



Geographic isolation and elevational gradients promote diversification in an endemic shrew on Sulawesi



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ABSTRACT

Phylogeographic research on endemic primates and amphibians inhabiting the Indonesian island of Sulawesi revealed the existence of seven areas of endemism (AoEs). Here, we use phylogenetic and population genetic analyses of one mitochondrial gene and 15 nuclear loci to assess geographic patterns of genetic partitioning in a shrew (*Crocridura elongata*) that is endemic to Sulawesi, but occurs across the island. We uncover substantial genetic diversity in this species both between and within AoEs, but we also identify close relationships between populations residing in different AoEs. One of the earliest divergences within *C. elongata* distinguishes a high-elevation clade from low-elevation clades. In addition, on one mountain, we observe three distinct genetic groups from low, middle, and high elevations, suggesting divergence along a single elevational gradient. In general, our results show that *C. elongata*, like several other Sulawesi endemic taxa, harbors extensive genetic diversity. This diversity is structured in part by known AoE boundaries, but also by elevational gradients and geographic isolation within AoEs.

1. Introduction

Insular Southeast Asia holds an important place in the history of biogeography and indeed, in the history of evolutionary biology (Wallace, 1869, 1876, 1880). Early naturalists documented sharp zones of faunal turnover and remarkable levels of endemism (e.g., Huxley, 1868; Wallace, 1869; Dickerson, 1928; Taylor, 1934). Despite these early discoveries, the fauna of this megabiodiverse region remains poorly known in many respects, and modern expeditions frequently uncover new species of vertebrates, including mammals (e.g., Heaney et al., 2011, 2014; Esselstyn et al., 2012, 2013; Rowe et al., 2016). It is perhaps unsurprising then that the biogeographical factors that shaped the region's current patterns of diversity and endemism remain incompletely understood (Lohman et al., 2011; Brown et al., 2013; Sheldon et al., 2015). Nevertheless, within-island diversification, facilitated by topographic complexity, is emerging as a significant contributor to the phylogenetic diversity of insular faunas (Heaney and Rickart, 1990; Heaney et al., 2011; Esselstyn et al., 2013; Hosner et al.,

2013; Toussaint et al., 2014; Justiniano et al., 2015; Demos et al., 2016). Several studies have identified species endemic to single mountains or mountain ranges, with close relatives found in neighboring ranges (e.g., Heaney et al., 2011; Esselstyn et al., 2013; Justiniano et al., 2015). This suggests that unsuitable lowland habitats, competitive exclusion by closely related lowland species, or both represent long-term ecological barriers to dispersal for these taxa. Furthermore, elevational gradients on individual mountains may generate diversity if divergent natural selection promotes reproductive isolation and the formation of parapatric species. However, documented examples of this phenomenon are rare and often debatable (Caro et al., 2013; Demos et al., 2016).

The island of Sulawesi is large (11th largest globally), topographically complex (several mountains exceed 3000 m elevation), and shaped like a “K”, with its four peninsulas together comprising a greater land area than the island's central core (Fig. 1). In addition, Sulawesi is a composite island, formed as no fewer than four (and perhaps seven or more) prehistoric landmasses collided between ~25 and 2 Ma (Hall,

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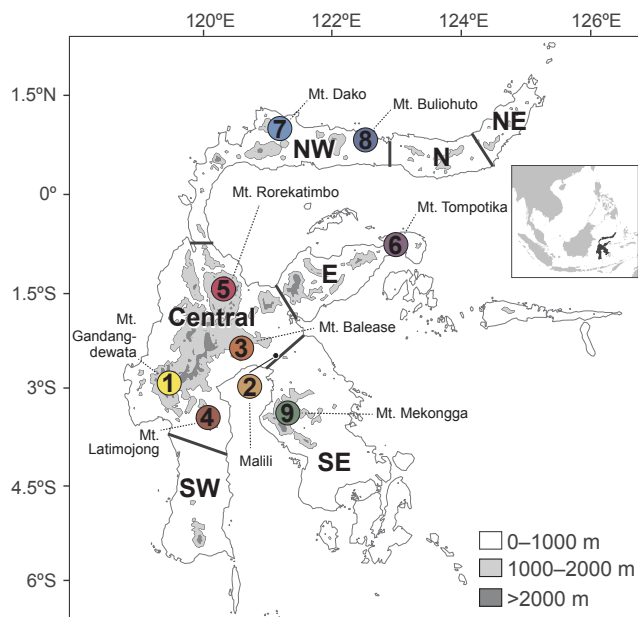


Fig. 1. Map of Sulawesi with black lines corresponding to AoE boundaries. Numbers indicate the locations of sampling localities as follow: 1 = Mt. Gandangdewata, 2 = Malili, 3 = Mt. Balease, 4 = Mt. Latimojong, 5 = Mt. Rorekatimbo, 6 = Mt. Tompotika, 7 = Mt. Dako, 8 = Mt. Buliohuto, and 9 = Mt. Mekongga. Bold text indicates the abbreviated name of each AoE. Inset shows the position of Sulawesi in SE Asia.

