

Climate-Mediated Movement of an Avian Hybrid Zone

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Summary

The interaction between sibling species that share a zone of contact is a multifaceted relationship affected by climate change [1, 2]. Between sibling species, interactions may occur at whole-organism (direct or indirect competition) or genomic (hybridization and introgression) levels [3–5]. Tracking hybrid zone movements can provide insights about influences of environmental change on species interactions [1]. Here, we explore the extent and mechanism of movement of the contact zone between black-capped chickadees (*Poecile atricapillus*) and Carolina chickadees (*Poecile carolinensis*) at whole-organism and genomic levels. We find strong evidence that winter temperatures limit the northern extent of *P. carolinensis* by demonstrating a current-day association between the range limit of this species and minimum winter temperatures. We further show that this temperature limitation has been consistent over time because we are able to accurately hindcast the previous northern range limit under earlier climate conditions. Using genomic data, we confirm northward movement of this contact zone over the past decade and highlight temporally consistent differential—but limited—geographic introgression of alleles. Our results provide an informative example of the influence of climate change on a contact zone between sibling species.

Results

Hybrid Zone Movement and Geographic Introgression

Genomic comparisons show that the chickadee hybrid zone in southeastern Pennsylvania has moved north between historical (2000–2002) and contemporary (2010–2012) periods (Figures 1A–1C; Figure S1 available online). From the 1425 locus dataset, which consisted of 167 individuals, 75 loci showed clinal geographic variation and had cline widths less than 100 km. Of these clinal loci, 23 had significantly different cline center estimates (i.e., nonoverlapping 95% confidence intervals) between periods after Bonferroni correction (Table S1). Averaging

across these 23 loci, the center of the hybrid zone shifted north by ~11.5 km over the past decade (Figures 1A and S1).

There were two genetic clusters in both periods (Table S2). Analyses with the program STRUCTURE revealed (1) genetic admixture within historical and contemporary Nolde Forest (NF) and Hawk Mountain (HM) populations and (2) the absence of genetic admixture at Great Marsh (GM), Villanova University (VU), and Tuscarora State Forest (TU) (Figure 1C). Eleven individuals showed admixture in the historical sample, which we determined by examining parental species membership coefficient proportions: proportions < 0.99 in either parental category indicate admixture (Figure 1C, using membership coefficient proportions outlined in [6] and [7]); six (56%) of these had the signature of F1 hybrids. Seven individuals showed genetic admixture in the contemporary sample; four (57%) of these possessed genetic signatures of F1 hybrids.

Geographic introgression of alleles was highly variable across the genome, with individual loci showing either consistency or inconsistency between periods (Figures 1A and 1B; Table S1). A subset of loci exhibited generally concordant cline center estimates clustered around the contact-zone center, whereas other loci showed variable extents of northward introgression (Figure 1B). Loci within these two clusters were partially consistent between time periods (Table S1). The loci exhibiting narrow cline widths and concordant centers were significantly more likely to be located on the Z chromosome than on autosomes and to be identified as interspecific F_{ST} outlier loci in previous analyses (Table S1) (S.A.T., R.L.C., I.L., T.A.W., and V.F., unpublished data).

Distribution and Climate

Independent eBird data allowed us to map contemporary and historical locations of the contact zone between *Poecile atricapillus* and *Poecile carolinensis* across a broader geographic extent than the transect of genetic sampling locations (Figures 2A and 2B) and similarly revealed the hybrid zone movement seen in the genomic data. Changes in proportions of *P. carolinensis* within the region of each sampling site further match anecdotal data from the sites (Figure 2C; Table 1).

Cold winter temperatures appear to limit the northern extent of *P. carolinensis*. The northern range limit of *P. carolinensis* is not coincident with a physical boundary or habitat shift, but instead closely aligns with the mean minimum winter temperature -7°C isotherm [8, 9]. Physiological experiments have shown that *P. atricapillus* tolerates low winter temperatures better than *P. carolinensis* does [10]. We used eBird data and climate records from the PRISM database (2011, PRISM Climate Group; map created July 6, 2013) to evaluate the relationship between mean minimum daily winter temperature ([MDWT]; December to February) and the location of the chickadee contact zone (Figures 3A and 3B). We chose to build the model using MDWT given the aforementioned evidence of a relationship between the northern range limit of *P. carolinensis* and this parameter. By considering evidence for cold temperatures limiting the northward limit of *P. carolinensis*, we believe that MDWT is the best-available temperature indicator from PRISM, reflecting both typical minimum temperatures and extreme fluctuations. Note that mean and minimum temperatures are typically correlated.

