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Tramps in transition: genetic differentiation between populations of an iconic “supertramp” taxon in the Central Indo-Pacific

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Abstract

The island monarch (*Monarcha cinerascens*) was an original example of the “supertramp strategy”. This involves well-developed dispersal specialisation, enabling a species to colonise remote islands but leaving it competitively inferior. Supertramps are hypothesised to be excluded from larger islands by superior competitors. It is the only original Melanesian supertramp to occur in Wallacea, home also to the sedentary pale-blue monarch (*Hypothymis puella*). We interrogate the supertramp strategy and its biogeographical underpinnings by assessing the population structure of these two monarchs. We sampled island and pale-blue monarchs in Wallacea, collecting DNA and morphological data. We investigated monarch population structure by applying ABGD and Bayesian and Maximum Likelihood methods to their ND2 and ND3 genes. We constructed linear models to investigate the relationships between genetic divergence, dispersal ability, and island area, elevation, and isolation. Wallacea’s deep waters restrict gene flow even in a supertramp, as the Wallacean and Melanesian island monarchs are likely separate species (mean genetic distance: 2.7%). This mirrors the split of the pale-blue monarch from Asia’s black-naped monarch (*Hypothymis azurea*). We found further population structure within Wallacean and Melanesian island monarch populations. Their genetic divergence was related to elevation, area, and isolation of islands, as well as dispersal ability of birds. However, dispersal ability was independent of island elevation and area. Rather than being *r*-selected on small, disturbance-prone islands, our results support the view that the island monarch’s supertramp lifestyle is a temporary stage of the taxon cycle, i.e. supertramps may transition into resident species after colonisation. Our models suggest that more dispersive monarchs reach more distant islands, and divergence is promoted on islands that are more distant or larger or more permanent, without selection against dispersal ability *per se*. We suggest that supertramp lifestyle helps determine the distribution of species across islands, not necessarily the divergence occurring thereafter.

Highlights

- This work interrogates and helps to develop a framework that has been influential in biogeography since the 1970s, that of the “supertramp strategy”.
- We were able to integrate DNA, distribution data and morphology for the first time, allowing us to assess both the dispersal ability and population structure of the study populations.
- We found substantial population structure in the island monarch, one of the original examples of a supertramp, suggesting dispersiveness is not maintained after colonisation.
- We found no population structure in the pale-blue monarch, suggesting that it maintains both competitive ability and higher dispersiveness than some other Sulawesi endemics.
- Our findings provide evidence for the view that “supertramp” populations represent incipient species, but not for any clear links between competition and dispersal abilities.

Keywords: Dispersal, island biogeography, Melanesia, Monarchidae, *r* selection, speciation, supertramp strategy, taxon cycle, Wallacea

Introduction

Animals vary in their ability to move or disperse through the environment, and these differences affect not only the range size of individual species (Sheard et al. 2020), but broad patterns of speciation (Smith et al. 2014, Manthey et al. 2020) and even the biogeographic division of life between regions of the Earth (White et al. 2021). The word “supertramp” originated in the autobiography of migrant worker WH Davies, “a free knight of the highway [who] lived like a pet bird on titbits” (Shaw 1908) and was later introduced into the scientific literature by Diamond (1974) to describe the life history strategies of nine bird species with wide distribution ranges, which occur only on small, isolated, or recently defaunated islands. Diamond attributed the life history strategy of these nine supertramps, which he studied on the Bismarck and Solomon islands in Melanesia (Mayr and Diamond 2001), to an extreme form of *r* selection (MacArthur and Wilson 1967), which selects “for dispersal ability and reproductive potential at the expense of competitive ability” (Diamond 1974). Small islands are prone to disturbance and so these conditions would select for highly dispersive birds, but due to their low competitive ability these species would be excluded from larger islands inhabited by stronger competitors (Diamond 1974).

Diamond’s nine supertramps comprised a varied assortment of species: in updated taxonomy (this paper follows Gill et al. 2021) they include three doves (*Ptilinopus solomonensis*, *Ducula pistrinaria*, and *Macropygia mackinlayi*), a kingfisher (*Todiramphus tristrami stresemanni*), and five passerines: one monarch flycatcher (*Monarcha cinerascens*), one white-eye (*Zosterops griseotinctus*), one whistler (*Pachycephala melanura dahlia*), and two honeyeaters (*Myzomela sclateri* and *Myzomela pammelaena*). This disparate grouping allows us to compare supertramps to relatives with contrasting life histories. The “supertramp” label has since been applied to additional Melanesian birds by Mayr and Diamond (2001), and to other birds and non-avian taxa by numerous authors (e.g. Cronk et al. 2005, Balke et al. 2009, Cibois et al. 2011, Pedersen et al. 2018, Le Pepke et al. 2019). The supertramp strategy has been examined using genetic studies on white-eyes (Linck et al. 2016) and cuckoo-shrikes (Pedersen et al. 2018, Le Pepke et al. 2019). Linck et al. (2016) found population structure in the Louisiade white-eye, one of Diamond’s original supertramps, with populations on larger and higher islands the most genetically distinct. In their studies on cuckoo-shrikes, Pedersen et al. (2018) and Le Pepke et al. (2019) found some young taxa to be widespread and undifferentiated. They dubbed these supertramps and contrasted them with older taxa which show greater genetic differentiation between populations. Linck et al. (2016) and Le Pepke et al. (2019) built a case that, rather than being selected for by *r* selection on small islands, the supertramp strategy is temporary and will be replaced by a sedentary lifestyle over time. We sought to build on this view by incorporating data on dispersal ability and

extending it to another of the original supertramps, the island monarch (*Monarcha cinerascens*) (Temminck 1827), using data from Wallacea as well as some of the Melanesian islands where the theory originated.

