







## RESEARCH ARTICLE

# Diversification and community assembly of the world's largest tropical island

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## Abstract

**Aim:** The species diversity and endemism of tropical biotas are major contributors to global biodiversity, but the factors underlying the formation of these systems remain poorly understood.

**Location:** The world's largest tropical island, New Guinea.

**Time period:** Miocene to present.

**Major taxa studied:** Passerine birds.

**Methods:** We first generated a species-level phylogeny of all native breeding passerine birds to analyse spatial and elevational patterns of species richness, species age and phylogenetic diversity. Second, we used an existing dataset on bill morphology to analyse spatial and elevational patterns of functional diversity.

**Results:** The youngest New Guinean species are principally distributed in the lowlands and outlying mountain ranges, with the lowlands also maintaining the majority of non-endemic species. In contrast, many species occurring in the central mountain range are phylogenetically distinct, range-restricted, endemic lineages. Centres of accumulation for the oldest species are in montane forest, with these taxa having evolved unique bill forms in comparison to the remaining New Guinean species. For the morphological generalists, attaining a highland distribution does not necessarily represent the end to dispersal and diversification, because a number of new species have formed in the outlying mountain ranges, following recent colonization from the central range.

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**Main conclusions:** We conclude that a general model of tropical montane diversification is that lineages commonly colonize the lowlands, shifting their ranges upslope through time to become range-restricted montane forest endemics, attaining novel functional adaptations to these environments.

**KEYWORDS**

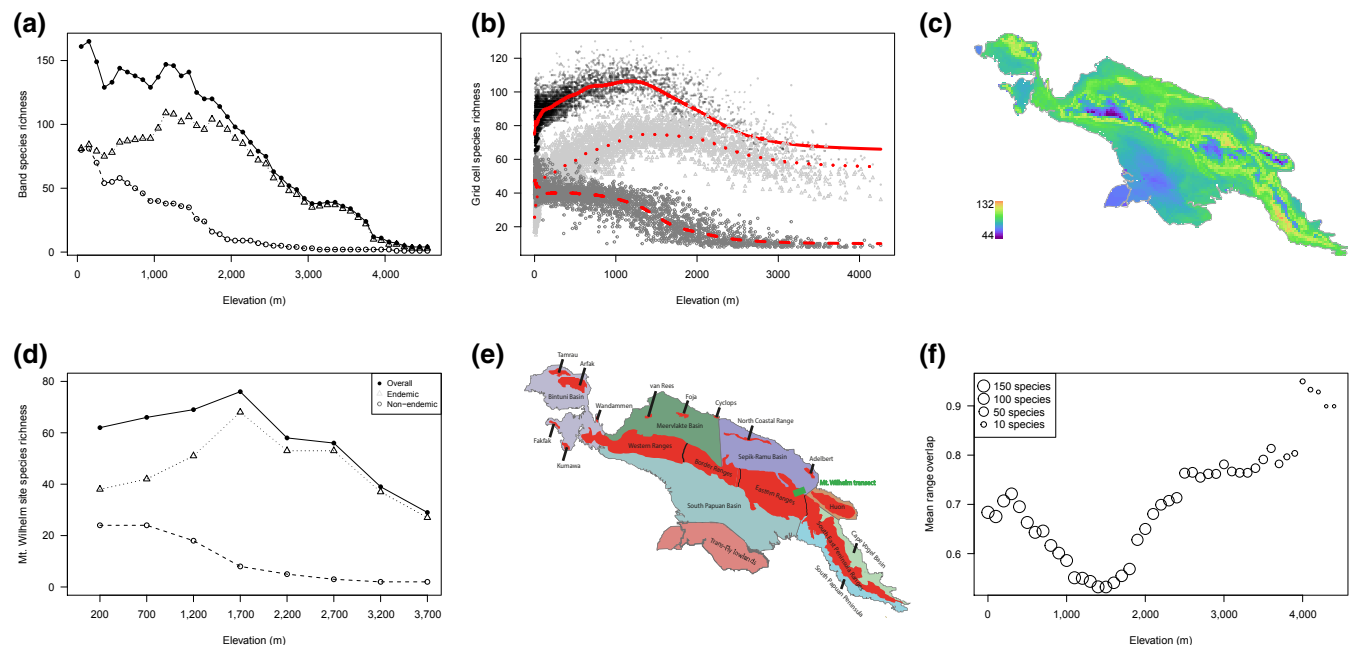
community assembly, elevational gradient, island diversification, New Guinea, taxon cycle, tropical speciation

## 1 | INTRODUCTION

Understanding the processes determining the diversity and composition of assemblages is a central aim of the biological sciences (Ricklefs, 1987). Speciation, extinction and dispersal are the ultimate mechanisms by which species are added to or removed from regional biotas, with subsets of these taxa able to form local communities of sympatric species. Climatic, geological and biotic factors all influence which species are able to coexist at the local scale; therefore, studying systems that possess strong environmental gradients can provide general insights about the relative importance of the processes that govern the formation of species assemblages (McCain, 2009). Specifically, topographically complex areas in the tropics represent global hotspots of biodiversity because of the variability in evolutionary and ecological processes at different elevations that influence patterns of speciation and extinction through time (Fjelds  et al., 2012; Jarzyna et al., 2020; Price et al., 2014). Following

mountain formation, lineages may disperse between or within elevational zones, such that given enough time (and area), new species can form and become established in local communities. However, to date, investigating the interaction between regional and local assembly processes has been significantly hampered owing to the difficulties in defining meaningfully bounded study systems in complex continental faunas, where the majority of global biodiversity is distributed. To address this issue, we study the world's largest tropical island, New Guinea, to gain a greater understanding of elevational variation in the processes associated with lineage diversification and community assembly.

