

BIOGEOGRAPHY

Paleoenvironments shaped the exchange of terrestrial vertebrates across Wallace's Line

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Faunal turnover in Indo-Australia across Wallace's Line is one of the most recognizable patterns in biogeography and has catalyzed debate about the role of evolutionary and geoclimatic history in biotic interchanges. Here, analysis of more than 20,000 vertebrate species with a model of geoclimatic and biological diversification shows that broad precipitation tolerance and dispersal ability were key for exchange across the deep-time precipitation gradient spanning the region. Sundanian (Southeast Asian) lineages evolved in a climate similar to the humid "stepping stones" of Wallacea, facilitating colonization of the Sahulian (Australian) continental shelf. By contrast, Sahulian lineages predominantly evolved in drier conditions, hampering establishment in Sunda and shaping faunal distinctiveness. We demonstrate how the history of adaptation to past environmental conditions shapes asymmetrical colonization and global biogeographic structure.

The world's major biotic interchanges have had a disproportionate impact on the distribution of the world's terrestrial fauna (1–3). Well-known systems include the American interchange, which followed the formation of the Panamanian isthmus between North and South America (4), and the Indo-Australian interchange, which followed the convergence of the Australian and Eurasian tectonic plates and was shaped by complex dynamics of island formation (5). Far from an even diffusion of species between regions, interchanges have displayed an asymmetry in the direction of exchange (6–8) and have been dominated by particular functional traits (9, 10). This unevenness may reflect a predisposition for dispersion in particular groups of organisms, because successful colonization is dependent on the ability both to disperse to a new region and to establish within new environmental conditions and ecological communities (11). Dispersal ability may act as a primary filter on colonization success (12), but lineages with broad environmental tolerances, or those with the ability to adapt to new environments, might contribute more to an interchange in the presence

of environmental gradients between regions (9, 13). To date, our ability to distinguish between hypotheses regarding the processes that shape the unevenness of different biotic interchanges has been limited by the available process-based methodologies and paleoenvironmental reconstructions.

Distributional patterns of terrestrial vertebrates in the Indo-Australian archipelago have fascinated naturalist for centuries (14) and have provided a model system for understand-

ing biotic interchange. As the Australian continental plate approached the Eurasian plate, subduction at the northern boundary led to the formation of a geologically complex archipelago, today composed of thousands of islands and known biogeographically as Wallacea (5) (Fig. 1). The oceanic boundary separating the Sunda continental shelf (including Myanmar, Cambodia, Vietnam, Laos, Thailand, Malaysia, and Indonesia west of Lombok on the Eurasian plate) from Wallacea and the Sahul continental shelf (including Australia and New Guinea on the Australian plate) is named Wallace's Line after Alfred Russell Wallace (14) (Fig. 1), who noted a clear disjunction in the distribution of some taxa across it (14, 15). Today, Wallace's Line marks the boundary of the Indomalayan and Australasian zoogeographic realms (2, 16) (Fig. 1), but there are many lines in the region that mark turnover between a predominantly Sundanian or Sahulian fauna (15), such as the Heilprin-Lydekker Line (Fig. 1). The persistent presence of oceanic barriers has led to the dominant idea that dispersal limitation is the primary process shaping interchange (12). For example, the mammalian faunas of Sunda and Sahul are largely endemic, and only vagile rodents (17) and bats (18) have been successfully exchanged between continents. However, environmental niche traits may also have played a role (19, 20) as the distinctly drier Australian continent (20, 21) shaped the evolution of

