

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.

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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 (Verhoeve 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

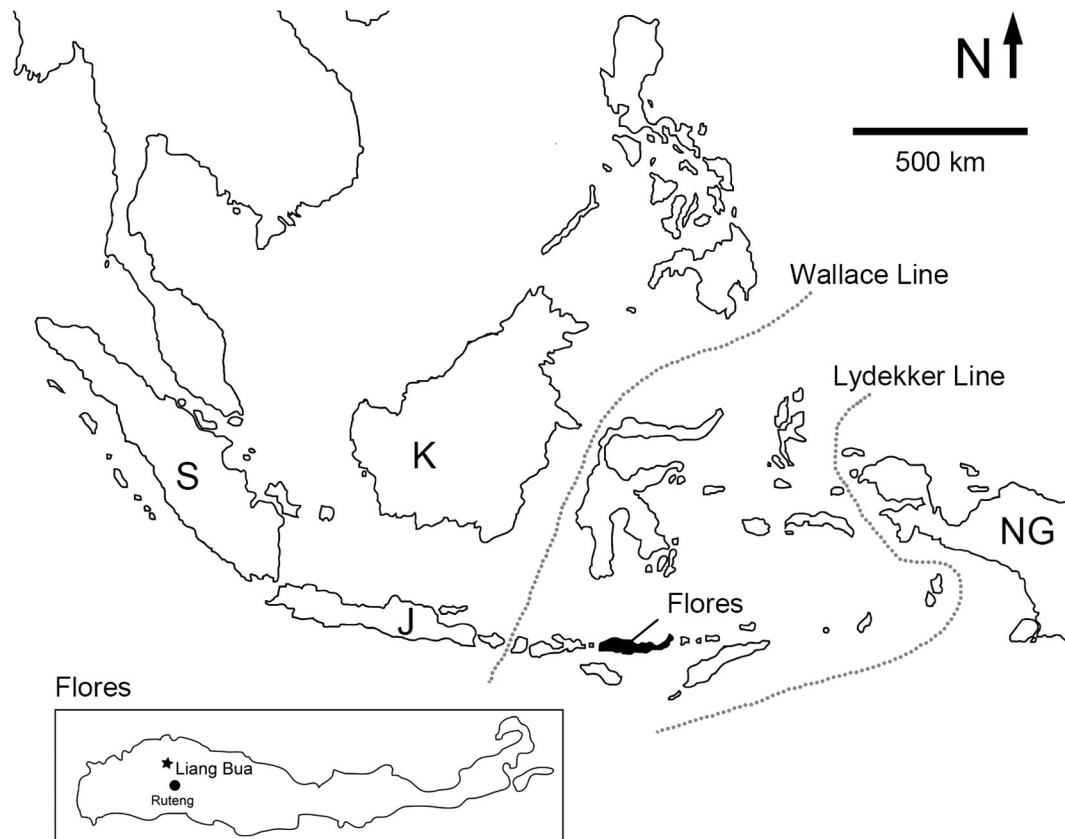


Fig. 1. Map of Island Southeast Asia with the location of Flores (in black). Gray lines denote the western and eastern limits of Wallacea by respectively the Wallace Line and the Lydekker Line. Inset shows the location of Liang Bua in western Flores. Abbreviations: J, Java; K, Kalimantan; NG, New Guinea;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

Table 1

Non-passerine avian taxa and their abundances (number of identifiable specimens, NISP) recovered from the Pleistocene sequences of Liang Bua's Sectors XI (Meijer et al., 2013) and XII. Shaded taxa were excluded from the analyses because they could not be identified to genus level or beyond. † extinct species, (†) possibly extinct species, * does not presently occur on Flores.