Most of Diamond’s original supertramps are confined to Melanesia. The island monarch is unique among them in that its range stretches to Wallacea in central Indonesia, a region of deep water between the Sunda and Sahul shelves (Ali and Heaney 2021), full of small and isolated islands (Figure 1). As in Melanesia, the deep waters of Wallacea act as a barrier to the dispersal of many species, offering us a “natural laboratory” (Whittaker et al. 2017) for the study of the movements of this supertramp. Although it is present in both Wallacea and Melanesia, it is absent from New Guinea and other large islands in between, a peculiarly disjunct distribution shared with 23 other dispersive bird species (White et al. 2021). Despite their dispersal abilities, the island monarch and these other 23 species do not occur west of Sulawesi and are thus subject to classical biogeography’s most famous boundary line (Wallace 1863, Ali and Heaney 2021). The “Wallace Line” marks the edge of the Sunda Shelf, suggesting that this boundary between deep and shallow water is significant to even the most dispersive species.

To maintain gene flow across a distribution that spans Wallacea and Melanesia, the island monarch must have the greatest dispersal abilities of all the supertramps considered by Diamond (1974). Alternatively, this apparently wide distribution could be a relic of outdated taxonomy: since Diamond’s work, some of the Melanesian supertramps have been split from Wallacean relatives, like the Melanesian kingfisher (*Todiramphus tristrami*, formerly *Halcyon chloris stresemanni*). Indeed, recent investigations suggest that the island monarch may warrant division into multiple species (Eaton et al. 2021). If the Melanesian and Wallacean island monarchs are separate species, despite their similar appearances (i.e. cryptic species), we would expect them to exhibit genetic divergence equivalent to that between other *Monarcha* species. The identification of such cryptic species is vital to developing a full understanding of biodiversity, in this region and around the world (Fišer et al. 2018). As Wallacea has been relatively little studied, distributions of species in this region have also been unclear. Older distributions for the island monarch (e.g. del Hoyo et al. 2006) marked it as a year-round resident on larger Wallacean islands like Sulawesi and Timor and absent from the smaller Menui (also spelled Manui) and the Wakatobi islands (also called Tukangbesi). Mayr and Diamond (2001) allow for cases where a species exhibits a supertramp distribution in one archipelago, while occurring on both small and large islands in another (this they term a tramp distribution). However, recent work has clarified that the island monarch exhibits a true supertramp distribution in Wallacea, as it does in Melanesia, being resident only on small islands, including Menui and the Wakatobi, and not on larger islands (Martin et al. 2012, Rheindt et al. 2014, O’Connell et al. 2017,