The island of New Guinea lies slightly south of the equator, covers an area of 821,400 km<sup>2</sup> and comprises seven geologically distinct lowland basins, a central mountain range (running the majority of the north-west to south-east axis of the island) and 10 smaller outlying mountain ranges to the north and north-west (Deiner et al., 2011; Diamond, 1985; Figure 1). Together, these areas represent an



**FIGURE 1** (a–d) Species richness patterns at three different spatial scales within New Guinea: (a) 100 m elevational bands; (b,c) the number of species overlapping each 0.1° grid cell; and (d) Mount Wilhelm sites. (e) Lowland basin and montane regions proposed by Deiner, et al. (2011). (f) Mean range overlap of all species present in each 100 m elevational band. In panels (a,b,d), filled circles represent the trends for all species, open triangles for species endemic to New Guinea and open circles for the non-endemic species

archipelagic microcosm of the world's tropical and temperate environments, encompassing a vast mosaic of habitats and climates that range from sweltering tropical rainforests to permanently frozen barren mountaintops. New Guinea is rich in endemic taxa for a wide variety of organismal groups (Allison, 1996; Beehler & Pratt, 2016; Cámara-Leret et al., 2020) and covers a large enough area that a significant proportion of the avifauna has formed via *in situ* speciation. The large number of range-restricted and species-poor lineages distributed on the island suggests that it might serve as a museum of biodiversity; an area of high lineage persistence through deep historical time (Jønsson et al., 2017). In contrast, many other lineages maintain distributions within New Guinea having diversified recently from taxa distributed in the surrounding areas, meaning that the island could also represent a cradle of diversity, an area of rapid recent species formation (Jønsson et al., 2017). Taken together, these hypotheses are well aligned with taxon cycle theory, in which lineages undergo predictable phases of geographical range expansion across the lowlands (cradle), differentiation/speciation in a geologically and topographically complex region and subsequent contraction into the high mountains (museums). An upslope shift in species distributions through time is proposed to be associated with the evolution of increased specialization in habitat preferences and niche-based functional traits (Wilson, 1961). We assess whether these predictions are consistent with the distribution of endemic lineages, species age, phylogenetic diversity and an important ecomorphological trait (bill form; a trait strongly associated with species ecology) among the passerine fauna in New Guinea.

Given that New Guinea is clearly defined by oceanic boundaries in the present and demonstrates extensive variability in habitat and climate, we are able to quantify various aspects of passerine biodiversity from regional to local scales. Specifically, we assess elevational gradients in diversity at the whole-island scale, in individual lowland basins or mountain ranges, and across an elevational transect of local sites. Building a complete phylogeny for all 336 native breeding passerine bird species and combining this with highly resolved geographical distributions and three-dimensional measurements of bill form, our analyses provide a framework to investigate the origin, dispersal and assembly of the New Guinea passerine avifauna.

## 2 | METHODS

### 2.1 | Phylogenetic, morphological and distributional data

Our molecular phylogeny of New Guinean passerine birds sampled 336 species, following the taxonomy of Beehler & Pratt (2016). We used GenBank to source mitochondrial (*cytb*, *ND2* and *ND3*) and nuclear genes (*ODC*, *GAPDH* and *Myo2*) for our supermatrix assembly, supplementing this with our own newly generated sequences for 42 species (Supporting Information Table S1). We analysed the derived supermatrix using Bayesian methods, calibrating the phylogeny with

a number of fossil calibration points. The full methodology relating to DNA sequencing and phylogenetic tree building can be found in the Supporting Information (Methods), and GenBank accession numbers are provided in the Supporting Information (Table S1). The maximum clade credibility tree from these analyses is shown in the Supporting Information (Figure S1).

We collated three-dimensional images of the upper beak for 258 of 336 (77%) New Guinean passerine species (Supporting Information Figure S2) from museum study skins, using data generated by Chira et al. (2018) and Cooney et al. (2017). Four landmarks and 75 semi-landmarks were defined on the three-dimensional beak images by Chira et al. (2018), before being subjected to a generalized Procrustes analysis in the R package *geomorph* (Adams & Otarola-Castillo, 2013). A principal component analysis was then performed on the Procrustes-aligned coordinates for the New Guinean passerine species. Given that the first five principal component axes explained > 95% of the variation in bill shape, we focused our analyses of functional diversity upon the species-level scores of these axes.

Minimum and maximum elevational ranges reflecting breeding distributions were determined from the studies by Beehler and Pratt (2016) and Pratt and Beehler (2014) within 100 m elevational bands (Supporting Information Table S2). Using these same sources, we also recorded species presence or absence in seven lowland basins, four central mountain ranges and 10 outlying mountain ranges (Figure 1e; Supporting Information Table S2). These regional delimitations followed Deiner, et al. (2011) and Diamond (1985) and represented the units from which we assessed patterns of lineage turnover and exchange across New Guinea.

Breeding range polygons were compiled by BirdLife International (BirdLife International and Handbook of the Birds of the World, 2016). In the few instances where there was a discrepancy between the taxonomy followed by BirdLife International and that of our phylogeny, we either separated a single range polygon into two or more new ranges where a previously recognized species had been taxonomically split or created additional novel distributions based on available information in QGIS (QGIS.org, 2021) for recently discovered species that were not split from other congeners.

Species diversity at local sites distributed along a 30 km elevational transect on Mount Wilhelm in the Central Range of Papua New Guinea were obtained from Sam et al. (2014, 2019), subset to include only passerine species (Supporting Information Table S2). The Mount Wilhelm transect extends from lowland floodplains to the treeline and consists of eight evenly spaced sites (200, 700, 1,200, 1,700, 2,200, 2,700, 3,200 and 3,700 m).

