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Colonization and diversification of the white-browed shortwing (Aves: Muscicapidae: *Brachypteryx montana*) in the Philippines

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ABSTRACT

Molecular phylogenetic approaches have greatly improved our knowledge of the pattern and process of biological diversification across the globe; however, many regions remain poorly documented, even for well-studied vertebrate taxa. The Philippine archipelago, one of the least-studied 'biodiversity hotspots', is an ideal natural laboratory for investigating the factors driving diversification in an insular and geologically dynamic setting. We investigated the history and geography of diversification of the Philippine populations of a widespread montane bird, the White-browed Shortwing (*Brachypteryx montana*). Leveraging dense archipelago-wide sampling, we generated a multi-locus genetic dataset (one nuclear and two mtDNA markers), which we analyzed using phylogenetic, population genetic, and coalescent-based methods. Our results demonstrate that Philippine shortwings (1) likely colonized the Philippines from the Sunda Shelf to Mindanao in the late Miocene or Pliocene, (2) diversified across inter-island barriers into three divergent lineages during the Pliocene and early Pleistocene, (3) have not diversified within the largest island, Luzon, contrary to patterns observed in other montane taxa, and (4) colonized Palawan from the oceanic Philippines rather than from Borneo, challenging the assumption of Palawan functioning exclusively as a biogeographic extension of the Sunda Shelf. Additionally, our finding that divergent (c. 4.0 mya) lineages are coexisting in secondary sympatry on Mindanao without apparent gene flow suggests that the speciation process is likely complete for these shortwing lineages. Overall, these investigations provide insight into how topography and island boundaries influence diversification within remote oceanic archipelagos and echo the results of many other studies in demonstrating that taxonomic diversity continues to be underestimated in the Philippines.

1. Introduction

The Philippines has long served as a model island archipelago, playing a crucial role in informing our understanding of the mechanisms of evolution in an insular and geologically dynamic setting (Dickerson, 1928; Diamond & Gilpin, 1983; Heaney, 1986; Brown et al., 2013). However, despite the Philippines' importance as a natural laboratory and status as a 'biodiversity hotspot' (Myers et al., 2000), knowledge of the pattern and process of diversification across the archipelago remains largely incomplete. Even within well-studied vertebrate groups, new species are regularly described from the Philippines, largely resulting from both increased sampling efforts and the widespread application of molecular phylogenetic tools in taxonomic research (Posa et al., 2008; Welton et al., 2010; Heaney et al., 2009; Heaney et al., 2011; Heaney et al., 2016; Hosner et al., 2013a). Consequently, estimates of endemism for Philippine taxa have risen substantially, and currently range from 56 to 80% for terrestrial vertebrate taxa (Brown et al., 2013). These figures will likely continue to rise as more cryptic taxa are uncovered by molecular approaches (Lohman et al., 2010; Hosner et al., 2014; Campbell et al., 2016). Such research underscores the importance of intensive field and taxonomic research in informing conservation priorities, especially in poorly studied regions of the world (Mace et al., 2004; Posa et al., 2008).

The proliferation of well-sampled molecular phylogenies for Philippine taxa has also greatly increased our knowledge about the historical processes of colonization and diversification in the

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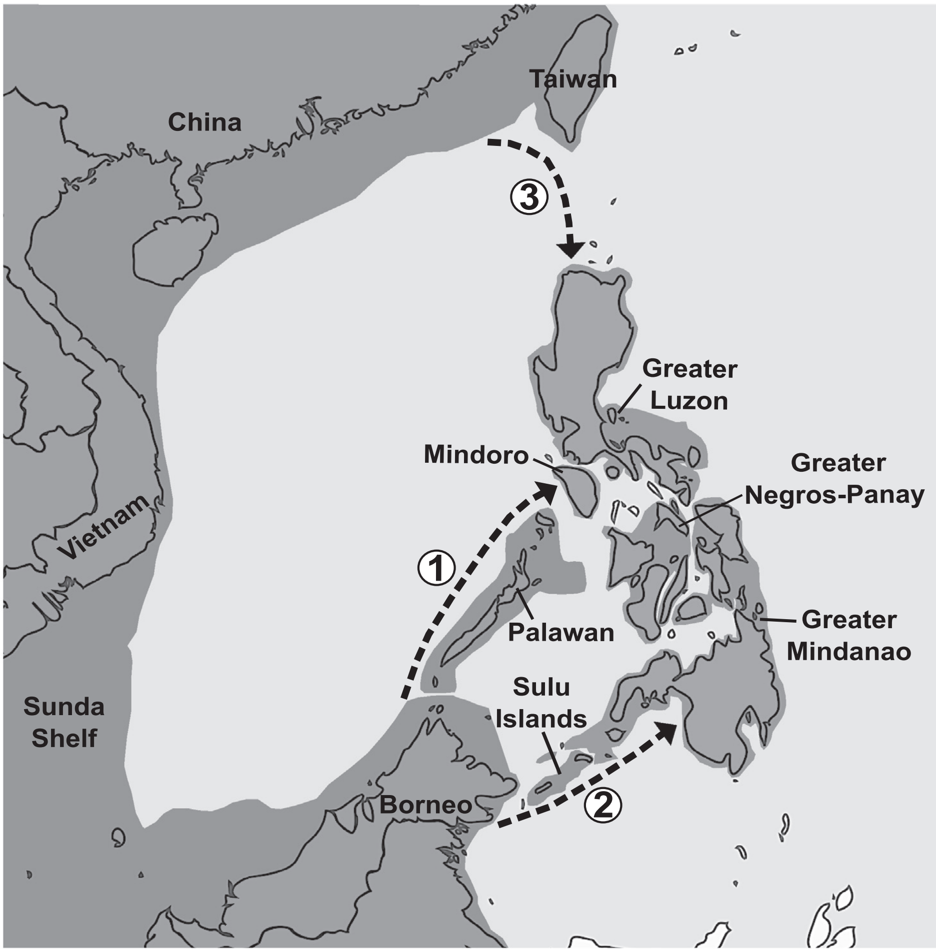