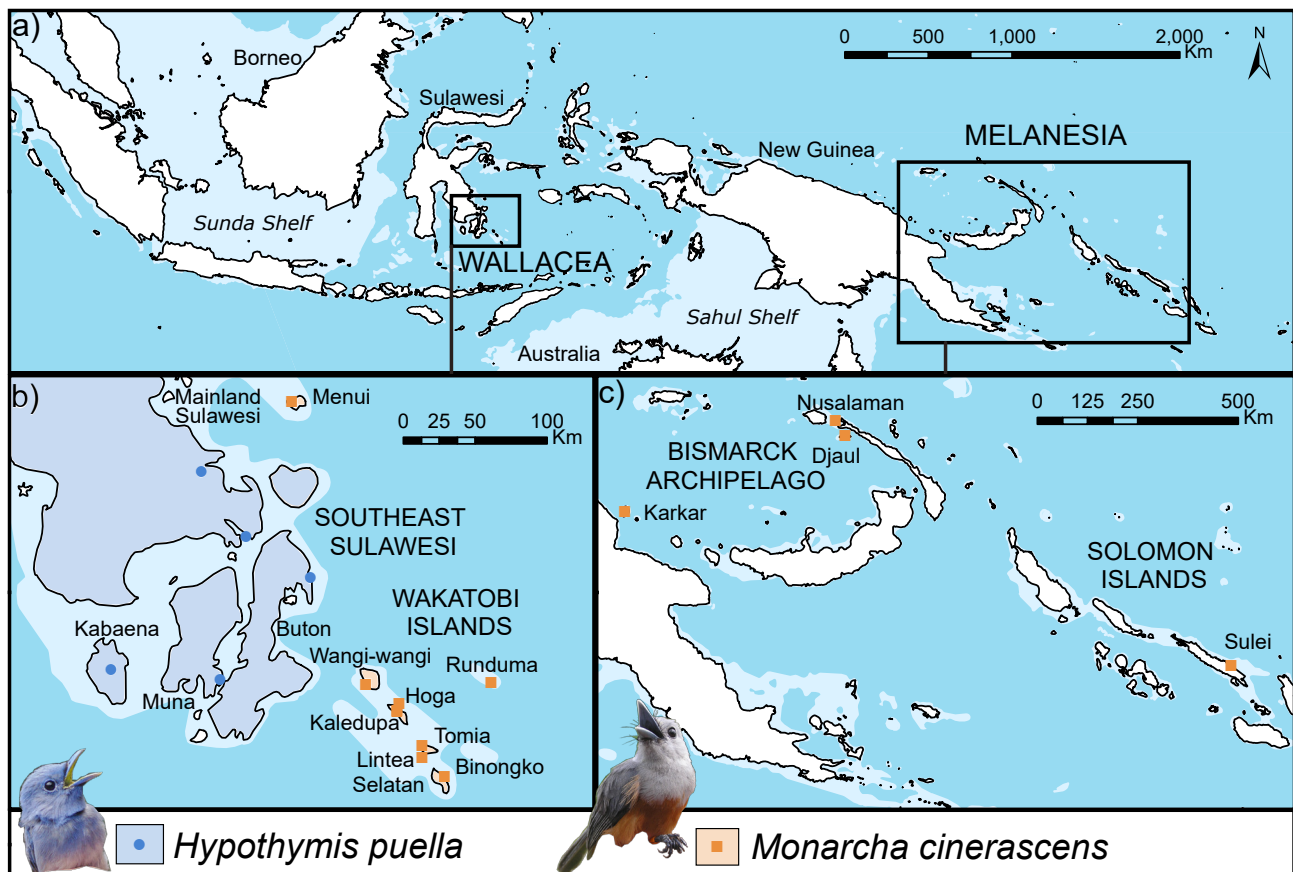


Figure 1. a) Map of the Indo-Pacific with the Wallacea and Melanesia regions labelled. Seas deeper than 200 metres are drawn in a darker blue. b) Map of Southeast Sulawesi and associated islands in Wallacea. Pale-blue monarch range is shown in blue, island monarch range in orange, both based on the authors' observations in the region. Islands where we sampled monarchs are labelled. Pale-blue monarch sampling sites are marked as blue circles, island monarch sampling sites as orange squares. There were no islands on which both species occurred. c) Map of Melanesia. Islands where Andersen et al. (2015a) sampled island monarchs in the Bismarck and Solomon archipelagos are labelled and marked with orange squares. Pale-blue monarch photo taken by Emma Shalvey, island monarch by DJK.

Monkhouse et al. 2018, O'Connell et al. 2019c, O'Connell et al. 2020, Eaton et al. 2021).

Wallacea is famed as a transition zone between Asian and Australo-Papuan faunas (Ali and Heaney 2021). The island monarch, representative of the Australo-Papuan genus *Monarcha*, is joined in Wallacea by the Asian monarch genus *Hypothymis* in the form of the pale-blue monarch (*Hypothymis puella*). This species was described by Wallace (1862), then lumped with the black-naped monarch (*Hypothymis azurea*) by Rand (1970) and split once again by Fabre et al. (2012). This split has been upheld by Gill et al. (2021). The black-naped monarch occurs all over the Sunda Shelf and as far west as India, so this split shows Wallacea's water barriers can block the dispersal of even widespread species. Like many Indo-Pacific bird families, the systematics of monarchs remained unclear until molecular sampling improved in recent years (Andersen et al. 2015a). Andersen et al. (2015a) placed *Hypothymis* and *Monarcha* in two separate clades of the Monarchidae, providing DNA sequences

for four island monarchs from Melanesia. The pale-blue monarch is endemic to a few of Wallacea's larger islands, including Sulawesi and nearby land-bridge islands Kabaena, Muna, Buton, and Wawonii (Figure 1). These islands were all connected to one another, and to the Sulawesi mainland, during geologically recent glaciations (Nugraha and Hall 2018). As the only other monarch in this part of Wallacea, the pale-blue monarch could fill the role of the *K*-selected sedentary competitor excluding the supertramp island monarch from larger islands. Such a role was outlined for other non-supertramp monarch species in Melanesia by Mayr and Diamond (2001) and a similar exclusionary relationship was hypothesised between the whole *Monarcha* and *Hypothymis* genera by Rand (1970).

Unlike the land-bridge satellite islands occupied by the pale-blue monarch, the nearby Wakatobi and Menui islands have been separated from Sulawesi since they first rose from the deep surrounding seas (Nugraha and Hall 2018), although the waters between the Wakatobi islands themselves are shallower

(Figure 1). Deep, permanent water barriers are a key factor in the genetic isolation that leads to the evolution of new species (Wallace 1887), and several endemic bird taxa have been named from the Wakatobi (Hartert 1903, Collar and Marsden 2014, Kelly et al. 2014, O'Connell et al. 2019d). The Wakatobi, being islands of varying shapes, sizes and distances from one another, thus provide an adequate context for testing the relationship between geography and genetic divergence, including the effects of island area, island elevation, and isolation by distance, following the approach of Linck et al. (2016). The four main islands of Wangi-wangi, Kaledupa, Tomia and Binongko (whence the name “WaKaToBi”) all have maximum elevations over 200m and areas 53–155 km², while Lintea Selatan and Hoga are just 8.3 km² and 3.5 km², respectively, and are less than 20m above sea level. Menui is 183km from the Wakatobi.