### 2.2 | Elevational gradients in species richness, range size and age

To assess elevational gradients in species richness across spatial scales, we analysed the presence-absence matrices of the elevational bands, range maps and local sites. For analyses of the range polygons, we first gridded the data at the 0.1° scale (c. 123 km<sup>2</sup>) and

calculated the number of overlapping ranges using the R package *BiSaT* (<https://github.com/ghthomas/BiSaT>). We also determined the richness gradients among the species endemic to New Guinea [including species distributed on nearby offshore islets and islands (e.g., D'Entrecasteaux Islands), but not those separated by larger water gaps (e.g., New Britain)], members of families wholly endemic to New Guinea and species that extended their ranges into other landmasses (herein, non-endemics). Finally, we downloaded the global elevation layer from WorldClim v.2.1 (Flick & Hijmans, 2017) at the scale of 30 arc s, overlaid this onto our 0.1° grid cells and calculated the mean elevation per cell.

The elevational bands are units containing different amounts of land area, owing to the mountainous nature of New Guinea (i.e., there is greater land area at sea level compared with 4,000 m). Given that species richness is strongly correlated with area at the regional scale, we assessed outliers in this association among the bands to determine elevations where richness was higher or lower than expected. Using the R package *sp* (Pebesma & Bivand, 2005), we calculated the number of cells in our elevational raster layer occurring within each elevational band. We then calculated the residuals from a linear model assessing species richness as a factor of  $\log_{10}$ -transformed band area (number of cells), plotting these against elevation. In addition, we estimated how the average range overlap between species changed between elevational bands. Range overlap was calculated between all species pairs using the range polygons, as the proportion of the smaller ranged species range encompassed by the larger ranged species.

To derive the age of speciation events leading to the New Guinean passerine species, we used the terminal branch lengths from the most recent well-sampled species-level phylogenies of larger relevant clades (e.g., Ericson et al., 2020; Jönsson et al., 2016; Marki, Jönsson, Irestedt, Nguyen, et al., 2017). In the relatively small number of instances where there was a lack of a suitable phylogeny for these purposes, we blasted the mitochondrial sequences on GenBank to identify the closest relative. We considered a 2.2% sequence difference to equal 1 Myr (Weir & Schluter, 2008). For cases where the sister taxa were well known to occur within New Guinea, but not sampled in a broader species-level phylogenetic analysis, we used the terminal branches from the phylogeny produced in this study. Ages from the phylogeny produced in this study and from the larger species-level trees were strongly correlated for the majority of species (Supporting Information Figure S3). We estimated the mean, median and *SD* of species age for all species (also for the endemics and non-endemics) in the elevational bands, grid cells and local sites.

### 2.3 | Phylogenetic and functional diversity

To assess how the distribution of bill morphologies and phylogenetically distinct lineages vary with elevation, we estimated different aspects of phylogenetic and functional diversity. Using the R package *picante* (Kembel et al., 2010), we measured evolutionary diversity and relatedness within assemblages with the following metrics:

(1) the total branch length of an entire assemblage [phylogenetic diversity (PD)]; (2) the average amount of branch length separating all species pairs [net relatedness index (NRI)]; and (3) the average branch length separating closest relatives of each species within the assemblage [nearest taxon index (NTI)]. The functional diversity of assemblages was calculated using the principal component scores derived from the bill scans. Calculated in the R package *dispRity* (Guillerme, 2018), the following metrics were chosen to capture analogous properties of functional trait space to those estimated for phylogenetic diversity: (1) convex hull volume (the total volume of morphological space occupied by an assemblage); (2) the mean pairwise (Euclidian) distance between all species; and (3) the mean nearest neighbour (Euclidian) distance. For both phylogenetic and the functional diversity metrics, we calculated standardized effect sizes (SEs) to control for the variation in species richness among our assemblages. The SES values were determined in association with a null model, where species of an equivalent number present in each assemblage were drawn randomly from the overall pool of New Guinea species before each functional or phylogenetic metric was recalculated. We generated null distributions from 1,000 random draws, then used these distributions to calculate SES values to determine the regions/local sites that were significantly clustered (negative SES) or overdispersed (positive SES) compared with these expectations.

Given that the same morphological volume can be occupied at different densities by alternative sets of species, we calculated five dimensional (principal components 1–5) hypervolumes in the R package *hypervolume* (Blonder et al., 2014) to determine the distinct areas of morphospace occupied at different elevations and how the endemic/non-endemic lineages contributed to these patterns. Hypervolumes were estimated using a multidimensional kernel estimation procedure, and bandwidths were determined using the Silverman bandwidth estimator (Blonder et al., 2014). Overlap in the hypervolumes and the unique fraction of morphospace occupied between pairwise comparisons was calculated using the Sørensen index, which ranges from zero to one, representing a complete lack of overlap to identical hypervolumes, respectively.

### 2.4 | Lineage turnover between regions and elevations

To determine the phylogenetic distinctiveness and dissimilarity of elevational assemblages, we calculated phylogenetic  $\beta$ -diversity, which consists of two components: (1) nestedness, indicating how the losses or gains of lineages between assemblages reflect differences in species richness; and (2) turnover, which characterizes the replacement of lineages between assemblages (Baselga, 2010). The turnover and nestedness components of phylogenetic  $\beta$ -diversity were estimated using the R package *betapart* (Baselga et al., 2018) for the lowland basins/montane regions (both individually and combined), the 100 m elevational bands and the local Mount Wilhelm sites. To investigate the turnover of lineages between the central

and outlying mountain ranges in more detail, we combined the tax lists from all central and outlying montane regions and determined the number of taxa unique to each area (e.g., species/genera/families found only on the central ranges but not on the outlying mountain ranges, and vice versa).

