

UC Merced

Frontiers of Biogeography

Title

Birds and barriers: present and past seas are dominant correlates of avian turnover in the Indo-Australian Archipelago

Permalink

<https://escholarship.org/uc/item/1kq0f5vd>

Journal

Frontiers of Biogeography, 15(2)

Authors

Prasetya, Audrey M.
Moritz, Craig
Joseph, Leo
et al.

Publication Date

2023

DOI

10.21425/F5FBG58189

Supplemental Material

<https://escholarship.org/uc/item/1kq0f5vd#supplemental>

Copyright Information

Copyright 2023 by the author(s). This work is made available under the terms of a Creative Commons Attribution License, available at

<https://creativecommons.org/licenses/by/4.0/>

Peer reviewed



Birds and barriers: present and past seas are dominant correlates of avian turnover in the Indo-Australian Archipelago

Audrey M. Prasetya^{1,2*} , Craig Moritz¹ , Leo Joseph² ,
Maisie W. Stelling¹ and Paul M. Oliver^{3,4} 

¹Division of Ecology and Evolution, Research School of Biology, and Centre for Biodiversity Analysis, The Australian National University, Building 116, Daley Road, Acton, ACT 2601, Australia.

²Australian National Wildlife Collection, CSIRO National Research Collections Australia, Canberra, ACT, Australia.

³Centre for Planetary Health and Food Security, Griffith University, Nathan, QLD, Australia.

⁴Biodiversity and Geosciences Program, Queensland Museum, South Brisbane, QLD, Australia.

*Correspondence: Audrey M. Prasetya, audrey.prasetya@anu.edu.au

Abstract

The Indo-Australian Archipelago (IAA) is a geologically dynamic area of high biotic endemism that spans the continental shelves of Sunda and Sahul and intervening oceanic islands. We provide a comprehensive quantitative assessment of how bird communities are structured across the IAA using beta diversity indices. We focus on three key questions. Are the islands of Wallacea a biogeographically cohesive unit or a more heterogeneous transition zone? Is the rich biota of New Guinea and the East Melanesian islands most closely linked to that of Sunda, Sahul or Wallacea? What are the geographic and environmental correlates of biotic structuring across the region and how does this compare with determinants of plant diversity? We measure the dissimilarity of bird species composition between eleven major areas within the IAA using a new compilation of distribution data and calculate taxonomic beta diversity at species, genera, and family levels. To compare with recent analyses of plants, we analysed potential correlates of turnover, focusing on geographic proximity, sea barriers, land area, and climatic variation. We also used connectivity analyses to estimate the minimum number of connection events needed to explain the current distribution of shared taxa. We found that islands recently connected by land have lower beta diversity than oceanic islands. Additionally, avifaunas on the islands of Wallacea have little biotic cohesion, reflecting their complex geological history. The avifaunas of New Guinea and the Eastern Melanesian islands are very distinctive. Where New Guinea birds are most similar to Australia, East Melanesian birds are more similar to either Sahul or Wallacea, depending on taxonomic level. Isolation through space and time had the strongest influence on avifaunal turnover at all taxonomic scales, in contrast to plants for which climatic variation was the strongest predictor. Further analyses incorporating phylogeny, biome, trait, and biotic interaction data are needed to investigate the processes that have caused biotic turnover across this fascinating biogeographic region.

Abstrak

Indo-Australian Archipelago (IAA) adalah area yang dinamis secara geologis dan kaya akan endemisme biotik. Daerah ini meliputi landas benua Sunda, Sahul, serta pulau-pulau *oceanic* di antara mereka. Kami melakukan penilaian kuantitatif secara menyeluruh tentang bagaimana komunitas burung terstruktur di sepanjang IAA menggunakan indeks keanekaragaman beta. Kami memusatkan studi ini pada tiga pertanyaan besar. Apakah pulau-pulau di Wallacea merupakan unit biogeografi yang koheren atau zona transisi yang lebih heterogen? Apakah kekayaan biota di Guinea Baru dan Kepulauan Melanesia Timur lebih terkait erat dengan biota Sunda, Sahul, atau Wallacea? Apa faktor geografis dan faktor lingkungan yang berkaitan dengan struktur biotik di wilayah ini dan bagaimana hasil ini dibandingkan dengan hasil determinan dari taksa tumbuhan? Kami mengukur perbedaan komposisi spesies burung di sebelas area utama IAA menggunakan kompilasi data distribusi dan mengkalulasi keanekaragaman beta pada level spesies, genus, dan famili. Sebagai bahan perbandingan dengan analisis terbaru dari tumbuhan, kami menganalisis variabel yang dapat berkorelasi dengan *turnover* spesies, dengan menitikberatkan pada jarak geografis, penghalang laut, luas daratan, dan variasi iklim. Kami menggunakan analisis konektivitas untuk memperkirakan jumlah peristiwa koneksi minimum yang diperlukan untuk menjelaskan distribusi spesies yang terbagi antar daerah saat ini. Kami menemukan bahwa pulau-pulau yang baru saja terhubung oleh daratan memiliki keanekaragaman beta yang lebih rendah dibandingkan dengan pulau-pulau *oceanic*. Selain itu, komunitas burung di pulau-pulau Wallacea tidak memiliki kohesi biotik yang kuat. Hal ini mencerminkan sejarah geologis yang kompleks daerah tersebut. Burung-burung di Guinea Baru dan Kepulauan Melanesia Timur sangat berbeda. Burung di Guinea baru lebih mirip dengan Australia, sementara burung Kepulauan Melanesia Timur lebih mirip dengan Sahul atau Wallacea, bergantung pada tingkatan taksonomi. Isolasi secara ruang dan waktu memiliki pengaruh terbesar pada *turnover* spesies burung pada semua level taksonomi. Hal ini sangat kontras dibandingkan dengan tumbuhan, di mana variasi iklim merupakan prediktor terkuat. Analisis lebih lanjut yang memadukan data filogeni, bioma, sifat, dan interaksi biotik diperlukan untuk menyelidiki proses yang mempengaruhi daerah pertukaran hayati di wilayah biogeografis yang menarik ini.

Keywords: Australia, beta diversity, biogeography, biotic interchange, birds, Melanesia, South-east Asia, Sunda, Sahul, Wallacea

Highlights

- Melanesia (New Guinea and East Melanesian Islands) holds the highest number of bird species in the Indo-Australian Archipelago, despite having a smaller land area than nearby Australia and the combined islands of the Sunda shelf.
- The most significant correlate of turnover in bird species of the IAA is historical connectivity and not climatic variation, which contrasts with previous research on plants in the region.
- The avifauna of Wallacea is not a cohesive assemblage: islands within the region do not consistently cluster together, unlike areas within the Sunda or Sahul regions.
- Birds of New Guinea are more similar to Australia than Asia, and this contrasts with previous studies on the plants within the same region.
- The Eastern Melanesian island fauna is very distinctive, clustering with Sahul at the species level but with Wallacea at higher taxonomic scales.

Introduction

Biotic interchanges across regions occur when a barrier between two (or more) previously separated areas weakens and there is increased exchange among previously isolated biotas (Lohman et al. 2011, Sheldon et al. 2015, Christensen et al. 2017). Locations where biotic interchanges develop are often points of great biogeographic interest due to the complex patterns of species richness and the interplay of dispersal and vicariance (Vermeij 1991, Weir et al. 2009). Biogeographic patterns are influenced by external processes such as environmental gradients and geological history in conjunction with dynamic biotic processes such as speciation, dispersal, and extinction (Vermeij 1991, Whittaker et al. 2008). By investigating biogeographic patterns at biotic interchanges, we have the opportunity to understand the interaction between geological, ecological, and biological processes and how they shape the assembly of regional biotas (Whittaker et al. 2008). Understanding patterns of turnover across a biotic interchange requires synthesising data from multiple taxa across key regions. Such comparisons can then be used to investigate the relevance of a range of potentially significant factors such as climatic variation, geological history, and the strength of barriers. Archipelagic systems, due to their dynamic nature and role in diversification, provide a superb opportunity to further investigate which variables correlate with biotic turnover (Whittaker et al. 2008, Lohman et al. 2011). One such example of a well-studied archipelagic system, which involves dynamic geology and interesting biogeographical patterns of biotic interchange, is the Indo-Australian Archipelago.

The Indo-Australian Archipelago (IAA) spans the region from Sundaland to Australia (Figure 1). The Sunda and Sahul continental shelves are the two largest components of the IAA. The Sunda shelf is the south-eastern extension of the mainland Eurasian plate whereas the Sahul continental shelf includes the Australian continental plate and a complex assemblage of accreted and uplifted terranes, forming the current island of New Guinea, along its northern edge (Hall 2011, Harrington et al. 2017). Between these continental shelves are an array of oceanic island groups with complex histories of movement, uplift and accretion going back at least 35 million years, and potentially much longer (Hall 2012). This history and geology make the IAA a model region for understanding patterns of differentiation and dispersal across biogeographic realms in connection with dynamic island processes (Filardi and Moyle 2005, Michaux 2010, Lohman et al. 2011, McCullough et al. 2022).

There is extensive scientific literature on biotic turnover across the IAA, especially concerning biogeographical boundaries among terrestrial biotas. To document and understand biotic differentiation in the IAA, biogeographers have delineated zones (or “lines”) where turnover is particularly marked (Figure 1; Simpson, 1977). The most famous of these are Wallace’s Line and Lydekker’s Line. Wallace’s Line was initially characterised by Wallace (Wallace 1860, Wallace 1869, Ali and Heaney 2021) and effectively demarcates the eastern edge of the Sunda continental plate. The line was modified by Huxley (1868) who considered the Philippines as ‘east of the line’. Lydekker’s Line (Lydekker 1896) effectively demarcates the western edge of the Sahul continental plate. Sandwiched between Sunda and Sahul is Wallacea, a complex assemblage of islands of greatly varying ages, sizes, and geological origins (Mayr 1944, Simpson 1977, Moss and Willson 1998, Michaux 2010, Zahirovic, Matthews, et al. 2016, Hermogenes De Mendonça and Ebach 2020, Oliver et al. 2023). Wallacea includes at least three broad contemporary areas (Lesser Sundas, Sulawesi, and Maluku Islands). Although not usually considered part of Wallacea, the Philippine archipelago is geographically close to the islands within Wallacea and was included in the initial definition of “Wallacea” (Ali and Heaney 2021). The Philippine archipelago has a similar history to Wallacea, in that most islands in this region have had little to no history of connections with nearby continents over the last 30 million years.

