Recent postglacial range expansion drives the rapid diversification of a songbird lineage in the genus Junco

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Pleistocene glacial cycles are thought to have played a major role in the diversification of temperate and boreal species of North American birds. Given that coalescence times between sister taxa typically range from 0.1 to 2.0 Myr, it has been assumed that diversification occurred as populations were isolated in refugia over long periods of time, probably spanning one to several full glacial cycles. In contrast, the rapid postglacial range expansions and recolonization of northern latitudes following glacial maxima have received less attention as potential promoters of speciation. Here we report a case of extremely rapid diversification in the songbird genus Junco as a result of a single continent-wide range expansion within the last 10 000 years. Molecular data from 264 juncos sampled throughout their range reveal that as the yellow-eyed junco (Junco phaeonotus) of Mesoamerica expanded northward following the last glacial maximum, it speciated into the dark-eyed junco (Junco hyemalis), which subsequently diversified itself into at least five markedly distinct and geographically structured morphotypes in the USA and Canada.

Patterns of low genetic structure and diversity in mitochondrial DNA and amplified fragment length polymorphism loci found in dark-eyed juncos relative to Mesoamerican yellow-eyed juncos provide support for the hypothesis of an expansion from the south, followed by rapid diversification in the north. These results underscore the role of postglacial expansions in promoting diversification and speciation through a mechanism that represents an alternative to traditional modes of Pleistocene speciation.

Keywords: speciation; postglacial expansion; phylogeography; Holocene; Junco

1. INTRODUCTION

Range expansions and colonization of new areas following glacial periods have resulted in some of the most remarkable radiations known in vertebrates (Schluter 2000; Coynes & Orr 2004). In North America, isolation of populations in refugia during Pleistocene glacial cycles is thought to have been largely responsible for the most recent speciation events in birds (Johnson & Cicero 2004; Weir & Schluter 2004), though the overall importance of the Pleistocene relative to older periods remains a topic of considerable debate (Klicka & Zink 1997; Avise & Walker 1998; Zink & Klicka 2004).

Bird populations underwent rapid continent-wide expansions following glacial maxima as ice sheets receded and climatic amelioration allowed the recolonization of northern latitudes, a process documented for a number of bird species as well as numerous other animal and plant taxa since the last glacial maximum (LGM) 18 000 years ago (Taberlet et al. 1998; Lessa et al. 2003; Hewitt 2004).

In birds, intraspecific tests of this ‘postglacial expansion hypothesis’ have documented patterns of low genetic diversity and structure in temperate and boreal populations relative to southern temperate and subtropical populations, demonstrating that the lack of genetic structure is due to shared ancestral polymorphism rather than gene flow (Milá et al. 2006; Ruegg et al. 2006).

Given that genetic distances between sister avian taxa generally correspond to divergence times ranging from 0.1 to 2 Myr (Klicka & Zink 1997; Johnson & Cicero 2004; Weir & Schluter 2007), it has been traditionally assumed that speciation took place in isolated refugia over one to several full glacial cycles (Mengel 1964; Hubbard 1973; Zink & Klicka 2006). The role of postglacial expansions themselves in driving speciation has received much less attention. Since continent-wide range expansions would subject advancing populations to a wide variety of unoccupied habitats with varying selective regimes, relatively short periods of isolation as new areas are colonized could potentially suffice to drive diversification in comparatively short periods of time. Considering that avian postglacial expansions are as short as a few 1000 years (Milá et al. 2006), and that this scenario does not invoke the need for long-term isolation in refugia, the postglacial expansion hypothesis poses an alternative to traditional modes of Pleistocene speciation.

