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

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ABSTRACT

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 after 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 counteracting mechanisms.

1. Introduction

Paleo-envionmental 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 Because much DNA sequence data have been archived, studies combining phylogenetic meta-analysis and paleo-environmental analysis hold promise in exploring the interplay between paleo-envionmental changes and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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Table 1
Species pairs analyzed in this study and their estimated divergence times.

Family name	Species pair	Nucleotide substitution model	Sequence divergence per lineage (%)	Estimated divergence time (Ma)	Reference
North American migratory species pairs					
Anatidae	*Bucephala islandica* vs *B. clangula* (Barrow's goldeneye vs Common goldeneye)	TN	1.65	1.57	Oates and Principato (1994)
Apodidae	*Chaetura pelagica* vs *C. vauxi* (Chimney swift vs Vaux's swift)	HKY + G	2.71	2.58	Price et al. (2004)
Calcariidae	*Calcarius pictus* vs *C.ornatus* (Smith's longspur vs Chestnut-collared longspur)	HKY + G	1.65	1.57	Klicka et al. (2003)
Turdidae	*Catharus fuscescens* vs *C. minimus* (Veery vs Grey-cheeked thrush)	HKY + G	0.52	0.49	Outlaw et al. (2003)
Emberizidae	*Melospiza lincolnii* vs *M. georgiana* (Lincoln's sparrow vs Swamp sparrow)	HKY	1.51	1.44	Carson and Spicer (2003)
Emberizidae	*Pipilo maculatus* vs *P. erythrophthalmus* (Spotted towhee vs Eastern towhee)	HKY + I	0.30	0.28	DaCosta et al. (2009)
Emberizidae	*Zonotrichia albicollis* vs *Z. leucophrys* (White-throated sparrow vs White-crowned sparrow)	TN + G	2.23	2.12	Carson and Spicer (2003)
Icteridae	*Euphagus carolinus* vs *E. cyanocephalus* (Rusty blackbird vs Brewer's blackbird)	HKY + G	2.70	2.57	Powell et al. (2008)
Icteridae	*Sturnella neglecta* vs *S. magna* (Western meadowlark vs Eastern meadowlark)	TN + G	2.45	2.33	Lanyon and Omland (1999)
Parulidae	*Geothlypis tolmiei* vs *G. philadelphia* (MacGillivray's warbler vs Mourning warbler)	HKY	1.14	1.09	Lovette et al. (2010)
Parulidae	*Oreothlypis virginiae* vs *O. luciae* (Virginia's warbler vs Lucy's warbler)	HKY + G	0.75	0.71	Lovette et al. (2010)
Parulidae	*Setophaga occidentalis* vs *S. townsendi* (Hermit warbler vs Townsend's warbler)	HKY + G	0.46	0.44	Lovette et al. (2010)
Parulidae	*Setophaga petechia* vs *S. pensylvanica* (American yellow warbler vs Chestnut-sided warbler)	HKY + G	2.47	2.35	Lovette et al. (2010)
Vireonidae	*Vireo cassinii* vs *V. solitarius* (Cassin's vireo vs Blue-headed vireo)	HKY	1.35	1.29	Cicero and Johnson (1998)
Median value ($n = 14$)			1.58	1.51	
North American migratory vs neotropical sedentary (less migratory) species					
Apodidae	*Chaetura pelagica*/*C. vauxi* vs *C. chapmani* (Chimney swift/Vaux's swift vs Chapman's swift)	HKY + G	3.75	3.57	Price et al. (2004)
Caprimulgidae	*Caprimulgus carolinensis* vs *C. rufus* (Chuck-will's-widow vs Rufous nightjar)	TN + G	3.69	3.51	Han (2006)
Caprimulgidae	*Caprimulgus vociferus* vs *C. arizonae*/*C. saturatus* (Eastern whip-poor-will vs Mexican whip-poor-will/Dusky nightjar)	TN + G	4.13	3.94	Lovette et al. (2012)
Cardinalidae	*Piranga ludoviciana* vs *P. bidentata* (Western tanager vs Flame-colored tanager)	HKY + G	3.01	2.87	Burns (1998)
