

Population genomics of the island thrush elucidates one of earth's great archipelagic radiations

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Abstract

Tropical islands are renowned as natural laboratories for evolutionary study. Lineage radiations across tropical archipelagos are ideal systems for investigating how colonization, speciation, and extinction processes shape biodiversity patterns. The expansion of the island thrush across the Indo-Pacific represents one of the largest yet most perplexing island radiations of any songbird species. The island thrush exhibits a complex mosaic of pronounced plumage variation across its range and is arguably the world's most polytypic bird. It is a sedentary species largely restricted to mountain forests, yet it has colonized a vast island region spanning a quarter of the globe. We conducted a comprehensive sampling of island thrush populations and obtained genome-wide SNP data, which we used to reconstruct its phylogeny, population structure, gene flow, and demographic history. The island thrush evolved from migratory Palearctic ancestors and radiated explosively across the Indo-Pacific during the Pleistocene, with numerous instances of gene flow between populations. Its bewildering plumage variation masks a biogeographically intuitive stepping stone colonization path from the Philippines through the Greater Sundas, Wallacea, and New Guinea to Polynesia. The island thrush's success in colonizing Indo-Pacific mountains can be understood in light of its ancestral mobility and adaptation to cool climates; however, shifts in elevational range, degree of plumage variation and apparent dispersal rates in the eastern part of its range raise further intriguing questions about its biology.

Keywords: island biogeography, great speciator, phylogeny, colonization, gene flow, Pleistocene climate changes, passerine birds, mountains

Layman Summary

Island radiations are powerful systems for studying evolutionary processes and biodiversity buildup. Here we use population genomics methods to investigate one of the most spectacular and perplexing archipelagic radiations among birds. The island thrush displays a complex mosaic of plumage variation and occupies a vast range across the Indo-Pacific despite being sedentary and largely restricted to mountains. We reconstruct its evolutionary relationships, demographic history, and population structure to provide a detailed picture of an explosive radiation from Asia during the Pleistocene. We illustrate how departure from the mainland and subsequent founder events degraded genetic variation, and detect considerable cross-population gene flow. Our results place focus on the dynamics of populations at the leading edge of radiations vs. those behind it.

Tropical archipelagos are natural laboratories that have shaped scientific understanding of evolution and biogeography (Darwin, 1859; MacArthur & Wilson, 1967; Mayr, 1942; Mayr & Diamond, 2001; Ricklefs & Cox, 1978; Wallace, 1869). The processes of

colonization, speciation, and extinction are manifested in the modern distribution of their biotas, from evolutionary relics stranded on single islands, to ultra-mobile colonizers ubiquitous across entire archipelagos. At the intersection of these extremes

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are the “great speciators” (Diamond et al., 1976). These species (or lineages) are sufficiently dispersive to broadly colonize island systems, but paradoxically show distinct differentiation between island populations, indicating incipient speciation (and limited dispersal ability). This dynamic makes great speciators an alluring model for investigating how lineage expansion and diversification shape global biodiversity patterns (Jönsson et al., 2014; Moyle et al., 2009; Pepke et al., 2019). Molecular phylogenetic studies (Andersen et al., 2013, 2014, 2015; Irestedt et al., 2013; Jönsson et al., 2014; Moyle et al., 2009; Kearns et al., 2020; Pedersen et al., 2018) have confirmed that great speciators represent rapid and geographically complex lineage radiations. However, those same attributes, combined with limited genetic sampling, have impeded precise evolutionary reconstruction of these radiations (though see Gwee et al. [2020] and Manthey et al. [2020]).

Another similar group overlaps with the great speciators: the montane species and lineages that have undergone expansive radiations across archipelagic highlands. This group represents a striking component of island species diversity in the Indo-Pacific that has held longstanding interest for researchers studying the formation of montane biodiversity (Mayr, 1944; Mayr & Diamond, 1976, 2001; Rensch et al., 1930; Stresemann, 1939). The rapid mountain colonizations inferred for these species seem doubly improbable because dispersers must overcome both terrestrial lowland and water barriers. The group is therefore central to the question of how past climatic oscillations contributed to modern species distribution patterns via land bridge formation and elevational habitat shifts (Mayr, 1944; Mayr & Diamond, 1976, 2001; Rensch et al., 1930; Stresemann, 1939). Despite this, the great montane island radiations have never been subjected to detailed molecular study.

The island thrush (*Turdus poliocephalus*) is both an archetypal great speciator (Mayr & Diamond, 2001) and one of the most prolific avian colonizers of island mountains (Clement & Hathaway, 2000; Collar, 2005). It is a sedentary species restricted to high montane forest across much of its range, yet it has radiated across islands spanning a 10,000 km distance from Sumatra to Samoa (Clement & Hathaway, 2000; Collar, 2005). Extraordinary differentiation between individual populations belies this evident propensity for inter-island dispersal. With some 50 recognized subspecies, the island thrush is arguably the world’s most polytypic bird (Clements et al., 2019; Gill et al., 2020), and certainly one of the most variably plumaged. Plumage color and pattern variation is both extreme and geographically incoherent, with similar color patterns often shared by widely separated populations (Peterson, 2007). This variation—in addition to variation in sexual dimorphism, body size, and elevational distribution—have confounded interpretation of the island thrush’s evolution. Preliminary molecular work (Batista et al., 2020; Jones & Kennedy, 2008; Nylander et al., 2008; Voelker et al., 2007) has left open the question of whether the island thrush is even monophyletic, or an artificial assemblage of unrelated forms.

For this study, we conducted a comprehensive sampling of island thrush populations, both living and historically extinct, and additionally sampled its hypothesized sister clade (Nylander et al., 2008; Voelker et al., 2007) from East Asia. We obtained genome-wide shotgun sequencing data and used single nucleotide polymorphisms (SNPs) to reconstruct the island thrush’s phylogeny, population structure, gene flow, and demographic history. This approach allows us to reveal, in unprecedented detail, the evolution of a great speciator.

Methods

Methods are briefly summarized here; the full Methods section is found in Supplementary File 6. We genetically sampled 71 individuals representing 48 of 50 island thrush subspecies, as well as five close relatives from East Asia. We generated resequencing data using an Illumina platform, and mapped the cleaned reads to a new *de novo* reference genome assembly of a common blackbird (*Turdus merula*). ANGSD (Korneliussen et al., 2014) was used to generate a genotype likelihood dataset of 8.5 million SNPs, and we used SAMtools v.1.4 and BCFtools v.1.5 (Danecek et al., 2021; Li et al., 2009) to generate a second dataset of hard genotype calls (0.6 million SNPs). We constructed genome-wide phylogenetic trees from pairwise distances and from pairwise F_{ST} using neighbor-joining (Saitou & Nei, 1987), performed a maximum likelihood phylogenetic analysis with IQ-TREE v.1.6.10-omp-mpi (Nguyen et al., 2015), and also conducted a Bayesian phylogenetic analysis of mitogenome data with BEAST v.1.8.4 (Drummond et al., 2012). Population structure and heterozygosity levels of the island thrush were analyzed using PCAngsd (Meisner & Albrechtsen, 2018) and ANGSD, respectively. The demographic histories of the island thrush and its relatives were inferred using the pairwise sequentially Markovian coalescent method (PSMC; Li & Durbin, 2011). We carried out additional analyses related to the island thrush’s mode of colonization and the evolution of sexual dichromatism within the species.