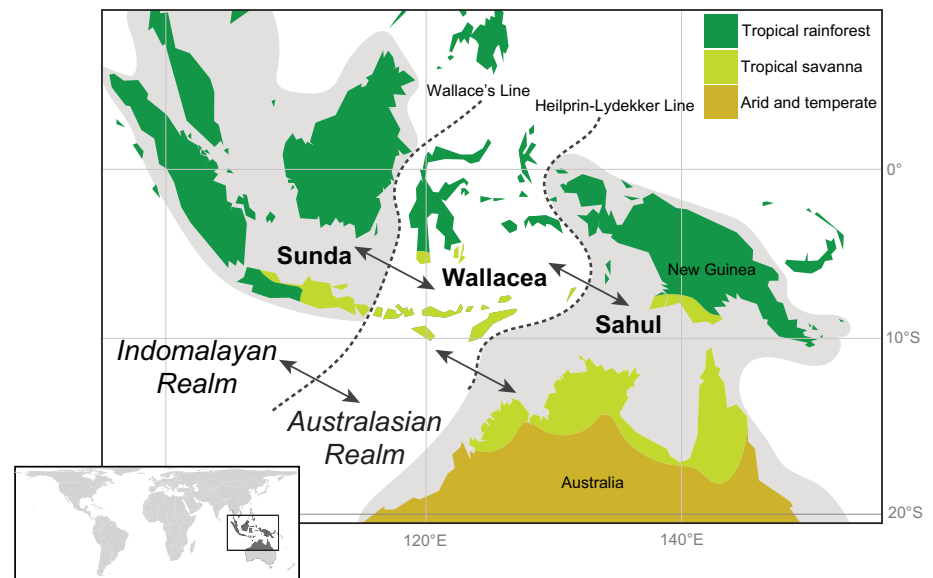


Fig. 1. Climate and geography of the Indo-Australian archipelago at present. The Sunda continental shelf is part of the Indomalayan zoogeographic realm and is separated from the Australasian zoogeographical realm by Wallace's Line. Wallacea is the island archipelago between the Sunda and Sahul continental shelves. The Sahul continental shelf, which includes the Australian mainland and New Guinea, is separated from Wallacea by the Heilprin-Lydekker Line. Sunda, Wallacea, and New Guinea are dominated by the tropical rainforest Köppen-Geiger climate belt, except for eastern Java, Bali, South Sulawesi, the Lesser Sunda isles, and southern New Guinea, which are dominated by the drier tropical savanna climate belt. The Australian mainland is dominated by tropical savanna, arid, and temperate climate belts. The climate maps are adapted from (48).

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an arid-adapted fauna (22). The interchange has been highly asymmetrical, with rates of exchange estimated to be at least twice as high from Sunda to Sahul than in the opposite direction (23). This could be shaped by the uneven sizes of the species pools, as stable areas of tropical rainforest in Sunda, connected to the Eurasian continent, supported a biodiverse fauna throughout the Cenozoic (24). Conversely, increasing aridity and a less connected continental area bound by oceans may have led to a reduced species pool in Sahul. Our current understanding of interchanges is pattern oriented, with historical biogeographic analyses determining where, when, and in which direction exchanges occur (2, 12, 15, 23, 25). A process-oriented understanding, however, requires the synthesis of paleogeographic and paleoclimatic information with biological traits and diversification histories across a range of taxa.

Paleoenvironmental and biological information united under a mechanistic modeling approach makes it possible to compare empirical observations with theoretical expectations and provides a framework with which to explore the mechanisms behind one of the world's major biotic interchanges. We hypothesize that, beyond a simple dispersal filter across oceanic barriers, paleoenvironmental niche dynamics also influence patterns of

change. In addition to each clade's dispersal ability (12) and the size of the species pool, exchange patterns should be related to either the variability in the environmental conditions in which species occur (25) (mean realized niche breadth) or the rate at which environmental niche traits change over time (13) (rates of niche evolution). Further, the spatial distribution of climate, and how it has changed through time, should also explain asymmetry and the spatial distribution of lineages with either Sundanian or Sahulian ancestry (19). Here, we combined paleoenvironmental reconstructions of temperature, precipitation, and plate tectonics over the past 30 million years (Ma) (26–28) with a mechanistic model of biodiversity (29) to explore how dispersal and niche traits interact with the environment to shape regional diversification and patterns of exchange through time (30). The selected time period captures the onset of the convergence of the Australian and Eurasian plates (5) and the origin of most terrestrial vertebrate families in the region (fig. S1). We used published, well-sampled phylogenetic and spatial information on 20,433 species belonging to all 227 families of terrestrial vertebrates present in the Indo-Australian archipelago to estimate phylogenetic and taxonomic β diversity across Wallace's Line as measures of compositional dissimilarity between the two

regions, as well as the number and direction of colonization events (31).

Trait-based drivers of faunal exchange

We estimated a minimum of 381 independent colonization events across Wallace's Line based on a conservative phylogenetic hypothesis for each family [figs. S2 to S5 (30)], explaining the widespread distribution across Sunda and Sahul of 87 out of 227 terrestrial vertebrate families (Fig. 2 and Fig. 3A). Older colonization events were associated with greater species diversity (Spearman $\rho = 0.68$; Fig. 2A), most likely because these older lineages had a longer time to diversify. Precipitation niche breadth was the most consistent predictor of exchange in the Indo-Australian archipelago, indicating that colonization is more common in lineages that can tolerate wider variation in precipitation. Using phylogenetic multiple regression (table S1), we found that families with broader precipitation niche breadths were more likely to be exchanged between regions, to have a larger number of exchange events, and to have lower taxonomic β diversity and phylogenetic β diversity (Fig. 3B and table S1) across Wallace's Line. Temperature niche breadth was negatively associated with exchange dynamics (Fig. 3B and table S1), because temperature and precipitation niche breadths are inversely related in vertebrates (32). The