There have been fewer quantitative analyses of patterns and correlates of turnover of terrestrial biotas across the entire IAA, and most have focused on plants (Sniderman and Jordan 2011, Van Welzen et al. 2011, Crayn et al. 2015, Joyce et al. 2021). One fundamental question is how current and past land connectivity and climatic difference interact to influence biotic turnover in an archipelagic system. Notably, the IAA comprises both continental islands that have had historical land connections, and also oceanic islands that have been isolated for all of their history (see Figure 1).

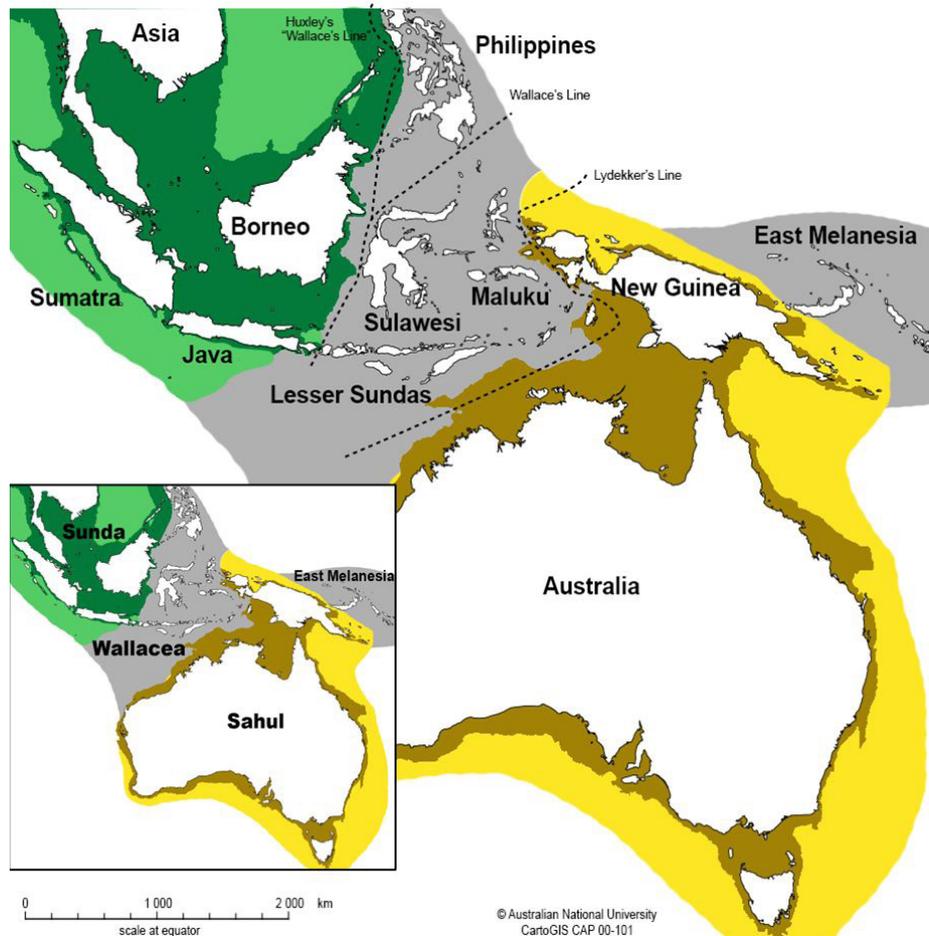


Figure 1. Map of the Sunda-Sahul Biotic Interchange located in the Indo-Australian Archipelago (IAA). Inset map shows clustering of areas into three groups represented by different colour highlights: Sunda (green), Islands (grey), and Sahul (yellow). Larger map shows the eleven areas discussed in the text within the three groups. Darker highlights indicate land above sea level during the last glacial maximum. New Caledonia and Vanuatu are not shown in this map but are included in East Melanesia in this study. Map reproduced with the permission of CartoGIS Services, Scholarly Information Services, The Australian National University.

Due to these past land connections species on the Sunda continental shelf islands of Java, Sumatra, and Borneo, may have had more opportunities to disperse through suitable habitats during glacial maxima as sea barriers receded into land bridges. However, during glacial lowstands, Sundaland also experienced substantial change to the extent of rainforest and savannah habitats. The interaction between changing geography and environment in Sundaland resulted in an east-west genetic structuring of some populations (Sheldon et al. 2015, Lim et al. 2017, McCullough et al. 2022), despite the high level of climatic similarity across these areas (Voris 2000, Sheldon et al. 2015). Across Sahul, north-south genetic structuring between New Guinea and Australia occurred due to changes in land connectivity over time as sea levels fluctuated (Peñalba et al. 2019). In contrast, the oceanic islands of Wallacea as well as the East Melanesian islands have mostly been separated from each other and nearby continents by sea barriers. The Wallacean islands are accordingly

dominated by taxa that can disperse overwater (Voris 2000, Stelbrink et al. 2012, Dalsgaard et al. 2014, White et al. 2021).

Studies of the IAA have started to integrate the relative extent to which turnover may be correlated with key factors such as sea barriers, land area, geographical proximity, and environmental variation. For birds and mammals across the entire IAA, White et al. (2021) identified dispersal potential as being important. For the Wallacean birds specifically, Dalsgaard et al. (2014) concluded that island area and elevation are positively associated with high species richness and endemism, with environmental variation playing only a small role in turnover. In contrast, Joyce et al. (2021) found that the environment is a better predictor of turnover in plants than geographic proximity. However, as these previous studies of biotic structuring have used very different approaches and focused at different spatial scales, it remains unclear to what extent climate and dispersal have different effects on plants and animals.

Wallace has presented longstanding challenges to synthesising and understanding patterns of biodiversity in the IAA, largely because of its complex geological history (Mayr 1944, Hall 2012). The classical biogeographic perspective which formerly distinguished Wallacea through clear-cut boundary lines has been replaced by a viewpoint that considers Wallacea as a transition zone (Ali and Heaney 2021). Wallacean islands first developed when the Sunda and Sahul plates began to collide from ~25 million years ago. This uplift likely triggered increased rates of biotic dispersal across the IAA (Jonsson et al. 2011, Moyle et al. 2016, Tänzler et al. 2016, Zahirovic, Flament, et al. 2016, Andersen et al. 2018, Rowe et al. 2019, Letsch et al. 2020, Oliver et al. 2020, Rheindt et al. 2020, Tsang et al. 2020, McCullough et al. 2022). The proximity of Wallacean islands to each other, and to nearby continental regions has also varied greatly over time. Most islands of Wallacea are isolated by permanent water barriers, although there are prominent exceptions including Sulawesi and some of its current offshore islands, and some parts of the Lesser Sundas (Voris 2000, Stelbrink et al. 2012). Moreover, Wallacean islands differ in environmental structure. Sulawesi consists predominantly of lowland and montane rainforests that are similar in climate to those found in Sunda and New Guinea (Kooyman et al. 2019). In contrast, the Lesser Sunda Islands have a much drier and more seasonal climate similar to parts of the Sahul region (Van Welzen et al. 2011, Stelbrink et al. 2012). Last, and certainly complicating the region, Sulawesi is geologically and tectonically composite island derived from multiple sources, and has varied in areal extent over time as different terranes have collided (Zahirovic, Matthews, et al. 2016).

This complex geological history resulted in Sulawesi being dominated by fauna derived from dispersal and having origins from both Sunda and Sahul (Stelbrink et al. 2012, Dalsgaard et al. 2014). There have also been varying results on the biotic associations of major areas such as Java and the Maluku Islands, with different taxa and studies suggesting closest affinities to either nearby continental shelves or other islands in the Wallacea transition zone (Van Welzen et al. 2011). In some analyses (especially of plants), Java is biotically associated with the Lesser Sundas as part of Wallacea, most likely through shared savannah habitats (Van Welzen et al. 2011, Louys and Roberts 2020). Thus, a complex interplay of sea barriers, distinct environments, and differing geographical distances render the elucidation of biogeographic regions within Wallacea, and between Wallacea and nearby areas perpetually challenging.

There is also uncertainty about the biogeographical cohesion of Sahul, particularly the affinities of New Guinea biota (Van Welzen et al. 2011, Joyce et al. 2021). Sahul's two main constituent landmasses, New Guinea (the largest part of Melanesia) and Australia, have been connected by land for much of the last 2.5 million years (and potentially much longer) and have many shared biotic elements (Lohman et al. 2011, Sniderman and Jordan 2011, Van Welzen et al.

2011, Crayn et al. 2015). However, some phylogenetic evidence suggests Melanesia (New Guinea and East Melanesian Islands) also has its own distinct and long isolated biota (e.g., birds - Jønsson et al. 2011, McCullough et al. 2022, reptiles - Oliver et al. 2018, frogs - Rivera et al. 2017, invertebrates - Toussaint, Tänzler, et al. 2015, Toussaint, Hendrich, et al. 2015). Recent reports of phylogenetically divergent lineages on East Melanesian islands also point to a long history of independent evolution of these faunas (Oliver et al. 2020). Reflecting this underlying complexity different studies have found contrasting patterns of association for elements within the biota of Sahul. On one hand, many faunal elements in Australia and New Guinea are closely associated, suggesting that land connectivity better predicts biotic similarity (e.g. rodents - Rowe et al. 2016). In contrast, other studies (especially of plants) have suggested that the biota of New Guinea and East Melanesia is much more associated with tropical islands on the Sunda shelf to the west (e.g. plants - Sniderman and Jordan 2011, Van Welzen et al. 2011, Joyce et al. 2021). This later results suggests greater importance of environmental similarity and high overwater dispersal ability than geographic proximity in explaining biotic turnover (Van Welzen et al. 2011, Joyce et al. 2021). To disentangle the apparent discrepancy between patterns across taxa, we need a consistent quantitative method that allows direct comparisons of results.