Family	Species recorded in the Pleistocene of Liang Bua	XI	XII	Overall
Anatidae	<i>Anas</i> sp.	1	1	2
Phasianidae	<i>Coturnix</i> sp.	0	1	1
Ciconiidae	<i>Leptoptilos robustus</i> †	23	0	23
Accipitridae	<i>Trionocephus</i> sp.*	18	5	23
	<i>Accipiter</i> sp.	2	0	2
	<i>Haliastur</i> cf. <i>indus</i>	3	0	3
	<i>Aquila</i> sp.	1	0	1
Rallidae	<i>Gallirallus</i> sp.	1	0	1
	<i>Porzana</i> sp.	2	1	3
Charadriidae	<i>Pluvialis fulva</i>	4	1	5
Scolopacidae	<i>Gallinago</i> sp.	17	32	49
	<i>Actitis hypoleucos</i>	2	6	8
Turnicidae	<i>Turnix</i> sp.	3	13	16
Columbidae	gen. et sp. indet	2	2	4
	aff. <i>Macropygia/Ptilinopus</i>	3	1	4
	<i>Macropygia</i> sp.	5	1	6
	<i>Ptilinopus</i> sp.	1	0	1
	<i>Geopelia striata</i>	0	4	4
Psittacidae	<i>Geoffroyus</i> cf. <i>geoffroyi</i>	5	2	7
Tytonidae	<i>Tyto</i> sp. (†)	5	0	5
Strigidae	<i>Otus</i> sp.	1	11	12
Apodidae	<i>Aerodramus</i> cf. <i>fuciphagus</i>	64	9	73
	<i>Collocalia esculenta</i>	4	3	7
Halcyonidae	gen et sp indet	4	0	4
	<i>Halcyon</i> sp.	9	2	11
Total		180	95	275

categories: C, carnivorous (including piscivorous); S, scavengers; I, insectivorous; O, omnivorous; N, nectarivorous; F, frugivorous; G, granivorous; and H, herbivorous. Habitat preference was scored for each species according to the 18 habitat types known to occur in Wallacea (Coates and Bishop, 1997): 1, ocean; 2, inshore waters; 3, offshore islets; 4, seashore; 5, mangroves; 6, littoral woodland; 7, coconut plantations; 8, swamp forest; 9, swamps, marshes and lakes; 10, ricefields; 11, grassland; 12, scrub; 13, savannah woodland; 14, lowland monsoon forest; 15, secondary forest and forest edge; 16, lowland rainforest; 17, montane forest; and 18, alpine grassland. In cases where a species occurs in more than one habitat, each habitat was scored as 1/n where n equaled the number of known habitats. The sums of the scores for each habitat result in a habitat spectrum for each assemblage. Data on geographic range sizes (in km²) were gathered from BirdLife International (2013), and island/landmasses occupied were taken from Coates and Bishop (1997). For fossil taxa identified to genus level only, the species with the smallest range within that genus was used. The distance between islands and their nearest continental landmass (including continental islands) was measured in Google Earth.

To test for statistically significant differences between the Pleistocene sample and the extant fauna in terms of dietary guild and body mass we used a 10,000-iteration randomized permutation test conducted in the R statistical environment (version 3.0.2, The R Foundation). The data for dietary guild were converted from letter categories to numerical values in order for a numerical average of dietary guild to be calculated.

3. Results

Of the 25 non-passerine bird taxa identified from Pleistocene sediments of Liang Bua's Sectors XI and XII, only 2 taxa (8%)—the giant marabou stork (*L. robustus*) and the vulture (*Trionocephus* sp.)—are

undoubtedly extinct (Table 1). The remains of a third taxon, the barn owl *Tyto* sp., may represent an extinct species (Meijer et al., 2013). The remaining 22 taxa still occur on the island today.

