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A lost world in Wallacea: Description of a montane archipelagic avifauna

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Birds are the best-known animal class, with only about five or six new species descriptions per year since 1999. Integrating genomic and phenotypic research with arduous fieldwork in remote regions, we describe five new songbird species and five new subspecies from a small area near Sulawesi, Indonesia, all collected in a single 6-week expedition. Two factors contributed to the description of this large number of species from such a small geographic area: (i) Knowledge of Quaternary Period land connections helped pinpoint isolated islands likely to harbor substantial endemism and (ii) studying accounts of historic collectors such as Alfred Wallace facilitated the identification of undercollected islands. Our findings suggest that humans' understanding of biogeographically complex regions such as Wallacea remains incomplete.

Birds (Aves) have long been a model organism across many biological disciplines because of our relatively detailed knowledge of their ecology, distribution, relationships, and global diversity (*1*). Their model status has become further entrenched with our planet's deepening man-made biodiversity crisis (*2*–*4*), which can often be evaluated most easily through the study of organismic groups that were already comprehensively known before being affected by modern anthropogenic processes such as habitat loss, the wildlife trade, and climate change.

The known global diversity of birds currently stands at ~11,000 species (*5*–*7*). In 1946, the late Ernst Mayr famously announced that "…the period of new discoveries is practically at its end. I doubt that in the entire world even as many as 100 new [bird] species remain to be discovered…" (*8*). Mayr's prediction was right until the 1990s: the 20th century saw a limited number of genuinely new species descriptions (*8*–*15*) even though taxonomic reassessments and so-called "species splits" have continued to contribute to an unhalting increase in the global species tally (*16*). Meanwhile, ornithology has entered a minor renaissance of species discovery in the 21st century, with average rates of bird descriptions slightly rebounding to ~5.6 species per year (a total of 95 descriptions from 2000 through 2016; table S1). Most of these new discoveries have come from South America (~61%), particularly the Andes and the Amazon, and refer to serendipitous finds blending into a slow trickle of single new species descriptions [e.g., tapaculos of the genus *Scytalopus* (*17*)]. Expeditions such as those of Johann Natterer in Brazil (1817 to 1835), which led to the description of ~40 bird species new to science (*18*), are not known to have occurred after the 19th century.

Description of five new species and five new subspecies of birds from a small area off Sulawesi

From November 2013 through January 2014, we conducted a bird-collecting expedition to three small, little-explored island groups off the northeastern coast of Sulawesi in present-day central Indonesia (*19*) (Fig. 1). Here, we formally describe five bird species and five subspecies from this expedition that are new to science and provide details of a long-overlooked local avifauna that has only come to light through recent exploration.

The three islands targeted by our collecting activity are situated in Indonesia's Wallacean region, an archipelago at the interface between the Oriental and Australian biogeographical realms (Fig. 1) named after Alfred R. Wallace, who was the most famous historical collector exploring this area. Six of our 10 new forms (three new species and three subspecies; Fig. 1) were found at higher elevations on Taliabu (~2950 km^2), the largest member of the Sula Islands, rising to over 1400 m. Three of the forms (two new species and one subspecies) were detected in the hills of Peleng (~2400 km^2), the largest island in the Banggai group, rising to just over 1000 m. One new subspecies comes from Batudaka (~250 km^2), the larger of the two main constituents of the Togian group, an agglomeration of low-lying islands barely reaching above ~350 m.

The description of this many bird species from such a geographically limited area is a rarity. Past examples include a series of consecutive collecting expeditions to multiple sites in northern Peru organized by Louisiana State University and collaborating teams >40 years ago (1970 to 1978), which produced type material for at least eight new bird species (*20*–*27*), three new species from the Kontum mountain range in central Vietnam collected by Jonathan Eames and coworkers during two expeditions (1996, 1999) (*28*–*30*), three new species in the African Rubeho mountains collected by Jacob Kiure during extended fieldwork across nearly 3 years (2000, 2002) (*31*–*34*), four new species in an unexplored type of Amazonian forest substrate ("white sand forest") near Iquitos (Peru) collected by José Álvarez Alonso between 1995 and 1999 (*35*–*38*), and four new species in a small Amazonian interfluvium between the Madeira and Aripuanã rivers collected by members of a mostly Brazilian group of collaborators during fieldwork between 2004 and 2011 (*39*–*42*). These latter cases raise the possibility that unexplored areas of bird endemism may await discovery.