Analysis of compositional dissimilarity - beta diversity - of assemblages from one area to another can inform us about potential connections between areas (Baselga et al. 2007, Baselga 2010, Baselga and Orme 2012). Beta-diversity was first introduced by Whittaker (1960) and refers to the variation in species or community composition between different locations or habitats. Repeating such analyses at different taxonomic scales can also provide insight into how these connections have varied from recent to deeper times, which is especially relevant in a dynamic region such as the IAA. Beta diversity indices can also be used to determine potential correlates of differentiation through multivariate analysis against factors such as the presence of sea barriers, geographic proximity, land area climatic variation (Baselga and Orme 2012, Joyce et al. 2021).

This study aims to investigate bird community structure across the IAA using a new compilation of distributional data and estimates of beta diversity. Birds are a species-rich and well-known group of terrestrial vertebrates in IAA and as such are an ideal group with which to quantify turnover. Information on their distribution is also readily available (Sullivan et al. 2009, BirdLife International and Handbook of the Birds of the World 2019). Here, we focus on three key questions. First, are the islands of Wallacea a biogeographically cohesive unit or a more heterogeneous transition zone? Second, are the rich biotas of New Guinea and East Melanesian islands most closely linked to those of Sunda, Sahul or Wallacea? Third, what are the geographic and climatic correlates of biotic structuring across the IAA and how do they compare

with determinants of plant diversity? We predicted that areas that were connected during the last glacial maximum would have relatively lower pairwise beta diversity values and more connection events. As with the plants of the IAA, we also expected that environmental factors and the size of landmass would be significantly correlated with the differences between area communities.

Materials & Methods

Data collection and region coding

A database of the bird species present in the Indo-Australian Archipelago was collated from country and region-based checklists obtained from Avibase (Lepage et al. 2014) and included a total of 3316 species (Appendix S1). To initially understand broad patterns in where species occur, presence/absence was recorded for eleven separate areas: Australia (AUS), New Guinea (NG), East Melanesian Islands (EMN), Maluku Islands (MAU), Sulawesi (SUL), Philippines (PHI), Lesser Sundas (LSU), Java (JAV), Borneo (BOR), Sumatra (SUM), and South-east Asia (SEA). For initial analyses of diversity and turnover between continental and non-continental regions, these areas were further clustered into three broad groups. Two of these groups correspond to largely continental shelf regions having histories of land connectivity through recent glacial oscillations, and potentially for much longer. These two groupings are: Sahul - comprising two areas 1) Australia and 2) New Guinea (including West Papua, Papua New Guinea, and Aru Islands); and Sunda - comprising 1) Borneo (both Indonesian and Malaysian Borneo), 2) Sumatra, 3) Java (including Bali), and 4) mainland South-East Asia (includes Peninsular Malaysia, Singapore, Thailand, Cambodia, Vietnam).

The third “islands” grouping includes five areas that do not represent a cohesive geographical entity. Rather, they are an amalgamation of islands that have had no or very few land connections to any nearby continental landmass through the Plio-Pleistocene, and in most cases much deeper into their history. This grouping includes 1) the Philippines; 2) three areas in the Wallacean region (Maluku Islands including both North Maluku and Maluku province, Sulawesi, Lesser Sundas up to Lombok Island); and finally, 3) the East Melanesian Islands (spanning the Bismarck Archipelago, New Caledonia, Solomons, Vanuatu).

The ‘Islands’ grouping is primarily one of convenience to enable comparison between areas that have or have not had histories of connection with continents. In most comparisons and analyses, we primarily focus on patterns of richness and turnover across the more granular “area” category. We use of the term ‘East Melanesia’ rather than “Melanesia”, is to reflect the fact that, contrary to some key avian literature (e.g., Mayr and Diamond 2001), many other biologists, and perhaps more importantly many indigenous people from the region consider New Guinea to be culturally and biotically part of ‘Melanesia’ (Narokobi 1983, de Boer and Duffels 1996, Sillitoe 1998, Tallowin et al. 2020, Oliver et al. 2023). To address this same issue

of this some bird literature has used the term ‘Island Melanesia’ (Dutson 2011) for what is here termed East Melanesia.

Presence/absence data were obtained from the online checklist Avibase (Lepage et al. 2014). The taxonomy and distribution range data were refined by crosschecking with presence/absence data from All the Birds of the World (del Hoyo 2020) as well as key references for the East Melanesian islands (Dutson 2011) and the Indonesian Archipelago (Eaton et al. 2021). Taxonomy is updated to match the IOC Bird Names Taxonomy Ver. 13.1 (Gill et al. 2020). Records of species from areas wherein they are considered introduced and vagrant were excluded from analyses. From this data, we collated an overview of avian diversity in the IAA and calculated the proportion of group endemic taxa in our dataset. We define ‘group endemic’ as taxa that are not shared by any areas in the other groups considered in this study.

Beta diversity indices

To measure dissimilarity of the bird species composition between the eleven major areas within the IAA, we calculated taxonomic beta diversity. We calculated beta diversity distance matrices for three taxonomic levels (species, genus, and family). Beta diversity was calculated using the package *betapart* (Baselga and Orme 2012) in R (R Core Team 2020). Beta diversity values range from 0 to 1. When comparing a pair of areas, a low beta diversity value means species communities are similar, whilst a higher beta diversity value indicates more differentiation. These beta diversity calculations comprise two different components of differentiation: nestedness and turnover (Baselga et al. 2007, Baselga 2010, Baselga and Orme 2012). Nestedness refers to the process of species loss where less diverse sites contain subsets of biota from richer ones (Ulrich et al. 2009, Baselga 2010). In contrast, turnover is indicative of different species occurring in different areas, a pattern that may be linked to environmental, geological or evolutionary constraints of dispersal (Qian et al. 2004, Baselga 2010). An overall beta diversity value was calculated along with overall nestedness and turnover components for the whole dataset as well for each pairwise comparison. Jaccard distance was used as our beta diversity index as it is less biased by differences in net diversity across regions.

Testing for correlation with environmental and geographical distance

To investigate correlates of beta diversity turnover we used multiple regression on distance matrices using the *MRMM* function Wang (2013) in R (R Core Team 2020). Jaccard’s (species, genus, family) beta diversity matrices were separately tested as a dependent variable against matrices of environmental distance (*EnvDist*), minimum geographical distance (*m.GeogDist*), size of landmass (*LandArea*), and connection during the last glacial maximum (*Shelf*). The *EnvDist* matrix was obtained from environmental variables downloaded from *WorldClim* (Fick & Hijmans, 2017, 2.5 minutes).

The average value of each environmental variable for each of the eleven areas (i.e. AUS, NG, BOR, etc.) was calculated using the Zonal Statistics plugin in QGIS (QGIS Development Team 2022). We selected five environmental variables from the WorldClim dataset that were least correlated with each other ($r^2 < 0.8$): Annual Mean Temperature (BIO1), Mean Temperature of Warmest Quarter (BIO10), Precipitation of Wettest Month (BIO13), Precipitation of Driest Month (BIO14), and Precipitation Seasonality (BIO15). An environmental distance matrix was obtained by calculating multivariate Euclidean distances of each pair of areas, thus simplifying the five selected environmental variables into a single environmental distance matrix. Minimum Geographic distance was obtained using the 'Join by nearest neighbour' tool in QGIS where the minimum distance between polygons from each of the areas were obtained. Contemporary land mass area was estimated by calculating the geometry area of polygons using QGIS. A LandArea matrix was obtained by summing up the landmass area for each area pair (i.e., SUM-BOR land area value would be the sum of area of Sumatra and Borneo). EnvDist, m.GeogDist, and LandArea were all divided by their respective maximum value in the matrix to obtain values from 0 to 1 in the matrix. Finally, previous connection of areas during the last glacial maximum was represented by the Shelf matrix, with a value of 1 for connected and 0 for not connected.

Connectivity Analyses

Our connectivity analyses followed the methods from Joyce *et al.* (2021). These analyses calculate the minimum number of dispersal events required between each pair of areas to result in the current distribution of all shared taxa. Species occurring in only one area ($n = 2170$) and species that occurred in all eleven areas ($n = 325$) were excluded from these analyses. We also excluded endemic and widespread genera ($n = 318$ and 80) and families ($n = 24$ and 49). In the end, 677 out of 3316 species, 389 out of 786 genera, and 67 out of 140 families were used. For these selected taxa, we

calculated the minimum number of connection events following Joyce *et al.* (2021):

$$p_{ij}(t) = \frac{1}{k}$$

where $p_{ij}(t)$ is the probability of a movement of this taxon between area i and area j within time t from when the taxon has evolved, and k is the total number of area states where the taxon is present. As defined by Joyce *et al.* (2021), connection events refer to the range of lineages that occur in multiple areas because of dispersal or vicariance. Connectivity analyses were undertaken separately for species, genus, and family level datasets to provide a broad proxy for temporal comparison through increasing depth in the evolutionary tree. We further weigh the number of connection events against the total species richness of area pairs to control for potential bias due to high richness.

Results

Overview of Avian Diversity

The final database comprised a total of 3316 resident or migratory species, 786 genera, and 140 family taxa recognised by the Handbook of the Birds of the World and IOC Birds List ver 13.1 (see Appendix S1).

Throughout the IAA, 70% of species are restricted to only one of the three regional groups (Figure 2). Total species richness is notably higher in the Islands group when compared to Sahul and Sunda, which were relatively similar. Sahul has the highest percentage of group endemic taxa at all three taxonomic levels (species, genus, and family). Sunda has a similar proportion of group endemic species to Sahul (~66%) but lower numbers of group endemic genera and families. The proportion of taxa shared between the three groups increases at higher taxonomic levels.