The distribution of mean body masses per species for the Pleistocene assemblage does not significantly differ from that of the extant avifauna (Figs. 2B, 3A–B, Table 2). For both the Late Pleistocene and modern avian community, a majority of birds (102 species or 59% of extant birds, 12 species or 55% of Pleistocene taxa) fall in the size category of 100–1000 g. The second-largest group includes 54 species (31%) of extant birds and 6 species (27%) of Pleistocene taxa in the 10–100 g category. The Glossy Swiftlet (*Collocalia esculenta*) is the only species in both samples with a body mass below 10 g. The largest body mass category (>10 kg) is only filled in the Late Pleistocene by the giant marabou stork (*L. robustus*). The observed difference between the mean body masses of the extant and Pleistocene assemblages, −0.043, is within the 95% confidence interval of the randomized permutation differences (Table 2). When the permutation test is performed on absolute body mass data (Fig. 3B, Table 2), the frequency distribution is heavily skewed by the presence of the large-bodied *L. robustus*. Nonetheless, the observed difference between the mean extant and Pleistocene body masses (−741 g) is still within the 95% confidence interval. Leaving out *L. robustus* yields a less skewed distribution (Table 2), and moves the new observed body mass difference (−34 g) toward the permuted mean.

There is a significant difference in dietary guild between the Pleistocene assemblage and the extant fauna. The observed difference between the mean Pleistocene and extant dietary guild (−1.050) falls outside the 95% confidence interval of the permuted mean differences (Fig. 3C, Table 2). Removing the scavengers from the Late Pleistocene assemblage results in no dietary guild difference between the samples (Fig. 3D, Table 2), as the extant Flores fauna lacks scavengers. Both (non-passerine) assemblages lack herbivores and nectarivores, and have a large proportion of carnivores (99 species, 57% of the extant fauna, and 8 Pleistocene taxa, i.e. 36%). Insectivores, omnivores and frugivores are about equally represented in both avifaunal samples, ranging between 10 and 20% of the total assemblage. Granivores are slightly more abundant in the Pleistocene assemblage (9% vs. 3% in the extant fauna).

The habitat spectrum for the extant fauna shows a strong representation of swamp, marsh and lake habitats (Fig. 2C), as well as marine habitats. When the modern fauna is split into migrants or residents, marine habitats are most strongly represented by migrant taxa, and less so by resident taxa. The opposite is true for forest habitats; savannah woodland, lowland monsoon forest, secondary forest and lowland rainforest are strongly represented by resident taxa but less so by migrant taxa. The Late Pleistocene fauna shows a strong component of species that use terrestrial-aquatic habitats, such as swamps, marshes and lakes, as well as grassland and scrub, and secondary forest and forest edge (Meijer et al., 2013). The estimated geographic ranges for extant taxa also present in the Late Pleistocene sample are mostly large and cover more than one island or island group (Table 3) with the possible exception of *Otus* sp., which may represent a taxon endemic to Flores. For most taxa, their range covers the Greater and Lesser Sunda Islands, and a few species, such as *Actitis hypoleucos*, *Haliastur indus* and *Aquila* sp. have extremely large ranges (BirdLife International, 2013). *L. robustus* shows adaptations to a terrestrial lifestyle (i.e. large body size and robust legs) (Meijer and Due, 2010) and presumably had a limited range. There are no indications that *Trionocephus* sp. had limited flight ability, but their low-aspect-ratio wings make vultures ill-suited for crossing water bodies (Kerlinger, 1985; Bildstein et al., 2009), and imply a limited range as well.

4. Discussion

Our analyses of the non-passerine Late Pleistocene and modern Flores avian assemblages failed to detect a large-scale shift in ecological structure of the avian community. A statistically significant difference was

