DOES NICHE DIVERGENCE ACCOMPANY ALLOPATRIC DIVERGENCE IN *APHELOCOMA* JAYS AS PREDICTED UNDER ECOLOGICAL SPECIATION?: INSIGHTS FROM TESTS WITH NICHE MODELS

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The role of ecology in the origin of species has been the subject of long-standing interest to evolutionary biologists. New sources of spatially explicit ecological data allow for large-scale tests of whether speciation is associated with niche divergence or whether closely related species tend to be similar ecologically (niche conservatism). Because of the confounding effects of spatial autocorrelation of environmental variables, we generate null expectations for niche divergence for both an ecological-niche modeling and a multivariate approach to address the question: do allopatrically distributed taxa occupy similar niches? In a classic system for the study of niche evolution—the *Aphelocoma* jays—we show that there is little evidence for niche divergence among Mexican Jay (*A. ultramarina*) lineages in the process of speciation, contrary to previous results. In contrast, *Aphelocoma* species that exist in partial sympatry in some regions show evidence for niche divergence. Our approach is widely applicable to the many cases of allopatric lineages in the beginning stages of speciation. These results do not support an ecological speciation model for Mexican Jay lineages because, in most cases, the allopatric environments they occupy are not significantly more divergent than expected under a null model.

KEY WORDS: *Aphelocoma*, birds, ecology, niche conservatism, niche modeling, speciation.

An outstanding question in evolutionary biology is whether ecology generally drives diversification, as in ecological speciation models in which divergent natural selection leads to reproductive isolation (Schluter 2001; Schluter 2009). Alternatively, ecological differences might accrue only after speciation, as in models in which species evolve in allopatry under similar ecological conditions (niche conservatism; Wiens 2004; Wiens and Graham 2005) and later come into contact through range expansion, after which they partition niche space (Diamond 1973; Price 2008). In the latter case, recently evolved lineages are expected to show a pattern of niche conservatism (Peterson et al. 1999; Wiens and Graham 2005). Until recently, the paucity of spatially explicit ecological data with comparable geographic coverage to phenotypic and genetic data has proven a formidable barrier to determine the relative prevalence of these two models in nature.

The recent availability of environmental data from satellites and weather stations has infused speciation research with large-scale ecological data for the first time (Kozak et al. 2008; Pearman

et al. 2008), allowing for tests of ecology's role in speciation (Peterson et al. 1999; Graham et al. 2004; Knouft et al. 2006; Kozak and Wiens 2006). These new sources of spatially explicit environmental data (also known as geographic information system [GIS] data) have increasingly been used in the framework of ecological niche models (ENMs) to assess niche divergence among species (Kozak et al. 2008). ENMs can generate geographic predictions of a species' distribution based on environmental data from known locality points (Austin 1985; Peterson 2001). Although their validity for predicting actual or potential geographic distributions for a single species is fairly well established, the comparison of ENMs between species—as is necessary when assessing niche divergence—poses new conceptual and statistical challenges. For example, an important role for ecology in speciation has often been posited when ENMs or niche visualizations in principal components space show little overlap between closely related taxa (e.g., Rice et al. 2003; Ruegg et al. 2006; Rissler and Apodaca 2007). However, the environmental data that underlie most ENMs (e.g., temperature and precipitation) are highly correlated with latitude and longitude (Costa et al. 2008), potentially confounding meaningful niche divergence with geographic distance. This problem of spatial autocorrelation in fact applies to all instances in which GIS data are compared between species—not just niche modeling—and it is especially acute when testing for divergence in the climatic niche between species with allopatric, neighboring ranges (see below).

Previous empirical and conceptual work have provided some hints as to how spatial autocorrelation in GIS data might be addressed when comparing species niches. First, studies that seek to investigate niche divergence between species could include ecological variables with more heterogeneity at local scales (Buermann et al. 2008). Soberón (2007) called these types of niche variables "Eltonian" in class because they describe resources and biotic interactions that are complex and dynamic at smaller scale. In contrast, the climatic niche (Grinnellian niche, sensu Soberón 2007) describes conditions, not resources, and is expected to show less spatial heterogeneity and therefore higher correlation among adjacent cells on a map (Soberón 2007). Whereas Grinellian niche characteristics are widely accessible and easily incorporated into ENMs in the form of climate layers for the Earth's surface (e.g., Hijmans et al. 2005), Eltonian niche variables are more difficult to measure over broad geographic areas without intensive field work (Soberón 2007). However, data from remote-sensing satellites on forest structure, species composition of vegetation, and tree cover potentially provide information about Eltonian niche characteristics at large scale. Although these variables are still rather temporally static, they nonetheless are more likely to capture more detailed aspects of the niche than climatic variables alone, especially given that they are more likely to vary at smaller scales. Indeed, remote sensing data on vegetation have been shown to im-

prove niche models when used in concert with climate variables (Buermann et al. 2008). Insofar as they can distinguish between vegetation types associated with different resources (e.g., deciduous vs. conifer forest; Frolking et al. 2006), they are also expected to show more spatial heterogeneity at local scales and—more so than climate variables—potentially correlate with resources important to ecological speciation.

Spatial autocorrelation can also be addressed using null models to test for niche divergence or conservatism (Warren et al. 2008). The basic idea behind the need for null models is that a pattern of niche divergence could result either from actual niche differences between species or simply due to spatial autocorrelation in environmental variables between the regions over which the species are distributed (hereafter background environmental divergence; Fig. 1). Examined in this framework, strong evidence for niche divergence requires two conditions: (1) niche characteristics differ between species; and (2) these differences are greater than background environmental divergence (Fig. 1; see also Broennimann et al. 2008; Warren et al. 2008). Niche conservatism, on the other hand, would be supported if niche differences are smaller than background environmental divergence (Fig. 1).