Results

Phylogenetic analyses

Phylogenetic analysis of SNP data

All three genome-wide phylogenetic trees built using SNP data recover the island thrush as monophyletic (Figure 1, Supplementary Figures S3 and S4). The topologies recovered by the pairwise distance (Figure 1) and pairwise F_{ST} (Supplementary Figure S3) analyses differ in some details. The pairwise distance tree shows a sequential branching pattern that indicates an origin in the Philippines, an expansion through the Greater Sundas and Wallacea, and further eastward colonization of the Pacific via New Guinea. The pairwise F_{ST} tree is broadly similar but suggests a more general western origin not necessarily centered in the Philippines. The maximum likelihood analysis (Supplementary Figure S4) recovers a topology of the island thrush very similar to the pairwise distance tree (Figure 1), and also indicates an origin in the Philippines. The most important differences are in the relationships of the island thrush’s close relatives and the arrangement of its earliest-branching clades.

Our reporting of the results of the phylogenetic analyses focuses mostly on the pairwise distance tree (Figure 1), calculated using the full 8.5 million SNP dataset. F_{ST} trees reflect differentiation due to intra-population genetic drift along each lineage. The pairwise distance tree provides a more direct estimate of phylogenetic distances, i.e., without confounding by intra-population drift. Unlike the pairwise F_{ST} tree, the pairwise distance tree strongly indicates a Philippine origin for the island thrush, which is supported by the maximum likelihood analysis (Supplementary Figure S4), by cross-population heterozygosity levels (Results: Population structure and heterozygosity levels) and by the demographic reconstructions (Results: Demographic history inference using PSMC). The pairwise distance tree and the maximum likelihood tree have high nodal support values, and the few nodes with < 100% bootstrap support appear to represent recent divergences between geographically proximate populations.

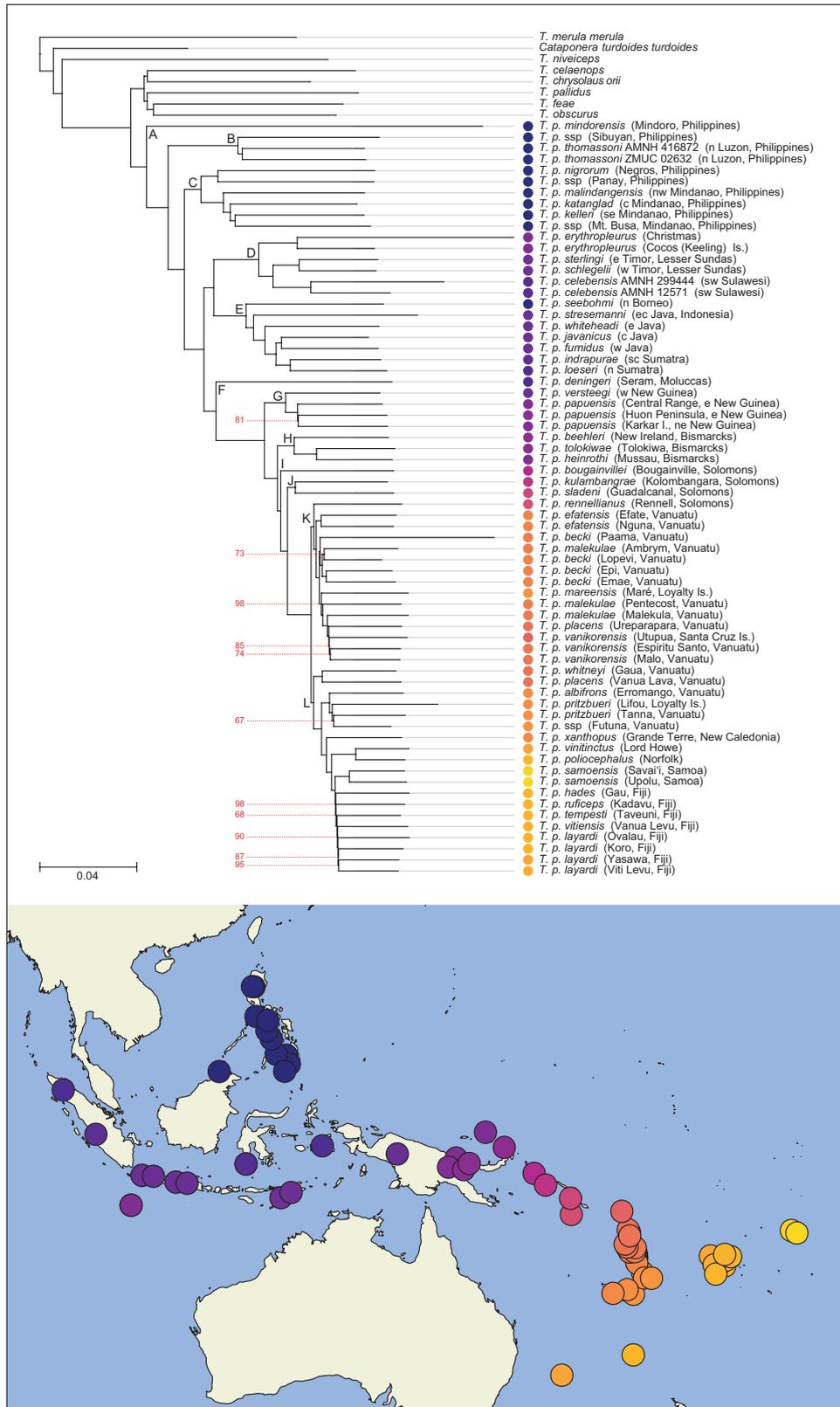


Figure 1. Phylogeny estimated from pairwise distances using neighbor-joining followed by subtree pruning and regrafting (top). Red lines indicate nodes with bootstrap support < 100% (from 100 non-parametric bootstrap replicates). Letters at nodes indicate clades referred to in the text. Island thrush individuals are colored by distance to a reference point at 30° N, 120° E, reflecting a hypothetical East Asian distribution of the species' mainland ancestor. The same colors are used to mark sampling localities on the map (bottom).

Five East Asian species constitute the sister clade of the island thrush. This in turn contains two subclades. The first contains *Turdus chrysolais* and *T. celanops*, which together have a breeding

range encompassing Japan, Sakhalin, and the Kuril Islands. The second contains *T. pallidus*, *T. feae*, and *T. obscurus*, which breed mostly in mainland East Asia. All phylogenetic analyses in this

study recover this five-species sister clade except for the maximum likelihood analysis (Supplementary Figure S4), which arranges the five taxa along four sequential branches below the base of the island thrush clade.

Detailed maps are provided in Supplementary Figure S5a–c showing the geographic distribution of island thrush populations and their phylogenetic relationships as recovered by the pairwise distance analysis. Island thrush Clades A, B, and C (Figure 1) are composed of populations from the Philippines. Clade A represents the Mindoro population, *T. p. mindorensis*. Clade B contains *T. p. thomassoni* from northern Luzon and an undescribed population from Sibuyan. Clade C contains (1) a subclade from the central Philippines islands of Negros (*T. p. nigrorum*) and Panay (undescribed); and (2) four populations from disjunct mountain ranges across Mindanao, including an undescribed population from Mt. Busa in the island's far south.