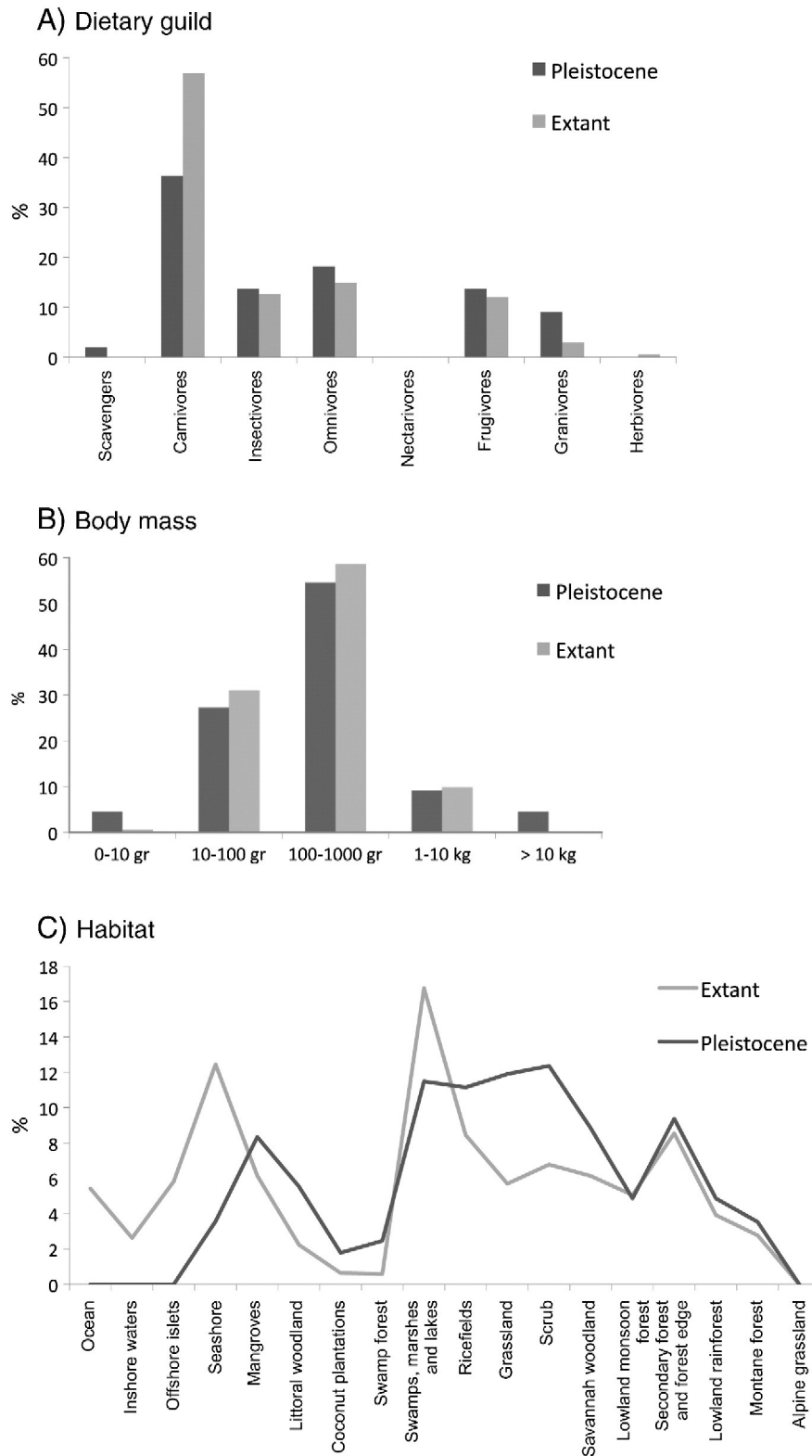


Fig. 2. Characteristics of the Late Pleistocene (dark gray) and Extant (light gray) avifaunas. A. Distribution of body mass within the Late Pleistocene and Extant avifaunas. B. Distribution across dietary guilds within the Late Pleistocene and Extant avifaunas. S, scavengers; C, carnivorous (including piscivorous); I, insectivorous; O, omnivorous; N, nectarivorous; F, frugivorous; G, granivorous; H, herbivorous. C. Habitat types represented by the Extant and Pleistocene avifaunas. 1, ocean; 2, inshore waters; 3, offshore islets; 4, seashore; 5, mangroves; 6, litt, woodland; 7, coconut plantations; 8, swamp forest; 9, wetlands (swamps, marshes and lakes); 10, ricefields; 11, grassland; 12, scrub; 13, savannah woodland; 14, lowland monsoon forest; 15, secondary forest and forest edge; 16, lowland rainforest; 17, montane forest; 18, alpine grassland.