### 3 | RESULTS

#### 3.1 | Species richness gradients

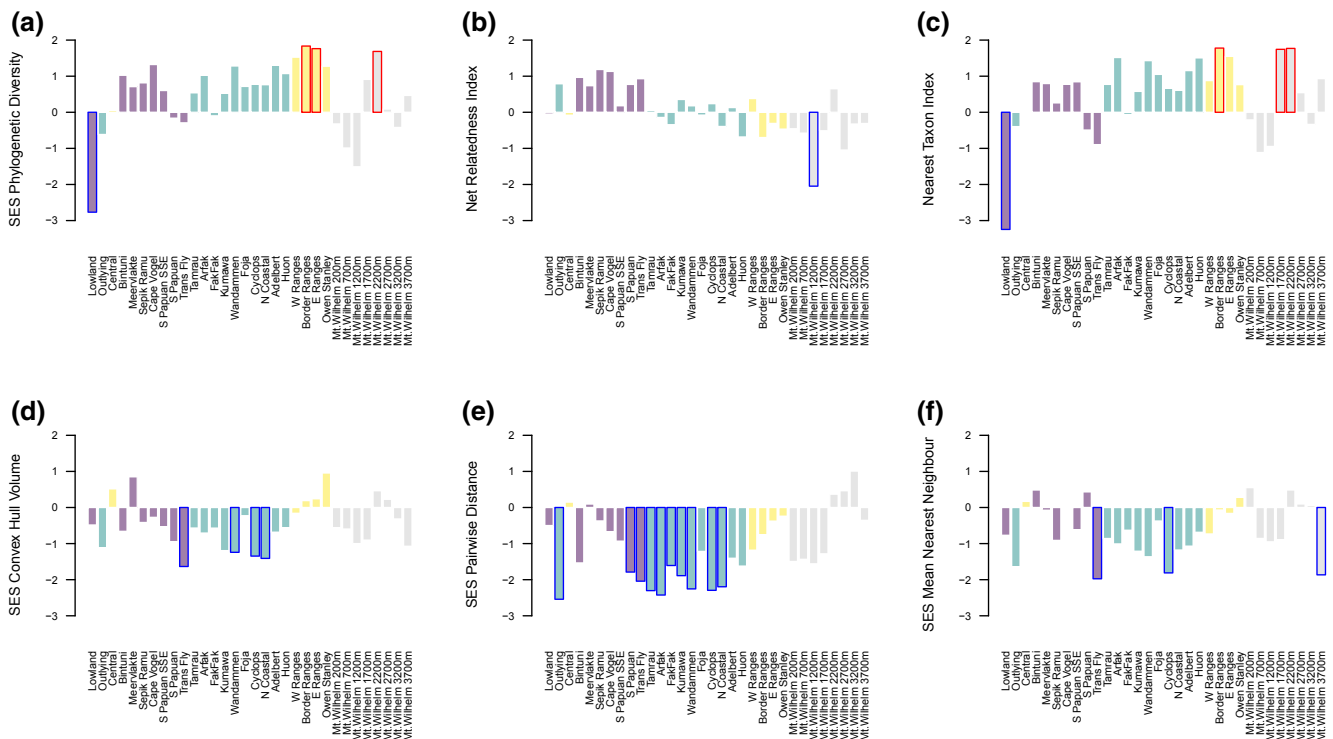
Variation in passerine species richness is strongly associated with elevation across New Guinea (Figure 1). Considering 100 m elevational bands that encompass the whole island, species richness is highest in the lowlands (Figure 1a), but above 1,800 m there is a continuous decline in species numbers towards the highest elevations. Upon accounting for the amount of available area per elevational band, we see that the highest number of species is between 1,000 and 2,000 m, being greatest at c. 1,500 m (Supporting Information Figure S4). A similar peak in species richness between 1,000 and 2,000 m is supported by analysis of the gridded range polygons (c. 123 km<sup>2</sup>) and Mount Wilhelm local sites (Figure 1).

Species geographical range size decreases towards higher elevations (Supporting Information Figure S5). Range size differs substantially among endemic and non-endemic lineages (Supporting

Information Figure S6) and, accordingly, endemism increases abruptly with elevation (Supporting Information Figures S7 and S8). The diversity of endemic species drives the peaks in species richness across spatial scales (Figure 1). Notably, species that are members of endemic families are responsible for the 1,700 m site on Mount Wilhelm being the most species rich along the gradient (Supporting Information Figures S7 and S9). Geographical range overlap among species declines to its lowest level in the elevational bands between 1,000 and 2,000 m (Figure 1f).

#### 3.2 | Phylogenetic diversity, functional diversity and species age

Phylogenetic diversity metrics generally trend towards overdispersion across spatial scales (positive SES values) in New Guinea (Figure 2), reflecting the co-occurrence of more distantly related species than expected. However, clustering arises when the seven lowland regions are analysed in combination, with a greater number of young closely related species co-distributed, as illustrated by the negative SES values of PD and NTI (Figure 2). Yet, when the lowland basins are analysed individually, there is a consistent non-significant tendency towards overdispersion (Figure 2). In comparison, two of the four regions in the central mountain range and the 1,700 and 2,200 m Mount Wilhelm sites support assemblages of distantly



**FIGURE 2** Standardized effect sizes (SESs) of phylogenetic and functional diversity metrics across different spatial scales within New Guinea. Purple bars represent lowland areas, pale green bars outlying montane ranges, yellow bars central mountain ranges and pale grey bars local sites on the Mount Wilhelm gradient. Clustering or overdispersion above the null expectation ( $p < .05$ ) is indicated by bars with the blue or red borders, respectively. Plots are shown for: (a) phylogenetic diversity; (b) net relatedness index; (c) nearest taxon index; (d) convex hull volume; (e) mean pairwise distance; and (f) mean nearest neighbour distance



related neighbouring taxa (Figure 2). All central and outlying mountain ranges trend towards overdispersion in PD and NTI (Figure 2). When comparing the average relatedness among all species with NRI, patterns of clustering and overdispersion were much weaker across spatial scales (Figure 2).