Columbidae	*Zenaida asiatica* vs *Z. meloda* (White-winged dove vs West Peruvian dove)	HKY + G	2.87	2.73	Johnson and Clayton (2000)
Columbidae	*Zenaida macroura* vs *Z. graysoni* (Mourning dove vs Socorro dove)	HKY	0.48	0.46	Johnson and Clayton (2000)
Emberizidae	*Pipilo maculatus*/*P. erythrophthalmus*/*P. chlorurus* vs *P. ocai* (Spotted towhee/Eastern towhee/Green-tailed towhee vs Collared towhee)	HKY + I	2.82	2.68	DaCosta et al. (2009)
Emberizidae	*Zonotrichia albicollis*/*Z. leucophrys* vs *Z. capensis* (White-throated sparrow/White-crowned sparrow vs Rufous-collared sparrow)	TN + G	4.40	4.19	DaCosta et al. (2009), Carson and Spicer (2003)
Hirundinidae	*Petrochelidon fulva* vs *P. rufocollaris* (Cave swallow vs Chestnut-collared swallow)	HKY	0.90	0.85	Sheldon et al. (2005)
Hirundinidae	*Stelgidopteryx serripennis* vs *S. ruficollis* (Northern rough-winged swallow vs Southern rough-winged swallow)	HKY + G	3.46	3.30	Sheldon et al. (2005)
Icteridae	*Icterus bullockii* vs *I. pustulatus* (Bullock's oriole vs Streak-backed oriole)	HKY	1.47	1.40	Jacobsen et al. (2010)
Icteridae	*Icterus galbula* vs *I. abeillei* (Baltimore oriole vs Black-backed oriole)	HKY	0.23	0.22	Jacobsen et al. (2010)
Icteridae	*Molothrus ater* vs *M. bonariensis* (Brown-headed cowbird vs Shiny cowbird)	HKY	0.66	0.63	Lanyon and Omland (1999)
Icteridae	*Quiscalus quiscula* vs other Quiscalus species (Common grackle vs other Quiscalus species)	HKY + G	2.43	2.31	Powell et al. (2008)
Icteridae	*Sturnella neglecta*/*magna* vs *S. bellicosa*/*S. militaris*/*S. loyca* (Western meadowlark/Eastern meadowlark vs Peruvian meadowlark/Red-breasted blackbird/Long-tailed meadowlark)	TN + G	8.06	7.68	Lanyon and Omland (1999)
Mimidae	*Toxostoma rufum* vs *T. longirostre*/*T. guttatum* (Brown thrasher vs Long-billed thrasher/Cozumel thrasher)	HKY + G	3.59	3.42	Lovette et al. (2012)
Parulidae	*Cardellina rubrifrons* vs *C. ruber*/*C. versicolor* (Red-faced warbler vs Red warbler/Pink-headed warbler)	HKY + G	2.44	2.33	Lovette et al. (2010)
Parulidae	*Oreothlypis virginiae*/*O. luciae*/*O. ruficapilla* vs *O. crissalis* (Virginia's warbler/Lucy's warbler/Nashville warbler vs Colima warbler)	HKY + G	1.32	1.26	Lovette et al. (2010)
Parulidae	*Setophaga discolor* vs *S. vitellina* (Prairie warbler vs Vitelline warbler)	HKY	1.26	1.20	Lovette et al. (2010)
Parulidae	*Setophaga occidentalis*/*S. townsendi* vs *S. adelaide* (Hermit warbler/Townsend's warbler vs Adelaide's warbler)	HKY + G	3.10	2.95	Lovette et al. (2010)
Parulidae	*Setophaga pinus* vs *S. pityophila* (Pine warbler vs Olive-capped warbler)	HKY + G	2.91	2.77	Lovette et al. (2010)
Turdidae	*Catharus fusescens*/*C. bicknelli*/*C. minimus* vs *C. frantzii* (Veery/Bicknell's thrush/Grey-cheeked thrush vs Ruddy-capped nightingale-thrush)	HKY + G	3.86	3.67	Outlaw et al. (2003)
Turdidae	*Catharus guttatus* vs *C. occidentalis* (Hermit thrush vs Russet nightingale-thrush)	HKY + G	3.53	3.36	Outlaw et al. (2003)
Tyrannidae	*Empidonax oberholseri* vs *E. affinis* (American dusky flycatcher vs Pine flycatcher)	HKY + G	0.30	0.28	Johnson and Cicero (2002)
Vireonidae	*Vireo gilvus* vs *V. leucophrys* (Warbling vireo vs Brown-capped vireo)	GTR	3.01	2.87	Johnson et al. (1988)
Median value ($n = 25$)			2.91	2.77	

journeys (>10,000 km; Alerstam et al., 2003). Therefore, evolution of migratory birds has been of special interest for a long period (Salewski and Bruderer, 2007). 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;