found for the distribution of dietary guilds (Figs. 2B, 3C–D, Table 2), but when scavengers were removed, no difference was observed. Furthermore, no difference in body size distribution was detected, and the distribution of species among habitat types is similar. These results are in

contrast to other oceanic islands, such as the Hawaiian Islands, New Zealand, and other Pacific Islands, where avian extinctions were more severe and significant ecological change was observed after the arrival of modern humans (Steadman and Martin, 1984, 2003; James and Olson,

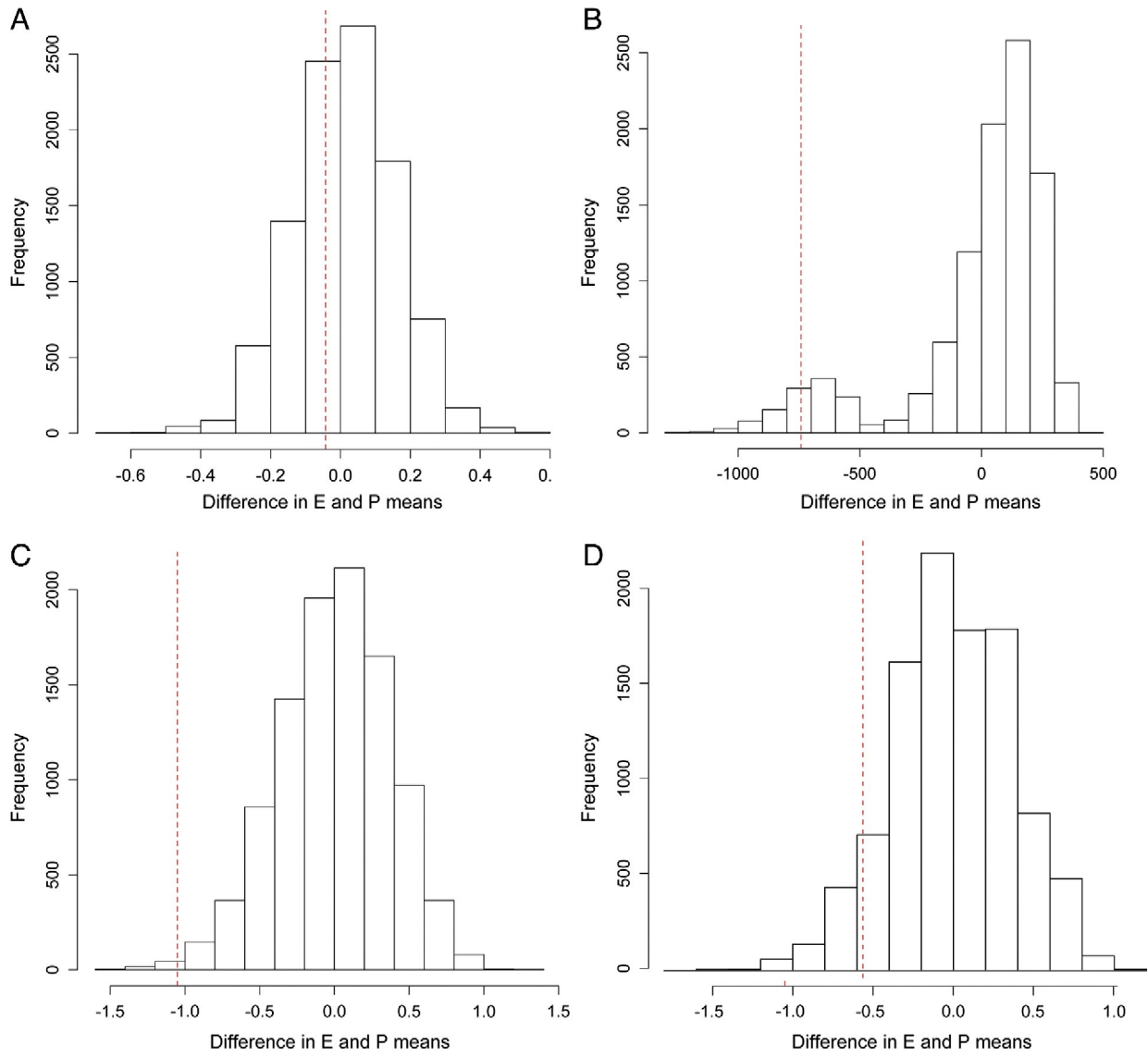


Fig. 3. Frequency distributions of 10,000 permutations of the difference between the mean for body mass (A–B) and dietary guild (C–D) of the extant (E) and Pleistocene (P) assemblages. A: body mass data grouped according to body mass categories. B, body mass data in absolute weights (grams). C, dietary guild data organized in categories. D, dietary guild data without scavengers. The red dotted line indicates the mean in the original data (see also Table 2). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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).

Flores' geographic location should be considered as an important factor contributing to the resilience of its avifauna. Despite being a true oceanic island, Flores is relatively close to nearby continental landmasses; the distance between Flores and the nearest continental landmass (~450 km) is much smaller than for other oceanic islands such as Hawaii (~3800 km) and New Zealand (~1500 km), where avian

extinctions were more severe. Flores is surrounded by other islands that lessen the water gaps, and thus the degree of isolation, between major land masses in the region. Less isolated islands allow more connectivity among avian populations on adjacent landmasses. Species with large geographic ranges may be less susceptible to extinction, either because their populations are replenished through relatively constant recruitment from other land masses or through repopulation from other land masses after local extirpation. Note that for relatively continuous recruitment to the local gene pool, population connectivity

Table 2

