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Geographic isolation drives divergence of uncorrelated genetic and song variation in the Ruddy-capped Nightingale-Thrush (*Catharus frantzii*; Aves: Turdidae) ☆

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ABSTRACT

Montane barriers influence the evolutionary history of lineages by promoting isolation of populations. The effects of these historical processes are evident in patterns of differentiation among extant populations, which are often expressed as genetic and behavioral variation between populations. We investigated the effects of geographic barriers on the evolutionary history of a Mesoamerican bird by studying patterns of genetic and vocal variation in the Ruddy-capped Nightingale-Thrush (Turdidae: *Catharus frantzii*), a non-migratory oscine bird that inhabits montane forests from central Mexico to Panama. We reconstructed the phylogeographic history and estimated divergence times between populations using Bayesian and maximum likelihood methods. We found strong support for the existence of four mitochondrial lineages of *C. frantzii* corresponding to isolated mountain ranges: Sierra Madre Oriental; Sierra Madre del Sur; the highlands of Chiapas, Guatemala, and El Salvador; and the Talamanca Cordillera. Vocal features in *C. frantzii* were highly variable among the four observed clades, but vocal variation and genetic variation were uncorrelated. Song variation in *C. frantzii* suggests that sexual selection and cultural drift could be important factors driving song differentiation in *C. frantzii*.
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1. Introduction

Diversification of montane taxa is an evolutionary phenomenon attributed to geographical isolation of populations and ecological factors that promote divergence by limiting exchange of genetic and cultural information (Price, 2008; Fjeldså et al., 2012). Once populations are geographically isolated, they may diverge in response to different ecologically based selection pressures. The rate of divergence may be accelerated when populations occupy different environments with different selection pressures (Orr and Smith, 1998; Lachlan and Servedio, 2004; Catchpole and Slater, 2008; Shaw and Mullen, 2011). The maintenance of barriers to gene flow is of considerable importance to understand speciation in montane systems.

Geographic isolation may also facilitate development of behavioral barriers to gene flow (West-Eberhard, 1983; Parker et al., 2012). Behavioral barriers are of particular interest in oscine songbirds, a lineage that is influenced by cultural evolution via song learning and sexual selection. As such, behavioral barriers have the potential to affect mate recognition and promote speciation in oscines (Lynch, 1996; Slabbekoorn and Smith, 2002b; Lachlan and Servedio, 2004; Podos and Warren, 2007; Catchpole and Slater, 2008; Price, 2008; Grant and Grant, 2010; Rowell and Servedio, 2012; Verzijden et al., 2012; Vokurková et al., 2013).

Vocalizations are useful characters for species diagnosis and delimitation in birds, especially across phylogeographic breaks (Payne, 1986; Isler et al., 1998; Tubaro, 1999). They can be used

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to study phylogenetic relationships among species (Payne, 1986; Price and Lanyon, 2002; ten Cate, 2004), and they are often congruent with molecular or morphologically based phylogenetic studies (Podos, 2001; Price and Lanyon, 2002, 2004; Price et al., 2007). Vocal variation across geography (e.g. vocal dialects) can offer clues in discriminating between genetically divergent populations (Baker et al., 1982; MacDougall-Shackleton and MacDougall-Shackleton, 2001). Indeed, in many bird species there is a positive correlation between vocal and genetic divergence in birds (e.g. Payne, 1986; MacDougall-Shackleton and MacDougall-Shackleton, 2001; Price and Lanyon, 2002; Soha et al., 2004; Nicholls et al., 2006; Alström et al., 2007; Irwin et al., 2008). However, studies using rapidly evolving genetic markers in a wide variety of song learners (mainly oscine songbirds and parrots), have failed to find genetic divergence coupled with song divergence (McDonald, 2003; Soha et al., 2004; Wright et al., 2005; Ruegg et al., 2006; Leader et al., 2008). The evolution of vocal traits, therefore, is thought to be driven by cultural processes analogous to genetic evolution: mutation, migration, drift, and selection (Lynch, 1996), but also by ecological factors like habitat structure and other environmental conditions (Larom et al., 1997; Slabbekoorn et al., 2002; Slabbekoorn and Smith, 2002a, 2002b; Catchpole and Slater, 2008).

Neotropical humid montane forests occur between 600 and 3000 m elevation from southeastern Mexico to northwestern Argentina, as well as the Tepuis and Atlantic Forest (Sánchez-González et al., 2008). In Central America and Mexico, humid montane forest is patchily distributed, but from Costa Rica through the Andes it is represented by a nearly 5000-km belt of continuous forest (Terborgh, 1971). Nearly 1700 bird species inhabit Neotropical humid montane forest (Stotz et al., 1996), many of which are composed of highly isolated, well-differentiated populations with minimal gene flow along their distributions (Peterson et al., 1992; García-Moreno et al., 2004; Bonaccorso et al., 2008; Navarro-Sigüenza et al., 2008; González et al., 2011; Barrera-Guzmán et al., 2012; Cortés-Rodríguez et al., 2013; Rodríguez-Gómez et al., 2013). Thus, this avifauna is ideal to study patterns of differentiation among isolated montane populations.