2002; Spakman and Hall, 2010; Hall, 2011). Moreover, because the individual landmasses constituting this proto-Sulawesi archipelago were divided further by periods of partial marine inundation (Whitten et al., 2002), the total number of prehistoric islands was even greater. As the centerpiece of the Wallacean biogeographic zone, Sulawesi has been colonized by faunal elements from up to three biologically diverse and distinctive areas: Sahul (Australia and New Guinea), Sunda (Borneo, Java, and Sumatra), and perhaps the Philippines (Stelbrink et al., 2012). Together, Sulawesi's geographical characteristics and geological history provide numerous plausible mechanisms for generating high levels of species diversity and concordant phylogeographic patterns.

Early taxonomic work on Sulawesi's vertebrate fauna showed that most species are endemic (e.g., Miller and Hollister, 1921a, 1921b), but it was not until much later that biologists began to notice geographic patterns of endemism within the island. Fooden (1969) first noted that macaque hybrid zones correspond to natural geographic boundaries separating the peninsulas from the central core, and individual components of the north peninsula from each other. More recent genetic comparisons demonstrated that these boundaries are consistent for various lineages of amphibians, reptiles, and mammals, suggesting that genetic diversity in these lineages has been influenced by shared mechanisms (Evans et al., 2003a, 2003b, 2008; McGuire et al., 2007; Shekelle et al., 2010; Setiadi et al., 2011). These studies defined seven areas of endemism (AoEs; Fig. 1) on Sulawesi that correspond to the island's central core, its east, southeast, and southwest peninsulas, and three areas on the north peninsula. However, some subsequent studies of Sulawesi taxa such as snails (von Rintelen et al., 2014), tarsiers (Driller et al., 2016), and bats (Campbell et al., 2007) have recorded geographic patterns only partially consistent with those observed in the monkeys and toads that defined Sulawesi's original AoEs (Evans et al., 2003a). Evans (2012) reviewed available evidence and noted that in addition to the original AoE boundaries, several lineages are partitioned within the central core area, and the geographic position of these boundaries is shared by some lineages. Because AoEs on Sulawesi have been defined solely by shared phylogeographic patterns, the roles played by various plausible mechanisms (such as paleo-island

geography, sea incursions, ecological barriers, and peninsular effects) in the formation of Sulawesi's AoEs are not well understood. As such, the extent to which the AoE paradigm can be applied to the whole of Sulawesi's biota remains unknown, and testing for the AoE pattern in additional organisms will help assess the importance of shared mechanisms of diversification, while also offering improved guidance to conservation efforts.

Whereas AoE patterns are inherently based on geographic distances, which have dominated discussions of within-island diversification on Sulawesi, elevational gradients provide potential alternative mechanisms of generating diversity and local endemism, as has been documented on other islands (e.g. Justiniano et al., 2015; Demos et al., 2016). Because studies that have investigated the AoE pattern on Sulawesi have not generally considered the elevational distribution of their focal lineage or its potential effect on geographic isolation and diversification, it is unclear whether elevational gradients serve as a cause of some reported AoE patterns of diversity, whether they act as an additional cause of diversification, or whether they have little influence on diversity and endemism.

Shrews of the genus *Crocridura* are represented on Sulawesi by six endemic species derived from two independent colonizations (Ruedi, 1995; Ruedi et al., 1998; Esselstyn et al., 2009). Among these shrews, *Crocridura elongata* offers a particularly promising opportunity to assess phylogeographic structure relative to AoE boundaries and along elevational gradients because it is widespread on the island, occurs from near sea level to the highest mountain areas that have been sampled, and its members are easily distinguished from other species by external characters (Ruedi, 1995). Here, we perform multi-locus population genetic, phylogenetic, and species delimitation analyses on *C. elongata* sampled from across Sulawesi to test if the species exhibits genetic structure associated with AoE boundaries, with elevational gradients, with both, or with neither.

2. Materials and methods

2.1. Taxon sampling

Specimens of *Crocridura elongata* were collected from 15 sites contained in nine general localities. These localities are spread across Sulawesi and represent four of the island's seven AoEs. Specimens are vouchered at the Field Museum of Natural History, Chicago (FMNH); Museum Victoria, Melbourne (NMV); Louisiana State University Museum of Natural Science, Baton Rouge (LSUMZ); Museum of Wildlife and Fish Biology, Davis (WFB); and Museum Zoologicum Bogoriense, Bogor (MZB). Our sampling includes multiple localities within the Central Core and Northwest (NW) AoEs, with one locality sampled from each of the Southeast (SE) and East (E) AoEs (Fig. 1; Table 1). All shrews were collected in forested habitats, with the majority taken in relatively undisturbed primary forest. Only the lowest site on Mt. Gandangdewata (also known as Gandadiwata) and the Malili locality consisted of secondary forest and shrubby, regenerating vegetation. Several of the mountains were sampled at multiple elevations (see above), often encompassing the major forest types of lowland tropical evergreen rainforest and montane forest (*sensu* Musser, 2014). We generally found *C. elongata* co-occurring with four to five other species of *Crocridura*.

2.2. DNA sequencing

DNA was extracted from tissue samples using the Qiagen DNeasy protocol or Promega Wizard SV kits. We amplified one mitochondrial gene (cytochrome *b* [cyt *b*]) and 15 nuclear loci via PCR. Of the 15 nuclear loci, eight (apolipoprotein B [ApoB]; brain-derived neurotrophic factor [BDNF]; breast cancer susceptibility gene [BRCA]; growth hormone receptor [GHR]; mast-cell growth factor [MCGF]; prostaglandin E2 receptor [PTGER]; recombination-activating gene

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