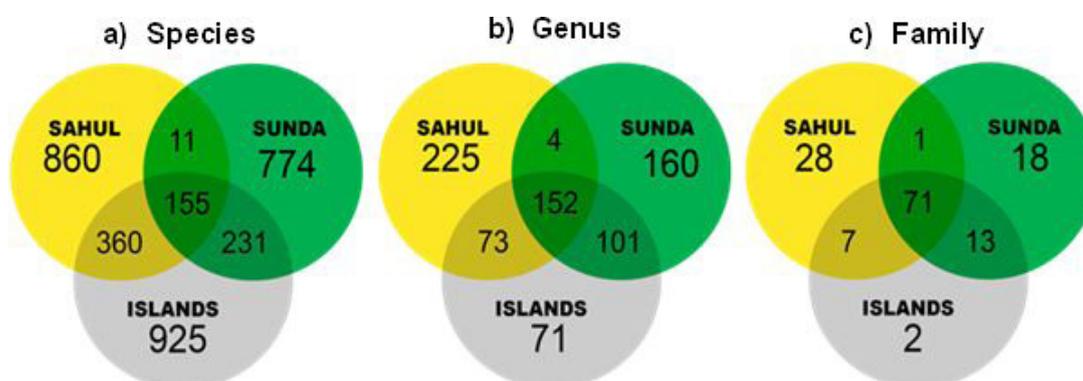


Figure 2. Venn diagram representing the richness of A) species, B) genera, and C) families of birds in the Indo-Australian Archipelago across the three groups: Sahul (yellow), Sunda (green), and 'Islands' with little or no history of connection to nearby continents (Wallacea + Philippines + East Melanesia) (grey).

The hyperdiverse and geographically composite islands group shows a very high number of group endemic species but a lower number of group endemic genera and families. Melanesia exhibits remarkable avian diversity, with a combined total of 1339 bird species when taking into account New Guinea and East Melanesia (Table S2).

Beta diversity between areas in bird communities

Pairwise beta diversity values between all eleven areas are high (Figure 3), having an average of 0.80 for species. As expected, values are lower at higher taxonomic levels – means of 0.57 for genus, and 0.30 for family. The turnover component makes up a large proportion (>90%) of total beta diversity when compared to the nestedness component at all taxonomic levels (Table S1). Overall beta diversity was lowest between the four areas in the Sunda group (mean sp = 0.73, gen = 0.51, fam = 0.27; Figure 3). The island area pairs with no history of land connection showed higher beta diversity values (mean sp = 0.78, gen = 0.49, fam = 0.21; Figure 3). This includes the East Melanesian islands which had consistently high beta diversity (> 0.78) relative to other areas. Beta

diversity for the Australia-New Guinea area pair (sp = 0.79, gen = 0.56, fam = 0.25; Figure 3) was higher than for the area pairs within the Sunda Shelf and higher than some island area pairs with no history of land connectivity (e.g. LSU-JAV (species), NG-MAU (genus)).

Hierarchical Clustering of Areas from Beta diversity

In hierarchical clustering analyses, continental areas form two consistent clusters across taxonomic scales (Figure 4), specifically the two areas of the Sahul group (Australia, New Guinea) and the four areas of Sunda group (SEA, Borneo, Sumatra, Java). Notably, at all taxonomic scales, the node separating Australia and New Guinea is deeper than those separating the components of the Sunda shelf (Figure 4); it is also deeper than several island-to-island area or island-to-continent area comparisons (e.g. Philippines to Java/Wallacean islands and Sulawesi to Lesser Sundas).

In comparison to the consistent clustering of the components in each of the Sahul and Sunda groups, the Islands group never forms a single cluster and associations are inconsistent across taxonomic scales (Figure 4). The Philippines area is typically associated with the Sunda cluster, except for its grouping within parts of western Wallacea (Sulawesi, Lesser Sundas) at the genus level. The three areas that are typically considered to comprise Wallacea do cluster at a species level, but not at a genus or family level. At family and genus level Sulawesi consistently pairs with the Lesser Sundas, while the more eastern islands of Maluku tend to group with Eastern Melanesia. Eastern Melanesia is most similar to the Wallacean islands subgroup, except at the species level where it aligns with the two areas of Sahul.

Correlates of Turnover

Beta diversity is positively correlated with geographical distance, landmass area and the absence of land bridges at the last glacial maximum (Table 1, Figure 5). In these analyses, the high beta diversity between Australia and New Guinea again stands out relative to other intra-continental comparisons. There is no significant relationship between environmental distance and beta diversity. These results are consistent across species, genus, and family levels.

Connectivity Analyses

Our analyses inferred absolute minimum number of connections between all possible pairs of areas. As predicted, we found higher numbers of connections between ‘continental’ landmasses that had land bridges at times of low sea levels (glacial maxima) and potentially also earlier (i.e., within Sunda and Sahul) than in comparison to more permanently separated areas (Figure 6). Area pairs with previous land connections had at least triple the overall number of events (i.e over 75% of inferred connections) than those that did not (Table S3). With respect to islands, not all geographically close areas showed the predicted pattern of high connectivity (Figure 6). Sulawesi in particular shows low levels of connectivity with geographically adjacent island areas of Maluku,

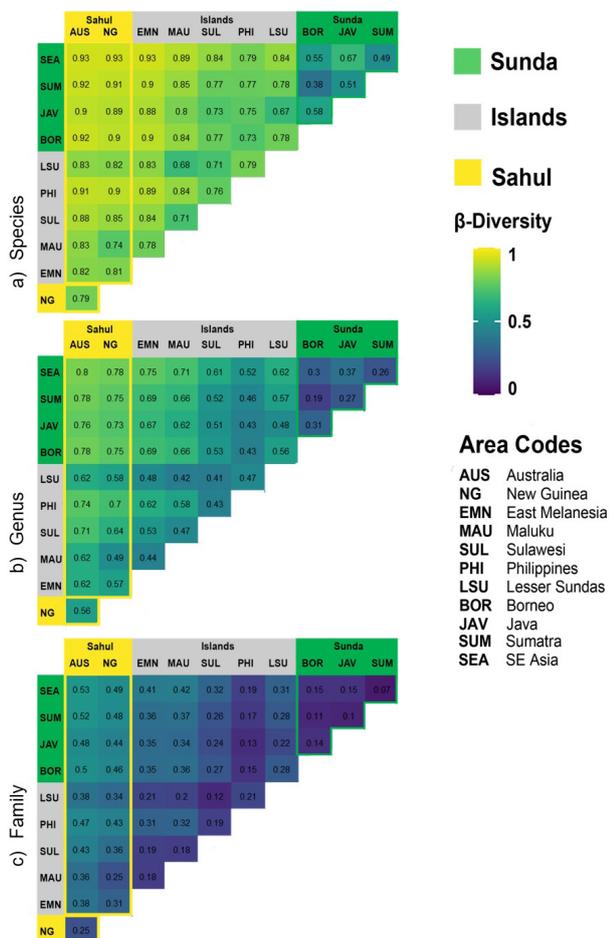


Figure 3. Heatmap matrix of taxonomic beta diversity for species, genus, and family level. Actual pair-wise beta diversity values are inside each cell.

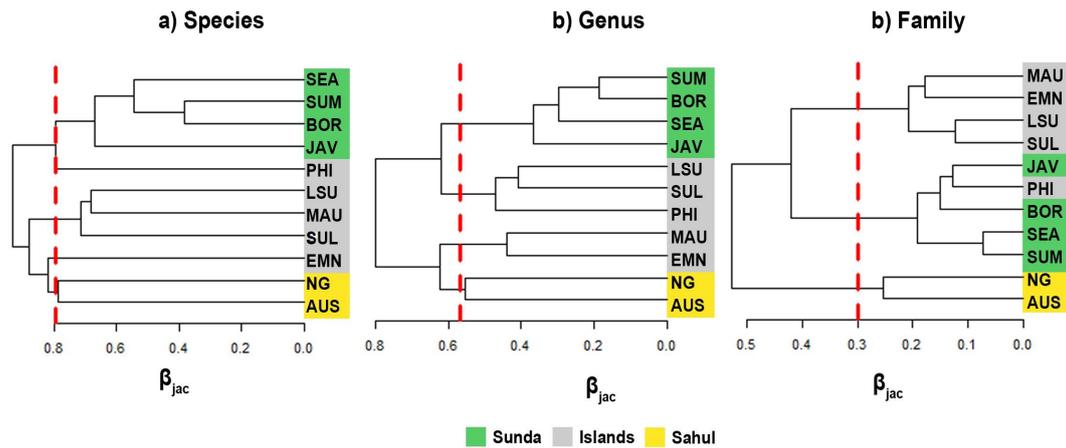


Figure 4. Hierarchical clustering dendrogram showing the relationships of eleven areas within the Indo-Australian Archipelago, clustered based on beta diversity calculated from bird community data. The length of the branches corresponds to the x-axis, where beta diversity is valued from low (0) to high (1). Dashed line represents mean beta diversity. Beta diversity was calculated separately on three levels: species (A), genus (B), and family (C).