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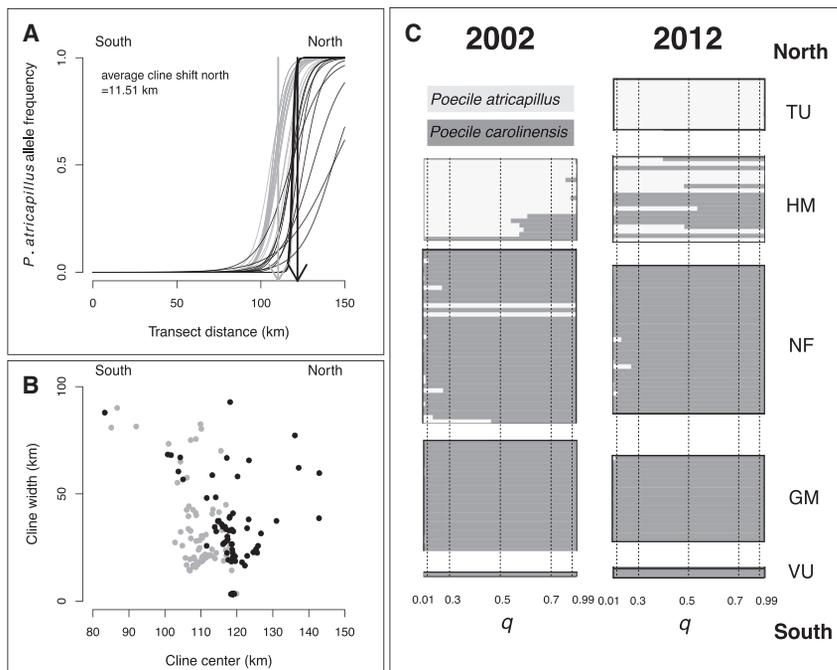


Figure 1. Genomic Evidence for Contact Zone Movement

(A) Locus-specific geographic clines depicting *P. atricapillus* allele frequencies for 23 loci with nonoverlapping 95% confidence intervals for both sampling time periods. Historical samples (2000–2002) in gray, contemporary samples (2010–2012) in black; arrows indicate mean cline center estimates.

(B) Locus-specific geographic cline centers plotted against cline widths. Contemporary samples in black, historical samples in gray.

(C) Bayesian assignment probabilities from STRUCTURE for *P. atricapillus* (light gray) and *P. carolinensis* (dark gray) at $K = 2$. Each horizontal line represents one individual. q = the probability of assignment to each genetic population. Dashed lines indicate threshold q values used to categorize individuals (see Results). Population acronyms as in Figure 2C.

significant predictive power with respect to the geographic location of the contact zone. We suspect that other features of the environment that potentially ameliorate the effects of winter temperatures

An eBird observation site was considered to be within the contact zone if at least 5% of the surrounding area was calculated to have both *P. atricapillus* and *P. carolinensis* (Figure 3A). The probability that an eBird observation site was within the contact zone was highly correlated with MDWT (Figures 3C and 3D). This correlation, however, changed slightly from east to west across Pennsylvania: the temperatures that predicted the location of the contact zone were warmer in the interior of Pennsylvania than at the coast (Figure 3D).

Accounting for longitudinal variation in the predictive ability of temperature, the statistical model describing the contemporary location of the contact zone (from eBird) based on current MDWT (from PRISM) was accurately able to predict (hindcast) the location of the contact zone a decade ago based on temperature data from that period (AUC = 0.91). Importantly, in the region of our genetic transect in southeastern Pennsylvania, mean minimum winter temperatures have increased over the past decade: model assessment site MDWT increased by 0.76°C during this time period (PRISM Climate Group). The predictive ability of the model is not an artifact of the absence of temperature change or contact zone movement over the past decade; rather, it captures observed temporal variation and movement in the chickadee contact zone.