Here, we use large-scale ecological data on vegetation and climate in concert with null models to investigate whether niche divergence accompanies speciation in a classic system for the study of niche evolution, the *Aphelocoma* jays. Specifically, we address the question of whether closely related allopatric taxa inhabit environments that are more different or more similar than expected based on background environmental divergence. Nonoverlapping ENMs generated from climate data have been interpreted as evidence for niche divergence in prior studies on *Aphelocoma* (Peterson and Holt 2003; Rice et al. 2003), and the genus has thus become a widely cited counterexample to studies on many other organisms supporting niche conservatism (reviewed in Wiens and Graham 2005; but see Losos 2008 for counterexamples). However, given that *Aphelocoma* jays occupy allopatric biogeographic areas, the degree to which divergence in ENMs results from spatial autocorrelation in GIS data is unknown. We therefore reassess whether niche divergence accompanies speciation among allopatric *Aphelocoma* lineages. Our study differs from previous work in that we incorporate vegetation characteristics and compare niche divergence to a null model of background environmental differences. To implement the null model, we used two approaches: a recently developed method using overlap in ENMs (Warren et al. 2008) and a conceptually similar approach that foregoes the use of ENMs and instead examines divergence over multiple, independent axes of multivariate niche space. This latter method is similar to other approaches for comparing divergence in niche space to divergence among targeted absence locations (Kozak and Wiens 2006) or visualizing niches within available
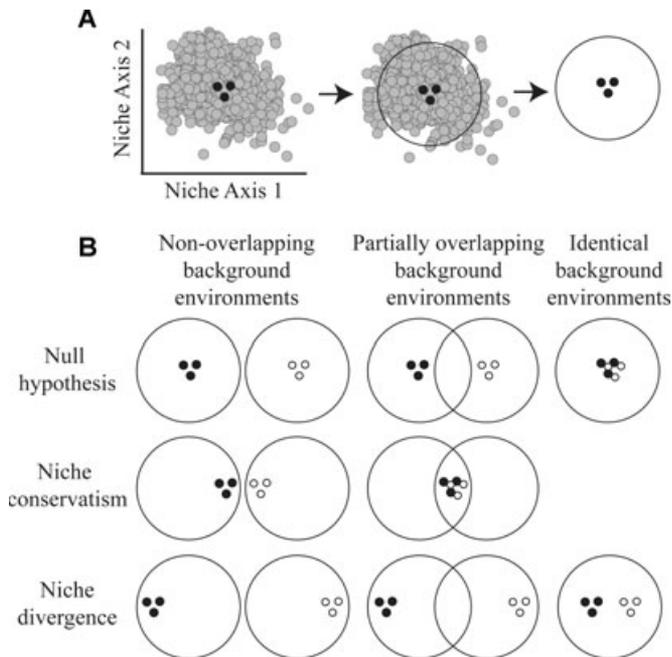
Figure 1. Testing niche divergence and conservatism against a null model of background divergence. Understanding the importance of comparing niche divergence to background divergence is aided by first considering a species' niche within the context of the available background environment. (A) Here, a simplified niche is considered on two axes. Values from species occurrence points (black dots) and random points from the geographic range of the species (gray dots) are plotted to show how the species occupies a portion of the total available environmental envelope. This representation can be further simplified (proceeding right with arrows) by removing the niche axes and circumscribing the background environment with a circle. (B) By adding another species (white dots), a conceptual framework for testing niche conservatism or divergence against a null model based on background divergence can be developed. The important point is that species' niches can appear divergent, but this might simply reflect divergence in their background environments (null hypothesis, top row), whether those environments overlap completely, partially, or not at all. Niche conservatism is supported when species' niches are more similar than expected based on their background environments (i.e., species are occupying niches that are as similar as possible given what is available). The strongest case for niche conservatism would be when both species only occupy the region where background environments overlap (middle row, far right). Niche divergence is supported when species niches' are more divergent than expected based on background divergence, with the clearest example being when niches are divergent despite identical background environments (bottom row, far right).

environmental space (Broennimann et al. 2008). However, unlike other approaches, it explicitly addresses the spatial autocorrelation in GIS data, using a null model for establishing a baseline expectation for the amount of divergence between allopatric regions (Fig. 1).

Our results suggest that autocorrelation of environmental variables may have confounded past interpretations from ENMs as supporting niche divergence among Mexican Jay lineages in the process of speciation. In allopatric regions Mexican Jays generally do not occupy habitats that are more divergent than expected. Taken together with evidence of niche divergence among *Aphelocoma* species, our results raise intriguing questions about the patterns of ecological diversity that have drawn attention to the genus (Rice et al. 2003). They are consistent with the idea that secondary contact is important for the generation of niche divergence, while such divergence does not necessarily accompany speciation in allopatry. The latter could be facilitated by the reduced gene exchange occurring between populations that are not adapted to unsuitable habitats between their disjunct geographic ranges (Wiens 2004).

Material and Methods
STUDY SYSTEM AND SELECTION OF TAXA
FOR ANALYSIS

The *Aphelocoma* jays have provided an important case study in the ecology of speciation (Peterson and Holt 2003; Rice et al. 2003). Due to their largely allopatric ranges, they also illustrate the need for null models when drawing inferences about ecology's role in speciation from GIS data. Our choice of study taxa within *Aphelocoma* was guided by a desire to test for niche divergence thoroughly within a clade where (1) speciation was in progress or recently completed and (2) lineages were alloparapatric and thus likely to be affected by spatial autocorrelation. The four monophyletic, allopatric lineages of Mexican Jays (currently recognized as one species, *A. ultramarina*, and hereafter referred to collectively as Mexican Jay lineages) identified by a recent phylogeographic study (McCormack et al. 2008) presented a suitable candidate clade for this purpose. The Mexican Jays are one of the three major clades within *Aphelocoma* and thus reflect about one-third of the overall diversity within the genus (J. McCormack, J. Heled, K. Delaney, A. Peterson, and L. Knowles, unpubl. ms.). Three of these lineages (Transvolcanic, West, and East) were previously analyzed by Rice et al. (2003), which concluded that they were ecologically divergent, but (as discussed above) the results may have been confounded by spatial autocorrelation of environmental variables. We include one further lineage that was later discovered to be phylogenetically distinct (Central, see Fig. 2; McCormack et al. 2008). Although they are currently considered a single species, a previous study including over 300 individuals showed that the four lineages are highly divergent in mtDNA and share no haplotypes (McCormack et al. 2008). Combined with evidence from the field for contact (e.g., West/Transvolcanic and Central/Transvolcanic; Pitelka 1951) and limited nuclear introgression (e.g., Central/East, McCormack et al. 2008) among
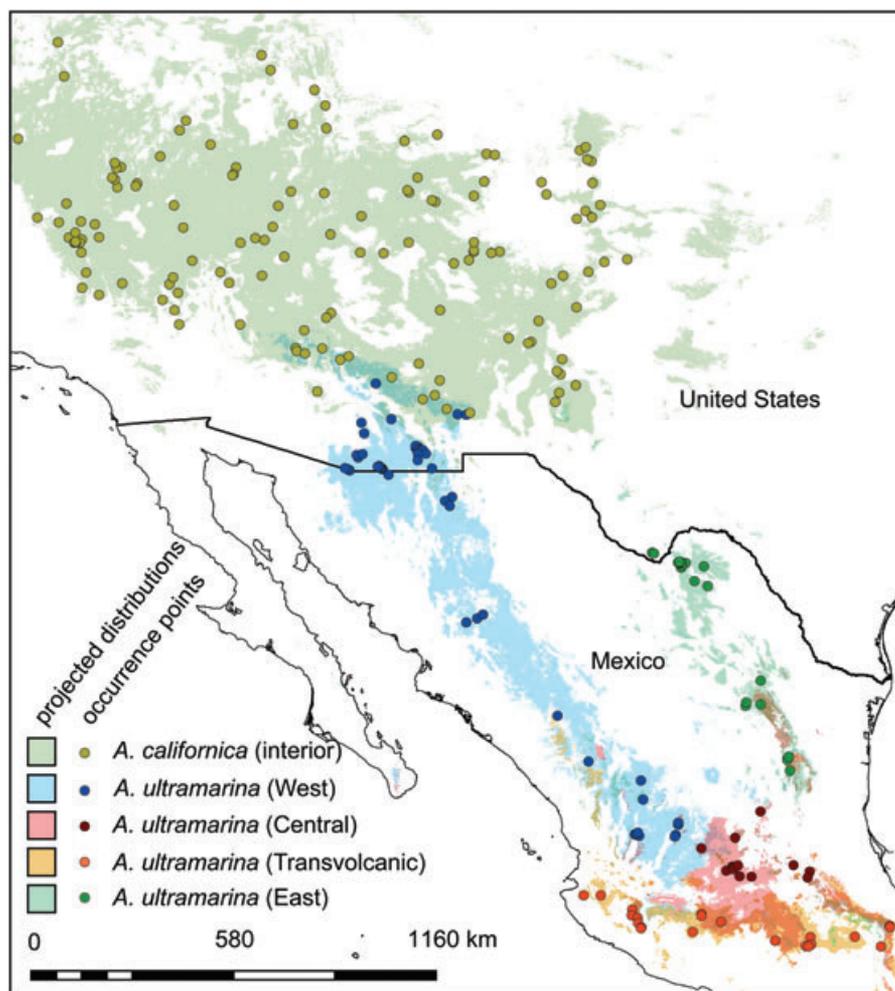
Figure 2. Locality data and niche models for *Aphelocoma* jays. Occurrence points and projected distributions from ecological niche models for the four Mexican Jay lineages (West, *n* = 53; East, *n* = 23; Central, *n* = 15; Transvolcanic, *n* = 22) and Interior Scrub-Jays (*n* = 128). Although projected distributions are shown here as suitable (shaded) or unsuitable (unshaded) based on a threshold habitat suitability score of 0.2 (corresponding closely to the lowest value of an actual occurrence points of each species) continuous measures of habitat suitability were used in ENM-based tests of niche divergence and conservatism (see Methods).