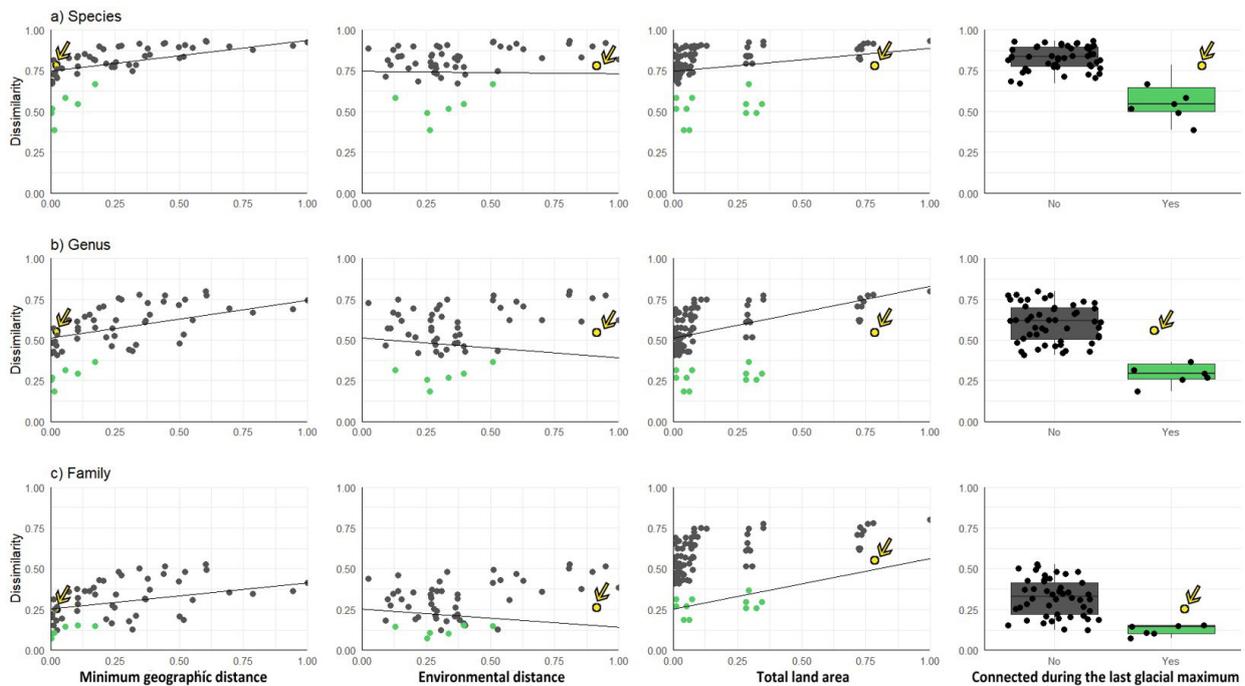


Figure 5. Beta diversity correlates for bird assemblages of the Indo-Australian Archipelago at a) Species level, b) Genus level, and c) Family level. Minimum geographic distance, environmental distance, land area and historical connection were tested using multiple regression on distance matrices. Colour corresponds to whether they are connected (green for Sunda, yellow for Sahul) or not connected (grey) to continental areas during the last glacial maximum. Comparisons between Australia and New Guinea, the most divergent of the two continental areas, are indicated by arrows.

Table 1. Results of multiple regression on distance matrices. Matrices between eleven area pairs with calculated taxonomic beta diversity at the species, genus, and family levels were tested against matrices of minimum geographic distance, environmental distance, total landmass area, as well as past connection during the last glacial maximum. Bold values are statistically significant ($p < 0.05$).

Taxonomic level	R2	Overall	m.GeogDist	EnvDist	LandArea	Shelf
Species	0.814	0.001	0.001	0.811	0.012	0.001
Genus	0.774	0.001	0.001	0.112	0.001	0.001
Family	0.666	0.001	0.004	0.164	0.001	0.001

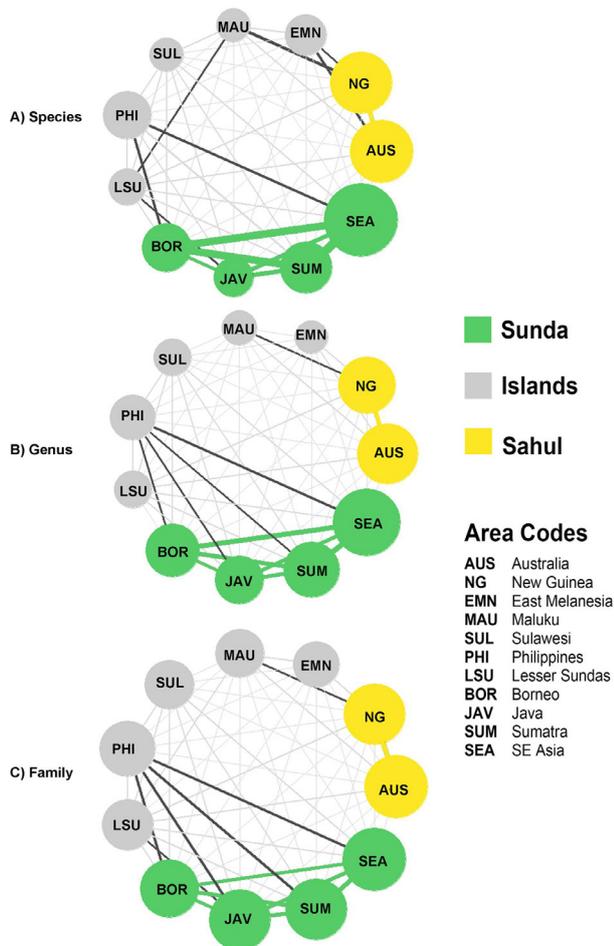


Figure 6. Network diagram visualising connection events of bird communities between eleven areas in the Indonesia-Australia Archipelago. The size of each area circle indicates area richness (no. of species/genera/families). Light grey lines represent <1% of total inferred connection events, Dark grey/green/yellow lines = >1% of total events. Width of line is weighted to number of connections.

the Philippines, Borneo, and the Lesser Sundas at the species level. These results are the same even when connection events are weighted against the total species richness of area pairs. Furthermore, frequency of connections between areas is not always correlated across different taxonomic scales (Figure 6). The Maluku Islands consistently have frequent connections to New Guinea and also, at species level, to the Lesser Sundas. For East Melanesia, there are frequent connections with New Guinea and Australia at species level, but no strong association with any other areas at deeper levels.

Discussion

We set out to provide a comprehensive quantitative assessment of avian turnover across the IAA. We focused on data and metrics that allow direct comparison with a recent study of turnover across this same region in plants (Joyce *et al.*, 2021). We found

that avian biodiversity in the IAA shows striking differentiation both across the three main groups and at finer scales across all eleven major areas included in our analyses. These data allowed us to investigate: 1) whether Wallacea is a biogeographically cohesive unit or heterogeneous transition zone, and 2) the extent to which the Melanesian avifauna is allied to that of Sunda, Sahul, or Wallacea. We also investigated potential correlates of turnover and found that sea barriers, geographic proximity, and land area are all significantly correlated with turnover, while environmental variation is not. Our quantitative assessments will guide how future comparisons with other taxa, and indeed in other biotic interchanges in other archipelagic systems, can be made more consistent.

Before discussing our results, we acknowledge several limitations of our current dataset. First, the use of checklists for distribution data often overestimates species richness in comparison to an expert-verified dataset (Cámara-Leret *et al.* 2020); this problem is more likely to be acute for groups such as plants or invertebrates that are more diverse and/or poorly known taxonomically relative to birds. Second, avian taxonomy in the IAA is still changing. Species in this region continue to be described either through *de novo* discovery (Saucier *et al.* 2019, Irham *et al.* 2022) or through populations of widespread species being taxonomically elevated to range-restricted subspecies or species rank (Rheindt *et al.* 2020). Finally, we also acknowledge that our dataset relies on the contemporary definition of each area/island and that our current presence/absence data may not reflect historical distributions. Considering these limitations, it is possible that beta diversity may be underestimated in our analyses, which could potentially make some results more conservative.

How cohesive is 'Wallacea'?

Our analyses of bird beta diversity show that the three areas within Wallacea as traditionally defined (Maluku Islands, Sulawesi and the Lesser Sundas) are highly differentiated and have inconsistent associations across taxonomic scales. At species level they form a cluster. However, at deeper taxonomic scales Maluku Islands associates with East Melanesia rather than with the geographically closer areas within Wallacea. Sulawesi also shows low connectivity to the nearby Maluku islands at all taxonomic scales. This high turnover and differentiation across Wallacea likely reflects a strong signal of endemic diversification across islands that never been connected by land. This result also supports the inference that the biota of the Wallacean islands as a whole is a depauperate subset of lineages from nearby continents, and those lineages that colonised have often undergone extensive *in situ* diversification (Moyle *et al.* 2016, Rowe *et al.* 2016, Tänzler *et al.* 2016, Rowe *et al.* 2019, Rheindt *et al.* 2020). The major island groups within Wallacea also have widely divergent geological histories, having little to no history of land connection (Michaux 2010, Zahirovic, Matthews, *et al.* 2016,

Hermogenes De Mendonça and Ebach 2020). Most famously, the largest island in Wallacea, Sulawesi, is a composite of multiple geological fragments (Zahirovic, Matthews, et al. 2016). Some regions in Wallacea may also have had longer histories of persistence than others, especially in Sulawesi and parts of the Maluku Islands. Here we show that just as Wallacea has little geological cohesiveness, it also appears that (at least for birds) the region has little biotic cohesiveness. Therefore, our results support the idea that Wallacea consists of a series of relatively discrete areas that have together acted as a transition zone between these two continental landmasses. It is thus not surprising that the many lines drawn within the biogeographical area are somewhat permeable and changing as 'Wallacea' itself was coined to describe an area with a heterogeneous biota (Ali and Heaney 2021).

The strength of biotic associations between key areas within Wallacea and bordering regions has also tended to vary across studies and taxa. In particular, some studies have suggested that Java is most closely allied to the nearby Lesser Sunda Islands (Huxley, 1868; Wallace, 1869; Lydekker, 1896; Simpson, 1977; Van Welzen *et al.*, 2011). Our analysis confirms that for birds at least, Java most strongly associates with other components of the Sunda shelf (Figure 4), emphasising the overarching importance of past land connections during the last glacial maximum (Voris 2000, Van Welzen et al. 2011, Hall 2012, Zahirovic, Flament, et al. 2016). In contrast, we found that Maluku has higher connectivity with New Guinea than with other areas in Wallacea (Figure 4, Figure 6). These data simultaneously emphasise the critical underlying role of sea barriers in shaping avian turnover, and the propensity for neighbouring regions to show more shared taxa.

Is the Melanesian biota Australian or Asian?