Discussion

Climate-Mediated Movement of the Chickadee Hybrid Zone

Climate change is causing northward movement of the chickadee hybrid zone, as seen in both our geographically focused genomic transect in southeastern Pennsylvania and more broadly in the eBird comparisons that span the past decade. Our use of genomic comparisons between sampling periods and our novel approach to contact zone modeling using the eBird database have allowed us to document consistency in observed hybrid zone movement between genomic and distribution data. We have also documented consistency between observed movement from distribution data and predicted movement from our climate model; additionally, MDWT has

may influence regions closer to the coast. For example, the minimum winter temperature records we used do not describe the duration over which cold temperatures are experienced. Coastal sites may experience their lowest temperatures for a shorter duration than inland sites, given the moderating effect of the Atlantic Ocean. The rate of hybrid zone movement exhibited by the chickadee hybrid zone in southeastern Pennsylvania (~1.0 km/year) generally matches the rate of hybrid zone movement of the chickadee hybrid zone recorded in Ohio (1.0–1.6 km/year) [1, 10–13] and in other moving hybrid zones [1].

It has been hypothesized that the chickadee hybrid zone is a tension zone in which maintenance of the narrow zone width is likely caused by strong intrinsic selection against hybrids [11]. Results from our geographic cline analysis support this assertion. Multiple loci, distributed through the chickadee genome, exhibit clinal variation across the hybrid zone and have narrow widths (Figure 1A; Table S1). This pattern is potentially the result of underdominant selection (heterozygote disadvantage) against admixed genomes in hybrids. Furthermore, the increased number of clinal loci that we detected on the Z chromosome follows expectations from Haldane’s rule and could reflect selection against heterogametic ZW individuals. Broadly, a pattern of increased differentiation of the sex chromosomes compared to the autosomes is common in birds and other organisms [14, 15]. Other explanations for this pattern include smaller effective population size of sex chromosomes and lower recombination rates, potential for a higher proportion of infertility alleles on sex chromosomes [16], meiotic drive [17], and Z-maternal interactions [18]. Differential response of the parental species to climate change (i.e., expansion of *P. carolinensis* northward), rather than differential survival of hybrids, is likely responsible for the rapid northward shift in hybrid zone location. The predictive ability of our model indicates clearly that climate is playing a role in the northward movement of this hybrid zone.

Northward movement of the chickadee hybrid zone may be facilitated by mate choice and superior competitive ability of

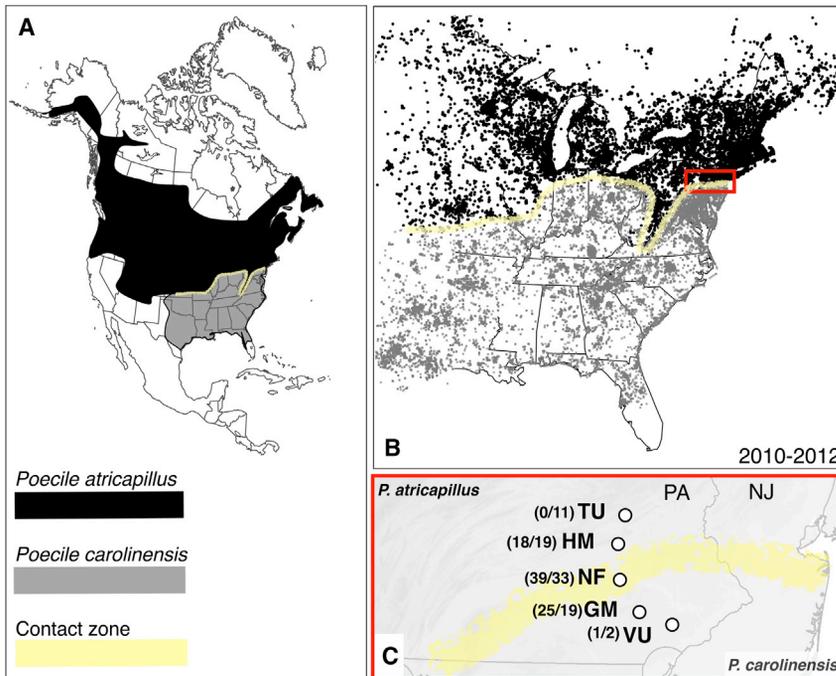


Figure 2. *P. atricapillus* and *P. carolinensis* Distributions, eBird Localities, and Study Sites

(A) Approximate ranges of *P. atricapillus* and *P. carolinensis* and contact zone.

