Gis-based niche models reveal unifying climatic mechanisms that maintain the location of avian hybrid zones in a North American suture zone

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Abstract

The existence of suture zones in North America has recently been verified, yet the environmental factors responsible for the maintenance of their structure and position have remained undetermined. The Great Plains suture zone in the US is perhaps the most significant and broadly studied in North America. Numerous avian hybrid zones that cluster in this region have been extensively studied over the last half-century. A primary result of this work is that exogenous factors present in this region have promoted and maintained avian species divergence. Yet, to date the variables most important in the generation and the clustered positioning of these hybrid zones in relation to one another have not been determined. The present study aims to advance our understanding of this North American suture zone by using niche modelling to quantify which environmental variables are most important in its formation and maintenance. Through the generation of fundamental niches for four hybrids and their parental species, similarities linking the hybrid zones were uncovered. The results show that temperature holds this suture zone in position and also suggest that temperature played a primary role in promoting niche differentiation among these sister species pairs during Pleistocene glacial cycles.

Introduction

Determining the endogenous and exogenous factors that generate and maintain hybrid zones has been a goal of evolutionary biologists for over half a century (Anderson, 1948,1949,1953; Remington, 1968; Endler, 1977; Moore, 1977; Barton & Hewitt, 1985; Rand & Harrison, 1989; Hewitt, 1996,1999,2001). These factors are of particular interest because the distribution of hybrid zones on a continent can provide valuable information concerning speciation, Pleistocene distributions, post-glaciation re-colonization routes and present day isolating mechanisms (Hewitt, 1996,1999,2001). Interestingly, hybrid zone locations from multiple taxa often cluster in discrete areas on a continent called suture zones (Anderson, 1953; Remington, 1968; Hewitt, 1999; Swenson &

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Howard, 2004,2005). More generally suture zones should not only be thought of areas where hybrid zones cluster, but also areas where contact zones and phylogeographic breaks cluster (Uzzell & Ashmole, 1970; Swenson & Howard, 2004,2005). Suture zones, in this broader sense, have been identified in terrestrial and aquatic environments suggesting their general importance across vastly different ecosystems (Remington, 1968; Hewitt, 1996,1999; Avise, 2000; Redenbach & Taylor, 2002; Swenson & Howard, 2005). The existence of suture zones has therefore been taken as evidence for the importance of Pleistocene climatic change, refugia and barriers to dispersal in generating diversity (Remington, 1968; Swenson & Howard, 2005). Further, because clustering of secondary contact must be maintained in order to detect and constitute a suture zone, similar past and present selective pressures are presumably acting upon all the present species pairs.

Recently, Swenson & Howard (2004) performed a general analysis of all of Remington's (1968) 13 North American suture zones. Their results found support for

two of those suture zones, suture zone 1 in the Great Lakes region on the Canadian border and suture zone 4 in the Great Plains region in the middle of the continent. Additional analyses of bird, mammal and tree contact zones provided more support for Remington's other 11 original suture zones and especially highlighted the importance of the Great Plains – Rocky Mountain ecotone in determining hybrid zone and contact zone locations in North America (Swenson & Howard, 2005). As the evidence supporting the existence of suture zones begins to accumulate, it is now important to identify if similar present day and historical factors are responsible for the generation and maintenance of multiple hybrid zones.

The avian hybrid zones that cluster in the Great Plains suture zone are ideal candidates for an analysis of how co-occurring hybrid zones are generated and maintained (Mengel, 1970; Moore & Price, 1993). Further they provide some of the most compelling evidence for the importance of allopatric speciation in North America (Coyne & Orr, 2004). This is because these hybrid zones have been under intense scrutiny individually since the 1950s and are therefore probably the most well characterized in the suture zone (Sibley & Short, 1959,1964; Mengel, 1964,1970; Rising, 1970; Anderson & Daugherty, 1974; Kroodsma, 1974a,b; Emlen et al., 1975; Kroodsma, 1975; Rising, 1983a,b; Moore & Buchanan, 1985; Moore & Koenig, 1986; Moore et al., 1991; Moore & Price, 1993; Rising, 1996). Additionally, North American parental bird species have had their locations mapped extensively for decades, thus giving a clear picture of their range structure.