Our analyses showed that Melanesia has exceptional bird diversity – a total of 1339 species if New Guinea and East Melanesia are considered together. Thus, despite having a smaller land area than Australia or the Sunda region, Melanesia has higher avian species diversity (Figure S1 and Table S2). Exceptionally high species diversity and endemism in Melanesia, and especially in New Guinea, has also recently been demonstrated in other taxa, namely plants and frogs (Cámara-Leret et al. 2020, Oliver et al. 2023). New Guinea's rich flora and fauna likely reflects a dynamic geological history and extreme topographic diversity that has promoted diversification (Rivera et al. 2017, Cámara-Leret et al. 2020). A striking difference in our analyses of birds when compared to plants and frogs is the much higher richness of species in East Melanesia: almost one-third of bird species from our Melanesian area are from East Melanesia. This emphasises the importance of dispersal limitations, as well as islands as generators of species diversity and endemism (Mayr and Diamond 2001).

Our beta diversity analyses group New Guinea with Australia for birds, albeit with high dissimilarity (Figure 3, Figure 4). This contrasts with analyses of

plants that allied Melanesia with parts of Sunda and Wallacea (Van Welzen et al. 2011, Joyce et al. 2021). Several factors potentially explain this discordance. Floristic exchange in the IAA has been asymmetric, Asia having dominated as a source (Sniderman and Jordan 2011, Kooyman et al. 2019). In contrast, two of the largest radiations of birds in the IAA, passerines and parrots, originated from Australia (Oliveros et al. 2019), and recent evidence suggest pigeons have deep insular origins in the IAA as well (Oliver et al. 2023). Many distinctively Australian (Gondwanan) plant lineages also show strong niche conservatism, and are associated with temperate or arid environments that are not widespread in most of Wallacea, Sunda and lowland New Guinea (Sniderman and Jordan 2011, Crisp and Cook 2013). Thus, a key implication here is that an important driver of community composition and turnover in plants has been environment and potentially niche conservatism, while geographic proximity has played a larger role in shaping turnover in birds.

The islands of East Melanesia, group with the New Guinea and Australia (Sahul) in the species-level analysis as expected given their proximity and many shared taxa. However, in a surprising result, East Melanesia clusters with the Maluku Islands in genus and family level clustering analyses (Figure 4). As there are no genera or families unique to Wallacea/East Melanesia, we hypothesize that these absences, combined with the many shared taxa and strong clustering of Australia and New Guinea, may be driving the unexpected association between the genera and family poor areas of Maluku and East Melanesia.

Although New Guinea clusters most strongly with Australia, there is high dissimilarity (beta diversity) between the two areas (Figure 3 and Figure 4). Indeed, the beta diversity value between New Guinea and Australia is the highest amongst all area pairs that had past land connection, and it is comparable with some beta diversity values between pairs of permanently isolated Wallacean islands. The high turnover between Australia and New Guinea may suggest despite periods of land connection and extensive exchange, there is a strong underlying signature of isolation between the two regions. This isolation may be linked to both geological history and isolation and marked environmental differences. While the island of New Guinea is a landmass comprising of accreted arc terranes to the north and the leading edge of the Australian shelf to the south, recent geological models suggest that much of 'proto-Papua' was isolated from the remainder of Australia for most of the last 20 million years (Harrington et al. 2017). In support of this isolation, phylogenetic evidence suggests that many radiations in New Guinea and Australia have had separate histories with only sporadic dispersals (Hugall et al. 2008, Jønsson et al. 2011, Oliver et al. 2018, Tallwin et al. 2020, McCullough et al. 2022). The environmental differences between New Guinea and most of Australia are also higher than other area pairs within the IAA that were connected during the LGM. Thus even though New Guinea and Australia

are geographically close to each other, and even the though turnover may be less marked than in plants, it is conceivable that niche conservatism (Crisp and Cook 2013) in birds may have still played some role in shaping turnover between the relatively temperate, arid seasonal environments of Australia and the more mesic, tropical and less seasonal forests of New Guinea.

What correlates with avian turnover in the IAA?

Our results suggest that overwater barriers are the most significant correlate and possible driver of turnover of bird communities in the IAA (Figure 5). Next in importance are geographic proximity and land area. We find the effect of environmental variation to be minimal. Recent analyses on plants found total land area and climatic variables to be significant correlates for turnover (Joyce et al. 2021). These contrasting results may be due to differences in environmental sensitivity in different taxa. For example, birds and indeed many vertebrates, may have more diverse strategies with which to respond to environmental fluctuations than plants do. These strategies include behavioural responses such as localised movement, which can buffer the organism from extreme weather events (Stelbrink et al. 2012, Dalsgaard et al. 2014, Weigelt et al. 2015). Plants, on the other hand, may be more tightly tied to a larger and thus more complex range of environmental indicators for their growth and establishment (Sniderman and Jordan 2011, Yap et al. 2018, Joyce et al. 2021).

Our inference that geographic distance is the best predictor of turnover is entirely consistent with the predictions of the theory of island biogeography: the further apart two populations are, the more distant dispersal must be to maintain gene flow between them (MacArthur and Wilson 1963, Whittaker et al. 2008). Likewise, we also found that larger landmass area also affects dispersal (Figure S1). This too is predicted by island biogeographic theory: larger landmasses provide more variable habitat and niche opportunities, as well as larger 'target' areas for dispersing individuals (MacArthur and Wilson 1963, Dalsgaard et al. 2014). Areas with a large total landmass would provide more space and, potentially, opportunities for more different kinds of species.

Despite the significance of geographic distance as a potential driver of turnover, it did not seem to limit the possibility of dispersal for many bird taxa. As regions geographically further from each other had more dissimilar bird assemblages, we predicted there would be more connection events between pairs of areas that are geographically closer together. Although most connection events occurred between areas that are closer to each other, this is not true for all geographically close area pairs. There are very minimal connection events between areas such as Philippines-Sulawesi and Sulawesi-Maluku Islands, despite their proximity. The definition of Wallace and Huxley's Line wavered between consolidating Sulawesi and Philippines, and no established biogeographical line currently exists between Sulawesi and Maluku (Figure 1). Overall, however the clear pattern is

that, more connection events occur not only when area pairs are close to each other, but also when they were historically connected by land (Figure 6). The importance of historical geography is shaping bird dispersal in the IAA has been emphasised in other studies (White et al. 2021). The results of our connection analysis are thus reflected in the lower beta diversity values between area pairs of the same continental shelf (Figure 3). Although some areas seem to be close to each other now, these areas may have been distant for much of their geological history, and some island area drifted and coalesced only relatively recently. For example, Borneo and the Maluku Islands have only been adjacent to a fully formed Sulawesi for the last 5-10 million years (Zahirovic, Flament, et al. 2016). In similar vein, only as the Australian continental plate has moved northward have the islands within Wallacea formed and moved closer to the Sunda Shelf. Thus, the main correlate of high bird turnover is not just geographic distance alone, but geographic distance in the presence of permanent sea barriers among areas (Peñalba et al. 2019).

The IAA is not the only example of a geologically dynamic island system in a region of biotic interchange (Vermeij 1991, Weir et al. 2009, Bansal et al. 2022). However, arguably, no other interchange has occurred in an area as tectonically active as the IAA (Lohman et al. 2011, Zahirovic, Flament, et al. 2016). Our inference that connectivity and distance are the strongest correlates of beta turnover may not be unique to Wallacea or the IAA more generally. Instead, these results could reflect general trends in the biogeography of geologically complex archipelagic systems resulting in a mixture of highly-vagile and widespread species and small-range island endemics within the same localities.

Conclusion

Our results indicate that high endemism of birds in the IAA reflects high turnover not just in one specific area (islands/island groups) but across all eleven areas analyzed. Differentiation is particularly marked over areas that have never been connected by land. In such a system, attempts to demarcate biogeographic boundaries are likely to be perpetually challenging and unstable. As such these results particularly highlight the need to reconsider and, potentially, abandon recognition of Wallacea as an entity in biogeography. The view that its component species are a natural assemblage of a biogeographic region having a shared evolutionary history does a disservice to the original view of the region as a transition zone, a view that our analyses support. Our results also highlight the exceptional richness of the broader Melanesian region, centred on New Guinea, but also including islands to the east. Despite having a smaller areal extent than the nearby Sunda regions and Australia to the south, this region has highest values for turnover, richness and endemism. Finally, comparisons with a similar study focused on plants of the IAA suggests that birds show a much weaker signature signature of turnover linked to the climate variation across the IAA. One potential

hypothesis to explain this difference is marked variation in the strength and role of niche conservatism in shaping distributions in different taxa.

Acknowledgements

The authors declare no conflict of interest. We also thank three anonymous reviewers whose detailed comments and suggestions substantially helped improve and clarify this manuscript. We would like to express our gratitude to M. Claus and Aprilia for their contribution in copy-editing the translated abstract of this journal article.

Author Contributions

AMP, PO, LJ, and CM conceived this study. AMP collected and analysed the data, with input from the other authors. MWS assisted in the data collation process and preliminary analyses. AMP, PO, LJ, and CM contributed to writing and revising the manuscript.