In Clade D, *T. p. erythropleurus* of Christmas Island in the Indian ocean is sister to a Wallacean group including *T. p. celebensis* from Sulawesi and two sister taxa on Timor. Clade E spans the Greater Sundas islands of Borneo, Java, and Sumatra. The Bornean population (*T. p. seebohmi*) is sister to the rest of the subclade, and Sumatran populations are embedded among Javan populations. The overall pattern indicates a southward spread from Borneo into eastern Java, followed by westward colonization across Java and into Sumatra.

Further eastward colonization into New Guinea appears to have proceeded via Seram in the Moluccas, represented by *T. p. deningeri* (Clade F). The relationships of *T. p. deningeri* with populations further west suggest that the island thrush may have crossed Wallace's Line twice—either two eastward colonizations or an eastward colonization followed by a westward back-colonization.

More recently, four clades diverged representing populations from New Guinea, the Bismarck Archipelago, and the Solomon Islands. Clade G contains New Guinea populations; *T. p. versteegi* from the west of the island is sister to more easterly populations, including the small offshore island of Karkar. Clade H contains populations from the Bismarcks. The uncollected population on the relatively large island of New Britain is not included; and we recover an unexpected sister relationship between the widely separated Tolokiwa and Mussau populations. Clade I comprises the Bougainville population, and Clade J contains populations further southeast Kolombangara and Guadalcanal.

Two large sister clades (Clades K and L) represent broad expansions into the Pacific. Clade K is distributed across southern Melanesia, while Clade L represents an even broader radiation across southern Melanesia, remote Tasman Sea islands, and Samoa. Sister to the rest of Clade K is the population from Rennell in the southern Solomon Islands. The rest of the clade is mostly distributed across Vanuatu, but two populations occur outside Vanuatu's central islands. The phylogenetic position of the extinct *T. p. mareensis* of Maré in New Caledonia's Loyalty Islands is unexpected, as other populations from New Caledonia and the southernmost islands of Vanuatu belong to Clade L. The clade also reaches Temotu, north of Vanuatu (*T. p. vanikorensis*). Plumage variation within Clade K is subtle, and three subspecies are not recovered as monophyletic: *T. p. becki*, *T. p. malekulae*, and *T. p. placens* (the latter including populations both from Clades K and L).

Sister to the rest of Clade L are populations from Gaua and Vanua Lava in the Banks Islands of northern Vanuatu. These populations are oddly interspersed between populations of *T. p. vanikorensis* (Clade K) spanning northern Vanuatu and Temotu. The next clade to diverge represents a distributional leap, encompassing populations in some of the southernmost islands of Vanuatu

(Erromango, Tanna, Futuna), as well the extinct population on Lifou in the Loyalty Islands. Our molecular results suggest that the undescribed Futuna population should be assigned to subspecies *pritzbueri*, which otherwise occurs on Tanna (and previously on Lifou). The next branch of the tree represents the extinct Grande Terre (New Caledonia) population of *T. p. xanthopus*. The remaining branches of Clade L represent the most extreme long-distance colonizations that can be inferred from the island thrush. The first branch represents a colonization of the distant Tasman Sea islands of Norfolk (the nominate subspecies) and Lord Howe (*T. p. vinitinctus*). Both taxa are now extinct. The second branch represents colonization of Fiji, where five subspecies form a clade, and the final branch represents colonization of Samoa (subspecies *samoensis*), which marks the eastern limit of the island thrush's radiation across the Pacific.

Phylogenetic analysis of mitochondrial genome data

The phylogenetic analysis of mitochondrial genome data (Supplementary Figure S6) also recovers the island thrush as monophyletic. The BEAST date estimate for divergence of the island thrush from its five-species sister clade is 2.4 Mya (95% HPD 2.0–2.8 Mya), and population divergence within the island thrush itself is estimated to have begun 1.3 Mya (95% HPD 1.1–1.5 Mya). The tree shows a sequential branching pattern that is roughly similar to the trees built with nuclear SNP data, again indicating a west-to-east stepping stone colonization pattern. However, while most nodes are strongly supported (posterior probability ≥ 0.99), the topology of the mitogenome tree differs in many details from the nuclear trees, reflecting specific patterns of mitochondrial inheritance that are not recovered from the average autosomal tree. For example, the mitogenome tree suggests two separate colonizations of the Philippines. A similar result was obtained by Jones and Kennedy (2008), who conducted a population analysis of the island thrush using the mitochondrial gene ND2. We stress that discordance between the mitochondrial tree and the nuclear trees is not unexpected, as the nuclear data encompass many distinct gene trees. The mitogenome tree does recover the same Greater Sundas/Wallacea/Christmas Island clade as the nuclear trees, as well as the same clade containing populations from New Guinea and all points east. These clades are both dated to about 0.8 Mya, indicating a very rapid radiation out of the Philippines that quickly reached Melanesia.

Population structure and heterozygosity levels

The PCAngsd MAP test suggests that six principal dimensions explain the population structure in the dataset, corresponding to 18.63% of the total variance (Supplementary Figure S7). Genetic correlation between pairs of individuals, which controls for individual variation in heterozygosity, is visualized in the heatmap in Supplementary Figure S8. Ancestry proportions for $k = 2$ to $k = 8$ putative ancestry components are illustrated in Supplementary Figure S9. These analyses suggest a genetic structure for the island thrush with strong differentiation between a western clade (Greater Sundas, Philippines, Wallacea) and an eastern clade (New Guinea and islands further east). The sequential branching pattern of the island thrush tree (Figure 1) implies strongly hierarchical levels of population structure, and the eastern Clades K + L (Figure 1) are heavily oversampled compared to the group's many smaller, early branching clades. This has the effect of overrepresenting variation within the eastern clade, while underrepresenting variation between the other clades. To test this interpretation, we reran the latent mixed-membership model analyses on a dataset that included the outgroup taxa.

This resulting plot (Supplementary Figure S10) shows the outgroup taxa to be homogenous, with a single common ancestry component for $k = 2$ to $k = 6$ ancestors, despite their deep divergences. The ingroup analysis (Supplementary Figure S9) suggests mixed ancestry in a number of populations, notably *T. p. mindorensis* (Mindoro, Philippines), *T. p. deningeri* (Seram, Moluccas), *T. p. seebohmi* (Borneo), *T. p. stressemanni* (east-central Java), and many populations in the islands east of New Guinea. While ascertainment bias due to uneven sampling and hierarchical levels of population structure are potentially problematic (Lawson et al., 2018; Puechmaille, 2016), explicit tests for gene flow using *D*-statistics (Results: Gene flow) support multiple gene flow events. Heterozygosity levels of individuals are visualized in Figure 2; there is a broad pattern of west-to-east decline, and levels tend to be higher in populations from larger islands.