Across the wide distribution of island monarchs, we hypothesised that genetic divergence would align with one of three general patterns:

Pattern 1. No divergence or limited divergence among populations across the entire species range, offering evidence of exceptional dispersal abilities that facilitate gene flow all the way from Melanesia to Wallacea.

Pattern 2. Two homogeneous sets of populations, one in Wallacea and one in Melanesia, divergent from one another but with little or no divergence within each set.

Pattern 3. Population structure within either Melanesia or Wallacea, or both, as well as genetic divergence between the two regions. This would indicate that the monarchs are not maintaining their dispersiveness after colonising these small islands, in turn suggesting that dispersiveness might not have been a selective response to these disturbance-prone conditions.

Divergence Pattern 1 would make the island monarch an example of “high dispersal facilities leading to a continuous swamping of semi-isolated populations” (Mayr 1942). Either of Patterns 1 or 2 would be in keeping with the original Diamond (1974) description of an archetypal supertramp. Pattern 3 would support an alternative conception, developed from genetic analyses of other supertramp taxa (Linck et al. 2016, Le Pepke et al. 2019), which sees the supertramps not as *r*-selected dispersal specialists, but as incipient species which will lose their dispersal abilities and form new island endemics. This developed from previous work on another class of highly dispersive birds, the “great speciators” (Moyle et al. 2009). In Divergence Pattern 3, supertramp status is not a permanent strategy but could instead be an early stage of the “taxon cycle” (Wilson 1959, 1961, Ricklefs and Bermingham 2002) of colonisation followed by range contraction (Le Pepke et al. 2019). The wider *r*-/*K*-selection hypothesis on which the supertramp theory was based has also evolved: where MacArthur and Wilson (1967) popularised a continuum of *r* selection

in disturbance-prone environments to *K* selection in stable ones, this has since developed into a broader understanding of life-history strategies influenced by multiple factors (e.g. Reznick et al. 2002).

As the pale-blue monarch is endemic to land-bridge islands in Wallacea, any genetic structure across this range would characterise it as a markedly non-dispersive bird. The Southeast Sulawesi land-bridge islands were connected by land relatively recently in geological history (Nugraha and Hall 2018), and most birds have uniform populations across all of these islands (O'Connell et al. 2019a, O'Connell et al. 2019d), but there are exceptions (Robinson-Dean et al. 2002, Ó Marcaigh et al. 2021a, Ó Marcaigh et al. 2021b). Thus, strong genetic structure across its range in Wallacea would indicate that this sedentary, *K*-selected monarch, which appears to exclude the island monarch from these larger islands, has been subjected to strong selection against dispersal. This would support the broader theory around supertramp taxa. In contrast, an unstructured population would provide no evidence for a connection between competitive ability and dispersiveness. The inclusion of the pale-blue monarch also serves as a “control” for the confounding effects of mischaracterized geologic history in our “natural experiment”.

We present here an exploration of the population structure of the supertramp island monarch across both Wallacea and Melanesia, and that of the related, sedentary pale-blue monarch endemic to Wallacea. If the supertramp strategy is a product of *r* selection on small islands, then it should be reinforced with time in these habitats, resulting in an unstructured population. In contrast, structure in the island monarch population would add more support to the supertramp strategy being a transient stage of the taxon cycle. Further, Linck et al. (2016) attributed the divergence of supertramps on larger and more elevated islands to selection against dispersal ability in these more stable habitats, but did not have morphological data to assess this directly. We have used morphologically-derived dispersal indices to investigate this hypothesis further. If mechanisms similar to those described in the Louisiade white-eye by Linck et al. (2016) were in effect, we predicted that larger, higher, and more isolated islands would hold the most genetically distinct populations. If this is driven by selection against dispersal ability, as could be expected under a relative *K* selection regime on larger and more permanent islands, we should also find populations on these islands to exhibit reduced dispersal ability. If they do not, this would imply a different relationship between dispersal, divergence and geography.

Materials and Methods

Sampling and DNA Sequencing

We sampled birds by mist-netting on expeditions between 1999 and 2017 across Southeast Sulawesi, its nearby land-bridge islands, and the Wakatobi archipelago (Figure 1). Birds were measured and photographed per Redfern and Clark (2001), to collect

data on wing length (maximum chord) and body mass (in grams). We collected a small number of contour feathers from the flank of each bird, to allow extraction of DNA while minimising risk of injury and avoiding disruption to flight abilities and plumage-based visual signals (McDonald and Griffith 2011).

