The Pliocene-Pleistocene transition had dual effects on North American migratory bird speciation

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A B S T R A C T

Paleo-environmental change is thought to substantially influence biological evolution. In particular, fragmentation of the geographical distributions of vertebrate faunas and subsequent speciation events occurred frequently due to glacial advances during the Pliocene-Pleistocene transition 2.5 million years ago (Ma). However, the effects of glacial advances on speciation between migratory and sedentary birds have not been systematically evaluated. Here, we conducted phylogenetic meta-analysis of 14 closely related pairs of the North American migratory species and 25 closely related pairs of the North American migratory and neotropical sedentary species and estimated their divergence times using cytochrome b. Whereas divergence events between migratory species were mostly in the Pleistocene (median 1.51 Ma) as previously reported, many divergence events between the migratory and sedentary bird species appear to date back to the Pliocene (median 2.77 Ma). These speciation patterns indicate that the Pliocene-Pleistocene transition may have accelerated speciation between migratory bird species, but did not accelerate that between migratory and sedentary species through countering mechanisms.

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1. Introduction

Paleo-environmental change substantially influences biological evolution (Webb and Bartlein, 1992). Systematic evaluation of effects of past environmental change on speciation is important for predicting the effects of future environmental changes on the biodiversity (Pearson and Dawson, 2003; Provan and Bennett, 2008). Phylogenetic methods have been used to infer the impacts of paleo-environmental changes on species distribution, genetic differentiation, and speciation (Avise et al., 1998; Cicero and Johnson, 1998). Because much DNA sequence data have been archived, studies combining phylogenetic meta-analysis and paleo-environmental analysis hold promise in exploring the interplay between paleo-environmental changes and biological evolution (Claramunt and Cracraft, 2015).

The Pliocene-Pleistocene transition 2.5 million years ago (Ma) represents one of the most fundamental climatic changes in geologic history (Yamane et al., 2015; Haywood et al., 2016). This transition was marked by an increase in the pace of glacial and interglacial cycles as well as an increase in the area of continental ice sheets, manifesting in more rapid and larger climatic and environmental oscillations (Lisiecki and Raymo, 2005). These changes had a major impact on the biodiversity. In particular, glacial advances southward were believed to have promoted speciation events by fragmenting the geographical distributions of vertebrate faunas at northern latitudes (Mengel, 1970), and this hypothesis is supported by phylogenetic analyses (Bermingham et al., 1992; Weir and Schluter, 2004; Lovette, 2005).

Many organisms, including birds, insects, fish, and mammals, migrate as an adaptation to seasonal and geographical variations in resource abundance (Dingle and Drake, 2007). Evolutionary transitions from residency to migration or vice versa, as well as changes in patterns of migration, have occurred frequently in these organisms (Alerstam et al., 2003) and promoted speciation events (Winker, 2000). Birds show striking evidence of frequent evolutionary transitions: closely related species include residents and short-distance and long-distance migrants (Alerstam et al., 2003), although the evolution of migration systems apparently involve costs associated with the migratory process in terms of time (e.g. losses of prior occupancy advantages), energy, and mortality (e.g. increased exposure to parasites). These variations are sometimes observed even between different populations of a single species (Alerstam et al., 2003; Milá et al., 2006), where some bird species travel extraordinary distances during their annual migratory

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The evolution of migratory systems can be promoted by ecological and biogeographic factors like seasonality, spatiotemporal distributions of resources, habitats, and predation and competition in winter and breeding seasons (Lundberg and Alerstam, 1986; Price et al., 2004; Klicka et al., 2003; Outlaw et al., 2003; Carson and Spicer 2003; Powell et al., 2008; Lanoy and Omland, 1999; Lovette et al., 2010; Johnson and Clayton, 2000; DaCosta et al., 2009; Carson and Spicer, 2003; Lanoy and Omland, 1999; Lovette et al., 2010; Lovette et al., 2010; Lanoy and Omland, 1999; Lovette et al., 2010; Lovette et al., 2010).

Table 1
Species pairs analyzed in this study and their estimated divergence times.