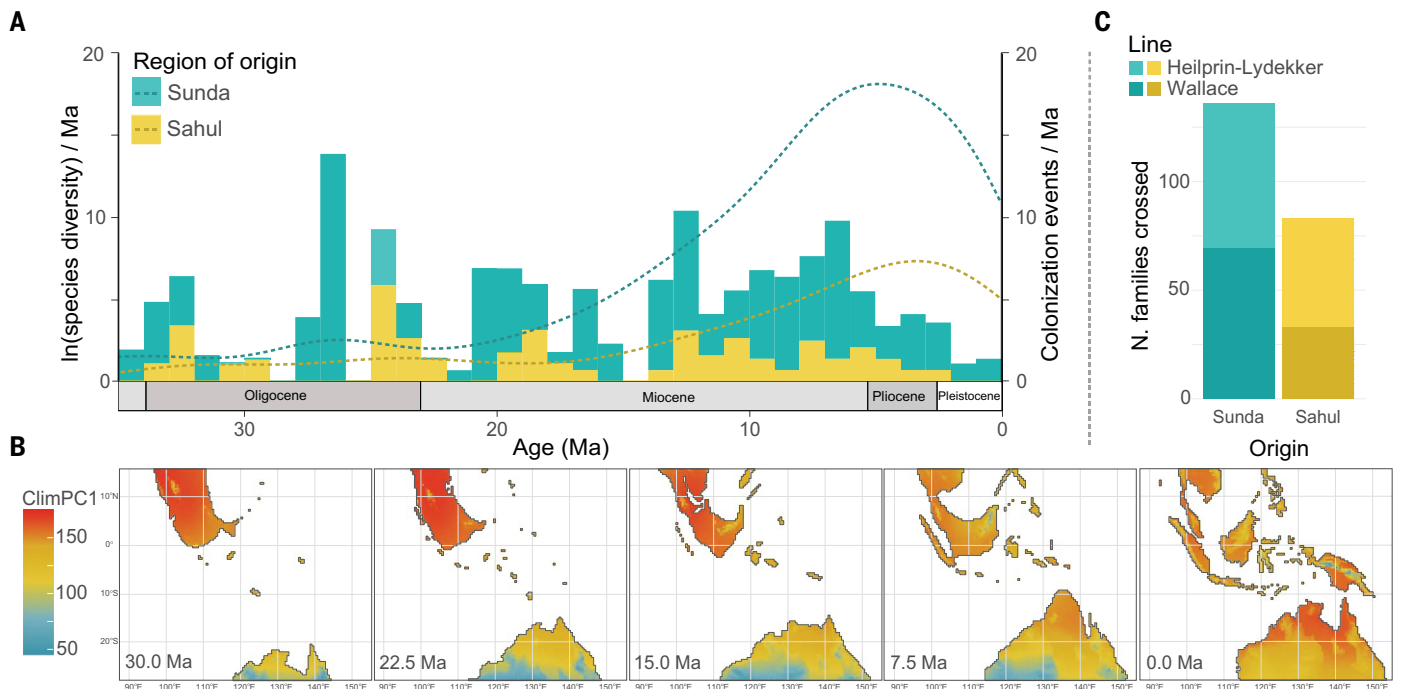


Fig. 2. Colonization dynamics of terrestrial vertebrates and geoclimatic changes in Indo-Australia. (A) Bars show the log-transformed number of species derived from independent colonization events across Wallace's Line from Sunda to Wallacea (blue) or in the opposite direction (yellow). Dashed lines show the number of colonization events through time. (B) Paleogeography (28) and paleoclimate (26, 27) of the Indo-Australian archipelago over the past

30 Ma (26, 28). (C) Numbers of families crossing between regions across two different biogeographic boundaries. Principle component analysis was performed on paleotemperature and paleoprecipitation to decompose a single climate axis (ClimPC1), explaining 88% of the variation in climate, where similar colors represent similar climates. Warm, wet conditions are shown in red; cold, dry conditions are shown in blue.

mechanistic model enabled the disentanglement of these factors and validated the role of broader precipitation niche breadths in the rate of exchange (table S2). Niche breadth may affect colonization dynamics through two pathways: (i) Clades more tolerant of a broad range of conditions may be less prone to extinction and therefore have a larger number of potential dispersing lineages (8), or (ii) they may be more able to establish in a diverse range of environmental conditions with greater establishment success. Our mechanistic model supports the second pathway, because higher rates of colonization were not associated with lower rates of extinction (fig. S6), but instead associated with certain dispersal and niche

characteristics of the modeled lineages. Although the simulation results cannot exclude the role of differential extinction on colonization dynamics [e.g., (8)], they do suggest that differences in the rate of lineage diversification are not required to explain asymmetrical exchange. These results support the hypothesis that the precipitation gradient between Sunda and Sahul is a sharp barrier to the establishment of range-expanding lineages (10, 33), and that lineages able to persist in a diversity of conditions can overcome this barrier.