We extracted DNA from feather samples using Qiagen DNeasy Blood and Tissue Kits. We followed the manufacturer's instructions but added 5 µl of 1M dithiothreitol (DTT) at the digest phase to release any genetic material shielded by keratin in the feather calamus. We carried out Polymerase Chain Reactions (PCRs) to target the mitochondrial ND2 and ND3 genes using a touchdown cycling protocol to increase yield (Korbie and Mattick 2008), beginning the reaction with an annealing temperature 10°C hotter than the melting temperatures of the primers and gradually reducing it (reagent quantities and protocol provided in Figure S1). Evolutionary histories inferred from mtDNA sometimes differ from those inferred from nuclear DNA (Rubinoff and Holland 2005, Phillimore et al. 2008), and introgression and male-mediated gene flow can obfuscate biogeographic patterns (Toews and Brelsford 2012). However, in recent radiations ND2 and ND3 have been found to provide the best phylogenetic resolution (Andersen et al. 2015b), and mitochondrial DNA's sensitivity to population structure has proven useful in studies on biogeographic concepts like the supertramp strategy (Linck et al. 2016). As we aimed to study divergence and structure at the level of populations, we therefore deemed ND2 and ND3 to be appropriate markers for our ends. We targeted the ND3 gene using the L10755-F and DOC-ND3-R1 primer pair (Chesser 1999, O'Connell et al. 2019a) and amplified ND2 in two halves using internal and external primers of our own design (Figure S2, Table S2). We screened our PCR products using 2% electrophoresis gels stained with GelRed (Biotium) at a 1X concentration, then had them Sanger sequenced by GATC EuroFins. We used the ClustalW function in BioEdit version 7.2.5 to align our sequences (Hall 1999) and concatenated the ND2 and ND3 sequences using Mesquite version 3.51 (Maddison and Maddison 2018), for a total of 1392 base pairs of DNA from each bird.

We used island monarch sequences from Andersen et al. (2015a) to represent the Melanesian population in our analyses. These represent three subspecies: *M. c. perpallidus* from Nusalaman and Djaul in the Bismarck Archipelago, *M. c. nigristrois* from Karkar, and *M. c. impediens* from Sulei in the Solomon Islands. However, the taxonomy of this species is "complex and not fully understood", and there is a proposal to lump these subspecies together (Clement 2020). We also utilised ten outgroup species from Andersen et al. (2015a), along with *Monarcha castaneiventris* sequences from Nyári et al. (2009). A complete list of samples used in our analyses is available in the Supporting Information (Table S1).

Genetic Analyses

We used both Maximum Likelihood (ML) and Bayesian approaches to investigate the phylogenetics of monarchs. Only one representative of each concatenated ND2/ND3 haplotype was included in the phylogenies. We used MEGA X version

10.1.8 (Kumar et al. 2018) to calculate the pairwise p-distances between these haplotypes (Tables S3 and S4). A p-distance is the proportion of sites that are different between the two sequences, uncorrected for multiple substitutions. We used the ModelFinder function (Kalyaanamoorthy et al. 2017) in IQTree version 1.6.12 (Nguyen et al. 2015) to select the most appropriate nucleotide substitution model for our alignment. Our ModelFinder analysis found strong support for a General Time Reversible model with a gamma shape parameter and a proportion of invariable sites (GTR+F+I+G4), supported by lower Bayesian Information Criterion (BIC) and Akaike Information Criterion (AIC) than other models.

We conducted our ML analysis in IQTree version 1.6.12 (Nguyen et al. 2015) using a GTR+F+I+G4 model. The confidence interval of the ML phylogeny was based on 1000 bootstraps (Felsenstein 1985). We used MrBayes version 3.2.7 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003) to carry out Bayesian phylogenetic inference using a GTR+G+I model. This comprised two independent Markov chain Monte Carlo (MCMC) runs, with four chains per run, sampling every 1000 generations. We discarded the first 25% of each MCMC run as a "burn-in" (Mau et al. 1999). We assessed convergence in TRACER version 1.7.1 (Rambaut et al. 2018), deeming it acceptable once average standard deviation in split frequencies (ASDSF) reached 0.01 and Effective Sample Size (ESS) of model parameters reached 200 (O'Connell et al. 2019d). Both of these requirements had been met by the time our MCMC algorithm reached 4 million generations. We exported a 50% majority rule consensus tree from MrBayes and imported both this and the ML tree into the R package "ggtree" (Yu et al. 2016). We produced a combined, simplified tree by omitting the outgroup and collapsing each major clade into a single branch, labelling the nodes with both ML bootstrap scores and Bayesian probabilities (Figure 2). We also made subtrees from the Bayesian tree, to display all haplotypes from *Monarcha* (Figure 3c) and *Hypothymis* (Figure 4c). Full versions of the Bayesian and ML trees, including all outgroup taxa, are provided in the Supplementary Material (Figures S3 and S4).

We carried out distance-based molecular species delimitation on *Monarcha* and *Hypothymis* haplotypes using Automatic Barcode Gap Discovery (ABGD) (Puillandre et al. 2012). This method uses pairwise genetic distances to group haplotypes into "species" so that there are smaller genetic distances within these "species" than between them. It takes a range of prior maximum intraspecific divergences, and for each of them it calculates a minimum threshold interspecific distance, the "barcode gap". It then splits the haplotypes into groups, with the distance between each group equalling or surpassing the barcode gap. The range of prior maximum intraspecific divergences allows the user to calibrate the species groupings for different genes and species. We ran our ABGD analysis on the web-server <https://bioinfo.mnhn.fr/abi/public/abgd/> using default settings (Pmin = 0.001, Pmax = 0.1,