Gene flow

Of the 67,525 calculated $D_{ij}(C)$ statistics, 15,055 are significant at FWER < 0.05 (Figure 3). The results indicate widespread ancient and recent gene flow within the island thrush and its five-species sister clade. Gene flow across early branches of the tree has in many cases left a visual pattern (Figure 3) of long rows of similarly shaded cells, with the genetic signature of early admixture

being inherited by descendent populations. Ancient gene flow is inferred within the island thrush’s sister clade, and also between members of this sister clade and the ancestral island thrush lineage. This is particularly evident in e.g., *T. pallidus*, and in the last common ancestor (LCA) of *T. celaenops* and *T. chrysolaeus*. Ancient gene flow is also inferred within the island thrush itself. We detected substantial admixture between the ancestral lineages that gave rise to populations in (1) the Greater Sundas, (2) Wallacea, and (3) islands from the Moluccas east to Polynesia. Admixture is also widespread among the deeper ancestral nodes of the clades representing populations east of New Guinea (Clades H–L in Figure 1). The results further indicate many instances of more recent gene flow between island thrush populations. Recent gene flow is much more prevalent among populations east of New Guinea, with gene flow inferred between several populations in the Bismarcks and Solomons (e.g., *T. p. heinrothi* and *T. p. beehleri*), and on many occasions between Clades K and L in the far east and south of the island thrush’s range. The few cases of inferred recent gene flow among western populations include those between e.g., *T. p. katanglad* (central Mindanao) and *T. p. malindangensis* (northwest Mindanao); and between *T. p. stressemanni* (east-central Java) and the LCA of *T. p. javanicus* and *T. p. fumidus* (west and central Java).

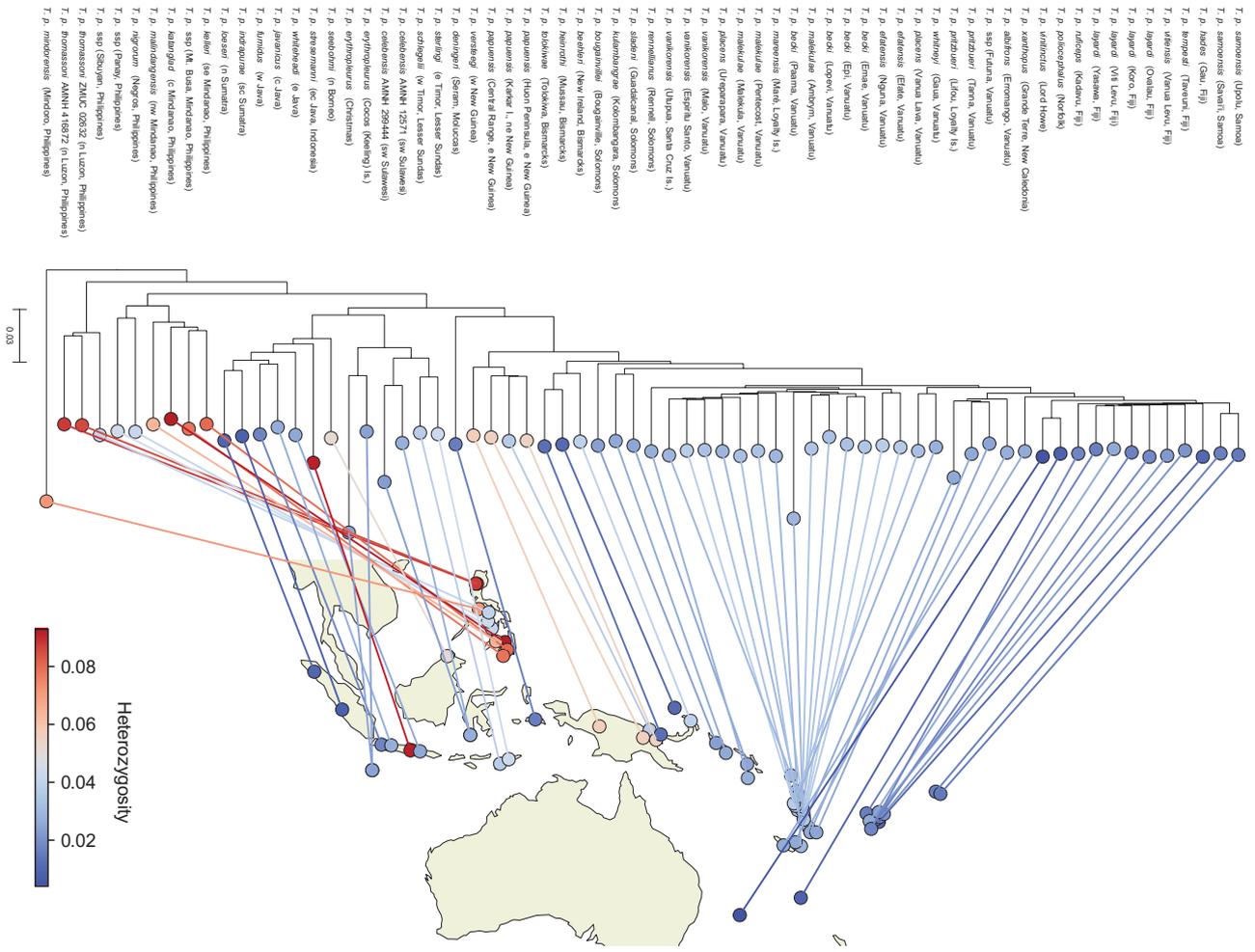


Figure 2. Heterozygosity levels of individuals, overlaid upon the pairwise distance tree. Lines connect leaf nodes to the geographic origin of the individual; crossing of lines has been reduced by sorting the left and right branches of internal nodes by the mean longitude of their respective leaf nodes. The overall pattern suggests a serial founder effect from a radiation that proceeded from the Philippines.