Fig. 1. Map of Southeast Asia depicting three potential colonization routes into the Philippines tested for *Brachypteryx montana,* including: (1) a northern route from Borneo to Mindoro via Palawan, (2) a southern route from Borneo to Mindanao via the Sulu Islands, and (3) a direct route from mainland Asia. Shading depicts late Pleistocene coastlines based on 120 m submarine bathymetric contour.

Philippines. Largely due to the Philippines' high degree of isolation from mainland Asia (Heaney, 1986; Heaney et al., 2016; Voris, 2000), colonization into the Philippines has been relatively limited for most terrestrial groups (Diamond & Gilpin, 1983; Heaney, 1985). For lineages that have colonized the oceanic Philippines (i.e., excluding Palawan, which may have formed land-bridge connections with the Sunda Shelf at times during the Pleistocene), numerous routes of arrival have been documented (Dickerson, 1928; Brown et al., 2013), including western or northern origin from mainland Asia or Taiwan (Jansa et al., 2006; Esselstyn & Oliveros, 2010), southern origin from Wallacea (Evans et al., 2003; Schweizer et al., 2012), and eastern origin from the Sunda Shelf (Diamond & Gilpin, 1983; Oliveros & Moyle, 2010; Brown & Siler, 2014). In particular, a large number of studies have focused on testing two potential routes originating from the Sunda Shelf, including: (1) a northern route characterized by colonization from Borneo to the northern Philippines via Palawan and Mindoro, and (2) a southern route consisting of colonization from Borneo to Mindanao via the Sulu archipelago, followed by expansion northward (Fig. 1; Diamond & Gilpin, 1983; Jones & Kennedy, 2008; Oliveros & Moyle, 2010; Brown et al., 2013; Brown & Siler, 2014; Hosner et al., 2013b). Although these routes were initially proposed based on avian distributional data (Diamond & Gilpin, 1983), molecular phylogenetic studies have found surprisingly little support for colonization of the oceanic Philippines along the northern route in birds (Jones & Kennedy, 2008; Oliveros & Moyle, 2010; Sheldon et al., 2012; Hosner et al., 2013b). Instead, some research suggests that Palawan may represent a biogeographic 'dead end' for many taxa (Oliveros & Moyle, 2010; Esselstyn et al., 2010; Brown et al., 2013), with few examples of widespread Philippine radiations originating from Palawan.

Regardless of their geographic origin, the lineages that have colonized the oceanic Philippines have often diversified substantially throughout the archipelago (Jansa et al., 2006; Esselstyn et al., 2009; Oliveros & Moyle, 2010; Siler et al., 2011; Hosner et al., 2013b). For many organisms, phylogeographic structure is coincident with present-day island coastlines, implicating water barriers as important barriers to dispersal and drivers of diversification (e.g., Steppan et al., 2003; Jones & Kennedy, 2008; Siler et al., 2011). In addition, numerous studies have documented the importance of Pleistocene sea-level fluctuations as determinants of genetic structure, due to their role in periodically connecting present-day islands by dry land (Fig. 2; Inger, 1954; Heaney, 1985; Voris, 2000; Brown & Diesmos, 2002; Roberts, 2006). Finally, a growing body of research has identified the importance of topographic features within islands as drivers of diversification (Esselstyn et al., 2009; Sanguila et al., 2011; Hosner et al., 2013a, b; Justiniano et al., 2015; Heaney et al., 2016; Kyriazis et al., 2017). In particular, these studies have highlighted the presence of numerous locally endemic species on the isolated mountain ranges of Luzon and Mindanao, thus implicating these 'sky islands' as drivers of diversification.

In this study, we combine extensive geographic sampling and multi-locus genetic analyses to study the patterns of colonization and diversification of the White-browed Shortwing (*Brachypteryx montana*) in the Philippines. *Brachypteryx montana* is a widespread montane forest species (family: Muscicapidae; Zuccon & Ericson, 2010) occurring through much of tropical Asia, ranging from the eastern Himalayas, to southeastern China, throughout much of the Sunda Shelf, and into the Philippines, where it is present on Luzon, Mindanao, Mindoro, Negros, Palawan, and Panay islands (Fig. 2). In total, 14 subspecies of *B. montana* have been described, 7 of which are endemic to the Philippines (Gill & Donsker, 2017). These subspecies tend to be distinctive in both