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Continental-style avian extinctions on an oceanic island

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ABSTRACT

The Indonesian islands have long been recognized for their rich and unique avifaunas, but little is known regarding how past processes and events have shaped current avian distributions. Here we compare the modern non-passerine avifauna of Flores with the Late Pleistocene non-passerine fossil assemblage from the cave site of Liang Bua to assess whether the Late Pleistocene assemblage differs from the modern avifauna. Randomized permutation tests failed to detect a statistically significant difference in body size distributions, but a significant difference in dietary guild was found, as the modern fauna lacks scavengers. The emerging pattern of avian extinctions on Flores is characterized by a low proportion of extinct species, a loss of large-bodied species, and apparently minor effects on avian community structure. This is in contrast to other oceanic islands, which experienced dramatic changes in avifauna after the arrival of modern humans. Flores' close proximity to other islands and landmasses likely allowed for population connectivity that buffered populations from extinction. Widespread species may also have been able to recolonize if local extirpations took place. The extinction of the large-bodied avian scavengers *Leptoptilos robustus* and *Trigonoceps* sp. on Flores is consistent with the pattern of human-caused extinctions on other oceanic islands. However, the loss of these two large scavenging species may be linked to the extinction of the pygmy proboscidean (*Stegodon florensis insularis*). Such a dependence of avian species on mammalian megafauna, leading to extinction by trophic cascade, is characteristic of continental Late Pleistocene extinctions.

1. Introduction

Fossil and archeological evidence from around the world shows that the arrival of modern humans initiated ecological changes in insular ecosystems. Pre-human avian assemblages from oceanic islands typically show low faunal turnover (James, 1987; Steadman, 1993; Hearty et al., 2005). However, with modern human arrival in island ecosystems, avian diversity often becomes significantly reduced, with extinctions sometimes affecting 50% or more of the resident species (Steadman and Martin, 1984, 2003; James and Olson, 1991; Olson and James, 1991; Steadman et al., 1991; Milberg and Tyrberg, 1993; James, 1995; Steadman, 1995, 2006; Worthy and Holdaway, 2002; Cheke and Hume, 2008). Although the magnitude and rate of avian extinctions vary from island to island due to differences in abiotic, biotic and cultural factors (Steadman and Martin, 2003; Duncan et al., 2013), extinction risk is significantly linked to intrinsic traits, including endemism, dietary guild and large body size, all of which can make a species more prone to extinction (Boyer, 2008, 2010; Duncan et al., 2013). As a result, significant losses of avian functional diversity have taken place over time (Steadman, 2006; Boyer and Jetz, 2014).

Island Southeast Asia is an area renowned for its unique biotas and one that has been the focus of biogeographical and zoological studies for more than a century (Wallace, 1869; Mayr, 1944; Myers et al., 2000). Despite its long history of scientific study, little is known regarding the extent of prehistoric avian extinctions, and how current avian distributions and diversity have been affected by Late Quaternary events. A major obstacle to reconstructing avian prehistory has always been the poor fossil record for birds in this region (Meijer, 2014). However, recent archeological excavations at Liang Bua—a cave site on the Indonesian island of Flores—have yielded a rich fossil avian assemblage (Meijer et al., 2013).

Liang Bua has provided one of the largest Late Pleistocene and Holocene faunal assemblages yet excavated in Island Southeast Asia, and it

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represents the first fossil record for birds in Wallacea (Meijer et al., 2013; Meijer, 2014). As a volcanic island within the Lesser Sunda island chain (Fig. 1), Flores has been separated from nearby islands by deep sea straits, even during times of low sea level. Many of Flores' terrestrial vertebrates likely evolved in relative isolation and display adaptations to an insular environment (Musser, 1981; van den Bergh et al., 2008, 2009; Meijer et al., 2010). During the Late Pleistocene, Flores hosted a number of insular endemics, including pygmy elephants (*Stegodon florensis insularis*), small-bodied hominins (*Homo floresiensis*), Komodo dragons (*Varanus komodoensis*) and giant marabou storks (*Leptoptilos robustus*), as well as vultures (*Trigonoceps* sp.) and a diverse set of murid and chiropteran taxa (Brown et al., 2004; Morwood et al., 2004, 2005; van den Hoek Ostende et al., 2006; van den Bergh et al., 2008, 2009; Hocknull et al., 2009; Meijer and Due, 2010; Meijer et al., 2010, 2013; Locatelli et al., 2012). In contrast, the Holocene deposits at Liang Bua document modern humans (*Homo sapiens*), pigs (*Sus scrofa*), civet cats (*Paradoxurus hermaphrodites*), macaques (*Macaca fascicularis*), and porcupines (*Hystrix javanica*), while *S. f. insularis*, *H. floresiensis*, *L. robustus*, and *Trigonoceps* sp. are all noticeably absent (van den Bergh et al., 2009; Meijer et al., 2013).

The specific reasons behind the disappearance of these large-bodied taxa toward the end of the Pleistocene remain poorly understood. However, Liang Bua's avifaunal record provides a first opportunity to assess the degree of ecological change between the Late Pleistocene and modern avian community structures of a Southeast Asian island, and to assess whether any such changes are consistent with those from other oceanic islands. To assess changes in community structure, we examine several factors that are known to be related to extinction risk in birds, including body mass, dietary guild, habitat preference, and geographic range size (Boyer, 2008, 2010).