<table>
<thead>
<tr>
<th>Family name</th>
<th>Species pair</th>
<th>Nucleotide substitution model</th>
<th>Sequence divergence per lineage (%)</th>
<th>Estimated divergence time (Ma)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anatidae</td>
<td>Bucephala islandica vs B. clangula (Barrow’s goldeneye vs Common goldeneye)</td>
<td>TN</td>
<td>1.65</td>
<td>1.57</td>
<td>Oates and Principato (1994)</td>
</tr>
<tr>
<td>Apodidae</td>
<td>Chaetura pelagica vs C. vauxi (Chimney swift vs Vaux’s swift)</td>
<td>HKY + G</td>
<td>2.71</td>
<td>2.58</td>
<td>Price et al. (2004)</td>
</tr>
<tr>
<td>Calcaridae</td>
<td>Calcaria pictus vs Carnatus (Smith’s longspur vs Chestnut-collared longspur)</td>
<td>HKY + G</td>
<td>1.65</td>
<td>1.57</td>
<td>Klicka et al. (2003)</td>
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<td>Turdidae</td>
<td>Catharus fuscens vs C. minimus (Veery vs Grey-cheeked thrush)</td>
<td>HKY</td>
<td>0.52</td>
<td>0.49</td>
<td>Outlaw et al. (2003)</td>
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<td>Emberizidae</td>
<td>Melospiza lincolni vs M. georgiana (Lincoln’s sparrow vs Swamp sparrow)</td>
<td>HKY</td>
<td>1.51</td>
<td>1.44</td>
<td>Carson and Spicer (2003)</td>
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<tr>
<td>Emberizidae</td>
<td>Pipilo maculatus vs P. euryrhyphalus (Spotted towhee vs Eastern towhee)</td>
<td>HKY + I</td>
<td>0.30</td>
<td>0.28</td>
<td>DaCosta et al. (2009)</td>
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<tr>
<td>Emberizidae</td>
<td>Zonotrichia albicollis vs Z. leucophrys (White-throated sparrow vs White-crowned sparrow)</td>
<td>TN + G</td>
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<td>2.12</td>
<td>DaCosta et al. (2009)</td>
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<td>Icteridae</td>
<td>Euphagus carolinus vs E. cyanocephalus (Rusty blackbird vs Brewer’s blackbird)</td>
<td>HKY + G</td>
<td>2.70</td>
<td>2.57</td>
<td>Powell et al. (2008)</td>
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<tr>
<td>Icteridae</td>
<td>Sturnella neglecta vs S. magna (Western meadowlark vs Eastern meadowlark)</td>
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<td>2.45</td>
<td>2.33</td>
<td>Lanoy and Omland (1999)</td>
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<td>Icteridae</td>
<td>Geothlypis tolmiei vs G. philadelphia (MacGillivray’s warbler vs Mourning warbler)</td>
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<td>1.14</td>
<td>1.09</td>
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<td>0.71</td>
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<td>Icteridae</td>
<td>Setophaga occidentalis vs S. townsendi (Hermit warbler vs Townsend’s warbler)</td>
<td>HKY + G</td>
<td>0.46</td>
<td>0.44</td>
<td>Lovette et al. (2010)</td>
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<td>Icteridae</td>
<td>Setophaga petechia vs S. pensylvanica (American yellow warbler vs Chestnut-sided warbler)</td>
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<td>2.35</td>
<td>Lovette et al. (2010)</td>
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<td>Vireonidae</td>
<td>Vireo casini vs V. solitarius (Cassin’s vireo vs Blue-headed vireo)</td>
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<td>1.29</td>
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<td>Median value (n = 14)</td>
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<td>1.58</td>
<td>1.51</td>
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<td>Anatidae</td>
<td>North American migratory vs neotropical sedentary (less migratory) species</td>
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<td>Apodidae</td>
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<td>HKY + G</td>
<td>3.75</td>
<td>3.57</td>
<td>Price et al. (2004)</td>
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<td>Caprimulgidae</td>
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<td>3.69</td>
<td>3.51</td>
<td>Han (2006)</td>
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<td>Caprimulgidae</td>
<td>Caprimulgus vociferus vs C. arizonae/C. saturatus (Eastern whip-poor-will vs Mexican whip-poor-will/Dusky nightjar)</td>
<td>TN + G</td>
<td>4.13</td>
<td>3.94</td>
<td>Lovette et al. (2012)</td>
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<td>Cardinalidae</td>
<td>Piranga ludovicianus vs P. bidentata (Western tanager vs Flame-colored tanager)</td>
<td>HKY</td>
<td>3.01</td>
<td>2.87</td>
<td>Burns (1998)</td>
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<tr>
<td>Columbidae</td>
<td>Zenaida asiatica vs Z. melodia (White-winged dove vs West Peruvian dove)</td>