Earth-historic insights guided our exploratory activity

On a global scale, our findings indicate that modern exploration to find undescribed species diversity can be targeted to areas of high promise. The more important of the two main reasons that we concentrated our field efforts on the islands of Taliabu and Peleng is a modern body of bathymetric data indicating the presence of deep sea between the latter two islands and Sulawesi (Fig. 1) (*43*). Sea depth is an important and long-neglected factor in determining the distinctness of an island's terrestrial communities. As the Earth has undergone a succession of 20 to 30 glacial periods over the past ~2 million years, global sea levels have repeatedly dropped by up to ~120 m during the peaks of ice ages, most recently at ~18,000 years before present (*44*, *45*), leading to land expansion especially in regions such as Australasia that are dominated by shallow shelf. Consequently, islands surrounded by sea greater than 120 m in depth would have remained isolated throughout the Quaternary Period (Fig. 1), increasing both rates of extinction and rates of endemism by severing gene flow between island populations. By contrast, islands that are linked to greater landmasses by areas of shallow sea (<120 m) would have merged with them through cyclical land-bridge formation, leading to gene flow between populations. Even small amounts of gene flow are powerful in counteracting biotic differentiation, reducing the potential for endemism on such islands (*46*).

Unaware of the exact earth-historic processes at the time, Wallace himself was likely

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the first to point out the uncanny faunal resemblance among shelf islands such as Borneo and Sumatra with mainland Asia while puzzling over the high levels of endemism on other, smaller landmasses such as Sulawesi and Halmahera that would appear no more isolated if one is oblivious that they are surrounded by deeper sea (*47*).

Although only separated by <15 km of sea water, Peleng has never been connected to Sulawesi (~180,000 km^2) owing to a deep sea channel separating the two (Fig. 1). Instead, the two smaller islands of Peleng and Taliabu have had Quaternary land connections with each other, forming one paleoisland (Fig. 1),