parapatric lineages, the lack of mtDNA introgression implies that some form of isolating mechanisms have evolved.

We also sought to conduct tests of niche divergence on representatives from the full range of phylogenetic and ecological diversity known from *Aphelocoma*. We focused on representative species from each of the three major clades within the genus: Mexican Jays (see above and Fig. 2), Western Scrub-Jays (three allopatric lineages currently considered one species, *A. californica*; Delaney et al. 2008), and Unicolored Jays (five allopatric lineages currently considered one species, *A. unicolor*; Pitelka 1951). These taxa, in addition to the phylogenetic diversity they represent, are geographically consistent with the goal of testing niche divergence among groups from similar climatic regions where spatial autocorrelation of environmental variables may be problematic. Specifically, tests of niche divergence among *Aphelocoma* species were conducted using (1) the West lineage of

Mexican Jays versus the interior lineage of Western Scrub-Jays (hereafter Interior Scrub-Jays, Fig. 2; Delaney et al. 2008), which co-occur in Arizona (Pitelka 1951), and (2) the Transvolcanic lineage of Mexican Jays versus the Sumichrasti lineage of Scrub-Jays (hereafter Sumichrasti Scrub-Jays, including populations of *A. c. sumichrasti* and *A. c. remota* that form a monophyletic group; Delaney et al. 2008), and the concolor lineage of Unicolored Jays (hereafter Unicolored Jays), which overlap geographically in eastern-central Mexico (see Fig. S1 for range maps of the latter two species). Collectively, we refer to these taxa as *Aphelocoma* species. Two other *Aphelocoma* species (the Florida Scrub-Jay, *A. coerulescens*, and Island Scrub-Jay, *A. insularis*) were not included because they are geographically restricted isolates within the larger Scrub-Jay complex and were thus not compatible with the study's focus on geographically proximate groups spanning many degrees of latitude and longitude. Practical limitations also

guided this selection in that *concolor* is the only one of five lineages of Unicolored Jay with a comparable number of occurrence points to other *Aphelocoma* species. Other Unicolored Jay lineages had <10 occurrence points with the level of precision that were necessary to generate accurate niche estimates (see below).

SPECIES OCCURRENCE POINTS

Before generating ENMs, range limits for all lineages were determined from previous phylogeographic studies (Delaney et al. 2008; McCormack et al. 2008) and vouchered occurrence points (Pitelka 1951). Primary occurrence data covered the fullest extent possible of each species' geographic range (see Fig. 2) and were taken by direct observation when possible and from eBird (www.ebird.com), a publicly available source of bird locality information that allows users to upload GPS points for bird sightings. Data uploaded to eBird are filtered and verified by local experts, and GPS points obtained in this manner were first vetted with Google Earth to ensure that they were found in plausible habitat (i.e., not within heavily urbanized areas). To construct niche models for the Mexican Jay lineages, we primarily used locality information obtained from direct observation by the authors and trusted ornithologists (2002–2008) because we were concerned with obtaining precise ENMs for groups with contiguous range borders in mountainous terrain where small errors in location can equate to large differences in environmental variables. Some georeferenced museum specimens (from the Museum of Vertebrate Zoology at UC Berkeley) were also used to augment sample sizes, but these represented a small fraction (6.7%) of the total occurrence points and were first vetted with Google Earth to ensure that forested habitat still occurred in collecting locations. We excluded occurrence points that were within 1 km of an existing point (i.e., the resolution of our environmental data, see below). For the interior lineage of Scrub-Jays, occurrence points were taken from eBird. Direct observation and eBird records for the Sumichrasti Scrub-Jays and Unicolored Jays were scarce, so we relied mostly on georeferenced museum specimens for these species.

ENVIRONMENTAL VARIABLES

Ecological data included four vegetation variables and 10 climate variables at 1 km resolution (Table 1). To provide information potentially relevant to resources and, therefore, divergent natural selection pressures, we used vegetation variables derived from satellite-borne remote sensors (NASA-MODIS/Terra data set, available at http://edcimswww.cr.usgs.gov/pub/imswelcome/) and a radar scatterometer (Quick Scatterometer). From MODIS, we used the Normalized Difference Vegetation Index (NDVI)—a measure of vegetation greenness—as well as the yearly standard deviation of NDVI (std_NDVI) and percent tree cover (TREE). The Quick Scatterometer (QSCAT) is a low-orbit satellite that measures reflected microwave radiation sensitive to subtle differ-

Table 1. Climate and vegetation variables used to test niche divergence.