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2. MATERIAL AND METHODS

(a) Taxonomy of the study group

The genus Junco is currently composed of three species—the dark-eyed junco J. hyemalis, the yellow-eyed junco J. phaeonotus and the volcano junco J. vulcani—although the actual number of species comprised in the dark-eyed junco complex remains a matter of debate (Nolan et al. 2002). The complex comprises at least five well-differentiated, largely allopatric morphotypes that differ prominently in plumage, beak colour and morphology (Miller 1941; Nolan et al. 2002). Formerly considered species (slate-coloured junco J. hyemalis, white-winged junco J. aikeni, Oregon junco J. oreganus, grey-headed junco J. caniceps and the Guadalupian island junco J. insularis), these five forms were recently lumped to form the dark-eyed junco (J. hyemalis; American Ornithologists’ Union 1973), though their assignment as subspecific ‘groups’ was intended to reflect the marked phenotypic differentiation between them, their allopatric breeding distributions and the stability of hybrid zones that exist between some groups (Nolan et al. 2002). In a recent monograph on the complex, Nolan et al. (2002) assert that with further investigation, the group is likely to be split again into multiple species. Indeed, a recent study on speciation times in birds has already considered two of the dark-eyed junco groups (J. oreganus and J. caniceps) as species based on evidence for lack of interbreeding when found in sympatry at some localities (Johnson & Cicero 2004). The yellow-eyed junco (J. phaeonotus) has been taxonomically stable and is composed of four different subspecies (phaeonotus, palliatus, fulvescens and alticola; Sullivan 1999). Finally, the volcano junco (J. vulcani) of southern Central America is considered a distant relative of other juncos and is included as an out-group for comparison. Given the unresolved status of Junco taxonomy, the number of species comprised by the genus ranges from a minimum of three to as many as seven. For consistency, we follow current
nomenclature which considers the genus to be composed of three species (dark-eyed, yellow-eyed and volcano juncos) and examine individuals from six dark-eyed junco morphotypes (slate-coloured Junco hyemalis hyemalis, white-winged Junco hyemalis aikeni, Oregon Junco hyemalis oreganus, pink-sided Junco hyemalis mearnsi, grey-headed Junco hyemalis caniceps and red-backed Junco hyemalis dorsalis), referred to here collectively as the ‘dark-eyed junco complex’, and from three of the four described subspecies of the yellow-eyed junco (phaeonotus, palliatus and alitoca).

(b) Sampling and mtDNA sequencing

Individuals were captured in the field using mist nets, and blood and/or feather samples were collected for genetic analysis. Three digital images of each individual were taken as photographic vouchers. Sampling localities, preceded by locality numbers in figure 1, referred to here collectively as the ‘dark-eyed junco complex’, and from three of the four described subspecies of the yellow-eyed junco (phaeonotus, palliatus and alitoca).

Sampling and mtDNA sequencing

We generated AFLP profiles for 142 individuals (for which blood samples were available) using a protocol modified from Vos et al. (1995). Whole genomic DNA extracted from blood samples using a Qiagen kit was digested with restriction enzymes EcoRI and MseI, and fragments were ligated to oligonucleotide adapters with T4 DNA ligase. A random sample of fragments was obtained through a pre-selective amplification using primers matching the adapters and enzyme restriction sites with an additional selective nucleotide in the 3’ end (E-tag and M-cgt). A final selective amplification was conducted with the same primers modified by the addition of three arbitrarily chosen nucleotides for each enzyme primer (E-tag and M-cgt), and labelled with the fluorescent dye 6FAM. Selectively amplified fragments were run in an ABI 3700 genetic analyzer using a LIZ500 size standard. Peaks were visualized using GENEMAPPER v. 7.0 and scored manually. Only unambiguously scorably loci and individuals were included in the analysis and peaks found in less than 2% of individuals were excluded. The average per locus methodological error rate for the AFLP data (assessed by running a subset of 10 individuals three times from the pre-selective amplification step) was 1.8%, similar to that of other AFLP studies on birds (Mock et al. 2002; Spaulding et al. 2006).

To assess genetic structure among samples, we used the program STRUCTURE v. 2.1 (Pritchard et al. 2000) and applied a model of no admixture as recommended for dominant markers (Pritchard & Wen 2004). The optimal number of populations (K) was calculated following the method by Evanno et al. (2005). We calculated Fst using ARLEQUIN v. 3.1., and tested for significance through 1000 random permutations of the dataset (Excoffier et al. 1992). We also obtained Weir & Cockerman’s Fst estimator θ (Weir & Cockerman 1984) using GENEPop (Raymond & Rousset 1995).

(d) Demographic history

We tested for population expansions using mtDNA sequence data and Fu’s test of neutrality (Fu 1997), which is particularly effective at detecting sudden changes in effective population size (Ramos-Onsins & Rozas 2002) by measuring departures from neutrality in situations characterized by an excess of rare alleles and young mutations. Large negative values of Fst reject population stasis. Significance of Fst values was evaluated with 1000 random permutations in ARLEQUIN v. 3.1. In addition, we compared mismatch distributions of pairwise nucleotide differences among CR haplotypes with expectations of a sudden expansion model (Rogers & Harpending 1992) using ARLEQUIN v. 3.1.