Data Accessibility Statement

The R code and biogeographic data used in our analyses is available in Supplementary Appendix S1 and can also be found in <https://figshare.com/s/e3b93f278a9c2c7c97a3>

Supplementary Material

The following materials are available as part of the online article at <https://escholarship.org/uc/fb>

Table S1. Turnover and nestedness components of beta diversity analyses

Table S2. List of ten areas included in this study with associated data of land area and no. of species

Table S3. Matrix of number of connection events for each area pair calculated from connectivity analyses

Figure S1. Species-area relationship curve

Appendix S1. R code used in analyses with all associated data, including list of all bird species included

References

- Ali, J.R. & Heaney, L.R. (2021) Wallace's line, Wallacea, and associated divides and areas: history of a tortuous tangle of ideas and labels. *Biological Reviews*, 96, 922–942. <https://doi.org/10.1111/brv.12683>
- Andersen, M.J., McCullough, J.M., Mauck, W.M., Smith, B.T. & Moyle, R.G. (2018) A phylogeny of kingfishers reveals an Indomalayan origin and elevated rates of diversification on oceanic islands. *Journal of Biogeography*, 45, 269–281. <https://doi.org/10.1111/jbi.13139>
- Bansal, M., Morley, R.J., Nagaraju, S.K., et al. (2022) Southeast Asian Dipterocarp origin and diversification driven by Africa-India floristic interchange. *Science*, 375, 455–460. <https://doi.org/10.1126/science.abk2177>
- Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity: partitioning beta diversity. *Global Ecology and Biogeography*, 19, 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Baselga, A., Jiménez-Valverde, A. & Niccolini, G. (2007) A multiple-site similarity measure independent of richness. *Biology Letters*, 3, 642–645. <https://doi.org/10.1098/rsbl.2007.0449>
- Baselga, A. & Orme, C.D.L. (2012) betapart: an R package for the study of beta diversity: Betapart package. *Methods in Ecology and Evolution*, 3, 808–812. <https://doi.org/10.1111/j.2041-210X.2012.00224.x>
- BirdLife International & Handbook of the Birds of the World (2019) Bird species distribution maps of the world. Version 2019.1. Available at <http://datazone.birdlife.org/species/requestdis>
- Cámara-Leret, R., Frodin, D.G., Adema, F., et al. (2020) New Guinea has the world's richest island flora. *Nature*, 584, 579–583. <https://doi.org/10.1038/s41586-020-2549-5>
- Christensen, B.A., Renema, W., Henderiks, J., et al. (2017) Indonesian Throughflow drove Australian climate from humid Pliocene to arid Pleistocene. *Geophysical Research Letters*, 44, 6914–6925. <https://doi.org/10.1002/2017GL072977>
- Crayn, D.M., Costion, C. & Harrington, M.G. (2015) The Sahul-Sunda floristic exchange: dated molecular phylogenies document Cenozoic intercontinental dispersal dynamics. *Journal of Biogeography*, 42, 11–24. <https://doi.org/10.1111/jbi.12405>
- Dalsgaard, B., Carstensen, D.W., Fjeldså, J., Maruyama, P.K., Rahbek, C., Sandel, B., Sonne, J., Svenning, J., Wang, Z. & Sutherland, W.J. (2014) Determinants of bird species richness, endemism, and island network roles in Wallacea and the West Indies: is geography sufficient or does current and historical climate matter? *Ecology and Evolution*, 4, 4019–4031. <https://doi.org/10.1002/ece3.1276>
- Dutson, G.C.L. (2011) *Birds of Melanesia: Bismarcks, Solomons, Vanuatu, and New Caledonia*. Princeton University Press, Princeton, N.J.

- Eaton, J.A., Balen, B. van, Brickle, N.W. & Rheindt, F.E. (2021) Birds of the Indonesian Archipelago: Greater Sundas and Wallacea, 2nd edn. Lynx Edicions, Barcelona.
- Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315. <https://doi.org/10.1002/joc.5086>
- Filardi, C.E. & Moyle, R.G. (2005) Single origin of a pan-Pacific bird group and upstream colonization of Australasia. *Nature*, 438, 216–219. <https://doi.org/10.1038/nature04057>
- Gill, F., Donsker, D. & Rasmussen, P. (2020) IOC World Bird List 10.1. <https://doi.org/10.14344/IOC.ML.10.1>
- Hall, R. (2011) Australia–SE Asia collision: plate tectonics and crustal flow. Geological Society, London, Special Publications, 355, 75–109. <https://doi.org/10.1144/SP355.5>
- Hall, R. (2012) Late Jurassic–Cenozoic reconstructions of the Indonesian region and the Indian Ocean. *Tectonophysics*, 570–571, 1–41. <https://doi.org/10.1016/j.tecto.2012.04.021>
- Harrington, L., Zahirovic, S., Flament, N. & Müller, R.D. (2017) The role of deep Earth dynamics in driving the flooding and emergence of New Guinea since the Jurassic. *Earth and Planetary Science Letters*, 479, 273–283. <https://doi.org/10.1016/j.epsl.2017.09.039>
- Hermogenes De Mendonça, L. & Ebach, M.C. (2020) A review of transition zones in biogeographical classification. *Biological Journal of the Linnean Society*, 131, 717–736. <https://doi.org/10.1093/biolinnean/blaa120>
- del Hoyo, J. (2020) All the birds of the world. Lynx edicions, Barcelona.
- Hugall, A.F., Foster, R., Hutchinson, M. & Lee, M.S.Y. (2008) Phylogeny of Australasian agamid lizards based on nuclear and mitochondrial genes: implications for morphological evolution and biogeography. *Biological Journal of the Linnean Society*, 93, 343–358. <https://doi.org/10.1111/j.1095-8312.2007.00911.x>
- Huxley, T.H. (1868) On the classification and distribution of the Alectoromorphae and Heteromorphae. *Proceedings of the Zoological Society of London*, 249–319.
- Irham, M., Prawiradilaga, D.M., Menner, J.K., O’Connell, D.P., Kelly, D.J., Analuddin, K., Karya, A., Meads, M., Marples, N.M. & Rheindt, F.E. (2022) A distinct new species of *Zosterops* white-eye from the Sulawesi region, Indonesia. *Ibis*, ibi.13148. <https://doi.org/10.1111/ibi.13148>
- Jønsson, K.A., Fabre, P.-H., Ricklefs, R.E. & Fjeldså, J. (2011) Major global radiation of corvid birds originated in the proto-Papuan archipelago. *Proceedings of the National Academy of Sciences USA*, 108, 2328–2333. <https://doi.org/10.1073/pnas.1018956108>
- Joyce, E.M., Thiele, K.R., Slik, J.W.F. & Crayn, D.M. (2021) Plants will cross the lines: climate and available land mass are the major determinants of phytogeographical patterns in the Sunda–Sahul Convergence Zone. *Biological Journal of the Linnean Society*, 132, 374–387. <https://doi.org/10.1093/biolinnean/blaa194>
- Kooyman, R.M., Morley, R.J., Crayn, D.M., Joyce, E.M., Rossetto, M., Slik, J.W.F., Strijk, J.S., Su, T., Yap, J.-Y.S. & Wilf, P. (2019) Origins and assembly of Malesian rainforests. *Annual Review of Ecology, Evolution, and Systematics*, 50, 119–143. <https://doi.org/10.1146/annurev-eolsys-110218-024737>
- Lepage, D., Vaidya, G. & Guralnick, R. (2014) Avibase – a database system for managing and organizing taxonomic concepts. *ZooKeys*, 420, 117–135. <https://doi.org/10.3897/zookeys.420.7089>
- Letsch, H., Balke, M., Toussaint, E.F.A., Narakusumo, R.P., Fiedler, K. & Riedel, A. (2020) Transgressing Wallace’s Line brings hyperdiverse weevils down to earth. *Ecography*, 43, 1329–1340. <https://doi.org/10.1111/ecog.05128>
- Lim, H.C., Gawin, D.F., Shakya, S.B., Harvey, M.G., Rahman, M.A. & Sheldon, F.H. (2017) Sundaland’s east–west rain forest population structure: variable manifestations in four polytypic bird species examined using RAD-Seq and plumage analyses. *Journal of Biogeography*, 44, 2259–2271. <https://doi.org/10.1111/jbi.13031>
- Lohman, D.J., de Bruyn, M., Page, T., von Rintelen, K., Hall, R., Ng, P.K.L., Shih, H.-T., Carvalho, G.R. & von Rintelen, T. (2011) Biogeography of the Indo-Australian Archipelago. *Annual Review of Ecology, Evolution, and Systematics*, 42, 205–226. <https://doi.org/10.1146/annurev-eolsys-102710-145001>