Although the avian hybrid zones in central North America have been studied for several decades, it was not until Moore & Price (1993) that more than one of these hybrid zones was analysed in unison. The outcome of this work was the suggestion that exogenous selection maintained hybrid zone structure and position in this region. The environmental variable that they regarded as the most influential was precipitation. To come to this conclusion Moore & Price (1993) overlaid avian range maps, hybrid zone maps and climate maps to see, which climatic isoclines lined up closest to range boundaries and hybrid zones.

In what appears to be an opposing view, Rising (1969) suggested that temperature is the most important environmental factor in determining the oriole hybrid zone (one of the hybrid zones analysed by Moore & Price, 1993) location in this suture zone. Rising's hypothesis was based on heat stress experiments, which showed that the Baltimore oriole's (*Icterus galbula)* range is restricted from progressing westward due to high temperatures, while the bullock's oriole (*Icterus bullockii*) is, most likely, restricted for moving eastward due to biotic interactions. This result is intriguing because it is based on experimental evidence and because many climatic variables

(i.e. temperature and precipitation) are often tightly correlated. Thus making them difficult to disentangle without experimentation or sophisticated niche modelling. Rising went on to suggest that differing temperature regimes among Pleistocene refugia and the present temperature gradient in the Great Plains may be responsible for the divergence between orioles and the present day maintenance of their hybrid zone structure and position, respectively (Rising, 1969,1970). To date no one has attempted to determine if the hypotheses proposed by Moore and Price or Rising hold true for the multiple avian hybrid zones in this suture zone using experimentation or ecological niche models.

There are obvious benefits in using ecological niche models, yet only two studies to date have used them in contact zone or hybrid zone research (Kohlmann et al., 1988; Cicero, 2004). The groundbreaking work of Kohlmann et al. (1988) used a BIOCLIM niche model (Nix, 1986) to predict the extent of an Australian cricket hybrid zone. Strangely, it was almost two decades before BIOCLIM was used again to better understand secondary contact (Cicero, 2004). This model addressed the distributions of the two parental species, *Baeolophus inornatus* and *Baeolophus ridgwayi*, which form an avian contact zone in Northern California. Ecological niche models have also been used successfully in recent phylogeographic studies providing exciting results (Hugall et al., 2002; Graham et al., 2004; Peterson et al., 2004). In particular, these three studies used BIOCLIM to better understand what past environmental variables were linked to diversification and to reconstruct paleo-distributions. All of the above studies are good examples of how powerful ecological niche models can be in evolutionary analyses.

The following study uses an alternative ecological niche model, the genetic algorithm for rule-set prediction (GARP, Stockwell & Nobel, 1992), and four hybrid zones analysed previously by Moore & Price (1993) to test the hypotheses that precipitation or temperature have played a predominant role in promoting and maintaining bird species divergence and thereby maintaining the position of a suture zone.

Materials and Methods

Parental species and hybrid zones

This study examined four avian hybrid zones and eight parental species' analysed by Moore & Price (1993) and recently discussed by Coyne & Orr (2004). The eight parental species selected were the following: black-headed grosbeak (*Pheucticus melanocephalus*); rose-breasted grosbeak (*Pheucticus ludovicianus*); red-shafted flicker (*Colaptes auratus cafer*); yellow-shafted flicker (*Colaptes auratus auratus*); bullock's oriole (*I. bullockii*); Baltimore oriole (*I. galbula*); lazuli bunting (*Passerina amoena*) and indigo bunting (*Passerina cyanea*). Each congeneric species pair forms a single hybrid zone.

Ecological niche models

Ecological niche models use known point locations for a species and values for environmental variables (i.e. elevation, precipitation and temperature) at those point locations to generate a fundamental ecological niche for that species. This ecological niche can then be projected onto a map of a study area in order to predict where that species could or may occur. Of the two most robust ecological niche models, BIOCLIM (Nix, 1986) and the GARP (Stockwell & Nobel, 1992), the latter was used because of its ability to provide accurate models with small sample sizes that are commonplace in hybrid zone research (Stockwell & Peterson, 2002). The desktop version of GARP used in this study was downloaded from the DesktopGARP homepage (http://www.lifemapper.org/desktopgarp/).