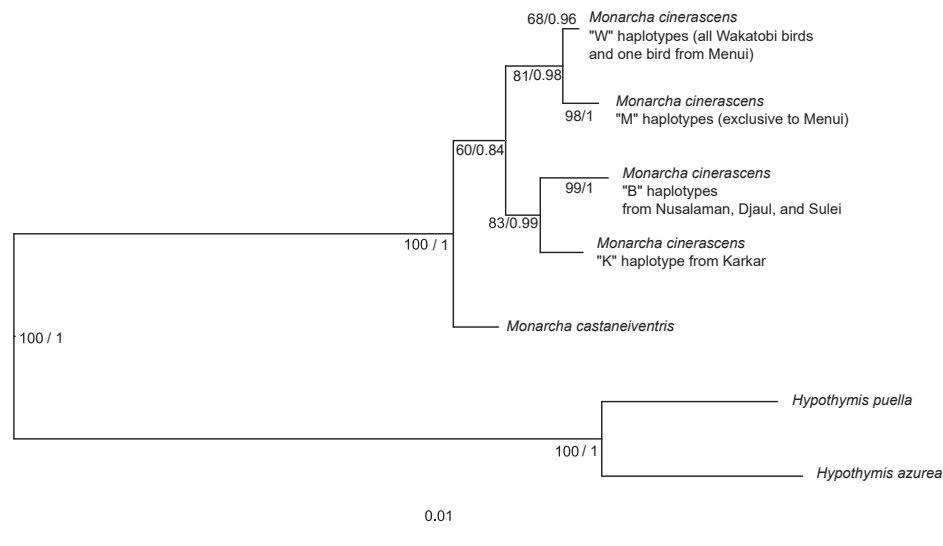


Figure 2. Simplified version of combined Maximum Likelihood (ML) and Bayesian phylogenetic tree of monarch species sampled in Wallacea and Melanesia. In this figure the outgroup is omitted and each major clade in the data is collapsed into a single branch. Nodes are labelled with ML bootstraps / Bayesian probability. Figures 3 and 4 include subtrees of the *Monarcha* and *Hypothymis* sections of the Bayesian tree, with individual haplotypes displayed. Full versions of the ML and Bayesian trees, including all outgroup taxa, are in the Supplementary Material (Figures S3 and S4).

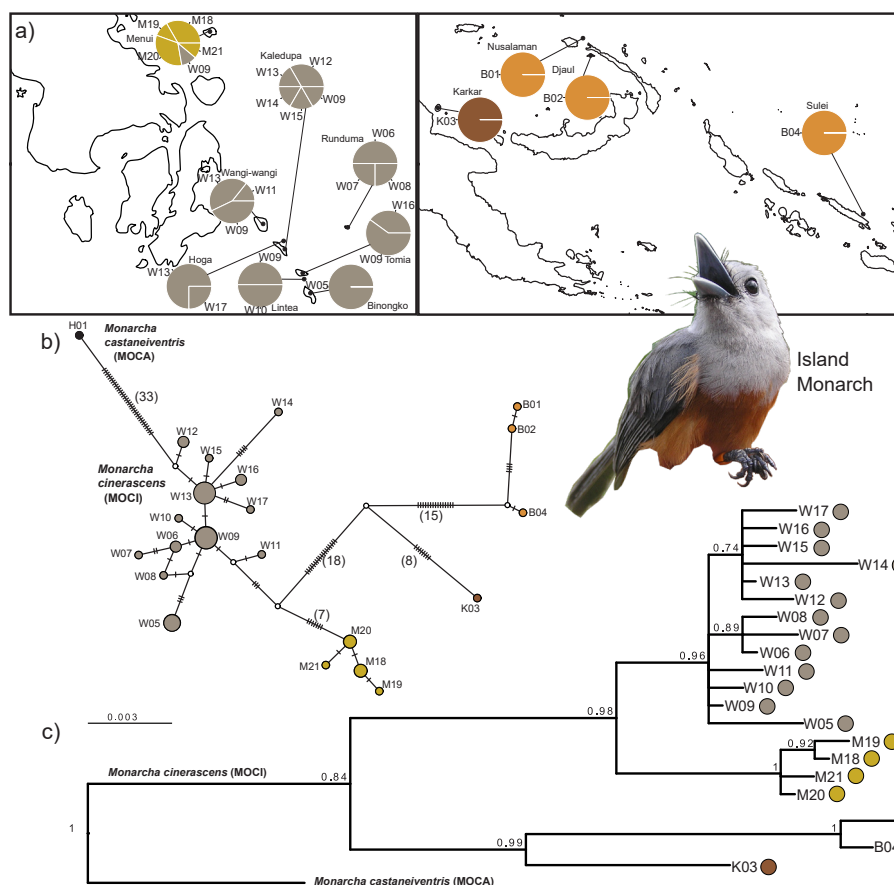


Figure 3. a) Geographic distribution of island monarch (*Monarcha cinerascens*) haplotypes in Wallacea and Melanesia. Each circle represents an island and the fractions within the circle the haplotypes found in that region, with the size of each proportion representing the frequency of each haplotype. The haplotypes are named and coloured according to clade. b) TCS Haplotype Network of *Monarcha* haplotypes. Each circle represents a unique ND2-ND3 haplotype, named and coloured according to clade and sized to represent how many birds carried that haplotype. The hatch marks represent mutations between haplotypes, also given as numbers in brackets for the wider divergences. The unfilled, white nodes represent hypothetical ancestral states. c) Bayesian consensus tree of *Monarcha* haplotypes. Nodes are labelled with Bayesian probabilities.