Environmental variable	Description
Bio1	Annual mean temperature
Bio2	Monthly temperature range
Bio4	Temperature seasonality (year st. dev.)
Bio5	Max temperature warmest month
Bio6	Min temperature coldest month
Bio9	Mean temperature driest quarter
Bio12	Annual precipitation
Bio15	Precipitation seasonality (coeff. var.)
Bio17	Precipitation driest quarter
Bio18	Precipitation warmest quarter
Bio19	Precipitation coldest quarter
NDVI	Normalized Difference Vegetation Index (greenness)
Std_NDVI	Greenness seasonality (yearly st. dev.)
TREE	Tree Cover (%)
QSCAT	Canopy or surface moisture and roughness

ences in vegetation canopy structure and moisture and, in areas of sparse vegetation, soil roughness, and wetness (Frolking et al. 2006). Data for QSCAT comprised a monthly composite for August 2001 compiled from 3-day composite data. The 10 climate variables were obtained from the WorldClim database and describe surface means of temperature and precipitation, seasonality, and potentially biologically limiting extremes (Hijmans et al. 2005). Nine of the 19 original climate variables were removed due to high correlations ($R > 0.95$) with other climate variables. This was done mainly to improve interpretability of niche axes in the multivariate analysis (see below). Rather than using axes from a principal components analysis (PCA) to construct ENMs, the individual environmental variables were used because we were interested in knowing the relative contribution of each variable to the ENMs.

PROJECTED DISTRIBUTIONS FROM ECOLOGICAL-NICHE MODELING

Occurrence data and environmental variables were used to generate ENMs using the program Maxent version 3.2 (Phillips et al. 2006). Maxent uses a probability distribution of maximum entropy to predict approximate species distributions from presence data. This method ranked high in a recent comparison of niche-modeling methods (Elith et al. 2006) and also performs well with small datasets (Pearson et al. 2007), although other methods are known to produce different predictions (Thuiller 2003; Pearson et al. 2006). Given problems with interpreting AUC scores as a means of model accuracy without absence data (Lobo et al. 2008; Peterson et al. 2008), and because range limits of the species in our study are well described, we assessed model performance by

visualizing projected distributions using a conservative threshold of the minimum value of an actual occurrence point (Pearson et al. 2007). Tree cover was excluded from Maxent analyses because missing information in this data layer caused the downstream analysis program ENMtools (see below) to crash when random points without data were drawn.

TESTING FOR NICHE DIVERGENCE AND CONSERVATISM

Objective

Our goal was to compare niches among the species while taking into account the fact that species have different habitats available to them in a spatially autocorrelated landscape. Thus, we were primarily concerned with environmental data from species occurrence points (see above) and other points from within the region inhabited by the species (see below). Comparison of environmental characteristics from these two classes of data should permit disentangling differences due to simple spatial autocorrelation caused by geographic distance from strong niche divergence that occurs because two species occupying different habitats. This approach is conceptually similar to methods that compare environmental data from species occurrence points to targeted absence points from regions between two species' geographic ranges (Kozak and Wiens 2006). Whereas the latter method focuses on the role of intervening habitats in reducing gene exchange between species, our method is agnostic to the role of gene flow because ecological differences can lead to speciation with or without gene flow (Schluter 2001).

Null model using ENMs

First, niche-overlap values were calculated from ENMs for each separate pairwise tests with the Schoener's D metric (Schoener 1968) using ENMtools (Warren et al. 2008). To test the null hypothesis that niches are similarly divergent compared to background environments, we used the background randomization procedure in ENMtools, which compares the observed niche-overlap values to a null distribution of 100 overlap values generated by comparing the ENM of one taxon to an ENM created from random points drawn from the geographic range of the other taxon (Warren et al. 2008). Because this process is then repeated for both taxa in the comparison, two null distributions are generated per analysis. The Hawth's Tools application in ArcMap version 9 was used to obtain random points, which were drawn from within a polygon that circumscribed the occurrence points for each taxon (see Warren et al. 2008 for details). The number of random points drawn from the background was equivalent to the sample size of the taxon from whose range the random points were drawn.

How the background area for each taxon is delimited affects the analysis by including regions that are more or less sim-

ilar to the niche (Warren et al. 2008). Ideally, background area should include accessible habitats and therefore should reflect information on dispersal ability (Soberón and Peterson 2005). Given the low dispersal capabilities of *Aphelocoma* jays (McCormack and Brown 2008), circumscribing the known occurrence points likely captures nearly all the accessible habitats. For other species with different dispersal capabilities, the approach of identifying background area would need to be adjusted to accommodate the species-specific details (Warren et al. 2008). To test whether our results are robust to different methods for delimiting background, we repeated our analyses using a more restrictive background delineated by each taxon's ENM set to a baseline threshold of the lowest occurrence point. This made our background areas less likely to include potentially inaccessible regions of the generally broad geographic ranges of *Aphelocoma* taxa.

Null model in multivariate niche space

Data for the 14 environmental variables were drawn from occurrence points and 1000 random background points from within the geographic range of each taxon with ArcMap. The 14 variables were reduced with PCA of the correlation matrix. For our dataset, this consistently returned seven principal components (PCs) that explained at least a modest portion of the overall variance ($>3\%$) and had a clear biological interpretation based on loading scores. On each of the seven axes, niche divergence and conservatism were tested against a null model of background divergence by comparing the observed difference in mean niche values on a given PC to the difference in mean background values (Fig. 3). Significance was assessed with 1000 jackknife replicates of the mean background values. A routine for running these analyses in Stata, version 10 (StataCorp 2003) is available from the corresponding author by request.

Results

ACCURACY OF ENMs

Projected distributions from the ENMs (Fig. 2), which provide a geographically explicit estimation of habitat suitability using joint information from all environmental variables simultaneously, closely conformed to known distributions except for the Unicolored Jay and Sumichrasti Scrub-Jay (see Fig. S1 for evidence of over-predicted distributions), which may reflect the low sample size or error in locality data given the source of the data (as discussed above). Considering that accurate ENMs are critical to downstream analysis including the generation of null distributions and observed niche overlap values (Warren et al. 2008), we did not use these lineages further in methods using ENM-based calculations. On the other hand, the conflation of errors in predicted environmental variables with projections from ENM-based calculations are not as severe for the multivariate PCA
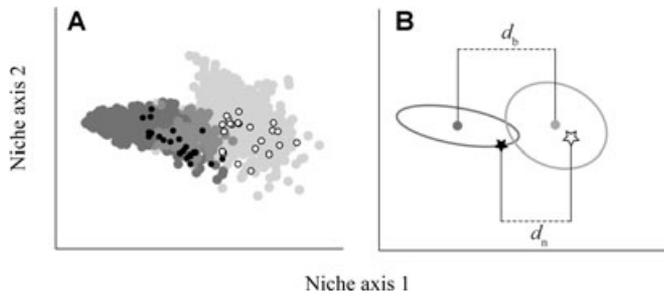
Figure 3. Implementation of the multivariate method. (A) An example on two niche axes showing occurrence points for two species (black and white dots) within their respective total available environmental space or background environments (visualized with 1000 random points drawn from their geographic ranges). (B) Divergence on a single niche axis is assessed by comparing divergence in means of background environments (d_b) to mean niche divergence (d_n), with the null hypothesis being $d_b = d_n$. Niche divergence is supported if $d_b < d_n$, whereas niche conservatism is supported if $d_b > d_n$. Significance was with 1000 jackknife replicates of d_b. Niche divergence was only supported if the observed niche divergence itself (d_n) was also significant (from *t*-tests).