(B) Cumulative distribution of eBird reports for *P. atricapillus* (black), *P. carolinensis* (gray), or both species/hybrids (yellow) in eastern North America during breeding (May to June) in 2010–2012.

(C) Approximate location of contact zone (yellow) and sampling transect in southeastern Pennsylvania. TU = Tuscarora State Forest (40.80N; –76.03W), HM = Hawk Mountain (40.65N; –76.00W), NF = Nolde Forest (40.28N; –75.96W), GM = Great Marsh (40.14N; –75.74W), VU = Villanova University campus (40.04N; –75.34W). Number of samples per site indicated in parentheses (2000–2002 or 2010–2012).

P. carolinensis males [12, 13]. The direction of movement of the chickadee hybrid zone we recorded matches predictions based on mating preferences of *P. atricapillus* females, which preferentially seek out extra pair copulations with *carolinensis*-like males [13], potentially because *carolinensis* tends to be dominant in interspecific male competitions [12]. We currently lack detailed data on differential fertility and/or survival of F1 hybrids and backcrosses that could explain the hybrid zone movement we detected without an influence of climate. However, hatching success of hybrid offspring is significantly lower than either parental species in southeastern Pennsylvania (R.C., unpublished data), like it is in Ohio [11], and multiple allelic clines indicate that selection against hybrids is strong, potentially due to underdominance. The high proportion of hybrids that are F1 and the low number of backcrossed hybrids in our data also suggest that the fitness of hybrid chickadees is low. In the absence of hybridization, we may expect the same directional movement of the hybrid zone, given that *P. carolinensis* appear to be dominant in interspecific interactions, which may aid in territory acquisition at the northern edge of their range [12].

Investigations into physiological tolerance differences between *P. carolinensis* and *P. atricapillus* suggest that *P. atricapillus* are better adapted to colder winter temperatures (to a large extent as a function of body size) and that increases in winter temperatures may facilitate northward

incompatibilities [10]. Concomitant strong selection against hybrids and increased dispersal of *P. carolinensis* into the contact zone in response to climate change would produce the pattern of a rapid northward movement that we see in both whole-organism and genomic data sets.

Hybrid Zone Movement and Climate

In a recent synthesis, 23 hybrid zones for which primary literature exists were shown to have moved at rates between 0.02 and 5.8 km/year over varying timescales; however, the underlying causes of hybrid zone movement were often unknown or anecdotal [1]. The fastest-moving hybrid zones involved species with high dispersal ability, including butterflies [19], birds [20–22], and invasive ants [23, 24], in hybrid zones thought or known to be tension zones [1, 25]. Similarly, 12 of 39 avian hybrid zones have moved within recorded history at varying rates and for multiple reasons [14]. When zones that are increasing steadily in width (unlike the chickadee hybrid zone) are excluded, 9 of 15 zones in which shifts could have been detected from repeated surveys show movement [14]. The mean rate of movement of these hybrid zones (~1 km/year) matches what we report for the chickadee hybrid zone, and the majority of the zones that show movement without concomitant broadening are moving along north-to-south axes [14]. Climate change was implicated as a causal factor for hybrid zone movement in 2 of 23 overall cases of hybrid zone movement and in 4 of 12 cases of moving avian hybrid zones [1, 14]. Notably, the well-studied carrion crow (*Corvus corone*)/hooded crow (*Corvus cornix*) hybrid zone is only moving where the line of contact runs east to west (allowing north-to-south movement) in Denmark and Scotland. This movement, which may be a response to climate change, is similar to what we report here [1, 14].