Point location data for the eight parental species' were obtained from the USGS North American Breeding Bird Survey (BBS) data set (USGS Patuxent Wildlife Research Center, 2004). For each species, the BBS presence only data was imported into ARCVIEW GIS 3.2 (Environmental Systems Research Institute Inc., 1999) and converted into a map layer suitable for GARP input. Point locations for hybrid populations were gleaned from the literature (Sibley & Short, 1959,1964; Rising, 1970; Anderson & Daugherty, 1974; Kroodsma, 1974a,b; Emlen et al., 1975; Kroodsma, 1975; Rising, 1983a,b; Moore & Buchanan, 1985; Moore & Koenig, 1986; Moore et al., 1991; Rising, 1996; Wiebe & Bortolotti, 2001). These hybrid point data, like the parental point data, were mapped in the GIS in order to create a map layer file for GARP input. Each hybrid zone point map layer included 30 or more points. This is important to note because a minimum of 20 training points are necessary to provide a robust GARP model (Stockwell & Peterson, 2002), while at the same it allowed the use of the remaining 10 or more points to test the accuracy of the GARP prediction (see below).

The physiographic data (elevation, slope and aspect) input into the models were initially obtained from the USGS Seamless Data Distribution System (http://seamless.usgs.gov/). The slope and slope aspect map layers were derived from the digital elevation model map layers in the GIS. The climate map layers (precipitation, minimum annual temperature, mean annual temperature, maximum annual temperature and radiation) were derived from data provided by the intergovernmental panel on climate change (http://www.ipcc.ch/) within the GIS. For each model, climate data was used that matched the years in which the species occurrence point data were recorded. The physiographic and climatic map layers were aligned with the GIS to ensure all layers overlaid properly inside GARP.

The GARP algorithm randomly sampled, with replacement, known point occurrences from the input GIS map layers and 'pseudoabsence' points in order to create independent training and test data sets (Stockwell &

Nobel, 1992; Oberhauser & Peterson, 2003). Through multiple iterations (up to 1000) GARP developed a 'rule' that described a fundamental niche for each species or hybrid. This process was repeated 100 times for each species or hybrid. Next, all but 20 models with the lowest levels of omission error (percentage of independent test points not predicted by the model) were discarded from the 100 replicate niche models. Next, 10 of these 20 models were selected as optimal based on their levels of commission error (percentage of predicted area that does not have a known point occurrence) as described in Anderson et al. (2003) and Oberhauser & Peterson (2003). Finally, this subset of 10 optimal models was imported into ARCVIEW GIS 3.2 (Environmental Systems Research Institute Inc., 1999) and overlaid to create one consensus predictive range map. Gird cells that were predicted as present by all 10 of these models were then extracted to give an optimal model for each species or hybrid (Anderson et al., 2003).

Model performance

In order to determine model accuracy, each GARP model from the initial set of 100 replicates was subjected to a chi-square test. The chi-square tested whether significantly more nontraining known occurrence points, test points, were predicted as positive by the model than expected at random. Next, a second GARP modelling procedure similar to that described above was performed for each species or hybrid. The difference in this second GARP modelling procedure was that some environmental map layers were randomly excluded from the formulation of each model. This jackknifing procedure allowed for analyses of which environmental variables were most crucial for accurate models (Peterson & Cohoon, 1999). Output data from the jackknifing procedure were analysed using a hierarchical partitioning approach (Chevan & Sutherland, 1991). Hierarchical partitioning was used in order to determine the relative contribution of each environmental map layer to model predictive accuracy (Peterson & Cohoon, 1999). That is, which map layers had the largest negative impact on model accuracy when it was excluded from the GARP modelling process. Presence – absence data for each environmental map layer (i.e. whether or not that layer was used in a model) were the independent variables and model predictive accuracy (i.e. extrinsic omission error) was the dependent variable. All statistical computations were performed using R statistical software (Ihaka & Gentleman, 1996).

Results

Ecological niche model accuracy

The chi-square test yielded significant results for 398 of 400 hybrid zone models produced ($P < 0.02$). This level of accuracy is typical of GARP models, which generally

have very low omission error rates. The optimum GARP hybrid zone predictive models are shown in Fig. 1.

The chi-square test yielded significant results for all 800 parental species models produced ($P < 0.00001$). Once again this was not a surprising result, particularly because of the large sample sizes obtained from the USGS database. Each con-generic species pair showed similar maps for eastern and western species suggesting similar mechanisms restricting ranges are shared (Figs 2–5).