In contrast to the phylogenetic diversity results, from the regional to local scale, all three measures of functional diversity consistently favoured morphospace clustering (negative SES values; Figure 2). Seven of the outlying mountain ranges (and the combined analysis of the individual outlying montane regions), in addition to the Trans Fly and South Papuan lowland regions, support species with significantly more similar bill forms than expected (Figure 2). The central range regions occupy a larger morphological volume than either the lowlands or the outlying regions (Supporting Information Figure S10), with the outlying montane ranges largely representing a taxonomic subset of the central range (Supporting Information Figure S11). Consequently, the morphospace the outlying range taxa occupy is largely nested within that of the central range (Supporting Information Figure S10). The main lineages driving these patterns are species that are members of the endemic families (Supporting Information Figure S12), which are proportionally and numerically far more prevalent in the montane regions (Supporting Information Figure S13). Despite morphological measurements being available for only 23 of 27 of the endemic family species, c. 40% of the hyper-volume they occupy is unique when compared with that of the remaining 235 measured New Guinea species (Supporting Information Figure S12).

As elevation increases, the mean (and median) age of species in the assemblage also increases (Figure 3; Supporting Information Figures S14 and S15). The endemic families are represented by species that are by far the oldest found on New Guinea (Supporting Information Figure S16), resulting in the increase in age between 1,700 and 3,000 m where they are most common (Supporting Information Figure S17). Assemblages that contain the oldest species tend to be located above the elevations at which the overall species richness peaks (2,000–4,000 m, as opposed to 1,000–2,000 m; Figures 1 and 3). In contrast, the majority of the youngest New Guinean species tend to be found in lowland regions, where the bulk of overall species are distributed (Supporting Information Figures S18 and S19), with a set of even more recently formed species endemic to the outlying mountain ranges (Supporting Information Figure S20).

### 3.3 | Lineage turnover

There is an abrupt turnover in phylogenetic  $\beta$ -diversity between lineages distributed in montane and lowland regions, such that these assemblages predominantly represent different portions of the New Guinea passerine phylogeny (Figure 4; Supporting Information Figures S21 and S22). These findings suggest that the substantial decrease in range overlap in the elevational bands between 1,000 and 2,000 m (Figure 1f) is attributable to segregation of the lowland

and highland faunas. These conclusions are also consistent when these analyses are repeated using the elevational band (Supporting Information Figure S21) or Mount Wilhelm local site data (Supporting Information Figures S22 and S23).

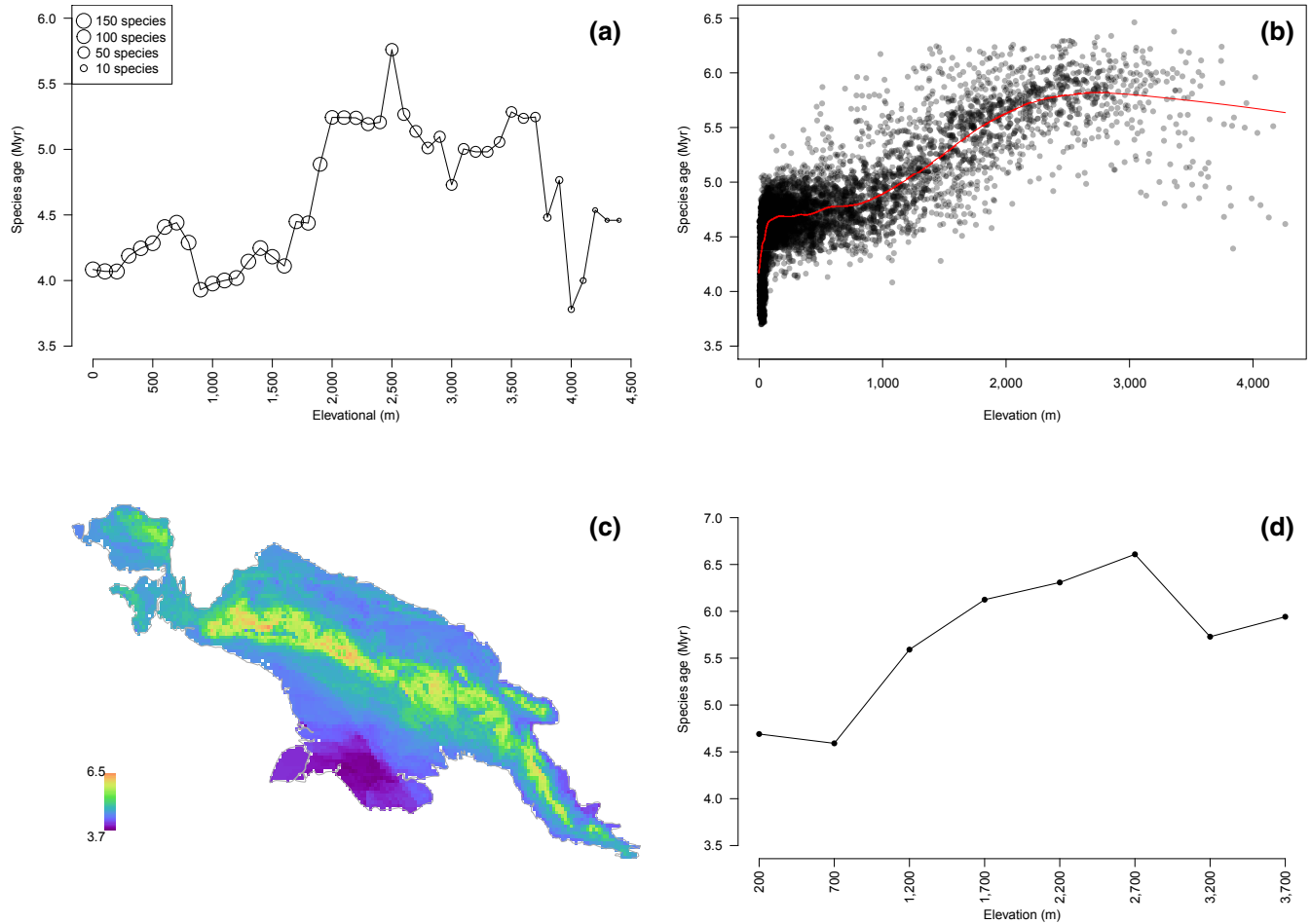
Turnover in phylogenetic  $\beta$ -diversity is generally small between different lowland basins but is greatest when contrasting the Trans Fly region against all other lowland basins (Figure 4). Among the different montane regions, branch length turnover is also generally low, but it becomes slightly elevated when compared between different outlying mountain ranges (Figure 4). However, consistent with the taxonomic results (Supporting Information Figure S11), rather than turnover, nestedness is more common when comparing the central and outlying mountain ranges (Figure 4). Although some of the outlying mountain ranges have generated endemic species, the central ranges maintain a greater number and proportion of endemic species, plus unique genera and families not found in any of the outlying mountain ranges (Supporting Information Figure S11).