method (i.e., only errors associated with the specific locality data itself, not additional misinformation associated with projecting species distributions). Therefore, we analyzed these species with the multivariate method (see below).

NICHE DIVERGENCE AMONG THE MEXICAN JAY LINEAGES

Compared to null models of background divergence, lineages of Mexican Jays in the process of speciation showed little support for niche divergence. Analysis using ENMs showed that five of the six pairwise comparisons among the four lineages showed significant evidence for niche conservatism with respect to at least one of the null distributions (Fig. 4). Although niche divergence was detected between the Central and Transvolcanic lineages, a sensitivity analysis revealed that results for this comparison alone differed with varied inclusions of background area. A more tightly circumscribed area based on ENMs produced results supporting niche conservatism (see Fig. S2), whereas results from the other comparisons differed little between the two methods.

To complement the ENM approach, we also tested for niche divergence and conservatism on independent niche axes using a multivariate analysis of the raw environmental data. Seven niche axes were identified that explained 91.6% of the total variation and availed themselves to biological interpretation (Table 2). Niche axes associated with climate explained most of the variation (e.g., PC 1–4), but were also highly correlated with latitude/longitude (see Table 2). Niche axes associated with vegetation (e.g., PC 5–7) explained smaller proportions of the variation, and showed less correlation to latitude/longitude (see Table 2). Evidence for niche
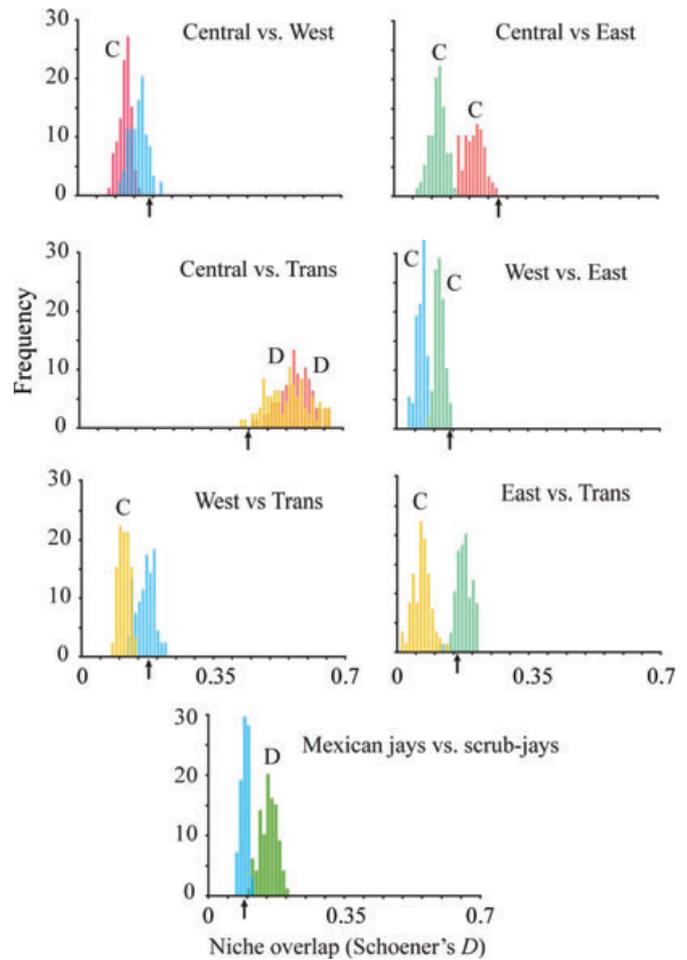

Figure 4. Tests of niche divergence and conservatism from niche models. Niche-overlap values (arrows) compared to a null distribution of background divergence. Each pairwise comparison produces two reciprocal analyses, one in which the niche model for group A is compared to a niche model generated from random points from the group B's geographic range and vice versa (hence, the two shaded distributions in each plot; the colors correspond to lineages in Fig. 2 and indicate the lineage for which the actual niche model is compared to the null model to generate the null distribution; see Methods for details). Overlap values smaller than the null distribution support niche divergence (D), whereas larger values indicate niche conservatism (C) (see Warren et al. 2008).

divergence was detected in only 11 of 42 tests, most of these involving the East lineage (eight of 11). Of the six pairwise lineage comparisons, the Central/Transvolcanic and East/Transvolcanic comparisons showed no evidence for niche divergence on any of the seven niche axes, and each supported niche conservatism on three axes. The West/Central, West/Transvolcanic, and West/East comparisons also showed little evidence for niche divergence (i.e., niche divergence was suggested on only one, two, or three of the seven axes, respectively). Only the Central/East comparison was characterized by a predominance of divergence, with two axes showing significant conservatism and five axes (primarily

Table 2. Divergence on independent niche axes among Mexican Jay lineages where speciation is in progress. Bold values indicate significant niche divergence (D) or conservatism (C) compared to null distribution (in parentheses) based on background divergence between their respective geographic ranges. To be divergent, niche values must also differ significantly between the two lineages.