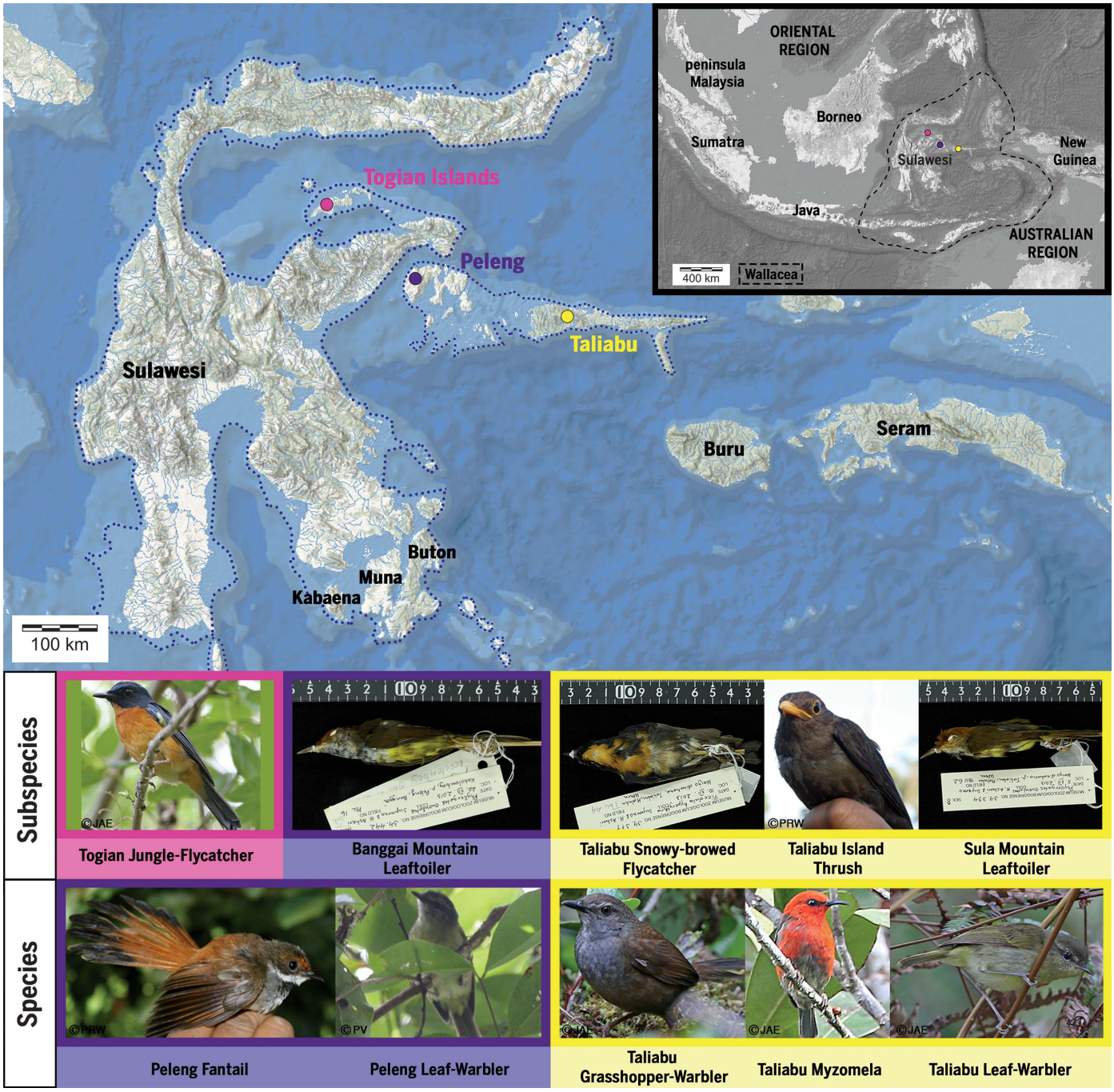

Fig. 1. Map of Sulawesi and satellite islands, with the fieldwork localities on Togian, Peleng, and Taliabu depicted by pink, purple, and yellow circles, respectively. The blue dotted line on the main map reflects the ~120-m isobath, roughly indicating land extent during glacial maxima. The map inset shows the Indonesian Archipelago, with the Wallacean region demarcated by a black dashed line. Photos representing each newly described taxon (labeled by their proposed English names), including three type specimens (aligned against rulers), are color coded with their respective island distribution. The seven live bird photos do not depict type specimens and were taken by photographers on independent visits to the islands. [Photos courtesy of James A. Eaton (JAE), Peter R. Wilton (PRW), and Philippe Verbelen (PV)]

which explains some of their faunal sharing (*48*, *49*). This bathymetric constellation was our strongest incentive to concentrate on these islands to search for new species diversity (*19*, *48*, *49*). Our approach has been further vindicated by the upgrade of five previously recognized avian subspecies from Peleng and Taliabu to species level after new bioacoustic and genomic data established an understanding of true levels of divergence (*50*–*53*).

The disproportionate importance of Quaternary land connections in defining how many individual species a landmass harbors can be gauged by contrasting Taliabu and Peleng with other satellite islands off Sulawesi. The southeastern arm of Sulawesi is surrounded by three comparably sized islands that provide a point of reference (Fig. 1): (i) Kabaena (~19 km from Sulawesi and ~900 km^2 in size); (ii) Buton (~6 km from Sulawesi and ~4400 km^2 in size); and (iii) Muna (~11 km from Sulawesi and ~2890 km^2 in size). Sea depth separating these three islands from Sulawesi is generally only 40 to 80 m at its deepest, indicating that all three have been repeatedly connected with Sulawesi by land bridges during glacial periods, including the Last Glacial Maximum only ~18,000 years before present (*44*, *45*). Not a single avian endemic species is known from these three islands despite exploratory activity over the past ~10 years equaling ours in methodology and effort [e.g., (*54*–*56*)]. This lack of endemism is notable compared with the 23 bird species recognized as being endemic to Taliabu, Peleng, and smaller surrounding islands (*57*) when including the five species newly described here and others upgraded in recent research (*50*–*53*).

Compared with other islands of a similar or greater size, Taliabu and Peleng are perhaps the last candidates in the Indonesian Archipelago that are both surrounded by deep sea and ornithologically undercollected. However, for other organismic groups, many such islands of high promise remain to be explored. Going forward, we recommend the use of bathymetry beyond birds and beyond the Indonesian Archipelago to predict how promising an island may be in terms of undiscovered diversity of a wide range of terrestrial organisms. Birds are generally volant and relatively large in body size, a combination that suggests they may, on average, be better dispersers than frogs, reptiles, and many invertebrates, which would render the presence or absence of land bridges an even more crucial determinant of endemism in the latter groups. In addition to sea depth, the elevational range and age of an island would also serve as an indicator to gauge potential for endemism. Previous work on Wallacean fauna has demonstrated the importance of topographic relief and high elevations for generating species endemism (*58*). On the contrary, the age of continuously emergent land is an unknown property for most Wallacean islands and is poorly characterized for others (*59*, *60*).

Knowledge of historic collection gaps was crucial in finding new birds

Alfred Wallace, aided by a number of helpers in addition to >100 contemporaneous, mostly European, explorers operating roughly until the world wars (after which collecting activity largely ceased), procured a comprehensive collection of Wallacea's birds that forms the basis of our understanding of the regional avifauna (*47*, *61*). Most islands larger than a few square kilometers have therefore been ornithologically explored to some extent. Beyond bathymetric considerations guiding our exploratory plans, we sought to focus on parts of Wallacea that had received the least coverage by historic collectors, which would therefore hold the highest promise of harboring undescribed avian diversity. Studying the routes and operations of historic collecting expeditions and identifying gaps has been a fruitful approach to pinpoint focal areas in our case, just as it was instrumental in generating some of the high new species totals during exploratory fieldwork in northern Peru almost half a century ago (*20*–*27*).