## 4 | DISCUSSION

As Earth's largest tropical island, New Guinea maintains staggering levels of species diversity and endemism (Cámara-Leret et al., 2020). For the passerine avifauna of the island, we demonstrate the strong predictive power of elevation upon patterns of species richness, endemism and age (Figures 1 and 3; Supporting Information Figure S7). Species richness is highest at mid-elevations (between 1,000 and 2,000 m; Figure 1) and is driven by the coexistence of predominantly endemic lineages (Supporting Information Figures S7 and S8). The lowland basins maintain many non-endemic species (Figure 1), thus appearing to represent the main areas of island colonization. Over time, species shift their ranges upslope, reduce their overall range size (Supporting Information Figure S5) and evolve unique bill morphologies (Supporting Information Figures S10 and S12) as they become endemic at higher elevations. However, colonization of the highlands does not always represent a dead end for the continued diversification of lineages, because many young endemic species are distributed in the outlying mountain ranges, with their closest relatives found in the central range. These findings attest to the generation of new species within New Guinea following dispersal between mountain ranges. Importantly, montane areas are of substantial importance for maintaining ancient, phylogenetically distinct species over long periods of evolutionary time.

### 4.1 | Elevational gradients of species diversity

Species richness gradients display heterogeneous associations with elevation across Earth's surface, including monotonic declines, low-elevation plateaus and mid-elevation peaks (McCain, 2005, 2009; Rahbek, 1995). The variable shapes of these relationships reflect not only environmental variability among mountain ranges, but also whether elevational gradients in species diversity are quantified



**FIGURE 3** Mean species age (in millions of years) at three different spatial scales across New Guinea: (a) 100 m elevational bands; (b,c)  $0.1^\circ$  grid cells; and (d) the local Mount Wilhelm sites

at the regional or local scale (McCain, 2009). Here, we show that regional patterns of elevational diversity do not directly mirror those at the local scale (Figure 1), and we add that this also applies to phylogenetic and functional diversity estimates (Figure 2). In New Guinea, an elevational plateau in species richness from 0 to 1,700 m is followed by a monotonic decline when evaluating distributions among elevational bands across the entire island (Figure 1a). However, as the spatial scale is reduced to  $123 \text{ km}^2$  grid cells, or local sites, a pronounced mid-elevation peak in species richness becomes apparent (Figure 1b–d). A major factor explaining these different trends is the large number of wide-ranging lowland allospecies that elevate the richness of these elevational bands across the whole island (Supporting Information Figures S5 and S6) but which are not sympatric in high numbers at local scales (Figure 1).

Available area positively predicts elevational band richness (Supporting Information Figure S4), with area declining from the lowlands towards the mountain peaks. This trend is consistent with the species–area relationship (McCain, 2005), yet elevational bands between 1,000 and 2,000 m maintain higher numbers of species than expected from a linear association with available area (Supporting Information Figure S4). The elevational bands with the lowest range overlap (1,000–2,000 m) represent an area of abrupt

lineage turnover between the lowland and highland avifaunas (Figures 1f and 4). This suggests a strong imprint of biogeographical history on the formation of the elevational diversity gradient (for a similar pattern among Himalayan birds, see White et al., 2019) and that faunal mixing might be an important explanatory factor of the mid-elevational diversity peaks. However, the species richness trends along Mount Wilhelm (Figure 1d) are also well correlated with the underlying distribution of arthropod resources (Sam et al., 2019) and the large number of insectivorous passerine species present (Schumm et al., 2020). The association between insectivores and arthropod abundance could be a common driver of insectivorous avian diversity gradients in tropical montane systems (Price, et al., 2014; Schumm, et al., 2020; Supriya et al., 2019).

## 4.2 | Phylogenetic and functional diversity vary with elevation and spatial scale

Phylogenetic diversity metrics show that species assemblages generally consist of distantly related species, whereas bill forms (a phenotypic character strongly associated with species ecology) within an assemblage tend to be more similar to one another (Figure 2).