Mean body mass and dietary guild for the Extant and Pleistocene assemblages, the difference in body mass and dietary guild between the Extant and Pleistocene assemblages, and the 95% confidence interval of permuted differences. Significant differences in bold.

	Mean Extant	Mean Pleistocene	Difference	95% confidence interval	
Body mass (categories)	2.775	2.818	-0.043	-0.298	0.264
Body mass (in grams)	403	1144	-741	-809	309
Body mass (in grams, excluding storks)	403	437	-34	-341	228
Dietary guild	2.086	3.136	-1.050	-0.794	0.690
Dietary guild (excluding scavengers)	2.086	2.65	-0.564	-0.786	0.718

is necessary, whereas repopulation after local extinction stems from fluctuating geographic ranges and discontinuous gene flow. With regard to geographical range, the majority of birds in the Late Pleistocene assemblage are extant species with a large geographical range (Table 3). With the possible exception of *Otus* sp. (the range of the endemic *Otus alfredi* is approximately 330 km²), all extant taxa that are also present in the Late Pleistocene assemblage are likely to have had a geographic distribution larger than 500,000 km² (including areas of ocean), covering a significant part of the Indonesian archipelago, as well as the Asian and Australian continental landmasses (BirdLife International, 2013).

These findings agree with those of Biber (2002), who showed that the degree of isolation for islands is positively correlated with the proportion of bird species, both modern and fossil combined, that have gone extinct (although intrinsic traits, rather than isolation, are the primary explanatory variables for avian extinctions in the Pacific area) (see Boyer, 2010). Under the hypothesis that less isolated islands allow for more population connectivity or for recolonization after local extirpation, it would follow that other Wallacean islands experienced similarly few avian extinctions. Interestingly, Steadman et al. (1999) suggested that New Ireland's relatively low extinction rate may have been related to the avifauna evolving alongside native rodents. Murid diversity is high in Southeast Asia (van den Bergh et al., 2009; Thomson et al., 2014), and murid presence may have been an additional factor affecting the avifauna's resilience. Another possible alternative or contributing factor is the likely long-term presence of pre-modern hominins on Flores since around 1 million years ago (Brumm et al., 2010).