The three islands we targeted were characterized by a particularly incomplete historic coverage (Fig. 1): (i) Taliabu and its neighbors, together forming the Sula group, were only briefly visited by eight historic collecting expeditions, all of which remained in coastal areas and failed to penetrate the highlands of the interior because of poor accessibility (*61*); (ii) Peleng and the remaining islands of the Banggai group were visited along their coastline by only three historic collectors who never ventured far uphill into the interior (*61*); and (iii) the Togian Islands (including Batudaka) were frequented by only two historic bird collectors (*61*) but have been targeted by modern Indonesian collecting expeditions (*62*, *63*).

Against this background of historic collecting activity, it is perhaps not surprising that nine of the 10 new forms we here describe come from the higher elevations of Taliabu and Peleng (roughly >800 m). When we first penetrated these areas (*48*, *49*), we found a highly distinct montane local avifauna comprising an unusual number of birds that had remained undiscovered by historic collectors. The only modern ornithologists frequenting the taller mountains of Taliabu before our first visit (*48*) were probably P. J. Davidson and co-workers, who in 1991 undertook an exploratory survey up to ~800 m, where they made the first observations of four of the six new forms that we describe here (*64*) but obtained no biological material for formal descriptions. Peleng remained equally unexplored to modern ornithology: before our own first observations (*19*, *49*), we are only aware of Mochamad Indrawan and colleagues' occasional exploratory forays in the 1990s and early 2000s (*49*).

New taxon descriptions

To confer nomenclatural availability on the 10 new bird forms, the supplementary materials (sections SM1 to SM11) provide full species and subspecies descriptions, including detailed information on the description of each holotype, diagnosis, etymology, variation within the taxon, history of discovery, distribution, status, taxonomic rationale, and a list of specimens examined. Our baseline taxonomy follows Eaton, van Balen, Brickle, and Rheindt (*57*), and ZooBank Life Science Identifiers (LSIDs) are given for each newly described taxon to comply with article 8.5.3 of the code of the International Commission on Zoological Nomenclature (*65*).

Species delimitation is a perennially contentious scientific topic that has variably divided the biological community into different factions, each following its own "species concept" (*66*). Even when strict standards and criteria are followed, there is a large gray zone within which decisions to confer species versus subspecies rank can be seen as subjective. We adopt the "multidimensional biological species concept" (*67*), an updated version of modern biology's first species concept (*68*, *69*), which continues to be the most widely applied such concept in ornithology and probably in all of biology. Although the criteria of the original biological species concept hinged strongly on the interpretation of "reproductive isolation," more modern versions are careful to note that reproductive isolation is not absolute and can be inferred through numerous proxies, e.g., a lack of gene flow as suggested by character discreteness or genomic divergence.

We used an integrative approach that relies on a combination of characters, variously including morphology, bioacoustics, ecology, genetic, and genomic data depending on taxon. In our application of the multidimensional biological species concept, we frequently resort to the "yardstick approach" (*70*), which compares the magnitude of differences among our island populations with differences between members of closely related, well-studied species pairs in which species-level divergence is firmly established. We have tried to remain conservative in our taxonomic decisions, conferring species rank only where our evidence base is strong and retaining subspecies rank in one or two cases where some colleagues may have opted for species rank. Although all five of our new species can by various definitions be assigned to larger radiations within genera that combine sets of species that geographically replace one another (*68*), they often

belong to the bioacoustically most unusual members within their respective radiation, and their status as distinct species long overlooked by modern ornithology is not in doubt.

Conservation implications

Both Taliabu and Peleng have suffered from rampant forest destruction. On both islands, virtually no primary lowland forest remains, and most highland forests have been affected by some form of logging and/or forest fires, the latter presumably caused by recent climate change (*48*, *49*). Although most of the new forms here described seem to tolerate some form of habitat degradation and were readily detected in secondary forest and edge, some may be threatened, and one of them, the Taliabu grasshopper warbler, is of particular concern as its habitat on the mountain tops of Taliabu may have shrunk to a few square kilometers, some of which was burned in the 1980s and logged in the 1990s (see supplementary materials, section SM3). Urgent, long-lasting conservation action is needed for some of the new forms to survive longer than a couple of decades beyond their date of description.

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SUPPLEMENTARY MATERIALS

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Figs. S1 to S15
Tables S1 to S6
References (*71*–*137*)

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Finding new species

Thousands of species have been described, and, although most may agree that many thousand remain undiscovered, identifying new taxa of charismatic vertebrates, like birds, is rare. Rheindt *et al.* describe five new songbird species and five new subspecies found on a single small island near Sulawesi, Indonesia, over a single 6-week expedition (see the Perspective by Kennedy and Fjeldså). They targeted the area because of its geological history and complexity and the historical notes of other explorers. They argue that similar approaches in other regions could also lead to the discovery of new species.

Science, this issue p. 167; see also p. 140