Supplementing the effect of climatic niche breadth, our empirical and *in silico* model results support the importance of dispersal ability and the species pool in exchange pat-

terns. More diverse biotas might facilitate interchange by having a greater number and variation of potential colonist species, increasing the number of potential colonization attempts (34), and this pathway is considered the null expectation in invasion biology (35). We found that the size of the source species pool was positively associated with exchange success and the number of colonization events in terrestrial vertebrates (Fig. 3B and table S1), as well as with all exchange metrics in the mechanistic model (table S2). As a key dispersal trait, flight was negatively associated with phylogenetic β diversity (Fig. 3B), and most exchanged taxa were highly volant, with 64% of families being either birds or bats,

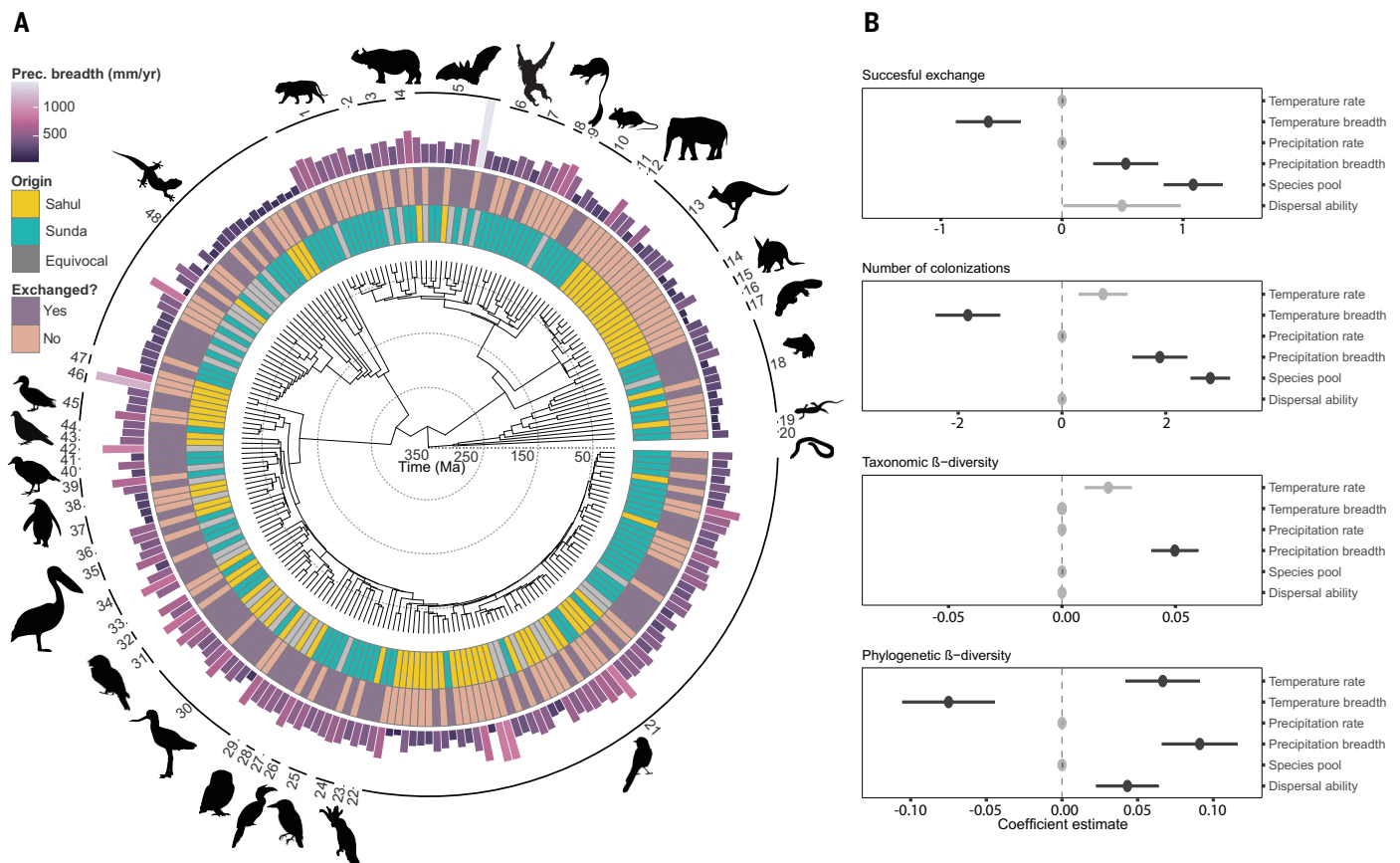


Fig. 3. Exchange dynamics and precipitation niche breadth of terrestrial vertebrates on a family-level phylogenetic tree and effect size of the predictors of exchange. (A) The circle in the center displays each family's reconstructed origin as Sunda, Sahul, or uncertain (equivocal support) based on biogeographic estimation models. The middle colored ring shows whether the family is present in both Sunda and Sahul and was reconstructed to have been exchanged across Wallace's Line. In the outer colored ring, the color and height of the bars represent the mean precipitation niche breadth of the family. Niche breadth was measured as the SD of mean annual rainfall across each species distribution (in millimeters per year). The numbered lines at the perimeter indicate the number of taxonomic orders, with representative taxa highlighted as silhouettes (images are from PhyloPic: <http://phylopic.org/>). 1, Carnivora; 2, Pholidota; 3, Cetartiodactyla; 4, Perrissodactyla; 5, Chiroptera; 6, Eulipotyphla; 7, Primates; 8, Scandentia; 9, Dermoptera; 10, Rodentia;

11, Lagomorpha; 12, Probosidea; 13, Diprotodontia; 14, Dasyuromorphia; 15, Peramelemorphia; 16, Notoryctemorphia; 17, Monotremata; 18, Anura; 19, Caudata; 20, Gymnophiona; 21, Passeriformes; 22, Psittaciformes; 23, Falconiformes; 24, Piciformes; 25, Coraciiformes; 26, Bucerotiformes; 27, Trogoniformes; 28, Strigiformes; 29, Accipitriformes; 30, Charadriiformes; 31, Apodiformes; 32, Caprimulgiformes; 33, Eurypygiformes; 