<td>HKY + G</td>
<td>2.87</td>
<td>2.73</td>
<td>Johnson and Clayton (2000)</td>
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<td>Columbidae</td>
<td>Zenaida macroura vs Z. graysoni (Mourning dove vs Socorro dove)</td>
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<td>0.48</td>
<td>0.46</td>
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<tr>
<td>Emberizidae</td>
<td>Pipilo maculatus/P. euryrhyphalus/P. chlorurus vs P. ocai (Spotted towhee/Eastern towhee/Green-tailed towhee vs Collared towhee)</td>
<td>HKY + I</td>
<td>2.82</td>
<td>2.68</td>
<td>DaCosta et al. (2009)</td>
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<td>Hirundinidae</td>
<td>Petrochelidon fulva vs P. rufocollaris (Cave swallow vs Chestnut-collared swallow)</td>
<td>HKY</td>
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<td>0.85</td>
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<tr>
<td>Hirundinidae</td>
<td>Stelgidopteryx rhipidum vs S. rubicollis (Northern rough-winged swallow vs Southern rough-winged swallow)</td>
<td>HKY</td>
<td>3.46</td>
<td>3.30</td>
<td>Sheldon et al. (2005)</td>
</tr>
<tr>
<td>Icteridae</td>
<td>Icterus bullockii vs I. pustulatus (Bullock’s oriole vs Streak-backed oriole)</td>
<td>HKY</td>
<td>1.47</td>
<td>1.40</td>
<td>Jacobson et al. (2010)</td>
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<td>Icteridae</td>
<td>Icterus galbula vs I. abfolii (Baltimore oriole vs Black-backed oriole)</td>
<td>HKY</td>
<td>0.23</td>
<td>0.22</td>
<td>Jacobson et al. (2010)</td>
</tr>
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<td>Molothrus ater vs M. bonariensis (Brown-headed cowbird vs Shiny cowbird)</td>
<td>HKY</td>
<td>0.66</td>
<td>0.63</td>
<td>Lanoy and Omland (1999)</td>
</tr>
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<td>Icteridae</td>
<td>Quiscalus quiscula vs other Quiscalus species (Common grackle vs other Quiscalus species)</td>
<td>HKY</td>
<td>2.43</td>
<td>2.31</td>
<td>Powell et al. (2008)</td>
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<td>Icteridae</td>
<td>Sturnella neglecta/magna vs S. hellicosa/S. militaris/S. loyca (Western meadowlark/Eastern meadowlark/Peruvian meadowlark/Red-breasted long-tailed blackbird/Long-tailed meadowlark)</td>
<td>TN + G</td>
<td>8.06</td>
<td>7.68</td>
<td>Lanoy and Omland (1999)</td>
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<td>Parulidae</td>
<td>Cardellina rubrifrons vs C. ruber/C. versicolor (Red-faced warbler vs Red-faced warbler/Pink-headed warbler)</td>
<td>HKY + G</td>
<td>2.44</td>
<td>2.33</td>
<td>Lovette et al. (2010)</td>
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<td>Parulidae</td>
<td>Oreothlypis virginiae/O. luciae/O. rufacippella vs O. crissalis (Virginia’s warbler/Lucy’s warbler/Nashville warbler vs Colima warbler)</td>
<td>HKY</td>
<td>1.32</td>
<td>1.26</td>
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<td>Setophaga discolor vs S. vitellina (Prairie warbler vs Viteline warbler)</td>
<td>HKY</td>
<td>1.26</td>
<td>1.20</td>
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</tr>
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<td>Parulidae</td>
<td>Setophaga occidentalis/S. townsendi (Hermit warbler/Townsend’s warbler vs Adaline’s warbler)</td>
<td>HKY + G</td>
<td>3.10</td>
<td>2.95</td>
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<td>Parulidae</td>
<td>Setophaga pinus vs S. pityophila (Pine warbler vs Olive-capped warbler)</td>
<td>HKY</td>
<td>2.91</td>
<td>2.77</td>
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<td>Turdidae</td>
<td>Catharus fuscens/C. bicknellii/C. minimus vs C. frantzii (Veery/Bicknell’s thrush/Grey-cheeked thrush vs Ruddy-capped nightingale-thrush)</td>
<td>HKY + G</td>
<td>3.86</td>
<td>3.67</td>
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<td>Turdidae</td>
<td>Catharus guttatus vs C. occidentalis (Hermit thrush vs Rusty nightingale-thrush)</td>
<td>HKY + G</td>
<td>3.53</td>
<td>3.36</td>
<td>Outlaw et al. (2003)</td>
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<td>Tyrannidae</td>
<td>Empidonax oberholseri vs E. affinis (American dusky flycatcher vs Pine flycatcher)</td>
<td>HKY + G</td>
<td>0.30</td>
<td>0.28</td>
<td>Johnson and Cicero (2002)</td>
</tr>
<tr>
<td>Vireonidae</td>
<td>Vireo gilvus vs V. leucophrys (Warbling vireo vs Brown-capped vireo)</td>
<td>GTR</td>
<td>3.01</td>
<td>2.87</td>
<td>Johnson et al. (1988)</td>
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<td>Median value (n = 25)</td>
<td></td>
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<td>2.91</td>
<td>2.77</td>
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