Linkages between climate change and hybrid zone movement have been explored rigorously in only a handful of cases. Most recently, climate change and hybrid zone movement

Table 1. Proportion of *P. carolinensis* Reported to eBird at Sites Surrounding Genomic Sampling Locations in Both Historic and Contemporary Time Periods

Site	2001	2011
Tuscarora State Forest	0	0
Hawk Mountain	0	0.09
Nolde Forest	0.86	0.91
Great Marsh	1.00	0.99
Villanova University campus	0.98	1.00

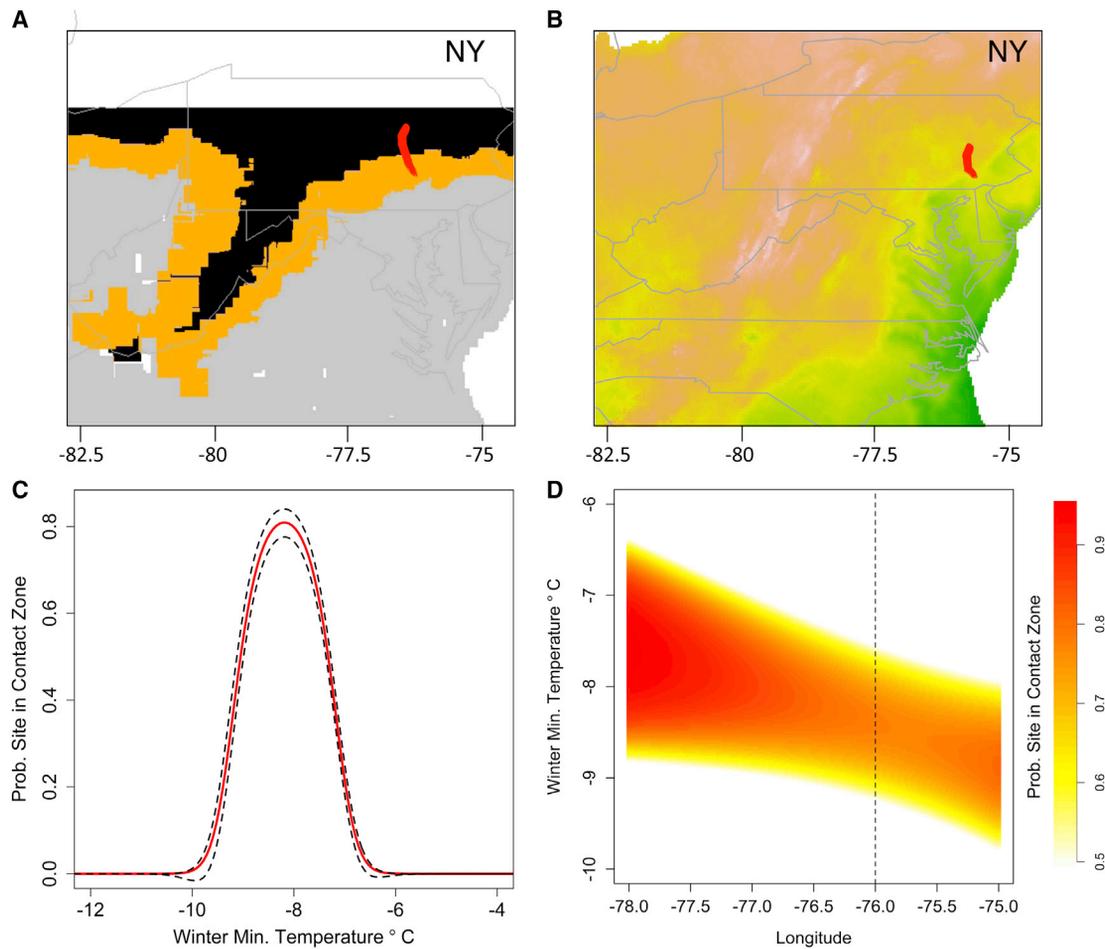


Figure 3. Association between Contact Zone Position and Temperature

(A) Chickadee contact zone mapped from eBird reports from 2010–2012 showing *P. atricapillus* (black shading), *P. carolinensis* (gray shading), and contact zone (minimum 5% of sites predicted to have both species, orange). Red line denotes approximate location of genomic sampling transect. (B) Mean daily minimum winter temperature in 2011. Red line denotes approximate location of genomic sampling transect. (C) Quadratic logistic regression of mean minimum daily winter temperature (December 2009 to February 2012) and contact zone position estimated from spring eBird data (2010–2012). (D) Heat map of complex relationship between predictive ability of daily minimum winter temperature and longitude for contact zone position.