- Louys, J. & Roberts, P. (2020) Environmental drivers of megafauna and hominin extinction in Southeast Asia. *Nature*, 586, 402–406. <https://doi.org/10.1038/s41586-020-2810-y>
- Lydekker, R. (1896) A geographical history of mammals. The University Press, Cambridge., <https://doi.org/10.5962/bhl.title.31155>
- MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution*, 17, 373–387. <https://doi.org/10.1111/j.1558-5646.1963.tb03295.x>
- Mayr, E. (1944) Wallace's line in the light of recent zoogeographic studies. *The Quarterly Review of Biology*, 19, 1–14. <https://doi.org/10.1086/394684>
- Mayr, E. & Diamond, J.M. (2001) The birds of northern Melanesia: speciation, ecology & biogeography. Oxford University Press, Oxford; New York.
- McCullough, J.M., Oliveros, C.H., Benz, B.W., Zenil-Ferguson, R., Cracraft, J., Moyle, R.G. & Andersen, M.J. (2022) Wallacean and Melanesian Islands promote higher rates of diversification within the global passerine radiation corvids. *Systematic Biology*, syac044. <https://doi.org/10.1093/sysbio/syac044>
- Michaux, B. (2010) Biogeology of Wallacea: geotectonic models, areas of endemism, and natural biogeographical units. *Biological Journal of the Linnean Society*, 101, 193–212. <https://doi.org/10.1111/j.1095-8312.2010.01473.x>
- Moss, S. & Wilson, M. (1998) Biogeographic implications of the Tertiary palaeogeographic evolution of Sulawesi and Borneo. In: *Biogeography and Geological Evolution of SE Asia* (ed. by Robert Hall and Jeremy D. Holloway), pp. 133–163. Backhuys Publishers, Leiden.
- Moyle, R.G., Oliveros, C.H., Andersen, M.J., Hosner, P.A., Benz, B.W., Manthey, J.D., Travers, S.L., Brown, R.M. & Faircloth, B.C. (2016) Tectonic collision and uplift of Wallacea triggered the global songbird radiation. *Nature Communications*, 7, 12709. <https://doi.org/10.1038/ncomms12709>
- Oliver, P.M., Bower, D.S., McDonald, P.J., et al. (2022) Melanesia holds the world's most diverse and intact insular amphibian fauna. *Communications Biology*, 5, 1182. <https://doi.org/10.1038/s42003-022-04105-1>
- Oliver, P.M., Heiniger, H., Hugall, A.F., Joseph, L. & Mitchell, K.J. (2020) Oligocene divergence of frogmouth birds (Podargidae) across Wallace's Line. *Biology Letters*, 16, 20200040. <https://doi.org/10.1098/rsbl.2020.0040>
- Oliver, P.M., Travers, S.L., Richmond, J.Q., Pikacha, P. & Fisher, R.N. (2018) At the end of the line: independent overwater colonizations of the Solomon Islands by a hyperdiverse trans-Wallacean lizard lineage (*Cyrtodactylus*: Gekkota: Squamata). *Zoological Journal of the Linnean Society*, 182, 681–694. <https://doi.org/10.1093/zoolinnean/zlx047>
- Oliver, P.M., Hugall, A.F., Prasetya, A., Slavenko, A., Zahirovic, S. (2023) Oligo-Miocene radiation within South-west Pacific arc terranes underpinned repeated upstream continental dispersals in pigeons (Columbiformes). *Biological Journal of the Linnean Society*, blad003. <https://doi.org/10.1093/biolinnean/blad003>
- Oliveros, C.H., Field, D.J., Ksepka, D.T., et al. (2019) Earth history and the passerine superradiation. *Proceedings of the National Academy of Sciences USA*, 116, 7916–7925. <https://doi.org/10.1073/pnas.1813206116>
- Peñalba, J.V., Joseph, L. & Moritz, C. (2019) Current geography masks dynamic history of gene flow during speciation in northern Australian birds. *Molecular Ecology*, 28, 630–643. <https://doi.org/10.1111/mec.14978>
- QGIS Development Team (2022) QGIS Geographic Information System. Open Source Geospatial Foundation Project.
- Qian, H., Ricklefs, R.E. & White, P.S. (2004) Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America: beta diversity in Asia and North America. *Ecology Letters*, 8, 15–22. <https://doi.org/10.1111/j.1461-0248.2004.00682.x>
- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rheindt, F.E., Prawiradilaga, D.M., Ashari, H., Suparno, Gwee, C.Y., Lee, G.W.X., Wu, M.Y. & Ng, N.S.R. (2020) A lost world in Wallacea: Description of a montane archipelagic avifauna. *Science*, 367, 167–170. <https://doi.org/10.1126/science.aax2146>

- Rivera, J.A., Kraus, F., Allison, A. & Butler, M.A. (2017) Molecular phylogenetics and dating of the problematic New Guinea microhylid frogs (Amphibia: Anura) reveals elevated speciation rates and need for taxonomic reclassification. *Molecular Phylogenetics and Evolution*, 112, 1–11. <https://doi.org/10.1016/j.ympev.2017.04.008>
- Rowe, K.C., Achmadi, A.S. & Esselstyn, J.A. (2016) Repeated evolution of carnivory among Indo-Australian rodents. *Evolution*, 70, 653–665. <https://doi.org/10.1111/evo.12871>
- Rowe, K.C., Achmadi, A.S., Fabre, P., Schenk, J.J., Steppan, S.J. & Esselstyn, J.A. (2019) Oceanic islands of Wallacea as a source for dispersal and diversification of murine rodents. *Journal of Biogeography*, 46, 2752–2768. <https://doi.org/10.1111/jbi.13720>
- Saucier, J.R., Milensky, C.M., Caraballo-Ortiz, M.A., Ragai, R., Dahlan, N.F. & Edwards, D.P. (2019) A distinctive new species of flowerpecker (Passeriformes: Dicaeidae) from Borneo. *Zootaxa*, 4686, 451–464. <https://doi.org/10.11646/zootaxa.4686.4.1>
- Sheldon, F.H., Lim, H.C. & Moyle, R.G. (2015) Return to the Malay Archipelago: the biogeography of Sundaic rainforest birds. *Journal of Ornithology*, 156, 91–113. <https://doi.org/10.1007/s10336-015-1188-3>
- Simpson, G.G. (1977) Too Many Lines; The limits of the Oriental and Australian Zoogeographic Regions. *Proceedings of the American Philosophical Society*, 121, 107–120.
- Sniderman, J.M.K. & Jordan, G.J. (2011) Extent and timing of floristic exchange between Australian and Asian rain forests: floristic exchange between Australian and Asian rain forests. *Journal of Biogeography*, 38, 1445–1455. <https://doi.org/10.1111/j.1365-2699.2011.02519.x>
- Stelbrink, B., Albrecht, C., Hall, R. & von Rintelen, T. (2012) The Biogeography of Sulawesi Revisited: is there evidence for a vicariant origin of taxa on Wallace's "Anomalous Island"? *Evolution*, 66, 2252–2271. <https://doi.org/10.1111/j.1558-5646.2012.01588.x>
- Sullivan, B.L., Wood, C.L., Iliff, M.J., Bonney, R.E., Fink, D. & Kelling, S. (2009) eBird: a citizen-based bird observation network in the biological sciences. *Biological Conservation*, 142, 2282–2292. <https://doi.org/10.1016/j.biocon.2009.05.006>
- Tänzler, R., Van Dam, M.H., Toussaint, E.F.A., Suhardjono, Y.R., Balke, M. & Riedel, A. (2016) Macroevolution of hyperdiverse flightless beetles reflects the complex geological history of the Sunda Arc. *Scientific Reports*, 6, 18793. <https://doi.org/10.1038/srep18793>
- Toussaint, E.F.A., Hendrich, L., Shaverdo, H. & Balke, M. (2015) Mosaic patterns of diversification dynamics following the colonization of Melanesian islands. *Scientific Reports*, 5, 16016. <https://doi.org/10.1038/srep16016>
- Toussaint, E.F.A., Tänzler, R., Rahmadi, C., Balke, M. & Riedel, A. (2015) Biogeography of Australasian flightless weevils (Curculionidae, Celeuthetini) suggests permeability of Lydekker's and Wallace's Lines. *Zoologica Scripta*, 44, 632–644. <https://doi.org/10.1111/zsc.12127>
- Tsang, S.M., Wiantoro, S., Veluz, M.J., Sugita, N., Nguyen, Y., Simmons, N.B. & Lohman, D.J. (2020) Dispersal out of Wallacea spurs diversification of *Pteropus* flying foxes, the world's largest bats (Mammalia: Chiroptera). *Journal of Biogeography*, 47, 527–537. <https://doi.org/10.1111/jbi.13750>
- Ulrich, W., Almeida-Neto, M. & Gotelli, N.J. (2009) A consumer's guide to nestedness analysis. *Oikos*, 118, 3–17. <https://doi.org/10.1111/j.1600-0706.2008.17053.x>
- Van Welzen, P.C., Parnell, J.A.N. & Slik, J.W.F. (2011) Wallace's Line and plant distributions: two or three phytogeographical areas and where to group Java? *Biological Journal of the Linnean Society*, 103, 531–545. <https://doi.org/10.1111/j.1095-8312.2011.01647.x>
- Vermeij, G.J. (1991) When biotas meet: understanding biotic interchange. *Science*, 253, 1099–1104. <https://doi.org/10.1126/science.253.5024.1099>
- Voris, H.K. (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography*, 27, 1153–1167. <https://doi.org/10.1046/j.1365-2699.2000.00489.x>
- Wallace, A.R. (1860) On the Zoological Geography of the Malay Archipelago. *Zoological Journal of the Linnean Society London*, 4, 172–184.
- Wallace, A.R. (1869) *The Malay Archipelago*. Macmillan, London.

- Wang, I.J. (2013) Examining the full effects of landscape heterogeneity on spatial genetic variation: a multiple matrix regression approach for quantifying geographic and ecological isolation. *Evolution*, 67, 3403–3411. <https://doi.org/10.1111/evo.12134>
- Weigelt, P., Daniel Kissling, W., Kisel, Y., Fritz, S.A., Karger, D.N., Kessler, M., Lehtonen, S., Svenning, J.-C. & Kreft, H. (2015) Global patterns and drivers of phylogenetic structure in island floras. *Scientific Reports*, 5, 12213. <https://doi.org/10.1038/srep12213>
- Weir, J.T., Bermingham, E. & Schluter, D. (2009) The great American biotic interchange in birds. *Proceedings of the National Academy of Sciences USA*, 106, 21737–21742. <https://doi.org/10.1073/pnas.0903811106>
- White, A.E., Dey, K.K., Stephens, M. & Price, T.D. (2021) Dispersal syndromes drive the formation of biogeographical regions, illustrated by the case of Wallace's Line. *Global Ecology and Biogeography*, 30, 685–696. <https://doi.org/10.1111/geb.13250>
- Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of oceanic island biogeography: a general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, 35, 977–994. <https://doi.org/10.1111/j.1365-2699.2008.01892.x>
- Yap, J.-Y.S., Rossetto, M., Costion, C., Crayn, D., Kooyman, R.M., Richardson, J. & Henry, R. (2018) Filters of floristic exchange: how traits and climate shape the rain forest invasion of Sahul from Sunda. *Journal of Biogeography*, 45, 838–847. <https://doi.org/10.1111/jbi.13143>
- Zahirovic, S., Flament, N., Dietmar Müller, R., Seton, M. & Gurnis, M. (2016) Large fluctuations of shallow seas in low-lying Southeast Asia driven by mantle flow. *Geochemistry, Geophysics, Geosystems*, 17, 3589–3607. <https://doi.org/10.1002/2016GC006434>
- Zahirovic, S., Matthews, K.J., Flament, N., Müller, R.D., Hill, K.C., Seton, M. & Gurnis, M. (2016) Tectonic evolution and deep mantle structure of the eastern Tethys since the latest Jurassic. *Earth-Science Reviews*, 162, 293–337. <https://doi.org/10.1016/j.earscirev.2016.09.005>

Submitted: 28 July 2022

First decision: 14 September 2022

Accepted: 10 March 2023

Edited by Robert J. Whittaker