Hybrid zone models

As expected the predicted hybrid zones runs longitudinally along the Great Plains – Rocky Mountains suture zone (Fig. 1). The two most important environmental variables in predicting hybrid zones were mean annual temperature and aspect (Table 1). For all four-hybrid zones GARP did not predict them to extend deep into Canada where some known hybrid locations exist (i.e. British Columbia; Wiebe & Bortolotti, 2001). This was

potentially due to the reduced levels of acceptable commission error implemented when selecting optimal models or by a general lack of available known training points located in Canada (Anderson *et al.*, 2003).

Parental species models

The eastern parental species were all predicted to have their ranges end approximately at the location of their respective hybrid zones. Conversely, the western species all had predicted ranges that extended far into eastern North America often reaching the Atlantic Ocean. It is important to note that the range predictions are based upon fundamental niches and thus inconsistencies between the model and the known distribution are presumed to be due to the difference between fundamental and realized niches. Figures 2–5 give the predicted maps for the grosbeak, flicker, bunting and oriole parental species pairs, respectively. In general, elevation and annual radiation were the two most important
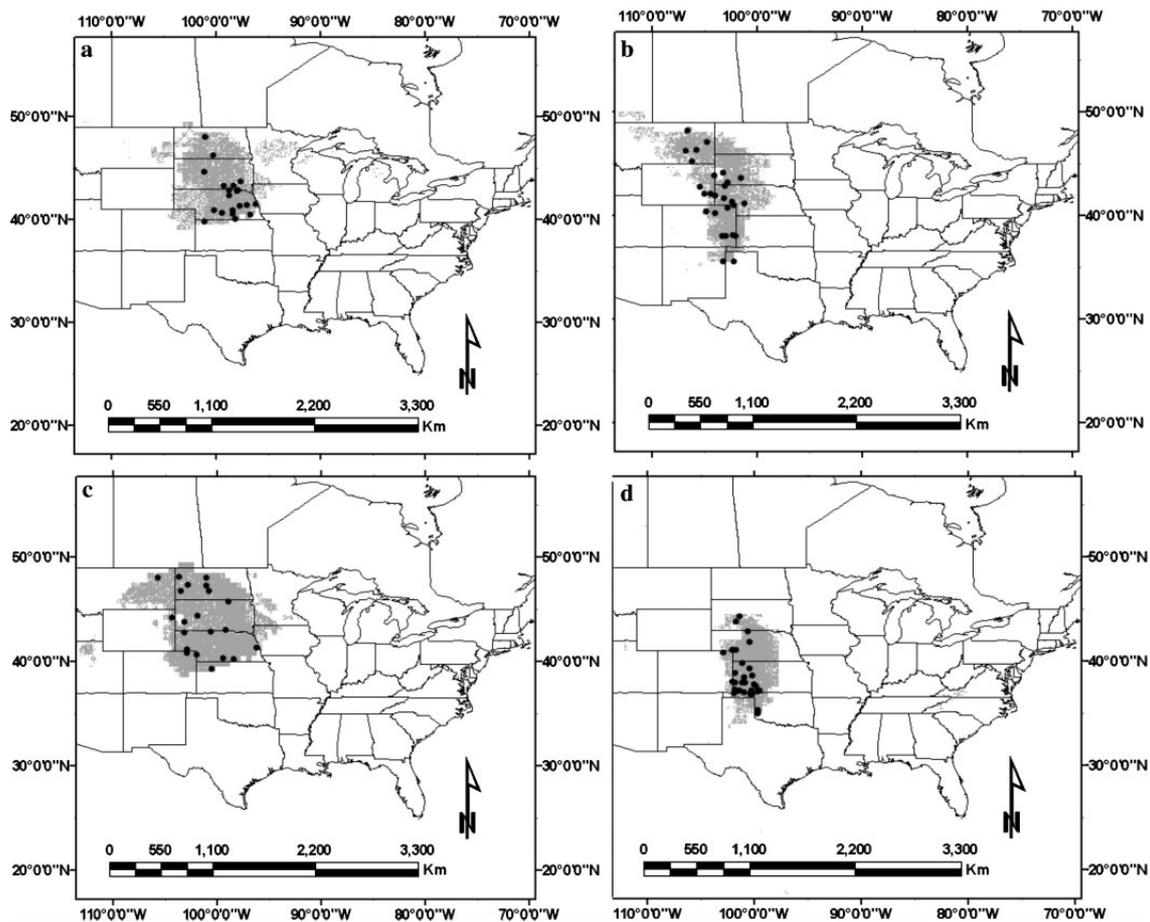