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. Unlike on other islands, there is no evidence for dramatic changes in the representation of species within feeding guilds, except for the loss of scavengers. Scavengers as a guild do not occur on most islands, thus their degree of vulnerability to extinction on islands is poorly understood. However, these birds are large in body size, which on other islands is a risk factor for extinction (Boyer, 2008, 2010). What is surprising is the combination of the scavenging guild disappearing completely while the rest of the avian community apparently remained unaffected. This pattern is reminiscent of Late Pleistocene continental extinctions, where the loss of large-bodied, scavenging and commensal birds is linked to the

disappearance of mammalian megafauna. Tyrberg (2008) showed that the 97 species of birds that went extinct in the Late Pleistocene across the five main continental landmasses were not a random sample of the affected avifaunas. Instead, more than half of the species that went extinct (52 species, 54%) were either flightless or large-bodied, being scavengers or raptors, colonial breeders, or possessing a combination of these traits (in contrast to 10% of extant birds). The pattern seems particularly strong for North America, where Steadman and Martin (1984) found that "many, if not all extinct genera of late Pleistocene birds can be attributed to ecological dependencies on mammals" (Steadman and Martin, 1984, p. 468). The extinction of large scavengers in an insular setting suggests that avian dependence on mammalian megafauna may not be limited to continental avifaunas but could also pertain to oceanic islands that support mammalian megafauna.

The disappearance of *L. robustus* and *Trigonoceps* sp. at the end of the Pleistocene is stratigraphically correlated with the disappearance of *S. f. insularis* and *H. floresiensis*. These four extinct taxa, along with *V. komodoensis*, are only known from the Late Pleistocene sediments at Liang Bua, as all of these large-bodied species are absent above a roughly 1-meter thick layer of tephra that was deposited toward the end of the Pleistocene (Morwood et al., 2004; van den Bergh et al., 2009; Meijer et al., 2013). In contrast, the Holocene layers document the arrival of modern humans and a new set of non-native species (van den Bergh et al., 2009; Meijer et al., 2010). The causes behind the extinction of the Flores megafauna remain poorly understood. Was the arrival of modern humans in the early Holocene the main driver of this extinction event? There is no denying the catastrophic impact, direct and indirect, of human arrival on naive island faunas (Milberg and Tyrberg, 1993; Steadman, 2006), but the earliest evidence for modern humans on Flores also derives from Liang Bua at ~11 ka, which is after the stratigraphic occurrences of the megafauna (van den Bergh et al., 2009). The presence of thick layers of volcanic ash separating the Pleistocene sediments from the Holocene ones (Morwood et al., 2004; Roberts et al., 2009) in combination with significant climatic change during the Late Pleistocene and early Holocene in this region (van der Kaars et al., 2001; Westaway et al., 2009) suggests that additional factors were at play. Regardless of the cause(s) behind the megafaunal extinctions, a population decline or extinction of *S. f. insularis* as a source of carrion, and *V. komodoensis* and *H. floresiensis* as carrion producers, would have resulted in a significantly reduced food base for

Table 3
Taxa recorded in Liang Bua's faunal sequence and their geographic ranges (data from BirdLife International, 2013). Note that for *Geopelia striata*, no exact range was given by BirdLife International other than 'very large'.