34, Suliformes; 35, Pelecaniformes; 36, Ciconiiformes; 37, Procellariiformes; 38, Sphenisciformes; 39, Gruiformes; 40, Cuculiformes; 41, Otidiformes; 42, Phaethontiformes; 43, Podicipediformes; 44, Columbiformes; 45, Galliformes; 46, Anseriformes; 47, Casuariiformes; 48, Squamata. (B) Coefficients of phylogenetic linear models of four exchange metrics with mean temperature and precipitation niche breadths, rates of temperature and precipitation niche evolution, dispersal ability, and species pool size. Predictors that were statistically significant based on phylogenetic linear models are in bold, and nonsignificant predictors are gray.

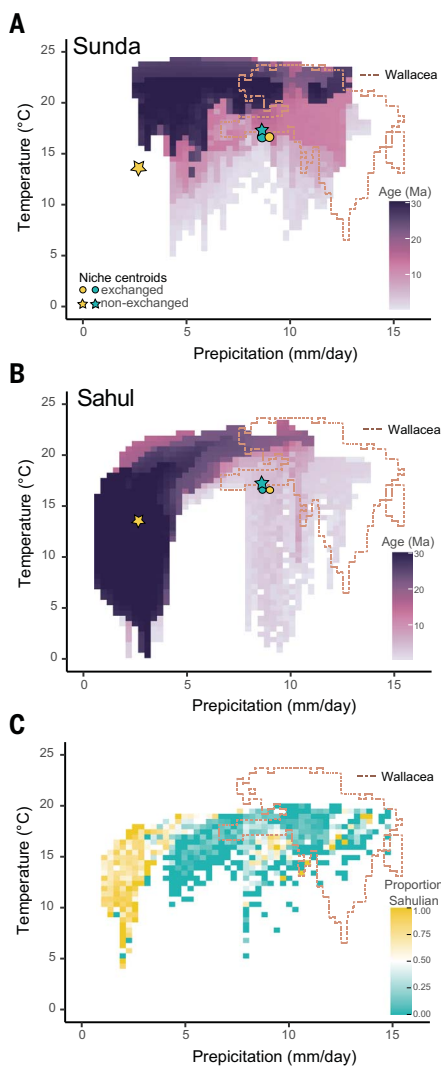


Fig. 4. Age of paleoclimatic space in the Indo-Australian archipelago and distribution of climatic niche centroids of terrestrial vertebrates. (A and B) Gridded representation of climate space defined by temperature and precipitation. Each tile in the grid represents a unique combination of these two variables. The tiles are colored by the age of that climate's first appearance in Sunda (A) and Sahul (B). Climate spaces that have been present longer are in darker colors. The climatic space occupied by the "stepping stone" region of Wallacea during the past 30 Ma is highlighted with an orange dashed line. This space has been present longer in Sunda than in Sahul. Symbols indicate the median climate niche centroid of species from Sahul (yellow) or Sunda (blue) that belong to families that have been exchanged (circle) or have not been exchanged (star). (C) Proportion of species of Sahulian origin in climate space. Species niche positions in climate space show that the area occupied by Wallacea is more densely filled with species from Sundanian families than with species from Sahulian families, and that species from both exchanged and nonexchanged Sundanian families are more commonly found in the climate space occupied by Wallacea.

accounting for 93% of the colonization events of Sunda. All exchange metrics were strongly positively associated with dispersal ability in the mechanistic model (table S2). We found that exchange of bird families across the Indo-Australian archipelago was proportionally higher than during other major biotic interchanges (36), reflecting the greater propensity of volant taxa to disperse over the deep-sea oceanic barriers such as Wallace's Line, which uniquely define the Indo-Australian interchange.