Pairwise comparison	Niche axes						
	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Central vs. West	**1.62[1] D**	1.74[1]	1.90[1]	1.33[1]	**0.53[1] C**	0.44	**0.05 C**
	(0.56,0.74)	(1.70,1.91)	(1.80,2.26)	(0.50,1.36)	(0.61,0.76)	(0.14,0.43)	(0.14,0.26)
Central vs. East	**0.95 C**	**1.43[1] D**	**1.50[1] D**	**0.49 C**	**1.04[1] D**	**0.54[1] D**	**0.87[1] D**
	(1.79,1.91)	(0.16,0.32)	(0.92,1.34)	(0.70,1.18)	(0.77,0.96)	(0.18,0.53)	(0.26,0.41)
Central vs. Trans	**2.46[1] C**	0.78	**0.03 C**	0.04	0.90	**0.03 C**	0.24
	(2.79,2.89)	(0.08,0.20)	(0.25,0.35)	(0.04,0.22)	(0.49,0.69)	(0.29,0.55)	(0.06,0.17)
West vs. East	**0.67 C**	**0.31 C**	**3.40[1] D**	0.84	**0.51[1] D**	0.10	**0.82[1] D**
	(1.09,1.31)	(1.44,1.69)	(3.11,3.28)	(0.03,0.78)	(0.15,0.20)	(0.03,0.11)	(0.12,0.17)
West vs. Trans	**4.07[1] D**	**0.96 C**	1.93[1]	**1.29[1] D**	0.36	0.47	0.19
	(3.41,3.57)	(1.56,1.78)	(1.54,1.94)	(0.44,1.17)	(0.06,0.13)	(0.10,0.17)	(0.06,0.10)
East vs. Trans	**3.41[1] C**	0.65	1.47[1]	**0.44 C**	**0.14 C**	0.56	0.63
	(4.64,4.75)	(0.02,0.20)	(1.24,1.61)	(0.51,1.12)	(0.24,0.30)	(0.01,0.13)	(0.06,0.10)
% variance explained	33.9	19.8	13.0	12.3	4.8	4.5	3.4
Top variable loadings[2]	bio12	*bio6*	*bio2*	*bio19*	*qscat*	ndvi_std	*(tree)*
	ndvi	*bio1*	bio15	*bio17*	(ndvi_std)	qscat	qscat
	(bio4)	bio9	bio9	bio4	(bio17)	(bio18)	bio17
Biological interpretation	rain & veg	temp	seasonality	rain	tree structure	complex (veg)	tree cover
Correlation latitude	−0.69	−0.35	0.27	0.41	0.21	0.17	−0.14
Correlation longitude	0.25	0.29	−0.73	−0.36	−0.20	−0.05	0.08

[1]Niche values differ significantly between lineage pair (*t*-test: Bonferroni-corrected *P*=0.0019).
[2]See Table 1 for variable descriptions. Parentheses indicate opposite sign. Values in italics reflect variables with particularly high contributions to a given PC axis (last eigenvector is 0.1 greater than next).

associated with vegetation variables) showing significant divergence (Table 2).

NICHE DIVERGENCE AMONG *APHELOCOMA* SPECIES

In a comparison between West Mexican Jays and Interior Scrub-Jays, which overlap in Arizona, ENM results supported niche divergence, based on rejection of one of the two null distributions (Fig. 4). From the multivariate method, niche divergence was detected consistently on niche axes associated with vegetation variables (PCs 5–7), whereas those niche axes associated with climate and correlated with latitude and/or longitude were conserved (Table 3).

Strong evidence for niche divergence was detected among the three *Aphelocoma* species that overlap in eastern-central Mexico. Despite high variance among Unicolored Jays (likely caused by low sample size), this species was highly divergent from both the Transvolcanic Mexican Jays and the Sumichrasti Scrub-Jays in the first niche axis associated with rainfall and the third niche axis associated with temperature seasonality (Table 4). In total, the Mexican Jay and Unicolored Jay were divergent in five of seven niche axes, involving both climate and vegetation variables, notably those representing greenness and tree cover. The Mexican Jay and Sumichrasti Scrub-Jay were divergent in three

of seven axes, all involving vegetation. The Unicolored Jay and Sumichrasti Scrub-Jay showed divergence in three of seven axes as well, but these were associated with aspects of seasonality, whereas vegetation axes were mostly conserved. The one axis where the Mexican, Unicolored, and Scrub-Jays showed a lack of divergence or conservatism was PC2, associated with temperature variables.

Discussion
DOES NICHE DIVERGENCE DRIVE SPECIATION IN MEXICAN JAYS?

When tested against null models of background environmental differences between their geographic ranges, results from both methods showed little support for niche divergence among the Mexican Jay lineages in the process of speciation. Cases in which the null hypothesis was rejected, it was usually in favor of niche conservatism (but see below for discussion of divergence in the East lineage). Due to the nonsymmetrical branching order of the *Aphelocoma* phylogeny (J. E. McCormack, unpubl. data), the analyses were not restricted to comparisons of sister taxa, and thus conclusions about speciation mechanisms for any specific case of lineage-splitting are difficult to draw from our

Table 3. Divergence on niche axes between West Mexican Jays and Interior Scrub-Jays with overlap in Arizona. Bold values indicate significant niche divergence (D) or conservatism (C) compared to null distribution (in parentheses) based on background divergence between their respective geographic ranges. For divergence, niche values must also differ significantly between the two lineages.

Pairwise comparison	Niche axes						
	PC1	PC2	PC3	PC4	PC5	PC6	PC7
West Mexican Jay vs.	**3.47[1] C**	**0.08 C**	**0.02 C**	0.28	**0.29[1] D**	**0.66[1] D**	**0.36[1] D**
Interior Scrub-Jay	(3.84,3.95)	(0.69,0.91)	(0.20,0.27)	(0.01,0.07)	(0.16,0.21)	(0.03, 0.07)	(0.10,0.13)
% variance explained	36.6	29.5	10.1	6.0	5.0	4.1	3.2
Top variable loadings[2]	(bio4)	*(bio5)*	bio19	*ndvi_std*	bio2	qscat	*tree*
	bio15	bio17	bio9	bio2	*(ndvi_std)*	(bio9)	(qscat)
	bio18	(bio1)	*(bio2)*	ndvi	*bio19*	tree	bio5
Biological interpretation	temp/rain seasonal	temp/rain	temp+rain seasonality	greenness seasonality	temp+veg seasonality	tree structure	tree cover
Correlation latitude	−0.90	0.19	0.22	0.15	0.08	0.05	0.06
Correlation longitude	0.52	0.15	−0.54	−0.04	−0.14	−0.10	0.00

[1]Niche values differ significantly between lineage pair (*t*-test: *P*<0.05).
[2]See Table 1 for variable descriptions. Parentheses indicate opposite sign. Values in italics reflect variables with particularly high contributions to a given PC axis (last eigenvector is 0.1 greater than next).

results. However, the consistent lack of niche divergence among Mexican Jays in general is compatible with a conclusion that niche divergence was likely not the major driver of speciation in this group. This is surprising considering that *Aphelocoma* jays are known for ecological innovation both within (Peterson 1993; Peterson and Vargas-Barajas 1993; McCormack and Smith 2008) and among (Pitelka 1951) species. This ecological diversity has had important consequences for local adaptation and the generation of phenotypic diversity at the intraspecific level (Peterson 1993; McCormack and Smith 2008), but our results suggest it is not the major factor driving species divergence. Rather, niche results from Mexican Jays—coupled with their geographic

Table 4. Divergence on niche axes between Transvolcanic Mexican jays, Sumichrasti Scrub-Jays, and Unicolored Jays with overlap in Eastern-Central Mexico. Bold values indicate significant niche divergence (D) or conservatism (C) compared to null distribution (in parentheses) based on background divergence between their respective geographic ranges. For divergence, niche values must also differ significantly between species.