In this study, we investigated patterns of genetic and vocal variation in the Ruddy-capped Nightingale-Thrush (Turdidae: *Catharus frantzii*), a non-migratory oscine bird that inhabits montane forests from central Mexico to Panama (Fig. 1). Across its wide distribution, *C. frantzii* inhabits humid to semihumid coniferous, pine-oak, and evergreen forest, 1500–3500 m above sea level (Howell and Webb, 1995). Populations are geographically and ecologically separated by deep valleys and lowland areas that serve as barriers to gene flow in other groups (González et al., 2011; Ornelas et al., 2013; Rodríguez-Gómez et al., 2013). Most isolated populations of *C. frantzii* differ in a suite of plumage characters that have been used to define eight or nine subspecies, depending on taxonomic authority (Phillips, 1991; Collar, 2005; Fig. 1). These phenotypic differences suggest some degree of divergence among populations of *C. frantzii*, but little is known of what, if any, vocal differences exist. Thus, the aim of our study is to reconstruct the phylogeographic history of the Ruddy-capped Nightingale-Thrush to examine the level of congruence between DNA sequence variation and song variation. We tested if long-isolated populations are both genetically and vocally more divergent than populations that are more recently diverged and/or show evidence of recent gene flow. This study contributes to our knowledge of differentiation in Mesoamerican montane birds, adds to a growing number of lineages with known phylogeographic histories for comparative

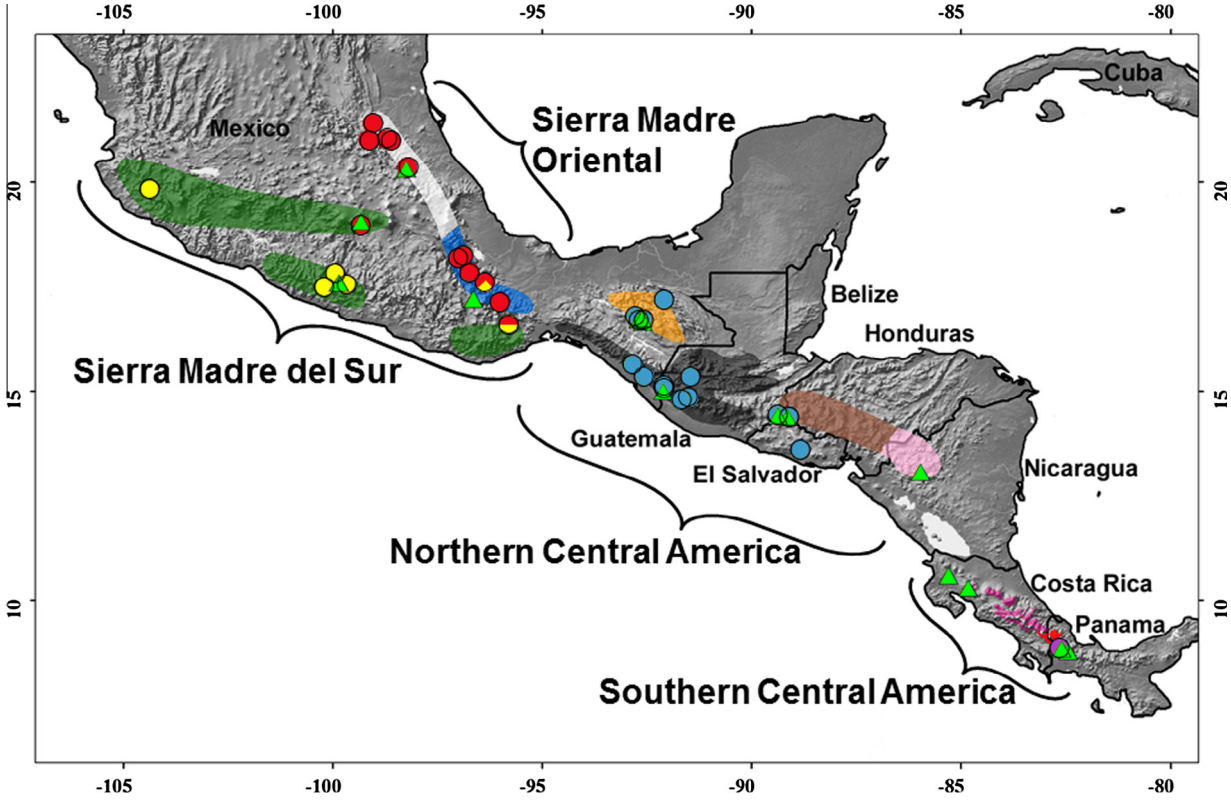

Fig. 1. Distribution map of the nine subspecies of *Catharus frantzii*. Color shades depict subspecies ranges. Green: *C. f. omiltemensis*; white: *C. f. confusus*; blue: *C. f. nelsoni*; orange: *C. f. chiapensis*; black: *C. f. alticola*; brown: *C. f. juancitonis*; pink: *C. f. waldroni*; purple; *C. f. frantzii*; and red: *C. f. wetmorei*. Colored circles depict localities of tissue samples used in this study; colors of circles reference the clades observed in the phylogenetic tree (Fig. 2), whereas green triangles depict localities of recordings used. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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