2. Material and methods

In total, 873 bird bones recovered from the excavated deposits of Liang Bua's Sectors XI and XII were examined. Of these, 275 are from the Late Pleistocene, and were positively identified to 25 non-passerine taxa, representing 14 families (Table 1). We compared this Late Pleistocene avian assemblage with the extant avifauna known from Flores. This fossil avian assemblage includes 180 bones from Sector XI (see Meijer et al. (2013) for descriptions) and 95 from Sector XII, which shares multiple aspects of its stratigraphy with Sector XI. These additional remains from Sector XII bolster the sample sizes for the Late Pleistocene avian taxa, and include two additional species not recorded previously in Sector XI; a quail *Coturnix* sp. and the zebra dove *Geopelia striata*. Only remains assigned to the genus level and below (22 taxa) were included for analysis. Any species designated as "cf." was treated as the conferred species. For the extant avifauna, a consensus list of 174 species of non-passerine bird species was compiled (see Supplementary Table 1) based on confirmed reports of species on Flores (Verhoeye and Holmes, 1998; Mees, 2006; Coates and Bishop, 1997).

For each fossil or extant taxon, the following data were compiled: resident or migrant, average body size in grams, dietary guild, and habitat preference. Data on body size for extant taxa were gathered from Dunning (2008). For fossil taxa identified only to the genus level, an average body mass was calculated based on published body masses of all species within that genus (Dunning, 2008). Body mass estimates for the extinct giant marabou stork (*L. robustus*) are from Meijer and Due (2010). Species were assigned to the following body mass categories: 1, 0–10 g; 2, 10–100 g; 3, 100–1000 g; 4, 1000–10,000 g; and 5, >10,000 g. Dietary guild was scored, based on data in Coates and Bishop (1997), by assigning each species to one of the following dietary

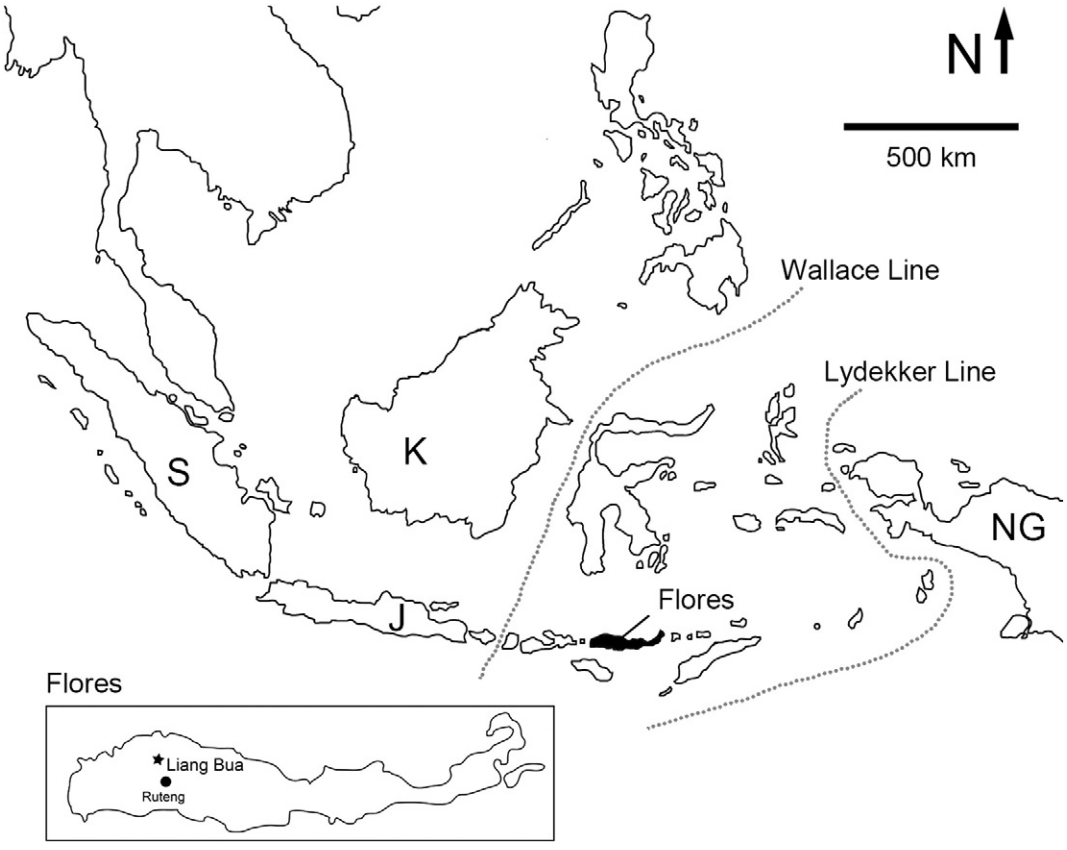

Fig. 1. Map of Island Southeast Asia with the location of Flores (in black). Gray lines denote the western and eastern limits of Wallacea by respectively the Wallace Line and the Lydekker Line. Inset shows the location of Liang Bua in western Flores. Abbreviations: J, Java; K, Kalimantan; NG, New Guinea; S, Sumatra.