Contrary to our prediction, rates of niche evolution were not commonly associated with exchange dynamics (Fig. 3B and tables S1 and S2), possibly reflecting the widespread phenomenon of niche conservatism, the tendency for lineages to retain their ancestral environmental niche through time (37), during transoceanic colonization (38). For instance, many families that we reconstructed as having a Sundanian origin, such as Colubrid snakes and Pteropodid bats, are typically restricted to similar biomes in Sahul. Instead of the ability to rapidly adapt to new environmental conditions, we show that broader precipitation niche breadths and higher dispersal ability were the primary biological traits that allowed lineages to expand their geographic ranges in the face of oceanic barriers and a steep precipitation gradient.

Paleoclimate and exchange asymmetry

We demonstrate that asymmetrical rates of exchange have been shaped by the distinctly different paleoclimatic histories of Sunda and Sahul. At least 46 families originating in Sunda (43% of all Sundanian families) crossed the Heilprin-Lydekker Line (Fig. 1 and table S3) to Sahul, whereas only 19 families originating in Sahul (24% of all Sahulian families) crossed Wallace's Line to Sunda. A necessary step to colonization involves crossing Wallacea (Fig. 1). Our paleoenvironmental reconstruction, which combines paleotopography (28), reconstructed Köppen belts (27), and a global circulation model (26), show that the humid climate space occupied by Wallacea emerged in Sunda at least 20 and 30 Ma (Fig. 4A and fig. S7) in a period associated with the spread of tropical rainforests (21, 24). Conversely, in Sahul, areas with similarly humid conditions were present during the mid-Miocene (fig. S8) (39) and only became widespread in their contemporary location on Sahul at least 10 and 5 Ma (Fig. 4B), after the northward movement of Sahul and the uplift of New Guinea (20, 24). An almost uninterrupted humid climate throughout the Indo-Australian archipelago, from Sunda to New Guinea, facilitated the establishment of Sundanian lineages in Sahul, and this can also explain the observation that Wallacean and New Guinean flora are compositionally more similar to the flora of Sunda than to that of the Australian mainland (33). Support-

ing this finding, we show that the climate space currently present in Wallacea and New Guinea is more densely occupied by vertebrate lineages from Sunda than by lineages from Sahul (Fig. 4C). By contrast, species from Sahul in families that did not colonize Sunda occupy an older and drier component of the Sahulian climate than species in families that colonized Sunda (Fig. 4C and fig. S9). A higher density of species in older climate space suggests that niche evolution has been truncated through time by the available climate on each continent, highlighting that niche conservatism limits exchange between Sunda and Sahul.

Greater connectivity of a humid climate at the interface of the exchange explains the observed patterns of asymmetrical interchange in terrestrial vertebrates, and this was supported by the mechanistic model. In the model, evolution of climatic niches was directed by the environmental conditions where species evolved (fig. S7). Therefore, Sundanian lineages evolved in niches closer to the conditions of Wallacea and colonized emergent Wallacean islands earlier (mean colonization = 15.27 Ma; fig. S10). In the opposite direction, Sahul lineages were generally unable to successfully colonize proto-Wallacea. Colonization events by Sahulian species across Wallace's Line generally occurred after the uplift of New Guinea's highlands (mean colonization time = 5.4 Ma; fig. S10), supporting the role of New Guinea as an ecological "stepping stone" between Wallacea and the Australian mainland (40).