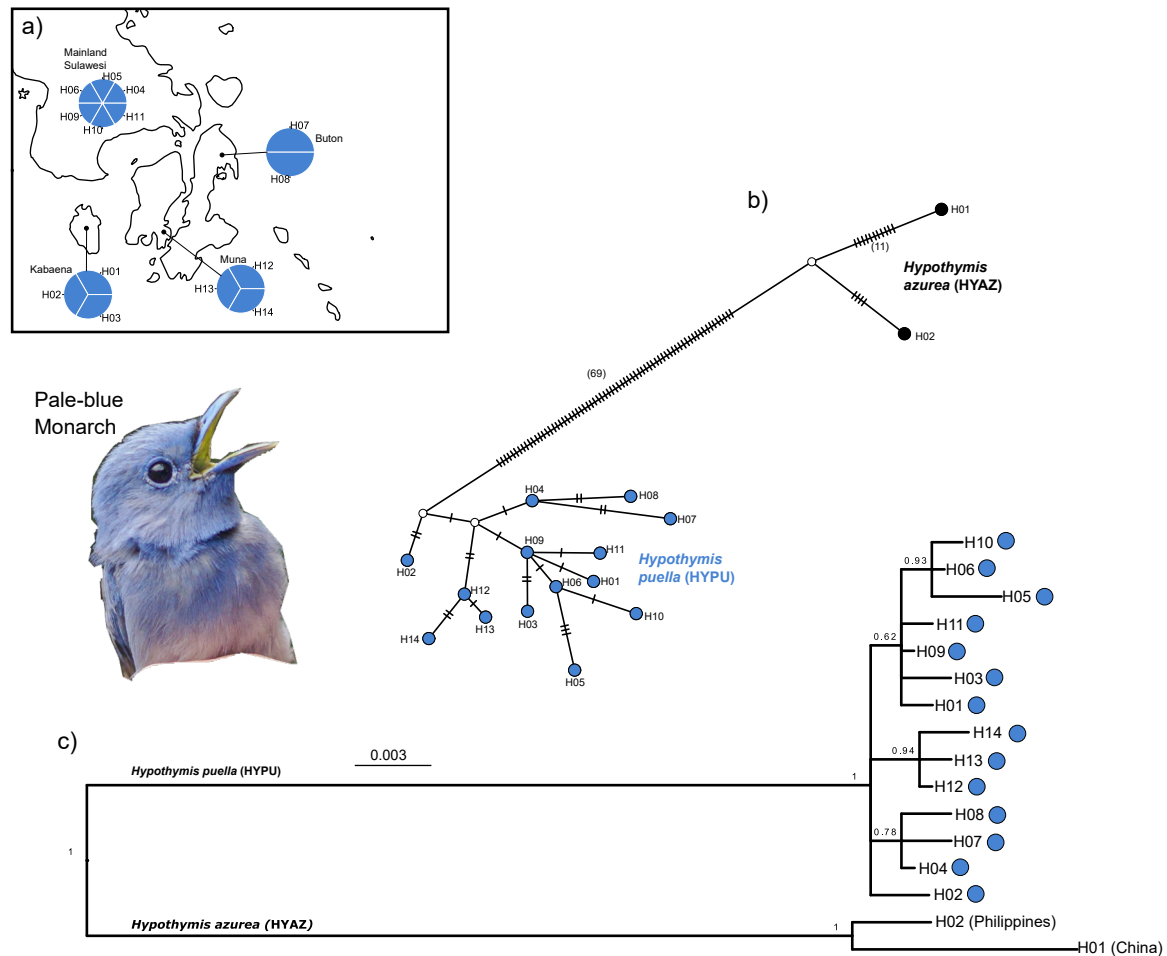


Figure 4. a) Geographic distribution of pale-blue monarch (*Hypothymis puella*) haplotypes in Wallacea. Each circle represents an island and the fractions within the circle the haplotypes found in that region, with the size of each proportion representing the frequency of each haplotype. All haplotypes are shown with the same letter (H) and colour (blue) because no population structure was found. b) TCS Haplotype Network of *Hypothymis* haplotypes. Each circle represents a unique ND2-ND3 haplotype, sized to represent how many birds carried that haplotype. The hatch marks represent mutations between haplotypes, also given as numbers in brackets for the wider divergences. The unfilled, white nodes represent hypothetical ancestral states. c) Bayesian consensus tree of *Hypothymis* haplotypes. Nodes are labelled with Bayesian probabilities.

Steps = 10, relative gap width = 1.5, Number of bins = 20) and a Kimura-2-Parameter (K2P) model.

To visualise any potential genetic structure in our monarch populations, we used PopArt version 1.7 (Leigh and Bryant 2015) to create TCS haplotype networks (Figures 3b and 4b). The TCS algorithm is agglomerative, progressively combining clusters that share one or more connecting edge (Templeton et al. 1992). This makes it well-suited to the analysis of divergence at the population level, where ancestral haplotypes are likely to be common in the population and variation is relatively low (Clement et al. 2000).