Family	Species	Reference species taken	Range (km ²)	Islands/landmasses currently occupied
Anatidae	<i>Anas</i> sp.	<i>A. gibberifrons</i>	788,000	Greater and Lesser Sunda Islands
Phasianidae	<i>Coturnix</i> sp.	<i>C. ypsilophora</i>	5710,000	Australasia
	<i>Leptoptilos robustus</i>		?	–
	<i>Trigonoceps</i> sp.	<i>T. occipitalis</i>	6910,000	Sub-Saharan Africa
Accipitridae	<i>Accipiter</i> sp.	<i>A. soloensis</i>	968,000	Greater and Lesser Sunda Islands, Philippines
	<i>Haliastur</i> cf. <i>indus</i>	<i>H. indus</i>	8730,000	Insular Southeast Asia, also Australia
	<i>Aquila</i> sp.	<i>A. fasciatus</i>	5440,000	Lesser Sundas, also Eurasia
Rallidae	<i>Gallirallus</i> sp.	<i>G. philippensis</i>	1950,000	Insular Southeast Asia and Australasia
	<i>Porzana</i> sp.	<i>P. fusca</i>	4430,000	Asia
Charadriidae	<i>Pluvialis fulva</i>	<i>P. fulva</i>	1730,000	Asia and Australia
Scolopacidae	<i>Gallinago</i> sp.	<i>G. megalala</i>	2840,000	Asia and Australia
	<i>Actitis hypoleucos</i>	<i>A. hypoleucos</i>	25900,000	Eurasia and Australia
Turnicidae	<i>Turnix</i> sp.	<i>T. maculosus</i>	1110,000	Wallacea, Philippines and Australasia
Columbidae	<i>Macropygia</i> sp.	<i>M. emiliana</i>	580,000	Greater and Lesser Sunda Islands
	<i>Ptilinopus</i> sp.	<i>P. melanospila</i>	498,000	Greater and Lesser Sunda Islands, Moluccas, Philippines
	<i>Geopelia</i> sp.	<i>G. striata</i>	Very large	Greater and Lesser Sunda Islands, Moluccas, Philippines
Psittacidae	<i>Geoffroyus</i> cf. <i>geoffroyi</i>	<i>G. geoffroyi</i>	793,000	Moluccas, Lesser Sundas, New Guinea and Australia
Tytonidae	<i>Tyto</i> sp.	<i>T. longimembris</i>	4270,000	Sulawesi and Lesser Sundas, South Asia, Australasia
Strigidae	<i>Otus</i> sp.	<i>O. alfredi</i>	330	Flores
Apodidae	<i>Aerodramus</i> cf. <i>fuciphagus</i>	<i>A. fuciphagus</i>	1420,000	Insular Southeast Asia
	<i>Collocalia esculenta</i>	<i>C. esculenta</i>	2750,000	Insular Southeast Asia
Halcyonidae	<i>Halcyon</i> sp.	<i>H. chloris</i>	3940,000	Insular Southeast Asia and Australasia

these scavenging birds. Thus, if both *L. robustus* and *Trigonoceps* sp. were dependent upon the megafauna for carrion, and particularly *Stegodon*, as a source of carrion (Meijer et al., 2013), the extinction of this large mammal could have produced a trophic cascade leading to the extinction of these scavengers.

Thinking more broadly, we might ask whether the extinction of mammalian megafauna across Southeast Asia explains the modern absence of large birds of prey across this landscape (Thiollay, 1998). Future findings of extinct large scavenging birds on Southeast Asian islands along with mammalian megafauna would lend support to this hypothesis. The presence of *Stegodon* may have served as a limiting factor to the distributional ranges of *L. robustus* and *Trigonoceps* sp. on Southeast Asian islands. Hypothetically, wherever *Stegodon* went, so did these birds. If this hypothesis turns out to receive support, and remains of these scavengers are found as far to the southeast as Timor, where *Stegodon* once occurred, then vultures succeeded in coming very close to Australia yet failed to establish themselves on that continent.

In conclusion, our analyses failed to detect large differences in avian community structure between the Late Pleistocene and modern non-passerine assemblages on Flores. In contrast to many other oceanic islands, Late Pleistocene avian extinctions on Flores apparently were limited, and although a guild of large scavengers was lost, did not significantly alter community structure overall. Flores' close proximity to other islands and landmasses likely buffered populations from extinction. We argue that the extinction of the large-bodied avian scavengers *L. robustus* and *Trigonoceps* sp. on Flores can be linked to the extinction of *Stegodon* on the island. Such a dependence of avian species on mammalian megafauna, leading to extinction by trophic cascade, is characteristic of continental rather than insular Late Pleistocene extinctions.

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