



# The effects of Pleistocene climate change on biotic differentiation in a montane songbird clade from Wallacea



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## ABSTRACT

The role of Pleistocene Ice Age in tropical diversification is poorly understood, especially in archipelagos, in which glaciation-induced sea level fluctuations may lead to complicated changes in land distribution. To assess how Pleistocene land bridges may have facilitated gene flow in tropical archipelagos, we investigated patterns of diversification in the rarely-collected rusty-bellied fantail *Rhipidura teysmanni* (Passeriformes: Rhipiduridae) complex from Wallacea using a combination of bioacoustic traits and whole-genome sequencing methods (dd-RADSeq). We report a biogeographic leapfrog pattern in the vocalizations of these birds, and uncover deep genomic divergence among island populations despite the presence of intermittent land connections between some. We demonstrate how rare instances of genetic introgression have affected the evolution of this species complex, and document the presence of double introgressive mitochondrial sweeps, highlighting the dangers of using only mitochondrial DNA in evolutionary research. By applying different tree inference approaches, we demonstrate how concatenation methods can give inaccurate results when investigating divergence in closely-related taxa. Our study highlights high levels of cryptic avian diversity in poorly-explored Wallacea, elucidates complex patterns of Pleistocene climate-mediated diversification in an elusive montane songbird, and suggests that Pleistocene land bridges may have accounted for limited connectivity among montane Wallacean biota.

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## 1. Introduction

Despite its status as one of the world's leading biodiversity hotspots (Myers et al., 2000; Brooks et al., 2002) and the extremely high levels of vertebrate endemism found there (Sodhi et al., 2004; Lohman et al., 2011), Wallacea in Indonesia remains one of the biologically most poorly-explored regions across the globe (Lohman et al., 2011), and biological diversification in this region is still largely uncharted and poorly understood. Wallacea is one of the most tectonically active areas in the world, and one of the only larger regions on the planet in which the distribution of land masses has drastically changed within the last 5 million years as a consequence of tectonic shifts (Hall and Holloway, 1998; Voris, 2000). In addition, global cyclical glaciations (called “ice ages”) and concomitant sea level fluctuations over the past ~2 million years (Voris, 2000; Siddall et al., 2003; Caputo, 2007) have resulted in complicated geographic patterns of land connections linking some islands but not others, subjecting biotic populations to repeated isolation and reconnection (Bintanja et al., 2005; Woodruff, 2010). From the time of Wallace's (1869) explorations of the region until now, there have been modest increases in our biological knowledge of even such well-known animal groups as birds (White and Bruce, 1986). In terms of diversification and differentiation, only a few avian taxa from the region have been subject to stringent integrative investigation linking population-genetics, phylogenetics and phenotypic traits such as bioacoustics (Jönsson et al., 2008; Irestedt et al., 2013; Andersen et al., 2015). The few studies conducted found complicated patterns of dispersal, diversification and speciation, including multiple colonizations and back-colonizations, and emphasize the importance of dispersal capability over vicariance in bird speciation. The recent advent of Next-Generation Sequencing (NGS) methodology now allows us

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to extend this approach and look, for the first time, into patterns of gene flow across Pleistocene land bridges in Wallacea, which provide insight into the effects of Pleistocene climate change on the evolution and diversification of Wallacean biota. These new methodologies allow us to test if Pleistocene land bridges constitute the main conduits of gene flow for terrestrial Wallacean biota, or if overwater dispersal across open sea also plays an important role in speciation in the region.

The rusty-bellied fantail *Rhipidura teysmanni* is a species complex endemic to Wallacea, ranging from Sulawesi eastwards to the Banggai and Sula archipelagos. These small-bodied passerines are resident in hill and mountain evergreen forests between 600 and 2300 m above sea level, where they actively pursue insect prey in the mid-storey and lower canopy (Boles, 2006). As montane forest inhabitants, these birds are subject to the same alternating cycles of isolation and separation throughout the Quaternary that heavily impact the evolution of other Wallacean biodiversity. Sulawesi and Peleng (the largest island in the Banggai archipelago) are separated by only ~13 km of open sea, while Taliabu (the largest island in the Sula archipelago) is positioned an additional ~80 km to the east; however, despite the larger geographical distance between them, Peleng and Taliabu have repeatedly been connected to form a single paleo-island during Pleistocene glaciation events (Voris, 2000). In contrast, even at the height of glaciations, the presence of a deep sea trench between Sulawesi and Peleng has ensured that the two landmasses have never been connected by land (Fig. 1).