Pairwise comparison	Niche axes						
	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Trans Mexican Jay vs.	**3.35[1] D**	**0.60 C**	**1.65[1] D**	**1.41[1] D**	**0.75[1] D**	**0.99[1] D**	0.18
Unicolored Jay	(2.60,2.80)	(1.62,1.77)	(0.73,0.90)	(0.78,0.90)	(0.32,0.42)	(0.06,0.13)	(0.02,0.11)
Trans Mexican Jay vs.	0.43	0.35	0.44	**1.47[1] D**	0.31	**0.89[1] D**	**0.52[1] D**
Sumichrasti Scrub-Jay	(0.33,0.47)	(0.06,0.22)	(0.14,0.33)	(1.07,1.17)	(0.11,0.22)	(0.30, 0.39)	(0.03,0.18)
Unicolored Jay vs.	**3.78[1] D**	**0.95 C**	**1.22[1] D**	**0.07 C**	**1.06[1] D**	**0.10 C**	0.34
Sumichrasti Scrub-Jay	(2.99,3.20)	(1.49,1.62)	(1.00,1.11)	(0.21,0.34)	(0.49,0.58)	(0.22, 0.29)	(0.01,0.07)
% variance explained	40.1	20.8	10.4	8.4	5.9	4.1	3.3
Top variable loadings[2]	bio12	*bio9*	*(bio4)*	ndvi	*(ndvi_std)*	*(tree)*	*(qscat)*
	bio17	*bio1*	tree	bio7	qscat	qscat	bio18
	bio19	bio15	ndvi	(bio6)	bio18	ndvi_std	bio2
Biological interpretation	rain	temp	seasonality + vegetation	vegetation + seasonal	vegetation seasonality	tree cover	tree structure
Correlation latitude	0.18	−0.18	−0.46	0.51	−0.14	−0.20	−0.03
Correlation longitude	0.10	−0.48	−0.10	−0.40	−0.10	0.26	0.00

[1]Niche values differ significantly between lineage pair (*t*-test: *P*<0.05).
[2]See Table 1 for variable descriptions. Parentheses indicate opposite sign. Values in italics reflect variables with particularly high contributions to a given PC axis (last eigenvector is 0.1 greater than next).

distributions—suggest a speciation model in which reproductive isolation builds up in allopatry without a significant contribution from ecologically mediated divergent natural selection.

THE QUESTION OF SCALE OF ENVIRONMENTAL DATA IN TESTS OF ECOLOGICAL SPECIATION

An important caveat to studies that test the role of ecology in speciation using large-scale ecological data is that niche axes important to divergent selection pressures across a group of organisms might be overlooked. This is especially relevant because divergence during ecological speciation is often driven by strong differences along a single niche axis (Nosil et al. 2009), as in crossbills where differences in the cones and scales of different pine species have led to an ecologically based radiation (Benkman 2003). This issue is related to the problem of scale discussed by Soberón (2007), where niche characteristics that are heterogeneous at local scales are expected to drive ecological speciation because they capture variation in resources, which are often important to divergent selection (another well-known example is Darwin's finches, Grant 1999).

Although it is possible that niche divergence important to speciation within Mexican Jays occurs in niche dimensions not included in our study, the vegetation variables we used (e.g., NDVI, QSCAT, tree cover) provide a link to at least one important niche characteristic known to drive adaptive intraspecific phenotypic divergence, the ratio between pines and oaks and their associated seeds (Peterson 1993; McCormack and Smith 2008). QSCAT, in particular, can detect differences between broadleaf and conifer forest (Frolking et al. 2006), providing information about this niche axis that showed little divergence among Mexican Jay lineages (Table 2). Both comparisons between Mexican Jays and Scrub-Jays—species that are known to prefer habitats with different compositions of pines and oaks (Pitelka 1951) and partition niches accordingly in areas of sympatry (Westcott 1969)—showed strong divergence on the niche axis associated with QSCAT (Tables 3 and 4).

The low correlation of vegetation variables with latitude and longitude also suggests that they are more heterogeneous at local scales than climate variables, which showed much stronger correlation with geographic space (Tables 2 and 3). This result supports previous work emphasizing that vegetation variables provide additional information that can improve niche estimates (Buermann et al. 2008) and stresses the importance of including vegetation variables in studies of the ecology of speciation using GIS data. Further research should investigate whether known cases of climatic niche divergence are more detectable in vegetation axes. One such study on *Anolis* lizards found little divergence in the climatic niche among different ecotypes (Warren et al. 2008), but vegetation variables were not included for comparison.

NICHE DIVERGENCE ASSOCIATED WITH SECONDARY CONTACT?

Contrasting with the ecological speciation model, niche divergence could be a consequence of secondary geographic contact and niche partitioning between species that diverged largely in allopatry (Diamond 1973; Price 2008). Supporting this idea, the East lineage of Mexican Jays that shows evidence for contact and nuclear DNA introgression (McCormack et al. 2008) with the Central lineage, was involved in most of the observed cases of niche divergence using the multivariate method (eight of 11 cases, five of them with the Central lineage; Table 2). Considering that these lineages are not sister taxa (McCormack et al. 2008), this geographic overlap likely represents a case of secondary contact. In contrast, the Mexican Jay lineage from the Transvolcanic Belt has been isolated for millions of years (McCormack et al. 2008) with little opportunity during this time for contact with other Mexican Jay lineages. This could explain its lack of substantial niche divergence compared to other groups (Table 2), despite its impressive phylogenetic distinctness (∼9% sequence divergence in coding mtDNA; McCormack et al. 2008). Confirmation that these differences reflect acceleration of divergence within the East lineage, as opposed to constraint with the Transvolcanic lineage await analysis of these data in an explicit phylogenetic context once there is a detailed molecular phylogeny for the genus. Similarly, it is not possible with this data alone to reject the hypothesis that unsuitable habitat between the ranges of the Mexican Jay lineages prevents gene flow and facilitates speciation (see Wiens 2004; Kozak and Wiens 2006).