We evaluated how climate connectivity explains exchange asymmetry by performing an in-silico counter-factual simulation experiment. Here, we either removed the precipitation or temperature constraints on species distributions or removed the tectonic history by holding the landscape constant with sea levels at the time period with maximum connectivity between the regions (Last Glacial Maximum, ~20,000 years ago). This effectively allowed dispersal within each continental region to be unconstrained by oceanic barriers and provided equivalent geographic isolation of each continental region from Wallacea. We found that the proportion of Sahulian species in Wallacea and New Guinea increased only when both the precipitation constraint and tectonic history were modified together, because this promoted more opportunities for dispersal and a higher likelihood of establishment (Fig. 5 and figs. S11 and S12). The proportion of simulations with colonization events between Sahul and Sunda was 16.6% in the full model, which was similar to the observed proportion in terrestrial vertebrates (24%). The proportion increased to 48.6% in the counterfactual model (fig. S11), which is more similar to the observed proportion of lineages moving in the opposite direction, from

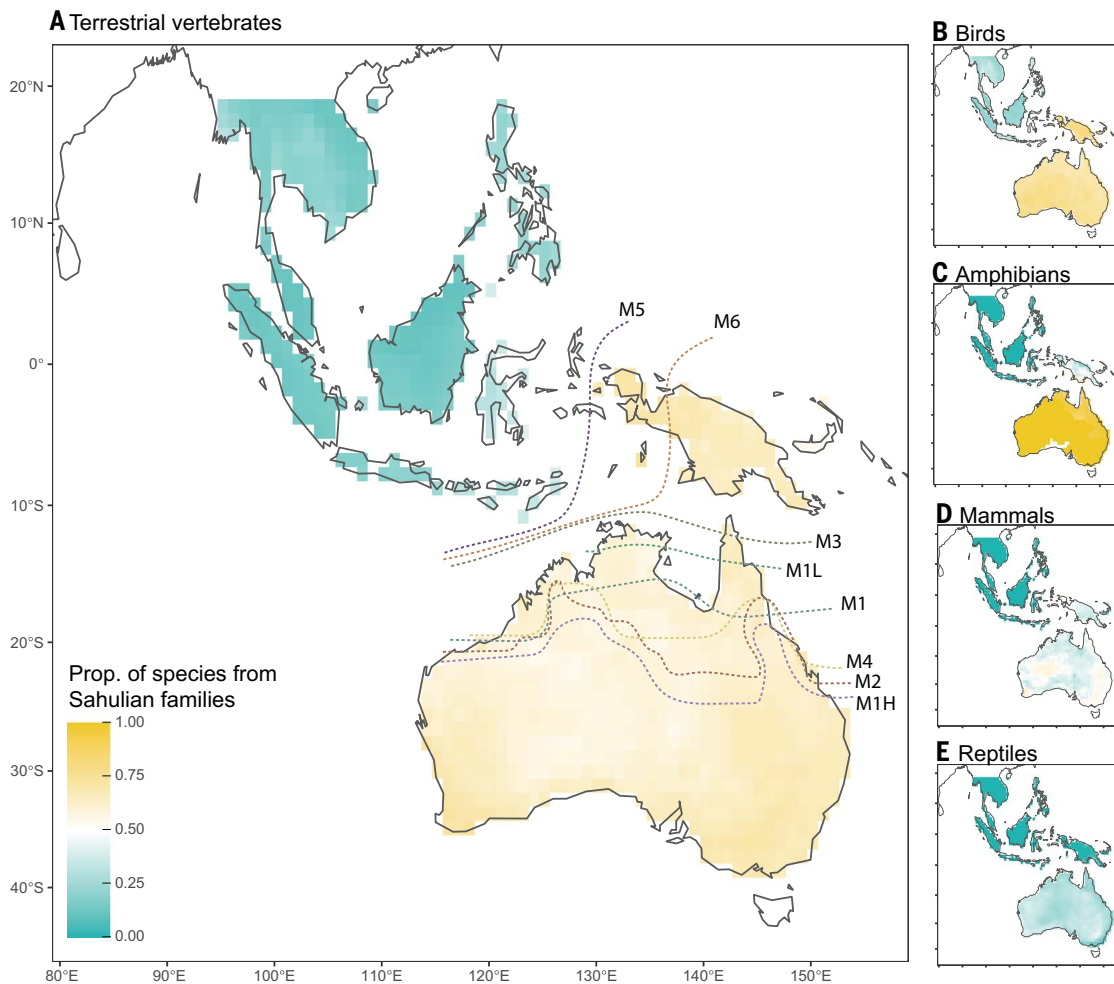


Fig. 5. Spatial distribution of the proportion of terrestrial vertebrate species of Sahul origin and biogeographic turnover predictions from the biodiversity simulation model. Proportion of total species richness in each grid cell that belongs to families of Sahul origin, based on biogeographic estimation, over the count of all species in the grid cell, for all terrestrial vertebrates (A), birds (B), amphibians (C), mammals (D), and reptiles (E). Dashed lines in (A) show the location of the sharpest spatial turnover of proportional Sahulian richness under six different simulation models (M1 to M6), as well as under high (M1H) and low (M1L) values of precipitation

niche breadth and dispersal ability parameters of the full model (M1). The precipitation constraint on species distributions is removed in M2, the temperature constraint is removed in M3, tectonic history is removed in M4, both the precipitation constraint and tectonic history are removed in M5, and both the temperature constraint and tectonic history are removed in M6. The dashed lines illustrate how removing certain constraints that limit colonization changes the distribution of species from families with either Sahulian or Sundanian ancestry. Grid cell size is 110 × 110 km for all panels (Behrmann projection).