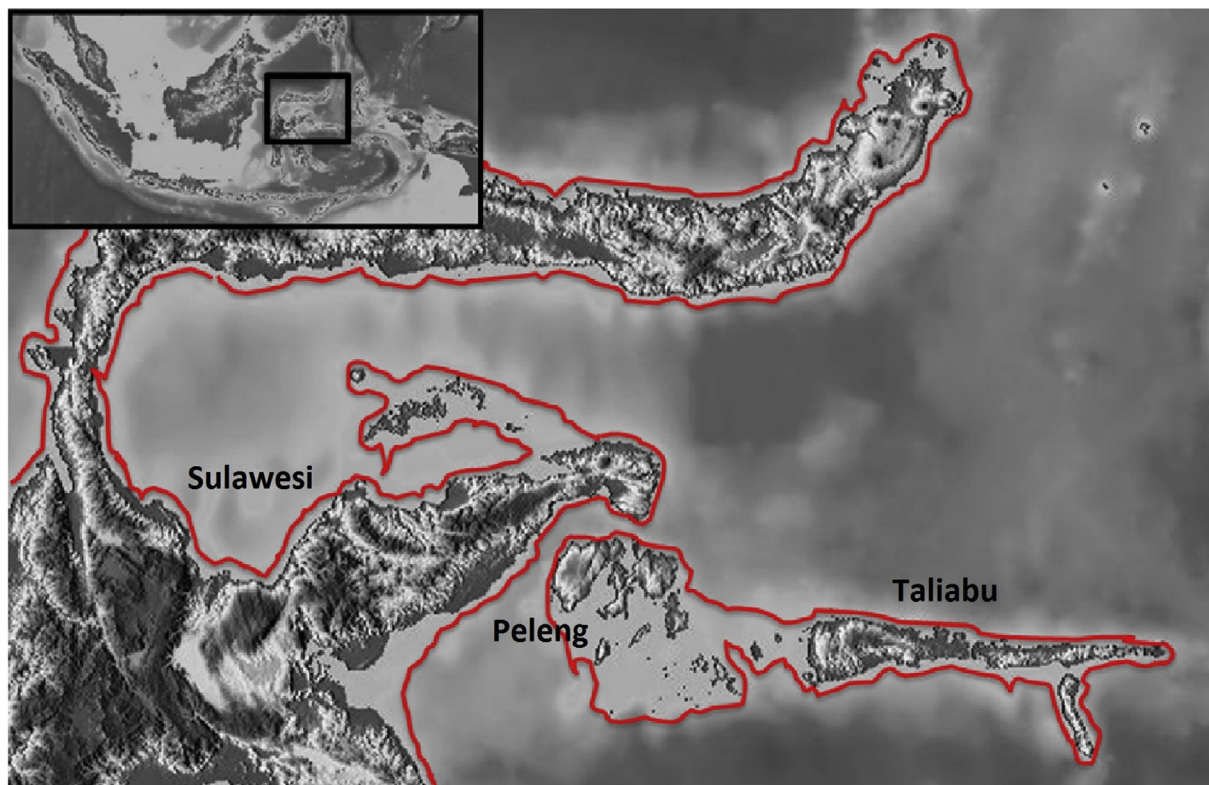
In this study, we use 16 samples of these elusive, rarely-collected fantails, procured from Sulawesi, Peleng and Taliabu, to explore patterns of divergence in this little-known species complex. The investigation of a non-dispersive songbird which inhabits montane forests allows us to test the importance of Pleistocene land bridges for the differentiation of highly terrestrial Wallacean

island biota. Our use of genome-wide data allows us to detect even small amounts of gene flow among deeply differentiated island lineages, which we combine with phenotypic markers in the form of bioacoustic characters to detect potential signs of clinality. Bioacoustic characters are especially important in songbirds, which use them in a wide range of behavioral contexts including mate recognition, territory maintenance, and sexual selection (Catchpole and Slater, 1995; Ball and Hulse, 1998; Nowicki et al., 1998; Marler and Slabbekoorn, 2004; Kroodsma, 2015). Bioacoustic divergence between closely related taxa has been found to be indicative of genetic differentiation, and has been a powerful predictor in the delimitation of genetically distinct taxa (Isler et al., 1998, 2007; Toews and Irwin, 2008; Rheindt et al., 2011; Ng et al., 2016; Ng and Rheindt, 2016; Garg et al., 2016). A combination of bioacoustics and genomic data thus allows us to comprehensively investigate patterns of divergence between islands linked by Pleistocene land bridges, and those that have remained separate throughout.

## 2. Materials and methods

### 2.1. Tissue sample collection

Fresh tissue samples were collected in December 2013 from three localities across the fantail's natural range: (1) Mt. Tumpu (~1°03'S, ~122°10'E) near Luwuk City in the Banggai Regency of Central Sulawesi; (2) the mountainous western peninsula of Peleng island (~1°21'S, ~122°51'E) in the Banggai archipelago; (3) and the highest mountainous area of Taliabu island (~1°47'S, ~124°48'E) in the Sula archipelago (Fig. 1). Mist-nets were set up between 0600 h and 1700 h at each location, and nets were checked every half hour for the retrieval of birds caught. Tissue samples were collected from the pectoral muscle and stored in 100% ethanol.



**Fig. 1.** Map showing the geographical locations of Peleng and Taliabu islands, to the east of Central Sulawesi. Solid lines represent the land extent during Pleistocene glacial maxima, when sea levels are ~120 m below modern day levels.

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