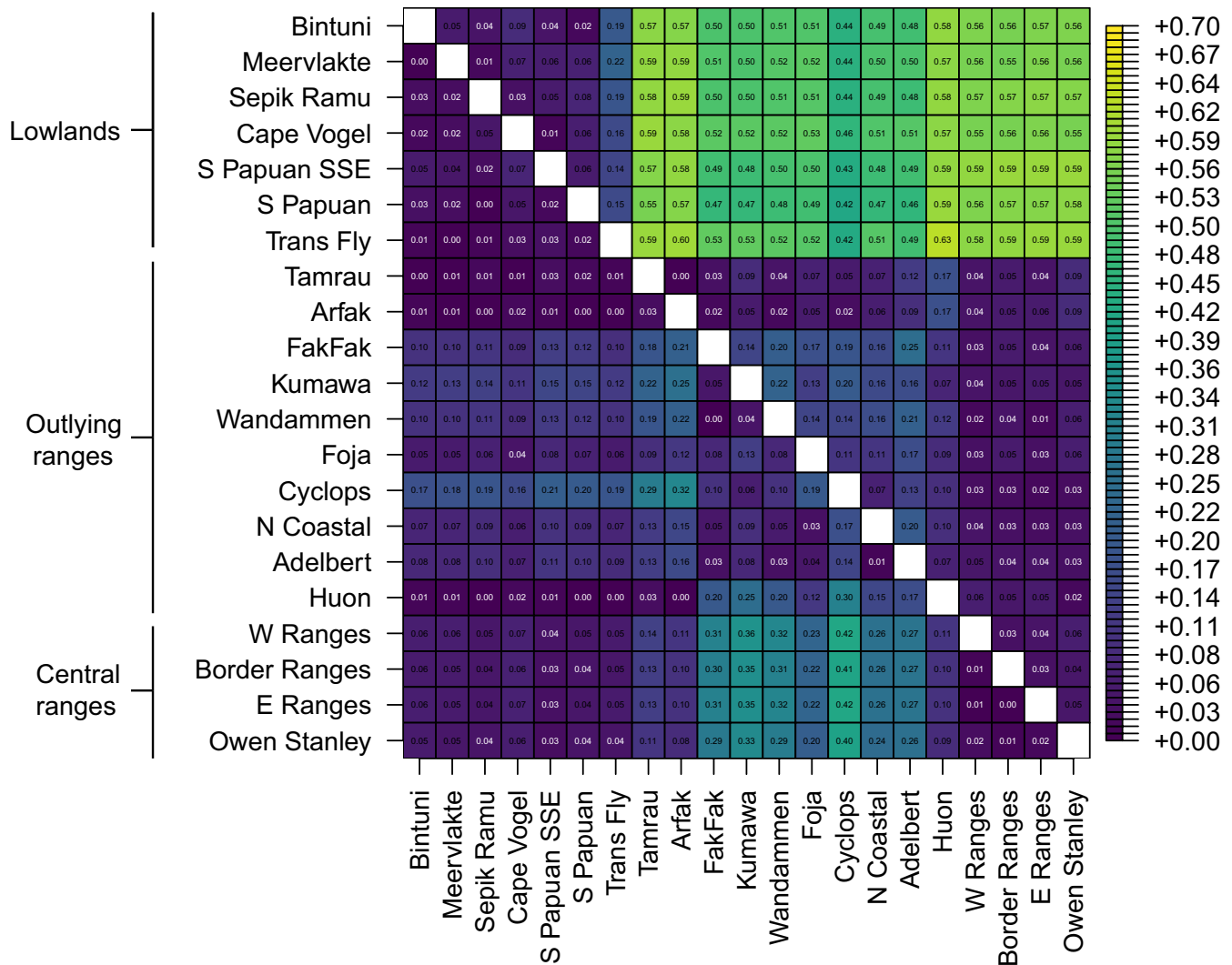


FIGURE 4 Matrix showing the phylogenetic lineage turnover (phylo-beta sim values; upper right triangle) and nestedness resulting from phylogenetic dissimilarity (phylo-beta sne values; lower left triangle) calculated among pairwise comparisons of the individual lowland and montane regions using the phylogeny of New Guinea passerines, following Baselga et al. (2018). Warmer colours on the heatmap indicate greater turnover/nestedness in the pairwise comparisons

Phylogenetic and morphospace diversity is greatest in montane regions (Figure 2), where the most phylogenetically distinct species are well represented (Schodde & Christidis, 2014). Members of the endemic families have distinct bill shapes (e.g., *Cnemophilidae*, *Eulacestoma* and *Toxorhamphus*) when contrasted to other New Guinean taxa, and these lineages account for much of the island-wide patterns of variation in functional diversity (Supporting Information Figure S12). Our results contrast with the monotonic elevational declines in both phylogenetic and functional diversity reported in a number of recent studies from tropical continental areas (Dehling et al., 2014; Hanz et al., 2019; Jarzyna, et al., 2020; Montaña-Centellas et al., 2020). Although c. 23% of the species in our analyses lack morphological data, these species have a relatively even distribution among assemblages/spatial scales and mainly represent members of clades from which close relatives have been measured (Supporting Information Figure S2).

As opposed to biases associated with unsampled species, we suggest a number of biological factors to be the most likely

explanations for the observed trends. First, the biotas of mountain ranges in continental settings, which have been the main focus of the majority of other studies, have inevitably accumulated a greater proportion of the fauna by immigration rather than by *in situ* radiation. In contrast, owing to the size and present-day insular nature of New Guinea, the majority of the avifauna has formed *in situ*, pre-dating the Pleistocene land connection to Australia (Supporting Information Figures S7, S13 and S18; Jønsson & Holt, 2015). Second, areas of montane forest might provide uniquely isolated, stable environmental conditions for the long-term accumulation of phylogenetically, functionally and ecologically distinct taxa (Fjeldså, et al., 2012; Kennedy et al., 2021; Slavenko et al., 2020). An obvious example of this influence is provided by the nine passerine families endemic to New Guinea, seven of which contain fewer than three species. In comparison to the remaining taxa, these endemic family species are both older (mean species age of  $9.33 \pm 6.5$  Myr, vs.  $4.2 \pm 3.3$  Myr for all other species in New Guinea) and occur at higher elevations



(mean mid-point elevation of  $1,613 \pm 901$  m for the endemic family species vs.  $1,151 \pm 917$  m for all other species in New Guinea). In addition, a smaller and more clustered functional trait space is also evident in some of the outlying mountain ranges and in the lowland basins (Figure 2). This appears to be a consequence of the biogeographical patterns of island colonization and range expansion, which have resulted in a large number of young species in the lowlands and outlying mountain ranges, as opposed to any obvious influence of environmental filtering. For example, a number of young endemic species in the outlying mountain ranges (Supporting Information Figures S19 and S20) share highly similar bill morphologies with their sister species distributed in the central montane regions from which they have recently diverged (e.g., *Ailuroedus*, *Parotia* and *Sericornis*). In many instances, these patterns seem to reflect the very recent formation of the northern accreted terranes, in comparison to the older central range (Baldwin et al., 2012; Toussaint et al., 2014; van Ufford & Cloos, 2005). Likewise, a comparison of the phylogenetic diversity metrics of the combined lowland regions and individual basins suggests that the lowlands harbour a number of very young allospecies distributed among the different basins (Figure 2).

