



## Evolutionary and ecological forces influencing population diversification in Bornean montane passerines



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### ABSTRACT

The mountains of Borneo are well known for their high endemism and historical role in preserving Southeast Asian rainforest biodiversity, but the diversification of populations inhabiting these mountains is poorly studied. Here we examine the genetic structure of 12 Bornean montane passerines by comparing complete mtDNA ND2 gene sequences of populations spanning the island. Maximum likelihood and Bayesian phylogenetic trees and haplotype networks are examined for common patterns that might signal important historical events or boundaries to dispersal. Morphological and ecological characteristics of each species are also examined using phylogenetic generalized least-squares (PGLS) for correlation with population structure. Populations in only four of the 12 species are subdivided into distinct clades or haplotype groups. Although this subdivision occurred at about the same time in each species (ca. 0.6–0.7 Ma), the spatial positioning of the genetic break differs among the species. In two species, northeastern populations are genetically divergent from populations elsewhere on the island. In the other two species, populations in the main Bornean mountain chain, including the northeast, are distinct from those on two isolated peaks in northwestern Borneo. We suggest different historical forces played a role in shaping these two distributions, despite commonality in timing. PGLS analysis showed that only a single characteristic—hand-wing index—is correlated with population structure. Birds with longer wings, and hence potentially more dispersal power, have less population structure. To understand historical forces influencing montane population structure on Borneo, future studies must compare populations across the entirety of Sundaland.

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### 1. Introduction

In contrast to the Neotropics and Africa, where comparative phylogeographic investigations of Pleistocene refuges, centers-of-endemism, and dispersal patterns of animals (Cracraft and Prum, 1988; Fjeldså and Bowie, 2008; Haffer, 1987) are common (e.g., Burney and Brumfield, 2009; Ditchfield, 2000; Huhndorf et al., 2007; Smith et al., 2014), such studies in Sundaland—the biogeographic region of Southeast Asia encompassing the Sunda continental shelf and its current land (Malay Peninsula, Sumatra, Java, Borneo, Palawan and small islands)—are rare. Only a handful exist

(Demos et al., 2016; Gorog et al., 2004; Lim et al., 2010; Lim and Sheldon, 2011). This is surprising, not only because studies in Sundaland helped inspire the science of Biogeography (Wallace, 1860), but because the region's potential for comparative phylogeographic study of Pleistocene vicariance, habitat refuges, colonization, community relaxation, and other modes of diversification and extinction is substantial and has been recognized for years (Brandon-Jones, 1996; Cracraft, 1988; Diamond et al., 1987; Heaney, 1991).

Among biogeographic features in Sundaland that merit greater study, the mountains of Borneo are paramount because of the important role they played in preserving and fomenting Southeast Asia's rainforest diversity (de Bruyn et al., 2014; Merckx et al., 2015; Sheldon et al., 2015). Borneo's main mountain chain runs diagonally from Sabah in the northeast, along the Sarawak-