Fig. 1 Optimal GARP models (gray) of the hybrid zones. (a) Grosbeak hybrid zone, (b) flicker hybrid zone, (c) bunting hybrid zone and (d) oriole hybrid zone. Black points represent hybrid populations reported in the literature that were used for model formulation and testing.
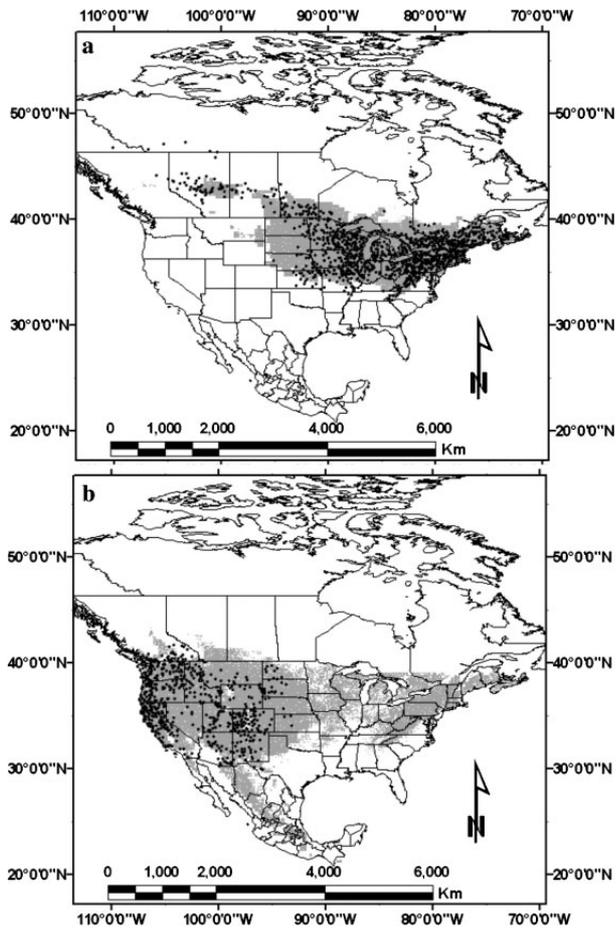
Fig. 2 Optimal GARP models (gray) for rose-breasted grosbeak (a) and blackhead grosbeak (b). Black points represent data from which the models were formulated and tested (i.e. the known present day range).

Fig. 3 Optimal GARP models (gray) for yellow-shafted flicker (a) and red-shafted flicker (b). Black points represent data from which the models were formulated and tested (i.e. the known present day range).

environmental variables when predicting the parental species ranges of these eight species. The eastern species range predictions, in particular, were heavily influenced by elevation and annual radiation. See Table 1 for a complete list of the contribution of different environmental variables to accurate range models for all eight parental species.

Discussion

The present work aimed to uncover whether precipitation or temperature are the environmental mechanisms generating and maintaining the location of multiple avian hybrid zones in a suture zone using ecological niche models. The models show that aspect, and more importantly, mean annual temperature is the two most important variables when determining avian hybrid zone structure and location in this suture zone. The only hybrid zone that temperature did not seem to be import-
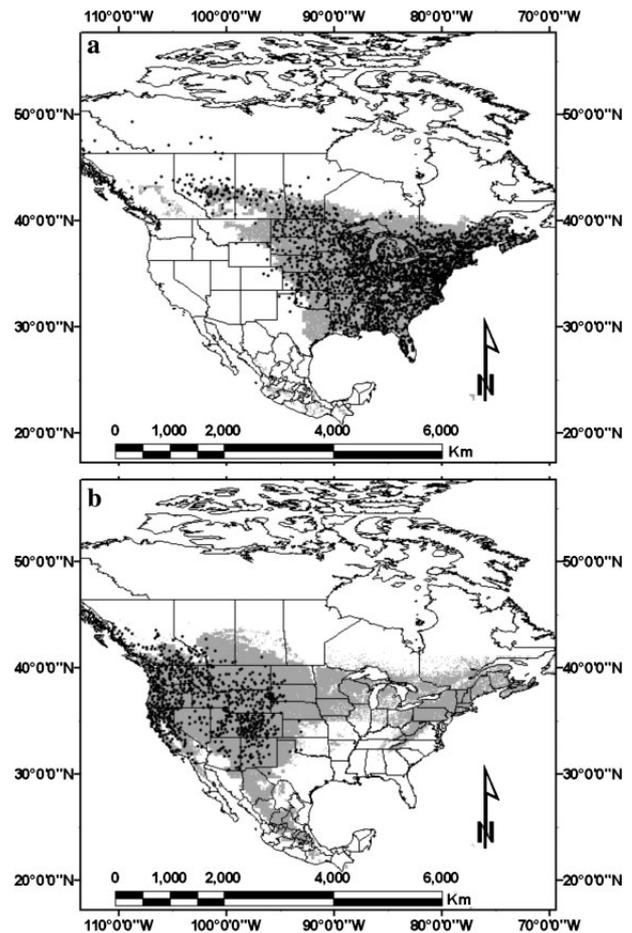
ant was the flicker (*Colaptes* sp.) hybrid zone, yet annual radiation is important in predicting the position of that zone. This evidence lends support to the physiological work of Rising (1969), who was the first to emphasis the importance of temperature in a hybrid zone in this region. At the same time the results also lend support to the work of Moore (1977) and Moore & Price (1993). This is because the hybrid zone locations do seem to be maintained by one or two dominate environmental factors and therefore exogenous selective pressures are shared.