### 4.3 | Cradles and museums of species diversity in New Guinea

At continental scales, areas of recent species formation, accumulation and historical maintenance commonly do not overlap in geographical space (Kennedy et al., 2014). In New Guinea, we find that areas of high overall species diversity are between 1,000 and 2,000 m (Figure 1), with these peaks comprising assemblages of species that encompass a broad range of ages (Supporting Information Figure S14). However, the peaks of species richness of the youngest and oldest species coincide with lower or higher elevations, respectively (Figure 3; Supporting Information Figures S8 and S19). The greater age, morphological distinctiveness and higher elevational distribution of the endemic family species could reflect both that higher elevations have been environmentally stable over long time periods (Fjelds a et al., 2012; Kennedy, et al., 2014) and that through time, species evolve to become specialists of interior highland forests (Ricklefs & Cox, 1978; Wilson, 1961).

The youngest New Guinean species are either lowland taxa or represent newly formed endemics from the outlying mountain ranges (Figure 3; Supporting Information Figures S19 and S20). Most of the lowland species are non-endemic (Figure 1; Supporting Information Figure S7), having distributions that extend outside New Guinea. Although greater numbers of species are distributed in the lowlands (Figure 1a), they have not formed more species-rich assemblages at local scales (Figure 1b–d). It is likely that many lowland allospecies are yet to evolve sufficient reproductive and ecological isolation from one another and are unable to coexist stably in sympatry (Price, 2008). The high proportion of non-endemic species (Supporting Information Figure S7) suggests that the lowlands represent the main area of island colonization within New Guinea.

For many lowland lineages, Australia represents a clear source fauna (Schodde & Christidis, 2014), such that the lowest degree of endemism is within the Trans Fly region that shared a land bridge connection during the Last Glacial Maximum. An obvious source fauna for the highlands seems less apparent. Considered in combination with the increasing age/endemism of the montane fauna (Figures 1 and 3) and the phylogenetic turnover between the lowlands and highlands (Figure 4), this implies that through time, lineages shift their ranges upslope. Upslope dispersal and subsequent dispersal/range fragmentation could plausibly result in some lineages maintaining isolated populations in the outlying mountain ranges that led to species-level divergence (Pujolar et al., 2022). Owing to their smaller area (and overall lower elevations, with associated reduced habitat diversity), younger age and greater isolation, the outlying mountain ranges harbour only a subset of the taxonomic and functional diversity found in the central range (Figure 4; Supporting Information Figure S11).

The taxon cycle hypothesis predicts deterministic patterns of increases in species age and ecomorphological specialization and decreases in range size with elevation (Ricklefs & Cox, 1978; Wilson, 1961) that are consistent with our results. Competitive interaction with more recent colonists is the original process proposed to generate these patterns (Ricklefs & Cox, 1978; Wilson, 1961). However, these same trends could also result if long-term climatic stability in montane forests lowers extinction rates at higher elevations (Fjelds a, et al., 2012). Clearly pertinent to understanding these patterns is that the montane areas where these species are currently distributed were largely absent until the last 5 Myr (Baldwin et al., 2012; Schodde & Christidis, 2014; van Ufford & Cloos, 2005), although the south-east Peninsula Ranges might be older (Toussaint et al., 2021). Coupled with significant uncertainty surrounding the tectonic history of New Guinea, it remains an open question how lineages that seemingly pre-date the age of the central range are currently endemic to these areas (Schodde & Christidis, 2014). Nevertheless, we argue that the most parsimonious explanation of the relationships between age, endemism, elevation and species richness is colonization of the New Guinea lowlands, followed by upslope range shifts and range fragmentation.

### 4.4 | Conclusions

For the world's largest tropical island, our multiscale analyses demonstrate dramatic elevational heterogeneity in the processes driving the diversification and community assembly of the passerine bird fauna. The high proportion of endemic taxa in New Guinea reflects a biota formed predominantly through *in situ* lineage diversification, with many of these taxa maintained in the highlands over long periods of time, whereas other lineages formed in the lowlands and the outlying mountain ranges in the more recent past. New Guinea can thus be viewed as both a cradle and a museum of passerine diversity. Lineages maintaining distributions outside of New Guinea are disproportionately lowland taxa, implying that the lowlands are

the main area of island colonization. Species richness of the oldest endemics is highest in areas of montane forest, and these functionally distinct taxa drive the peak in local community diversity at these elevations. We propose that the general mode of dispersal and diversification in New Guinea is lowland colonization, followed by upslope range shifts through time, such that lineages eventually become range-restricted highland endemics. Conservation of areas of montane forest is therefore crucial to maintain the most unique facets of New Guinean biodiversity.

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## CONFLICT OF INTEREST

The authors declare no conflicts of interest.

## AUTHOR CONTRIBUTIONS

Jonathan D. Kennedy, Petter Z. Marki and Knud A. Jønsson conceived the study. Petter Z. Marki, Mozes P. K. Blom, Martin Irestedt and Knud A. Jønsson generated the molecular data and the phylogenetic tree. Jonathan D. Kennedy performed the remaining analyses. Jonathan D. Kennedy and Knud A. Jønsson led the writing, and all authors contributed to interpretation of the analyses and editing the text.

## DATA AVAILABILITY STATEMENT

The phylogenetic tree can be downloaded from Dryad (<https://datadryad.org/stash/share/J58YcD-yEi7N7dN82wil8rQJSryahw1g>

QxxpNUDwKcM), and GenBank accession numbers are provided in the Supporting Information (Table S1). Elevational ranges and presence-absence matrices are shown in the Supporting Information (Table S2).

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