were investigated in a western European avian hybrid zone between migratory melodius warblers (*Hippolais polyglotta*) and icterine warblers (*Hippolais icterina*) using species distribution modeling [2]. Engler et al. sought to determine the relative influence of species interactions and climate on hybrid zone movement, concluding that biotic interactions (i.e., competition with *H. icterina*) are currently limiting range expansion of *H. polyglotta* northward [2]. These biotic limitations may impede the ability of *H. polyglotta*—the apparently less competitive species—to respond to climate change. It seems unlikely that biotic interactions will impede movement of the chickadee hybrid zone in response to climate change, given that the southern species, *P. carolinensis*, appears to dominate interspecific interactions [12]. In fact, mating preferences may even facilitate movement as previously discussed [13]. Not surprisingly, this comparison highlights that the influence of climate on hybrid zone movement will be complex and hard to predict, always influenced by species interactions and ecology. However, in both situations, climate change is having an impact, direct or indirect, on species interactions.

General Conclusions

We document an example of climate-mediated movement of a North American avian hybrid zone using a combination of temporal genomic, distributional, and climatic sampling, making use of the world’s largest citizen science database. The rate of hybrid zone movement we report is comparable to movement rate estimates for other hybrid zones, and our exploration of the association of the contact zone with mean minimum winter temperature provides the first robust evidence that climate change is influencing the movement of this hybrid zone. We encourage others to harness the power of comprehensive analyses and data sets for our understanding of the influence of environmental change on speciation and species interactions.

Experimental Procedures

Sample Collection and Preparation

Blood samples were collected as described in [13]. We chose samples from two periods that were 10 years apart (2000–2002 and 2010–2012). Within each period we selected unrelated individuals, with the goal of having as even a sampling as possible across available sampling locations in each

period. In 2000–2002, samples were only available from four locations (Figure 2C). An additional location, TU, was added to the sampling regime in 2006 to ensure that one sampling site remained ahead of the moving hybrid zone. This site is included in the 2010–2012 transect, with five sampling points (Figure 2C).

DNA was extracted from all samples using DNeasy extraction kits (QIAGEN) and standard blood extraction protocols, eluted in water, and concentrated using a vacuum centrifuge. Blood samples are archived at Villanova, and DNA extractions are archived at the Cornell Lab of Ornithology. Villanova University's IACUC approved protocols for all field methods.

Genomic Data

Genotyping-by-sequencing (GBS) libraries were prepared and analyzed at the Institute for Genomic Diversity (IGD) at Cornell [26], using the enzyme PstI for digestion and creating a library with 96 unique barcodes. GBS libraries were sequenced on two lanes of an Illumina HiSeq 2000 (100 base pairs [bp], single-end) at the Cornell University Life Sciences Core Laboratories Center. GBS data were processed as in [27]. See [Supplemental Experimental Procedures](#) for data filtering details.

Admixture Analyses

To examine temporal changes in population admixture, we used STRUCTURE version 2.3.1, analyzing each time period separately [28]. We present details of the STRUCTURE analyses in the [Supplemental Experimental Procedures](#).

Geographic Cline Fitting and Concordance

To quantify hybrid zone movement, we used a geographic cline approach. Details can be found in the [Supplemental Experimental Procedures](#).

Distribution Modeling and Climate Association

To map the distribution of the contact zone between *P. atricapillus* and *P. carolinensis*, we used records from the eBird database [29]. We looked for evidence that winter temperature determines the contact zone (Figure 3A) by using information on the contact zone derived from our eBird distribution map (as explained in the [Supplemental Experimental Procedures](#)) and information on MDWT from PRISM. We provide details of our distribution modeling and climate association approaches in the [Supplemental Experimental Procedures](#). We conducted all analyses of eBird data using the R statistical language [30], with the supplemental spatial analysis package sp [31] for manipulation of spatial data, the generalized linear model (GLM) function for conducting logistic regression analysis, and the supplemental PresenceAbsence package [32] for calculating AUC statistics.

Accession Numbers

The Dryad DOI for the SNP data reported in this paper is 10.5061/dryad.7gg47.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, one figure, and two tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.01.069>.

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