A role for secondary contact is also suggested by the patterns of niche divergence and geographical overlap among recognized *Aphelocoma* species from deeply divergent clades. Based on the two analyses among species whose ranges partially overlap, the results show clear evidence for niche divergence in accordance with natural history information. For example, Unicolored Jays, inhabiting cloud forest (Pitelka 1951), showed divergence from Transvolcanic Mexican Jays and Sumichrasti Scrub-Jays in a major niche axis (PC1) associated with rainfall (Table 4). In two separate comparisons, Mexican Jays also showed divergence from Scrub-Jays in vegetation, but not climate axes (Tables 3 and 4), supporting natural history data that both are found in hot, arid climates, although Mexican Jays tend to inhabit denser woodland (Pitelka 1951). As an ancillary point, our analyses also indicate further ecological differences not well known from field studies that warrant further detailed investigation. For example, some vegetation variables (e.g., greenness and tree cover) were similar between Unicolored Jays and Scrub-Jays in central Mexico even though Scrub-Jays inhabit drier, more seasonal climates (Table 4). Despite the clear niche differences and the partially sympatric ranges, it is not possible without comparing sister taxa

to say whether the observed niche divergence among *Aphelocoma* species played an important role in driving speciation or developed after speciation. Nevertheless, these results—combined with the lack of niche divergence seen observed among allopatric Mexican Jay lineages—are suggestive that postspeciational niche divergence has been important to the accumulation of ecological diversity in the genus.

CONTRASTING CONCLUSIONS WHEN NICHE DIVERGENCE IS ASSESSED WITH NULL MODELS

Previous research on *Aphelocoma* jays concluded that speciation events, including those within Mexican Jays, are marked by niche divergence (Peterson and Holt 2003; Rice et al. 2003). Our finding that there is little evidence for niche divergence among Mexican Jay lineages in the process of speciating, and that in many cases the tests support niche conservatism, cautions against using the degree of overlap of ENMs as evidence for niche divergence, as opposed to incorporating null models of background divergence (see also Warren et al. 2008). This is because allopatrically distributed species are expected to show divergence in climate variables simply by virtue of their disjunct geographic ranges. The high correlation we found between climate variables and latitude and longitude are indicative of this effect that would produce a pattern of apparent "niche divergence" from any two collections of geographic points, simply by virtue of being nonoverlapping in geographic space.

TESTING NICHE DIVERGENCE USING ENMS VERSUS MULTIVARIATE NICHE SPACE

In our study, two very different approaches that incorporated null models of background environmental divergence resulted in a similar conclusion that widespread niche divergence among the Mexican Jay lineages is lacking. However, consideration of the specific individual environmental variables important to the ENMs for Mexican Jays (Table 5, data from Maxent) suggests that, had strong divergence occurred in vegetation variables, it might have been missed by the ENM-based method because vegetation variables contributed little to ENMs, whereas climate variables contributed strongly. This raises the question of whether the environmental variables contributing most to a single species' ENM are really those best suited to assessing niche divergence between species. Because ENMs represent a single joint estimation of the niche with varying contributions from many environmental variables, comparing ENMs for two species to test for niche divergence is akin to a test along a single PC axis with different variable loadings. The difference is that although variable loadings in a PC axis are the same among species, the environmental contributions to ENMs differ among species, potentially leading, in the latter case, to comparison of niche estimations with very different properties (e.g., one ENM in which temperature was most important versus one ENM in which tree cover was most important). Therefore, another important conclusion is that studies of niche divergence using only an ENM-based approach might overlook smaller, but nonetheless important ecological differences. A multivariate method, such as the one we have developed here, provides more detailed information on niche divergence, as it is in better keeping with the Hutchinsonian idea of the niche as a multidimensional hypervolume (Hutchinson 1957), in which some axes will remain conserved while others diverge. As such, classification of divergence patterns as supporting niche divergence versus conservatism can be difficult (e.g., there is some evidence of divergence and conservatism for any single comparison; Table 2). Nevertheless, when considering the bulk of evidence in support of divergence versus conservatism across the multiple pairwise

Table 5. Contributions of specific environmental variables to ENMs.

Env variable	Transvolcanic % contribution	Central % contribution	East % contribution	West % contribution
bio_1	3.10	0.00	0.00	9.80
bio_2	0.40	6.50	17.30	2.40
bio_4	26.70	43.80	21.30	8.10
bio_5	43.90	4.20	19.00	2.50
bio_6	3.50	15.60	0.90	16.10
bio_9	0.00	3.00	17.50	6.30
bio_12	16.90	3.90	1.20	1.10
bio_15	0.00	3.90	9.00	13.40
bio_17	2.10	5.10	0.90	1.80
bio_18	0.10	7.80	0.00	24.00
bio_19	2.90	5.90	6.10	11.70
NDVI	0.00	0.00	3.30	0.90
NDVI_std	0.30	0.20	3.50	0.70
QSCAT	0.20	0.00	0.00	1.10

comparisons a general pattern emerges that suggests that niche conservatism among Mexican Jay lineages is replaced by a prevalence of niche divergence among the *Aphelocoma* species. These conclusions are qualitatively consistent with the results of the statistical tests of niche divergence from the ENM-based method of Warren et al. (2008).

IMPLICATIONS FOR TESTING THE ROLE OF ECOLOGY IN INCIPIENT SPECIATION

Our results and basic approach provide a framework for studying the role of ecology in speciation over a broad range of organisms. Even though we focused in detail on a relatively small radiation of birds, it is often the case, as in the Mexican Jay lineages studied here, that speciation involves the establishment of closely related lineages with largely disjunct geographic ranges (allospecies; Mayr 1963). This pattern is especially well documented in North American birds in which Pleistocene glacial periods promoted allospecies formation (Mayr 1963; Weir and Schluter 2004). Although our study does not provide conclusions about the speciation process for any specific pairs of taxa (practical considerations restricted the comparisons that could be made), the analyses point to a new general interpretation of this classic system for studying ecological divergence—namely, ecological divergence may accumulate after speciation (Rundell and Price 2009). If, as in Mexican Jays, other cases are discovered in which allospecies do not show strong signs of niche divergence (e.g., Peterson et al. 1999), then investigations should begin to determine what processes other than divergent natural selection contribute to the initiation of reproductive isolation. Possibilities include genetic drift, sexual selection, or the different adaptive mutations, or differential order of fixation of the same mutations in lineages experiencing similar ecological pressures (Mani and Clarke 1990; Schluter 2009). The latter possibility seems especially promising with increasing evidence that populations adapt to similar environments via different genetic pathways (Steiner et al. 2009), and the observation that reproductive isolation can arise rapidly due to incompatibilities in one or a few genes (Presgraves et al. 2003). Because competing speciation models invoke different roles for ecology, involve different evolutionary processes, and occur in different geographical contexts, determining their relative prevalence in nature would greatly influence our view of how evolution has generated organismal diversity.

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Supporting Information

The following supporting information is available for this article:

Figure S1. ENMs for Unicolored Jays and Sumichrasti Scrub-Jays (distributions in gray) showing overprediction compared to known geographic ranges (outlines).
Figure S2. Tests of niche divergence using a more restrictive, niche-based method for delineating background area (see Methods).

Supporting Information may be found in the online version of this article.

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