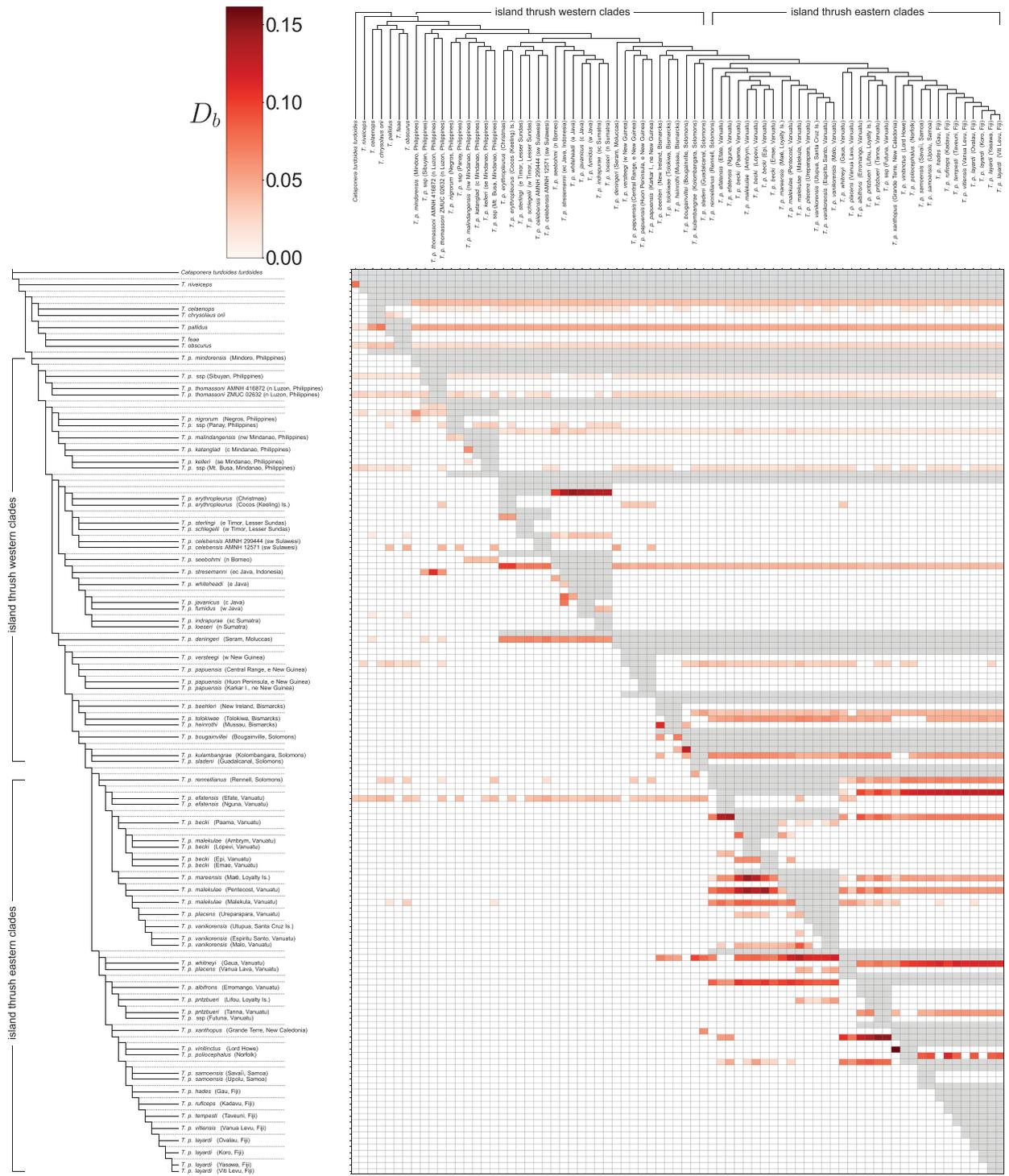


Figure 3. Tree violating branches and potential gene flow. The $D_b(C)$ statistic, analogous to the $f_b(C)$ statistic from Malinsky et al. (2018), summarizes the results of all D-statistic tests $D(A, B, C, T. merula)$ that are consistent with the phylogenetic tree (Figure 1). $D_b(C)$ measures excess allele sharing between individual (or ancestral node, indicated with dotted lines) C on the horizontal axis, and the branch of the tree b on the vertical axis (compared with b 's sister clade a). Each grid cell indicates one $D_b(C)$ statistic, where red cells correspond to significant values (more intense red indicates larger $D_b(C)$ values), white cells are non-significant, and gray corresponds to cells for which no statistic is consistent with the phylogenetic tree. Brackets indicate the island thrush's western clades (Clades A–J in Figure 1) and eastern clades (Clades K and L in Figure 1).

Patterns for certain populations suggest unlikely gene flow events. For example, the pattern for *T. p. efatensis* (Efate, Vanuatu) implies numerous individual admixtures with most eastern island thrush populations, as well as the island thrush's sister clade. This often occurs when two individuals from the same population (or two very closely-related populations) were sampled.

In pairs belonging to *T. p. thomassoni*, *T. p. erythropleurus*, *T. p. celebensis*, and the aforementioned *T. p. efatensis*, one member of the pair shows an unrealistic pattern of gene flow, while the other does not. The individuals that constitute these pairs differ from one another quite markedly in data quality (Supplementary File 4). To test whether these disparities in data quality influenced

the results, we reran the analysis without the four lower-quality individuals from the aforementioned pairs: *T. p. thomassoni* (AMNH 416872), *T. p. erythropleurus* (AMNH 768697), *T. p. celebensis* (AMNH 299444), and *T. p. efatensis* (AMNH DOT 21349). However, the results (Supplementary Figure S11) were nearly identical to those obtained in the original analysis (Figure 3).

Demographic history inference using PSMC

We used PSMC to infer the demographic histories of 60 individuals, representing 38 island thrush subspecies and six outgroup taxa (including *T. [poliocephalus] niveiceps*). We excluded individuals with sequencing depth < 10 ($n = 16$). The generated plots are presented in Figure 4 and Supplementary File 5. The analyses cover the time period from c. 10 Mya to 10 Kya; the dates and effective population sizes (N_e) reported here should be considered approximate, and reflective of temporal patterns of coalescent intensity (reflecting population structure), rather than census population sizes. However, the points at which PSMC curves diverge for different species correspond closely with the divergence time estimates from our mitochondrial genome tree (Supplementary Figure S6), and this guides our interpretation of the PSMC plots.

The common ancestral lineage had an estimated N_e of 600,000 individuals in the late Miocene. The outgroup taxon *T. merula* diverged from this lineage at 5–6 Mya, and maintained a fluctuating N_e of 200,000 to 1,000,000 until 10 Kya. The outgroup taxon *T. niveiceps* then diverged from the island thrush ancestral lineage at c. 5 Mya, and maintained a fairly stable effective population size of 300,000–700,000 until 10 Kya. The ancestral island thrush lineage increased steadily from that point. The island thrush diverged from its sister clade at 2 Mya, which coincides with a N_e peak at 1,000,000. Species within the sister clade experienced a continued rise in N_e before diverging from one another slightly before 1 Mya. The island thrush's N_e dropped steeply from its peak at 2 Mya. Philippines populations' N_e curves started to subtly diverge at 1 Mya, and declined at a lower rate than the remainder of the island thrush lineage. Non-Philippines island thrushes declined steeply until reaching a low N_e of 50,000–60,000 at 300 Kya. Western clades began to stabilize slightly earlier than eastern clades, but this subtle pattern should be interpreted with due caution bearing in mind the limitations of PSMC at recent timescales (Li & Durbin, 2011).

The curves present a very consistent overall pattern from 10 Mya to c. 300 Kya. The loss of concordance between 300 and 10 Kya likely reflects (1) that many populations were following variable individual trajectories at this point; and (2) that PSMC is unable to adequately resolve very recent coalescent events (Li & Durbin, 2011).

Geographic distance vs. genetic distance

We found a significant positive relationship between geographic distance and genetic distance (Supplementary Figure S12; $r^2 = 0.47$, $p < .001$), indicating isolation by distance (Slatkin, 1987, 1993) and supporting a stepping stone mode of colonization (Cibois et al., 2011; Irestedt et al., 2013).

Colonization in light of Pleistocene land bridge formation

Populations with inferred Pleistocene land bridge connections share close phylogenetic relationships, indicating that Pleistocene cooling aided inter-island colonization (Supplementary Figure S13).

Sexual dichromatism

Sexually dichromatic populations are scattered across the island thrush tree (Supplementary Figure S14), indicating that sexual dichromatism was gained and lost on numerous occasions.