The parental species niche models provided deeper insight into why these hybrid zones formed and are maintained in the Great Plains. This is primarily because GARP creates a species range based on a fundamental niche. Therefore, the models can predict species to occur in areas where the species have been excluded either by competition or by historical barriers to dispersal (Anderson *et al.*, 2002). This aspect of GARP was useful
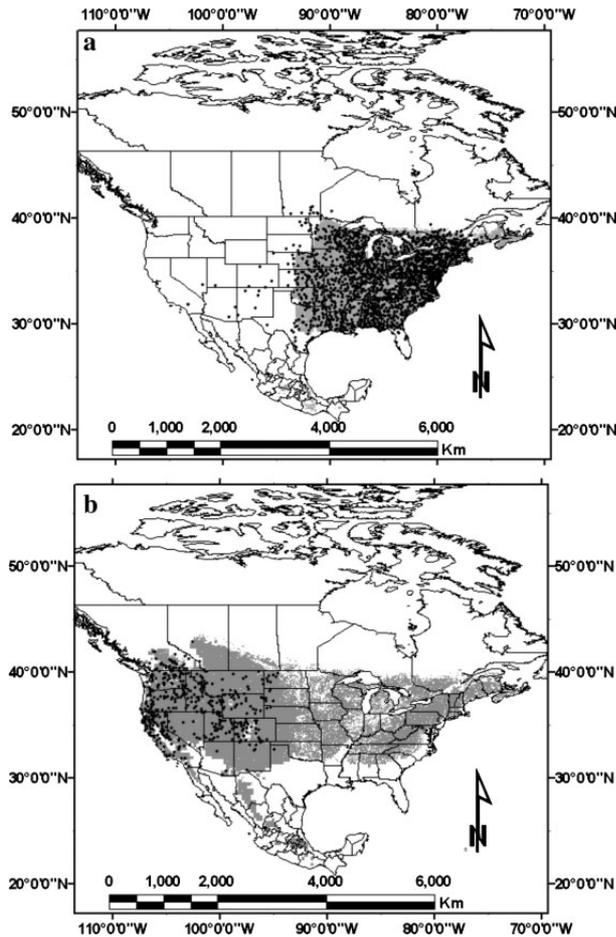
Fig. 4 Optimal GARP models (gray) for indigo bunting (a) and lazuli bunting (b). Black points represent data from which the models were formulated and tested (i.e. the known present day range).

Fig. 5 Optimal GARP models (gray) for Baltimore oriole (a) and bullock's oriole (b). Black points represent data from which the models were formulated and tested (i.e. the known present day range).