(e) Divergence times and diversification rates

Divergence times between taxa were estimated using three different methods. We applied a molecular clock using a range of calibrations to take into account the inter-taxon variability of CR mutation rates (Baker & Marshall 1997; Ruokonen & Kvist 2002). Given the lack of variation in the mtDNA coding regions surveyed (see electronic supplementary material) and the relatively higher levels of CR variation found in this study, we estimated the Junco CR mutation rate to be considerably higher than the 0.02 substitutions per site Myr−1 rate at which coding regions generally evolve (Garcia-Moreno 2004), and we used rates of 0.15, 0.10 and 0.05 substitutions
per site Myr$^{-1}$, which encompass rates generally found in birds (Baker & Marshall 1997). Much faster mutation rates, as those documented for the CR of penguins (0.30 substitutions per site Myr$^{-1}$; Lambert et al. 2002) or geese (0.21 substitutions per site Myr$^{-1}$; Quinn 1992), would make our diversification rate estimates even faster.

We also estimated diversification time with a coalescence-based model that generates non-equilibrium estimates of divergence time independent of gene migration (Nielsen & Wakeley 2001). We used Markov chain Monte Carlo simulations with the program M$^3$O (Nielsen & Wakeley 2001), which generates maximum likelihood estimates of $\theta$ (2$N_e \mu$); $T$, the divergence time between two populations scaled by population size; $M$, the gene migration rate between the two populations and time to the most recent common ancestor (TMRCA). We assumed uniform priors and set the two populations and time to the most recent common ancestor (TMRCA). We assumed uniform priors and set

\begin{equation}
T = \frac{2}{\mu k} \ln N_t
\end{equation}

where $N_t$ is the resulting number of species (Coyne & Orr 2004). We calculated NDI’s using $N_t=2$, 3 and 5, and the time divergence values obtained from M$^3$O using the three mutation rates described above. An $N_t$ of 5 would correspond to the yellow-eyed junco and a minimum number of dark-eyed forms (grey-headed, Oregon, slate-coloured and white-winged), and an $N_t$ of 2 would represent the most conservative assessment of variation in the group (yellow-eyed and dark-eyed juncoes).
juncos ($F_{st}$=0.003, $p=0.418$) was much lower than that between the dark-eyed junco complex and southern Mexico yellow-eyed juncos ($F_{st}=0.272$, $p<0.001$, table 2). These results suggest that yellow-eyed juncos from southern Mexico expanded through northern Mexico, rapidly diversifying into the various dark-eyed morphotypes after they arrived in temperate North America.

(b) AFLP analysis
A Bayesian analysis of population structure among all individuals using 75 AFLP markers revealed marked genetic similarity and an absence of structure among most dark-eyed junco morphotypes. The optimal number of populations in the assignment probability analysis using STRUCTURE was $K=4$ (figure 1b), with the four clusters corresponding broadly to Guatemala (yellow), Mexico (green), the white-winged junco population in the Black Hills and some pink-sided juncos from the nearby Bighorn Mountains (blue) and all remaining dark-eyed junco forms (red).

Also evident in the STRUCTURE results is the gradual pattern of differentiation between yellow-eyed and dark-eyed populations. When individuals are assigned to one of two clusters ($K=2$, figure 1b), each one corresponds roughly to yellow-eyed juncos (green) and dark-eyed juncos (red), with average assignment probabilities changing gradually with latitude. Interestingly, red-backed junco individuals (sites 12 and 13 in figure 1a) show similar assignment probabilities to the two clusters as predicted by their intermediate phenotype. For the optimal $K=4$ (figure 1b), yellow-eyed individuals from Arizona (site 11) show a higher average assignment probability to the dark-eyed cluster (red colour) than those in southern Mexico (site 5), which show a higher assignment probability to the Guatemalan cluster (yellow colour). This pattern is reflected in the $F_{st}$ analysis, with values between dark-eyed and northern yellow-eyed juncos being lower than between dark-eyed and southern yellow-eyed juncos (table 2).