Discussion

The island thrush represents a monophyletic island radiation that rapidly acquired its expansive geographic distribution within an estimated 1.3–2.4 million years. Its extreme plumage variation has obscured a biogeographically intuitive west-to-east stepping stone pattern of colonization from the Philippines through the Greater Sundas, Wallacea and New Guinea to Polynesia. With an aim to better understand the nature of archipelagic radiations and how they generate biodiversity, we here discuss the island thrush's evolutionary origins, spatiotemporal radiation, population admixture, demographic history, and ecological and morphological variability.

Evolutionary and geographic origins

The island thrush evolved from a clade of migratory *Turdus* thrushes with Palearctic/Sino-Himalayan breeding distributions (Batista et al., 2020; Nylander et al., 2008). Its probable sister clade comprises five East Asian species (Figure 1, Supplementary Figures S3, and S6; alternative arrangement in Supplementary Figure S4) that range from short-distance partial migrants to long-distance migrants (Collar, 2005). Four of five of these species are wholly or partly restricted to mountains within their breeding ranges (Collar, 2005). Given this evolutionary background, the island thrush's preference for cool (montane) habitat, and its evident ability to move across long distances, can be considered ancestral traits. The island thrush diverged from its continental sister clade c. 2.4 Mya, and began diversifying across the Indo-Pacific archipelagos c. 1.3 Mya (Supplementary Figure S6). Our results indicate that the first extant populations to be established were those from the Philippines, which correspond to the deepest splits in the tree (Figure 1). How the ancestral island thrush reached the Philippines is unclear. Given that its ancestors were likely Palearctic migrants, and that two species from its sister clade winter in the Philippines, it is possible that colonization occurred via settling down of wintering birds (Rolland et al., 2014). Alternatively, a non-migratory ancestor from East Asia or a now-extinct ancestral population from the Greater Sundas may have colonized the Philippines (Diamond & Gilpin, 1983; Jones & Kennedy, 2008). An entry into the Philippines via Mindoro could be inferred from the pairwise distance analysis, which recovers *T. p. mindorensis* as sister to the rest of Island Thrush (Figure 1). However, the sampled individual from Mindoro yielded relatively low-quality data (Supplementary File 4), and its position relative to the other Philippines clades is recovered slightly differently in each of our phylogenetic analyses (Figure 1, Supplementary Figures S3, S4, and S6).

Spatiotemporal dynamics of the radiation

Diversification of the island thrush occurred during the second half of the Pleistocene, starting c. 1.3 Mya (Supplementary Figure S6). This is in line with dating estimates for other great speciators, which also radiated explosively during the Pleistocene (Andersen et al., 2013, 2014, 2015; Irestedt et al., 2013; Jönsson et al., 2014; Kearns et al., 2020; Moyle et al., 2009; Pedersen et al., 2018). The sequential branching pattern of the island thrush tree (Figure 1) suggests that it expanded across most of its range following a stepping stone colonization path. Starting in the Philippines, it expanded into the Greater Sundas and Wallacea, colonized New Guinea and islands of Northern Melanesia, and then underwent overlapping radiations in southern Melanesia. In one of these radiations (Figure 1, Clade L), the pattern of incremental advances gives way to long-distance oversea dispersals to reach far-away outposts

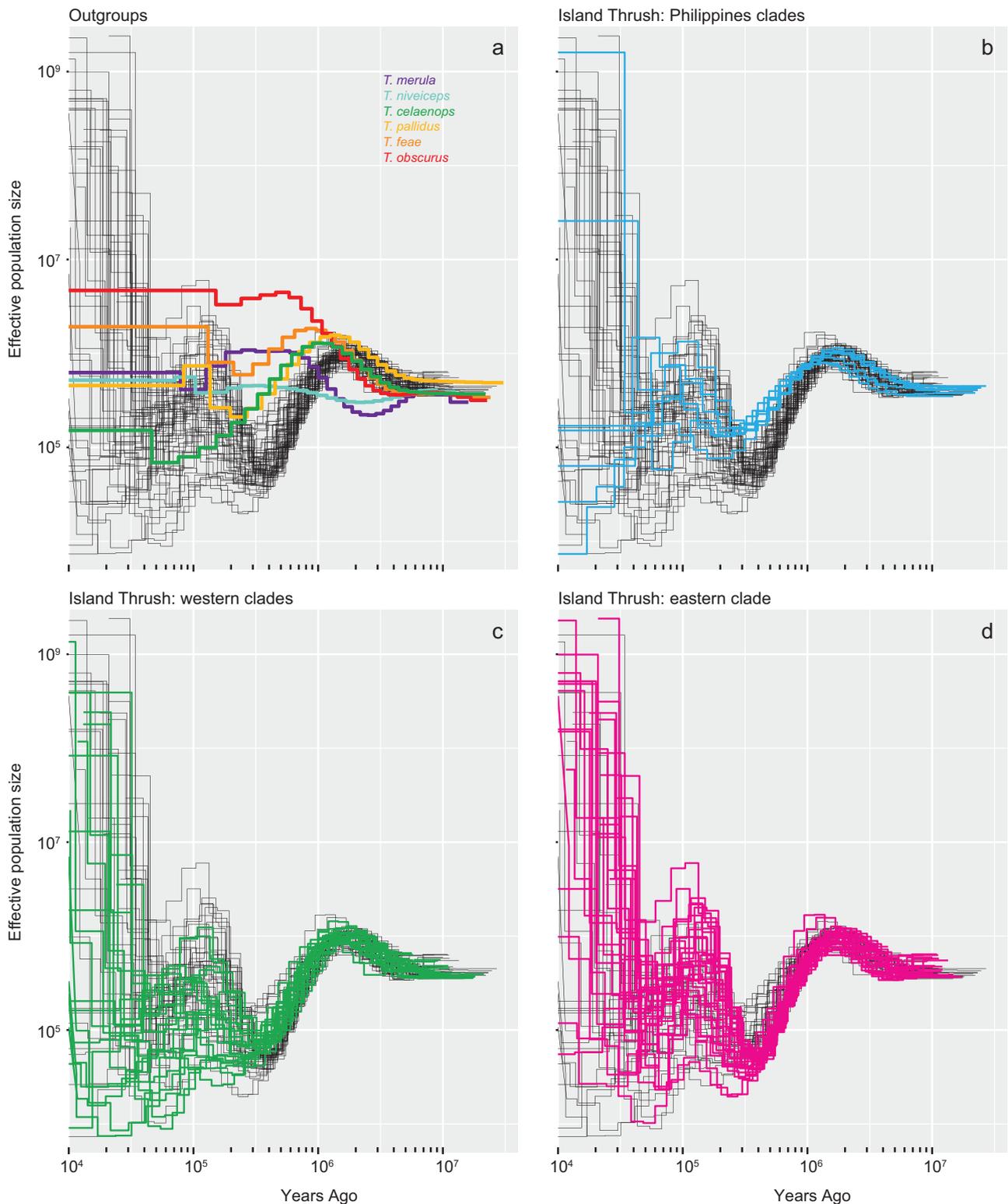


Figure 4. Pairwise sequentially Markovian coalescent (PSMC) plots illustrating demographic changes (effective population size; N_e) over time for the island thrush and related *Turdus* thrushes. Generation time is set at two years. The four panels show curves from all island thrush individuals analyzed (black lines, with groups of interest highlighted in color). (A) highlights outgroups; *T. celanops*, *T. pallidus*, *T. feae*, and *T. obscurus* belong to the island thrush's East Asian sister clade. (B) highlights Philippines populations, inferred to be those earliest established. (C) highlights all western clades outside the Philippines (Clades D–J in Figure 1), as far east as the Solomons; and (D) highlights the large eastern clade spanning southern Melanesia, Tasman Sea islands, and Polynesia (corresponding to sister clades K and L in Figure 1). Individual N_e trajectories show little consistency more recently than c. 300 Kya, and within this recent timespan there is no clear west vs. east regional pattern, or montane (C) vs. lowland (D) pattern.

in the Tasman Sea, Fiji, and Samoa. The overall stepping stone colonization process is supported by our regression analysis showing a positive relationship between geographic and genetic distance

(Supplementary Figure S12). A similar pattern has been found for some other Indo-Pacific bird radiations (Cibois et al., 2011; Irestedt et al., 2013; Pedersen et al., 2018), but not all (Ericson et al., 2019).