when trying to address if Rising's (1969) findings in orioles are transferable to the other parental species that form hybrids in the suture zone. Recall that Rising (1969) found that bullock's orioles (*I. galbula*), the western species, are not heat stressed at their range boundary while the Baltimore orioles (*I. bullockii*), the eastern species, are stressed at their boundary. This suggests that bullock's orioles are competitively excluded from the east, while Baltimore orioles are physiologically constrained from expanding further west. Interestingly, all of our con-generic species pairs show this same pattern of fundamental niches of western species expanding east beyond their known boundaries, while eastern species have fundamental niches not expanding past their known boundaries (Figs 2–5). The above results taken together suggest similar present day environmental factors maintain parental species and hybrid population distributions. In particular, the temperature gradient that defines the Great Plains suture zone should be considered
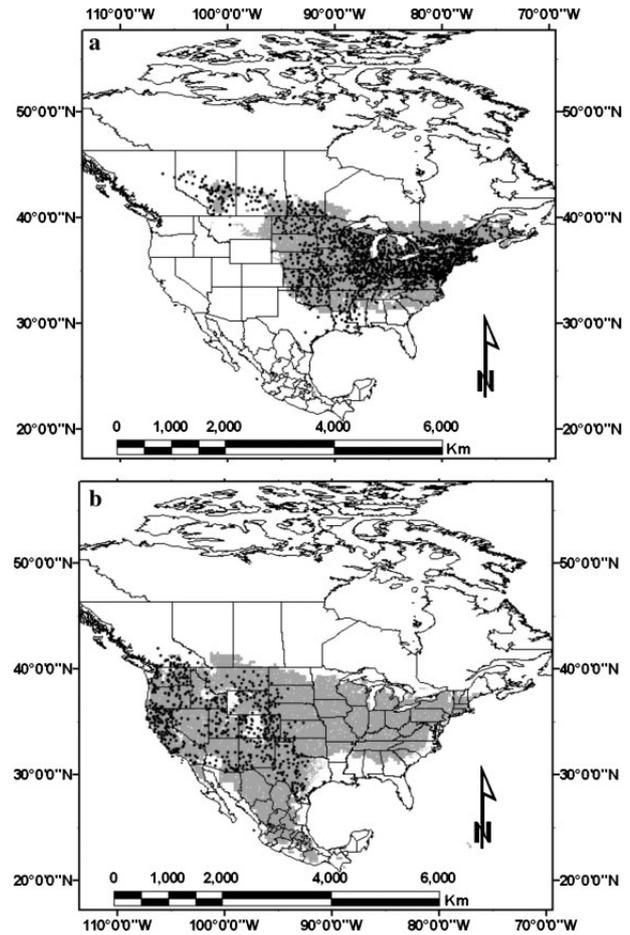
the primary mechanism maintaining the structure and position of these hybrid zones.

The results also lend additional support to the hypothesis that, while in a separate Pleistocene refugia, eastern species adapted to a cooler environment thus restricting them from expanding further into the arid west as the Laurentide ice sheet retreated towards the end of the Pleistocene approximately 18 000 years ago (Webb & Bartlein, 1992). If there were indeed two large Pleistocene refugia, with different temperature regimes, for all the taxa that collide in this suture zone, we would expect to see one range restricted biotically with the other restricted abiotically along a present day temperature gradient as is seen in the Great Plains.

Recent climatic modelling of ecoregions in North America during the Pleisotcene lends support to this refugial hypothesis (Hargrove & Hoffman, 2004). Hargrove and Hoffman show that the flora and fauna that currently reside in the Great Plains suture zone were

Table 1 Per cent of total predictive accuracy explained by different environmental variables.

Taxa or Hybrid Zone	Aspect	Elevation	Slope	Precipitation	Radiation	T_{min}	T_{mean}	T_{max}
Black-headed grosbeak	2.16	2.31	62.58	3.58	2.12	12.63	12.04	2.58
Rose-breasted grosbeak	6.57	41.95	2.86	12.1	28.61	2.11	2.12	3.68
Red-shafted flicker	9.64	2.63	62.68	12.42	4.95	3.12	2.44	2.12
Yellow-shafted flicker	5.76	33.28	5.37	6.94	27.35	2.21	15.4	3.68
Lazuli bunting	13.28	2.14	65.48	3.78	5.85	5.08	2.11	2.27
Indigo bunting	19.27	23.98	2.89	12.51	2.18	34.16	2.3	2.71
Bullocks oriole	5.55	24.95	2.04	4.37	48.74	8.12	4.05	2.17
Baltimore oriole	2.13	54.72	2.2	4.88	7.55	21.35	3.75	3.41
Grosbeak hybrid zone	34	10.74	3.37	6.25	8.25	6.21	29.01	2.17
Flicker hybrid zone	8.61	12.3	28.29	2.46	28.28	5.73	5.73	8.6
Bunting hybrid zone	31.78	2.12	8.71	2.12	11.99	2.12	38.4	2.77
Oriole hybrid zone	38.69	4.78	2.08	14.16	2.35	3.69	26.52	7.74

most likely distributed in separate refugia with disparate mean annual temperatures. Thus if this climatic scenario held true for all avifauna, and possibly for all taxa, forming a contact zone or hybrid zone in this suture zone, their parental range boundaries and hybrid zones are more than likely structured and positioned based on adaptations to different refugial temperature regimes they were subjected to during glacial cycles.