(c) Divergence times and diversification rates
The average genetic distance in mtDNA CR between the dark-eyed junco complex and yellow-eyed juncos was 0.019% when corrected for intraspecific polymorphism (Nei 1987). Applying a molecular clock, this value corresponds to divergence times ranging between 1300 and 3800 years BP using mutation rates of 15% Myr$^{-1}$ and 5% Myr$^{-1}$, respectively. The non-equilibrium estimates of time divergence between populations obtained with MDIV were 2548–7620 years BP, and TMRCA, or the time when genes last shared a common ancestor ranged between 26 764 and 80 028 years. Diversification time obtained from the distribution of pairwise differences among individuals provided comparable time estimates of 4046–11 976 years BP to the time of the population expansion, depending on mutation rate. Using a generation time of 2 years instead of 1 year, which might apply to small passerines with relatively high mortality rates, would double the time divergence estimates above. Finally, NDIs ranged from 0.0109 to 0.0016 Myr, depending on the mutation rate and the number of new taxa ($N_t$) considered to have been produced (figure 2).

4. DISCUSSION
Results from the mtDNA analyses provide strong support for a rapid postglacial expansion of the yellow-eyed junco from Mexico into temperate North America, and for a subsequent rapid burst of diversification that gave rise to at least five distinct morphotypes of the dark-eyed junco as expanding populations reached temperate latitudes. An alternative explanation for the genetic pattern found among dark-eyed junco morphotypes is the occurrence of a selective sweep by an adaptive mtDNA haplotype, which could have spread across previously differentiated morphotypes by crossing hybrid zones. The ubiquity of haplotype A in yellow-eyed junco populations (with whom dark-eyed juncos are not known to hybridize), the limited amount of gene flow evident in southern populations (e.g. haplotypes D and E are restricted to central Mexico, and G is restricted to Guatemala, see table 1) and the gradual latitudinal increase in the frequency of ancestral haplotype A, all strongly suggest that the predominance of haplotype A in northern populations reflects shared ancestral polymorphism resulting from a rapid population expansion, and not gene flow (Milá et al. 2006).

However, in order to confidently reject the selective sweep hypothesis, a congruent pattern of low genetic structure and diversity in dark-eyed juncos must be confirmed with unlinked nuclear markers. This is because factors such as bottlenecks and population expansions

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**Table 2. Differentiation between dark-eyed and yellow-eyed juncos based on mtDNA CR sequence data ($F_{st}$) and AFLP loci ($F_{st}$ and Weir and Cockerman’s $\theta$).**

<table>
<thead>
<tr>
<th></th>
<th>mtDNA</th>
<th>AFLP</th>
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<tr>
<td></td>
<td>$F_{st}$</td>
<td>$F_{st}$</td>
</tr>
<tr>
<td>DEJU versus NYEJU</td>
<td>0.003</td>
<td>0.129***</td>
</tr>
<tr>
<td>DEJU versus SYEJU (Mex only)</td>
<td>0.272***</td>
<td>0.200***</td>
</tr>
<tr>
<td>DEJU versus SYEJU (Mex + Gua)</td>
<td>0.193***</td>
<td>0.202***</td>
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**Figure 2.** Estimates of NDIs in the yellow-eyed and dark-eyed juncos based on mtDNA CR sequence, using three mutation rates (0.15, 0.10 and 0.05 substitutions per site Myr$^{-1}$), with three values for the number of diversified taxa ($N_t$), 2 (filled diamonds), 3 (filled squares) and 5 (filled triangles).
should affect the entire genome equally, whereas selective sweeps should only be detected in the locus under selection (and tightly linked loci; Galtier et al. 2000). The lack of clear structure in AFLP loci within the dark-eyed junco complex despite marked phenotypic differentiation and considerable geographical distances separating them is congruent with the mtDNA results and supports the hypothesis of rapid diversification following a recent expansion. The differentiation of the white-winged junco population was driven largely by the presence of three nearly diagnostic loci and could be due to founder events and the subsequent fixation of rare alleles in a population of small effective size, although the influence of natural selection cannot be ruled out. The fact that some pink-sided juncos from the nearby Bighorn Mountains of Wyoming and even some Oregon junco clusters with the white-winged junco suggests that the alleles involved appeared (or became fixed) in the small Black Hills population and spread west through gene flow across hybrid zones.