Many of the islands that the island thrush inhabits have never shared subaerial connections (Supplementary Figure S13), so it is clear that repeated oversea colonizations have driven its current distribution. Nevertheless, water barriers have impeded its dispersal, and land bridge formation via Pleistocene cooling facilitated colonization. This is evident from the findings that populations are usually most closely related to other populations from the same island, and that populations connected by land bridges during Pleistocene glacial periods are in all cases closely related (Supplementary Figure S13). We find that the downslope expansion of montane forest habitat during the Pleistocene (Garg et al., 2020; Hewitt, 2000) did not connect different populations on the same island (e.g., Mindanao, Greater Sundas, New Guinea) sufficiently to erase relatively deep genetic structure among them (Supplementary Figure S6).

Gene flow between populations

The island thrush's impressive dispersal capacity allowed it to repeatedly colonize new islands, but has also led to extensive admixture between established populations (Figure 3). In western populations (Clades A–G in Figure 1), most gene flow events appear to date back to the early phases of the radiation, when there was also admixture with the species' East Asian sister clade. Gene flow between island populations to the east and south of New Guinea (Clades H–L in Figure 1) is more recent and widespread. The many instances of gene flow between different branches of the island thrush phylogeny can help explain why topological inconsistencies exist across the phylogenetic trees (Figure 1 Supplementary Figures S3, S4, and S6).

The gene flow patterns provide new insight into the paradox of the great speciators (Diamond et al., 1976). A prominent hypothesis is that great speciators possess a uniformly moderate capacity for dispersal that is sufficient for colonization of new islands, but not sufficient for genetic and phenotypic homogenization across established populations (Diamond et al., 1976; Mayr & Diamond, 2001). This is not the case in the island thrush: in recent times, population admixture and colonizations across deep-water barriers are much more frequent in eastern populations than in western populations. Another hypothesis is that the dispersal capacity of great speciators changes over time, usually imagined as an initial burst of rapid colonization followed by a sedentary phase of differentiation (Diamond et al., 1976). This model does not fit the island thrush as a whole, again because of the different dispersal patterns of eastern and western populations. The island thrush radiation might be better characterized as a rapidly advancing colonization front that leaves more sedentary populations in its wake. This is a dynamic seen (at much shorter timescales) in the spread of the invasive cane toad (*Rhinella marina*) across Australia (Phillips et al., 2007), where high dispersiveness is selected for at the edge of the expansion (Phillips et al., 2010). A similar mechanism could operate in the island thrush, assuming that island populations are founded by exceptionally dispersive individuals, but that dispersiveness is selected against in established populations because oversea dispersers leave those populations.

Demographic history and genetic variation

The demographic history of the island thrush, and the modern genetic variation shown by its constituent populations, further elucidate its stepping stone colonization across the Indo-Pacific. The PSMC analyses (Figure 4) imply that the lineage that spawned the island thrush and its sister clade experienced continuous growth in effective population size (N_e) during the Pliocene and early Pleistocene, before diverging c. 2 Mya. This build-up

was likely accompanied by range expansion across East Asia, as reflected by the clade's current broad distribution across the region. As part of this expansion, the island thrush entered the Indo-Pacific archipelagos and experienced a steep N_e decline as gene flow with the continental lineage was lost. A similar rise-and-fall N_e dynamic is seen in *T. celanops*, which colonized isolated Japanese islands (Figure 4a), and in the snowy-browed flycatcher (*Ficedula hyperythra*) (Pujolar et al., 2022), another passerine super-colonizer of island mountains with likely origins on the Asian mainland (Moyle et al., 2015). This pattern suggests that mainland population build-up can trigger archipelagic radiations. The oldest island thrush populations in the Philippines declined less steeply than other groups (Figure 4b); this is likely because populations that were established earlier could regenerate genetic diversity earlier. Similarly, remaining western populations slowed their decline slightly earlier than eastern populations (Figures 4c, 4d), although this pattern is subtle and is seen at a recent time interval where inference by PSMC is less reliable (Li & Durbin, 2011). The substantial increases estimated for most populations starting c. 300 Kya (with some N_e estimates exceeding one billion) are technical artifacts reflecting the limitations of the dataset and of the PSMC method at recent timescales (Li & Durbin, 2011; Nadachowska-Brzyska et al., 2015, 2016); most modern populations actually have low heterozygosity levels.

Heterozygosity levels of modern island thrush populations (Figure 2) can be understood in light of the serial founder effect (Ramachandran et al., 2005). The oldest populations in the Philippines show the highest heterozygosity, probably retained in large part from the ancestral continental lineage. Repeated colonizations (and founder events) resulted in a general west-to-east pattern of decreasing heterozygosity. Most deviations from this pattern can be explained by island size (e.g., regionally low heterozygosity in small central Philippines island populations and regionally high heterozygosity in the large island of New Guinea). The most conspicuous exception to the overall pattern is the remarkably high heterozygosity of *T. p. stresemanni* of east-central Java, contrasted against the exceptionally low heterozygosity of the other six Javan and Sumatran subspecies. The analyses of population structure (Supplementary Figure S9) and gene flow (Figure 3) both suggest that this is due to admixture of *T. p. stresemanni* with the island thrush lineage now inhabiting the northern Philippines.