Mengel (1970) described the Great Plains as being a large isolating barrier to species during and just after the Pleistocene thereby promoting allopatric speciation. The reasoning for this is primarily due to the advance of glaciers along the Rocky Mountains immediately west of the Great Plains. These glaciers thereby effectively served as a wedge between a presumably once sympatric population of any given ancestral species. Given this Pleistocene scenario along with the present results leads to two interesting conclusions. First, is that the topography and historical climate of the Great Plains – Rocky Mountain ecotone drove each of the four ancestral species of the present day eight sister species to become isolated and to eventually speciate allopatrically. Second, is that the topography and present climate of this region maintains hybrid zone structure and forces these zones to cluster spatially. Ultimately, this suggests that the unique topography and climate, past and present, in this region has promoted species divergence and isolation as well as suture zone formation and maintenance.

Hybrid zone researchers and phylogeographers could and have greatly benefited from the use of explicit spatial information, in general, and ecological niche models in particular (Kohlmann *et al.*, 1988; Kidd & Ritchie, 2000; Ritchie *et al.*, 2001; Hugall *et al.*, 2002; Cicero, 2004; Graham *et al.*, 2004; Peterson *et al.*, 2004). Through the use of ecological niche models, the climatic mechanisms underlying present day patterns and past distributions can be uncovered. For example, if suture zones are truly indicators of secondary contact between numerous taxa, unifying environmental factors should control the hybrid zone and contact zone positions of not just birds but also mammals, reptiles, amphibians, insects and plants. As more museum parental species specimens and hybrids of these other taxa become geo-referenced, ecological niche models can be implemented to answer this question.

Second, if different con-specific populations are proposed to be diverging genetically due to differing abiotic environments, the implementation of an ecological niche model would prove interesting. By coding different genotypes as different species in a GARP model, e.g. one would be able to see how much or how little they overlap ecologically and what environmental factors in particular are the most important. Thus, the abiotic features selecting for different genotypes could be identified. Also if the two genotypes have small areas of sympatry in their fundamental niches these areas may be utilized to study diversifying selection and speciation much in the same way as interspecific hybrid zones have been utilized.

Third, ecological niche models have the ability to help a researcher confirm what type of hybrid zone they study (i.e. mosaic, bounded hybrid superiority or tension zone). If the hybrid zone is mosaic (Rand & Harrison, 1989), the pattern should become clear when the two parental maps and the hybrid zone map are overlaid within a GIS. If the hybrid zone is bounded (Moore, 1977), at least one of the parental species should have a fundamental niche expanding into the hybrid zone. Also the hybrid fundamental niche prediction should not expand far beyond the known boundaries of the hybrid zone and certainly not outside of the intermediate environment. If the hybrid zone is a tension zone (Barton & Hewitt, 1985), at least one of the two parental species and their hybrids should have predictions that expand beyond their known distributions. Even if the tension zone is resting in a 'trough', the fact that tension zones could have drifted back and forth across the landscape previously suggests that they are not governed by abiotic factors. This means that ecological niche models mirroring known current distributions, realized niches, would be unlikely in a tension zone.

Last, as described above ecological niche models hold the practical value of helping a researcher to determine where to study hybridization and speciation. For example if a researcher is knowingly or unknowingly studying only half of a hybrid zone, an ecological niche model will allow them to visualize its full size and shape. This will also allow the researcher to better determine where to sample for other hybrid populations in the future.

Spatial information and analyses are still vastly under-utilized by evolutionary biologists in general and phylogeographers and hybrid zone researchers in particular. The work presented here is a first step towards integrating spatial information of multiple species to understand general properties that cause hybrid zones to cluster in a suture zone. As evolutionary biologists integrate molecular information with explicit spatial information for analyses in the future, larger and more complex questions concerning diversification, and subsequent speciation, will be answered.

Acknowledgments

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