Sunda to Sahul (43%). Therefore, more symmetrical exchange could only be observed in the absence of climatic and dispersal barriers. A similar climate-mediated scenario has been suggested to explain exchange asymmetry during the American interchange (9, 41) and between India and Eurasia (7, 42). Our study clarifies how distinct climatic histories of continental regions can generate a near-ubiquitous pattern of asymmetrical terrestrial biotic interchanges.

Dispersal and environmental niche shape spatial patterns of faunal exchange

Patterns of turnover among taxa have long been a source of contention for designating bio-

geographic boundaries in the Indo-Australian archipelago (15) because there is a high discordance in the distributional extent of different taxa across the Indo-Australian archipelago. Across the four classes of terrestrial vertebrates, gradients of turnover from a predominantly Sundanian to a predominantly Sahulian fauna differed, with a high proportion of sites in Sahul having high richness of Sundanian reptile species (100% of sites; Fig. 5E) and mammal species (68.8%; Fig. 5D) (which is driven by the exceptional diversity of Sundanian squamates, rodents, and bats), but not for amphibian species (11%; Fig. 5C) or bird species (1.4%; Fig. 5B). In the mechanistic model, a combination of dispersal and niche traits

shaped gradients in biotic turnover, which could explain the emergence of these different patterns in vertebrates. When simulations were run with increased species' precipitation niche breadth and dispersal ability parameters, we found that lines demarcating turnover from a Sundanian to Sahulian biota (Fig. 5A) were located southward into regions of increased aridity, varying from a pattern corresponding with amphibians (Spearman's $\rho = 0.85$ to 0.87; Fig. 5C) to a pattern corresponding with mammals ($\rho = 0.71$ to 0.74; Fig. 5D), respectively. For birds, New Guinea is predominantly Sahulian, and this pattern was only reproduced by completely lifting the dispersal and precipitation constraints from the model

($\rho = 0.96$; Fig. 5B and fig. S11). This could be because birds have the broadest precipitation tolerances and the highest volancy of any class of vertebrate, and therefore have fewer constraints on colonization (fig. S13). Because the simulation model is agnostic to the taxa investigated, we expect a similar mechanism to operate across a range of taxa not explored here, and there is some evidence that niche and dispersal traits are important drivers of interchange and patterns of turnover in plants (10, 43).

Conclusion

The longstanding view of biotic interchange is that it is primarily governed by plate tectonics and dispersal ability, with rates of colonization in terrestrial organisms being directly proportional to the source pool size (I), the geographic distance between regions, and the emergence of land bridges (9). A more complete picture emerges when the deep-time legacy of climate connectivity and niche conservatism on species distributions are also considered. Advances in deep-time climate reconstructions make it possible to test this directly, and support for a key role of climate connectivity is emerging in the Indo-Australian archipelago (33) and more broadly in other systems such as Indo-Eurasia (7, 42) and the American interchange (41). The factors that shape colonization success are relevant in both a historical and a contemporary context, because biotic exchange is exacerbated by human intervention, and understanding these factors is therefore relevant for predicting the success of new biological colonizations and invasions (35). This is particularly true in the Indo-Australian archipelago, where biological invasions are contributing to some of the highest rates of native species extinction on the planet (45). An emerging view of global biodiversity patterns is that they are largely the outcome of historical changes in plate tectonics shuffling lineages around the planet, in concert with major fluctuations in precipitation and temperature shaping dispersal, speciation, and extinction dynamics through environmental niches (46, 47). A mechanistic

modeling approach enables us to move beyond “lines” in biogeography and instead consider the processes that shape global variation in biodiversity patterns.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.adf7122
Materials and Methods
Figs. S1 to S13
Tables S1 to S3
References (50–143)

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Paleoenvironments shaped the exchange of terrestrial vertebrates across Wallace's Line

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Editor's summary

The movement of species across newly connected continents millions of years ago still shapes flora and fauna today. Skeels *et al.* showed that species' dispersal ability, climate tolerances, and the climate in which they evolved help to explain why biotic exchanges are typically unequal, with more species spreading from one continent than the other. Using a model simulating species ranges and diversification paired with paleoenvironmental reconstructions, the authors found that precipitation tolerance influenced vertebrate species movements across Wallace's Line, which separates the distinct biota of Australia and New Guinea from that of Southeast Asia. Species that evolved in dry Australia were less able to cross to Asia, whereas the swath of tropical forest across the region allowed more species to move in the other direction through New Guinea. —BEL

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