Elevational distribution

The island thrush is mostly restricted to mountains in the western part of its range from Sumatra to the Solomons. Here it rarely occurs below 1000 masl, but it reaches sea level on Christmas Island in the Indian Ocean, Mussau in the Bismarck Archipelago, and Rennell in the southern Solomon Islands (Beehler & Pratt, 2016; Coates & Bishop, 1997; Dutson, 2011; Kennedy et al., 2000; MacKinnon & Philipps, 1993). By contrast, it occurs down to sea level, or nearly so, on the generally small and low islands in the Tasman Sea, southern Melanesia, and Polynesia (Collar, 2005; Dutson, 2011; Pratt et al., 1987). Preference for cool (montane) climates can be regarded as an ancestral trait, based on the ecology of the island thrush's close relatives (see above), and because montane populations correspond to the deepest splits in the island thrush phylogeny (Figure 1). Following this interpretation, its variable elevational distribution is the result of three individual shifts (or expansions) into the lowlands (on Christmas Island, Mussau, and islands south and east of the core Solomons). However, disentangling the mechanisms driving the island thrush's elevational distribution is not straightforward. Diamond

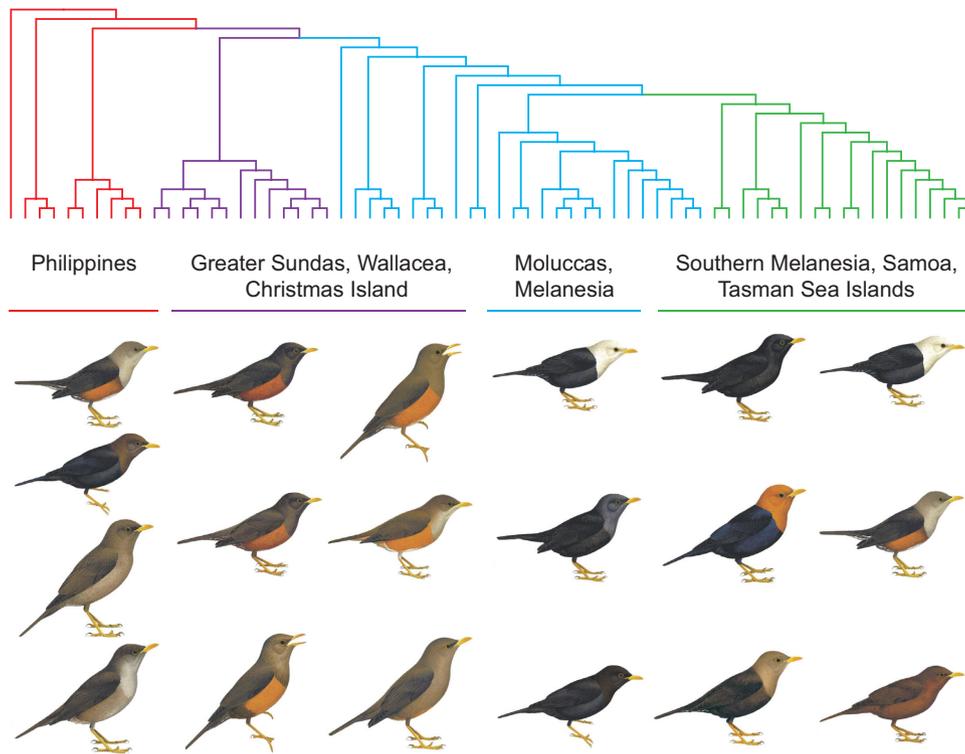


Figure 5. Plumage variation in light of phylogeny and geography. Tree topology matches that in Figure 1. A selection of subspecies encompassing the range of male plumage variation found within each of four geographic groups are shown (illustrations: Lynx Edicions). The tree is colored to indicate the phylogenetic positions of those groups. The illustration of *T. p. albifrons* was used to represent the similar-looking *T. p. deningeri*, and the illustration of *T. p. mindorensis* was used to represent the similar-looking *T. p. layardi*.

(1975) argues that populations' elevational ranges are governed by diffuse competition, being pushed into the mountains on islands with high bird species richness in the lowlands. However, those isolated islands with impoverished bird faunas (e.g., southern Melanesia, Tasman Sea Islands, Polynesia) also lack key nest predators such as *Rattus* rats and *Boiga* snakes, or did at least prior to anthropogenic introductions. An alternative explanation is therefore that nest predation pressure restricts some populations to mountains (Boyle, 2008; Jankowski et al., 2013; Skutch, 1985), which could explain the susceptibility of lowland island thrush populations to introduced rats (Collar, 2005; Villard et al., 2019). Either mechanism could explain the island thrush's striking absence from Australia, which is highly biodiverse but mostly lacks tall mountains.

Plumage color

Phylogenetic relationships alone do not explain the complex color variation in the island thrush, as populations that are not closely related often show convergent plumage types (e.g. *T. p. deningeri* of the Moluccas and *T. p. albifrons*/*T. p. pritzbueri* of southern Melanesia). Nevertheless, there is phylogenetic signal in its range-wide (male) plumage variation (Figure 5). The three major clades from the Philippines represent some of the oldest populations (Figure 1) and encompass a few distinct plumage types. Populations from the Greater Sundas, Christmas Island, and Wallacea west of Seram (Clades D and E in Figure 1) are dark brown birds that vary primarily in the extent of reddish coloration of the underparts. The Seram population marks a shift to blackish body plumage, but has a white head. Overall blackish plumage—with varying degrees of white in the vent and undertail coverts—is common to most of the rest of the complex, from New Guinea to southern Melanesia. The striking exception from

this pattern is the eastern Clade L (Figure 1), which encompasses massive plumage variation, even among geographically and genetically similar Fiji populations. Based on this clade's broad distribution in the Pacific, it is exceptionally dispersive, but it is not clear if or how this might be related to the pronounced variation in plumage. Overall, plumage variation is a poor proxy for phylogenetic distance in the island thrush.

The phylogenetic relationships of island thrush populations reveal numerous gains and losses of sexual dichromatism (Supplementary Figure S14). These transitions appear to occur haphazardly across the tree, having no obvious association with geographic region, island size, or elevational range. All members of the island thrush's sister clade are sexually dichromatic (Collar, 2005), as are most members of the broader Palearctic *Turdus* clade that it belongs to (Batista et al., 2020). Together with the fact that sexual dichromatism in the island thrush is mostly weak (Peterson, 2007), this is consistent with a general pattern that island populations are less sexually dimorphic than their congeneric mainland populations (Badyaev & Hill, 2003; Omland, 1997). The seemingly random appearance and disappearance of sexual dichromatism may be attributable to repeated founder effects (Kearns et al., 2020; Omland, 1997).

Conclusion

Our study provides a detailed phylogenetic reconstruction of a great speciator. We demonstrate that the island thrush represents one of the most simultaneously explosive, expansive, and phenotypically diverse radiations among birds. The island thrush evolved from Palearctic ancestors and rapidly island hopped across a quarter of the globe, a journey that was facilitated by Pleistocene land bridge formation, but driven by repeated oversea dispersals.

This stepping stone colonization left a clear signature of declining genetic variation from west to east. While representing extreme aspects of an archipelagic radiation, the island thrush provides a useful model for understanding Pleistocene interchange between Eurasian and Australo-Papuan faunas, and the role of mountains as pathways for temperate lineages to enter the tropics.

Supplementary material

Supplementary material is available online at *Evolution Letters* (<https://academic.oup.com/evlett/qrac006>)

Data availability

Raw Illumina sequences and the *Turdus merula* genome assembly are deposited in the NCBI Sequence Reads Archive (SRA) under the BioProject accessions PRJNA747885 and PRJNA747882, respectively.

Author contributions

A.H.R. and K.A.J. conceived the study. All authors contributed to build the dataset. A.H.R., G.G., F.R., and K.A.J. developed the analytical framework. G.G., M.P.K.B., B.P., P.G.P.E., and F.R. performed bioinformatics. G.G., J.M.P., and P.G.P.E. performed the phylogenomic analyses with input from A.H.R., F.R., and K.A.J. A.H.R. led the writing, and all authors contributed to the discussion of the results and the writing of the manuscript.

Conflict of interest

The authors declare no conflict of interest.

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