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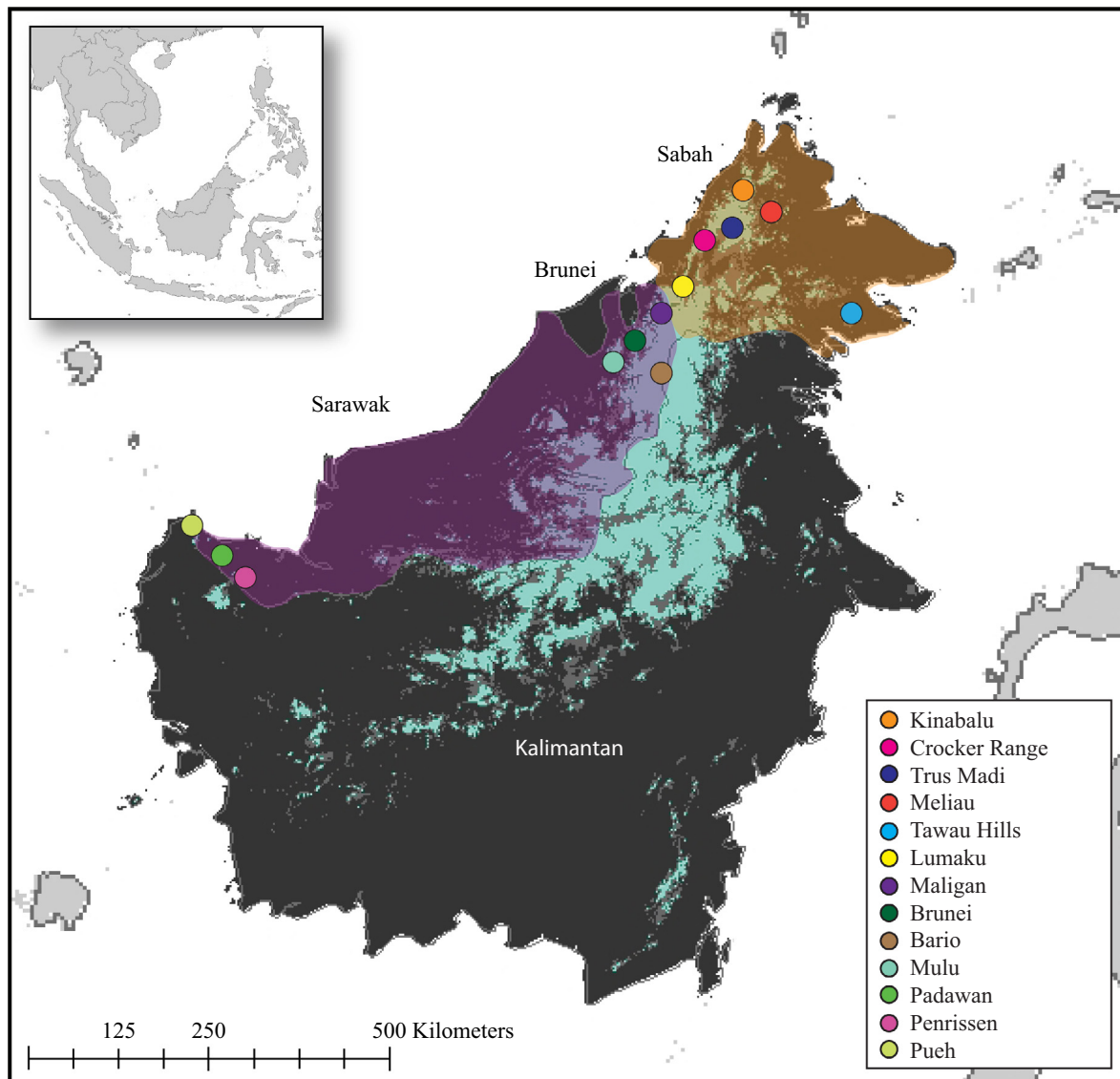
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Kalimantan border, toward the southwestern side of the island (Fig. 1). By virtue of their magnitude, longevity and position (especially in the northeast), these mountains helped maintain rainforest continuously throughout much of the Cenozoic, even during the cooler, drier times of the Oligocene, Pliocene, and Pleistocene, when rainforest was reduced in large areas of Sundaland (Morley, 2012). In respect to birds, Borneo's mountains not only helped preserve ancient (perhaps Eocene) rainforest lineages, but also fomented more recent diversification as a result of periodic rainforest isolation in the Pliocene and Pleistocene (Sheldon et al., 2015). In the warm, moist Miocene, when most of southern Asia was tropical (Morley, 2012), rainforest taxa surviving the Oligocene appear to have dispersed from Borneo, spreading to the other Sunda islands and mainland Southeast Asia (de Bruyn et al., 2014; Price et al., 2014). In the same epoch, taxa from the Himalayas and other mountains in Southeast Asia, including warblers and babblers, invaded Borneo (Moyle et al., 2012; Päckert et al., 2012). As a result of these dynamics, Borneo's montane avifauna now comprises a rich mixture of geologically ancient ende-

mic, middle-aged endemic and non-endemic, and younger immigrant taxa (Sheldon et al., 2015).

Although this scenario outlines the general forces responsible for assembling Borneo's montane avifauna, it fails to describe the more subtle dynamics that have shaped the composition and texture of Borneo's montane populations as they now appear. In truth, we know very little about the structure of Borneo's montane bird populations because almost all of our understanding comes from subjective assignment of subspecies based on plumage and size differences among populations separated from one another by hundreds of kilometers. We have no idea what these morphological differences signify in terms of evolutionary history.

Based on recent geographic events, we would expect little differentiation among bird populations in Borneo's mountains, first because montane habitat is largely continuous along the island's main mountain chain, and second because Borneo's montane habitat was certainly more expansive for most of the last 2.6 million years than it is currently (Manthey et al., 2017). During the Pleistocene, cooler climate resulting from long-lasting global glaciation events should have caused Sundaic montane forest to descend in



**Fig. 1.** Elevation map of Borneo with the Malaysian states of Sabah and Sarawak outlined and sampling sites marked with colored circles. Southwest (SW) Bornean populations: Padawan, Penrissen, and Pueh. Mid-Bornean populations: Lumaku, Maligan, Brunei, Mulu, and Bario. Northeast (NE) Borneo populations: Kinabalu, Crocker Range, Trus Madi, Meliau, and Tawau. Inset shows the region of Southeast Asia.

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