Several phenotypic characteristics of juncos are consistent with a history of diversification through a northward expansion from southern forms. The red-backed and grey-headed juncos of Arizona and the southern Rocky Mountains, in particular, are phenotypically intermediate between yellow-eyed and dark-eyed juncos. For example, the loss of the yellow iris in the red-backed junco (otherwise remarkably similar to its yellow-eyed neighbour), and the loss of the bicoloured beak in the grey-headed junco just to the north (figure 1c), appear to represent successive steps in the gradual evolution of dark-eyed forms, which subsequently and rapidly acquired their diverse plumage patterns (often with a prominent increase of eumelanic and pheomelanic). Recent divergence with fast plumage evolution (since the LGM) has been recently documented in Icterus orioles (Baker et al. 2003; Kondo et al. 2004), redpolls (Seutin et al. 1995), blue thrashers (Questiau et al. 1998; Zink et al. 2003), yellow wagtails (Ödeen & Björklund 2003) and yellow-rumped warblers (Milá et al. 2007). However, given the higher number and marked distinctiveness of plumage morphs and the short amount of time involved, the dark-eyed junco complex represents an exceptional case of fast plumage diversification.

Large-scale range expansions into formerly glaciated areas following glacial maxima have been reported for numerous animal and plant taxa during the Pleistocene (Hewitt 2000) and speciation during this period is thought to have been driven in part by isolation in glacial refugia (Weir & Schluter 2004). Previous studies on avian speciation rates have shown that coalescence times to the closest common ancestor of extant species pairs are typically in the range of 0.1–2.0 Myr (Avise & Walker 1998; Lovette & Bermingham 1999; Johnson & Cicero 2004; Weir & Schluter 2007) and often pre-date the Pleistocene (Klicka & Zink 1999). In a recent molecular study of 39 sister-species pairs of birds (Johnson & Cicero 2004), only two pairs showed splits younger than 50 000 years (Spizella breweri/Spizella taeniornis, two weakly differentiated taxa, and Junco oreganus/J. caniceps, two of the taxa in the dark-eyed junco complex examined here). In contrast, our molecular data indicate that diversification of dark-eyed juncos took place within the time span of a single postglacial expansion within the last 10 000 years, as ancestral yellow-eyed junco populations expanded their range through northern Mexico and into temperate North America following the LGM.

The occurrence of hybridization along contact zones between some forms in the dark-eyed junco complex (except for, at least, caniceps/hyemalis, caniceps/aikeni, and insularis), suggests that reproductive isolation between some morphotypes is not yet complete. However, the marked phenotypic differentiation between forms, their largely allopatric distribution, and the fact that most hybrid zones are of limited width and apparently stationary over at least a century (Miller 1941; Nolan et al. 2002), all suggest that dark-eyed junco forms are on distinct evolutionary trajectories and may represent a case of speciation in action. The rate of diversification presented here, even if only two species are considered, is among the fastest observed in vertebrates (Coyne & Orr 2004) and is similar to that reported for the cichlid fish species flock of Lake Nabugabo in East Africa, where five species evolved in less than 4000 years, which is thought to represent the fastest radiation within cichlids (NDI = 0.004 Myr; Coyne & Orr 2004). Because the Junco diversification is so recent, the probability of extinction of new taxa is low, which could account for the unusually low NDI values obtained. Potentially, similarly fast diversification bouts could have taken place in older lineages, yet because only a fraction of the original number of species has survived, speciation rates might be underestimated. However, given that none of the previously studied avian groups show similar recent bouts of diversification, and the fact that several bird taxa show similar signatures of postglacial population expansion over North America yet lack a comparable amount of phenotypic diversification (Ball et al. 1988; Zink & Dittman 1993; Milot et al. 2000; Kimura et al. 2002; Ruegg & Smith 2002; Veit et al. 2005; Milá et al. 2006), the rapid diversification in Junco appears to be exceptional.

Selection-driven evolutionary change can be especially fast in peripheral isolates such as those found at the leading edge of an expansion (Garcia-Ramos 1997; Gavrilets et al. 2000), and given the marked differences in plumage characters, sexual selection may have acted as the mechanism of divergence (Fisher 1930; Lande 1981; Barraclough et al. 1995). Indeed, a recently established Oregon junco population in southern California has evolved marked differences in a sexually selected trait (amount of white on outer tail feathers) after only several generations (Yeh 2004). The relative roles of female choice and male–male competition in the phenotypic divergence of juncos is unclear, although recent research on the slate-coloured junco suggests that both might be involved (McGlothlin et al. 2005). Our results underscore the role of postglacial expansions in driving diversification and speciation, and suggest that the colonization of new areas following glacial periods can lead to exceptionally rapid rates of evolution.

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