Morphological Analyses

Classic supertramp theory describes certain species colonising distant islands due to superior dispersal abilities, but the “taxon cycle” hypothesis predicts they will lose these abilities and become differentiated (Le Pepke et al. 2019). We tested this using morphological analyses on adult island monarchs

from Wallacea, carried out in R version 4.0.2 (R Core Team, 2020). These analyses investigated whether genetic divergence of populations was accompanied by a reduction in dispersal ability. Four adults were sampled in Menui, three of them processed by a different recorder (DOC) than the other birds in our dataset (which were processed by NMM). To test for differences between the measurements of DOC and NMM, five birds of various species were measured by both authors (Table 1). We ran a paired 2-sample *t*-test on their measurement data to check for inconsistent measurements.

Wing length alone is a poor indicator of dispersal ability (Dawideit et al. 2009). We therefore followed Garrard et al. (2012) and O’Connell et al. (2019d) by using our morphological data to derive an allometrically scaled “shape” parameter termed the “dispersal index”:

$$\text{Dispersal index} = (\text{wingspan})^3 / \text{body mass}$$

Table 1. Birds measured by both DOC and NMM for comparison of ringers.

ID	Species	Island	Wing length measured by NMM (mm)	Wing length measured by DOC (mm)
SUL2285	<i>Zosterops consobrinorum</i>	Muna	55	56
SUL2361	<i>Zosterops consobrinorum</i>	Muna	58	58.5
SUL2564	<i>Collocalia esculenta</i>	Menui	100	100
SUL2573	<i>Leptocoma aspasia</i>	Menui	59	60
SUL2581	<i>Monarcha cinerascens</i>	Menui	76	76

We calculated wingspan from wing length using the formula from Garrard et al. (2012), devised from species for which both wingspan and wing length were known:

$$\text{Wingspan} = 1.91 (\text{wing length}) + 0.06$$

Because of the physical constraints of flight, wingspan is expected to increase by three units whenever body mass increases by one unit (Garrard et al. 2012). The dispersal index is thus designed to be informative of variation in wingspan beyond that resulting from variation in body mass. We ran a *t*-test to compare the dispersal indices of the two clades suggested by the genetic analyses for which we had morphological data, and incorporated the dispersal index into our biogeographic analyses.

Biogeographic Analyses

Following Linck et al. (2016), we ran three linear models to test the effect of different biogeographic considerations on genetic divergence, measured as the mean *p*-distance between that island's monarchs and those of its closest neighbour. Model A was designed to test the effect of an island's area on genetic divergence, Model B the effect of island elevation, and Model C the effect of the island's geographic isolation (distance from the closest neighbouring population). Linck et al. (2016) described Models A and B as supertramp-specific, with a prediction of positive correlations between area/elevation and genetic divergence due to supertramps losing their dispersal abilities on larger and higher islands. Area and elevation are classic biogeographic proxies for the permanence of an island over geological time (MacArthur and Wilson 1967, Mayr and Diamond 2001). Model C is designed to test for more general "isolation by distance" (Wright 1943).

Our sampling allowed us to replicate these models using both Wallacean and Melanesian islands. We used NaturalEarth polygons and the R package "geodist" (Padgham et al. 2021) to find the closest points of islands and measure the distance between them. We collected data on area and elevation from the literature (Beehler and Pratt 2016, Monkhouse et al. 2018, O'Connell et al. 2019b, Kumar 2020). Because the Melanesian sampling of Andersen et al. (2015a) did not

cover the Eastern Bismarcks or Western Solomons, the Sulei population had an artificially inflated geographic distance to its "nearest neighbour", Djaul. Our Model C therefore used the logarithm of geographic isolation in order to better reflect the true variation in isolation. We compared models using base 2, base 10, and the natural log, and with the raw geographic isolation data with and without Melanesian data.

We also developed four additional biogeographic models that incorporated our island monarch morphology data, to test the conclusion of Linck et al. (2016) that supertramp species become differentiated on larger and more permanent islands due to selection against dispersal ability. These, Models W, X, Y, and Z, only covered Wallacea as we had no morphological data from Melanesia. Model W tested the relationship between genetic divergence, measured as the mean *p*-distance between that island's monarchs and those of its closest neighbour, and dispersal ability, i.e. the mean dispersal index of the island's monarchs. Model X tested the relationship between geographic isolation and dispersal ability. Model Y tested dispersal ability's relationship with island area, Model Z its relationship with island elevation. We drew lines of best fit to visualise the three models from Linck et al. (2016) (Figure 5) and our additional four models (Figure 6), using the packages "ggplot2" (Wickham 2016) and "ggrepel" (Slowikowski 2021).

Results

Genetic Results

In total we produced 42 new concatenated ND2-ND3 sequences for the island monarch and 14 for the pale-blue monarch (overview in Table 2, full list in Table S2). We have deposited these in GenBank (accession numbers MZ604441– MZ604552).

Bayesian and ML phylogenetic reconstruction sorted the island monarchs into four main clades (Figure 2), with geographic structure evident both from the trees and genetic *p*-distances. The mean genetic distance between Wallacea and Melanesia was 2.7% and there were also divisions within each of these regions. Clade W included all the birds netted on the Wakatobi islands and one immature bird netted on

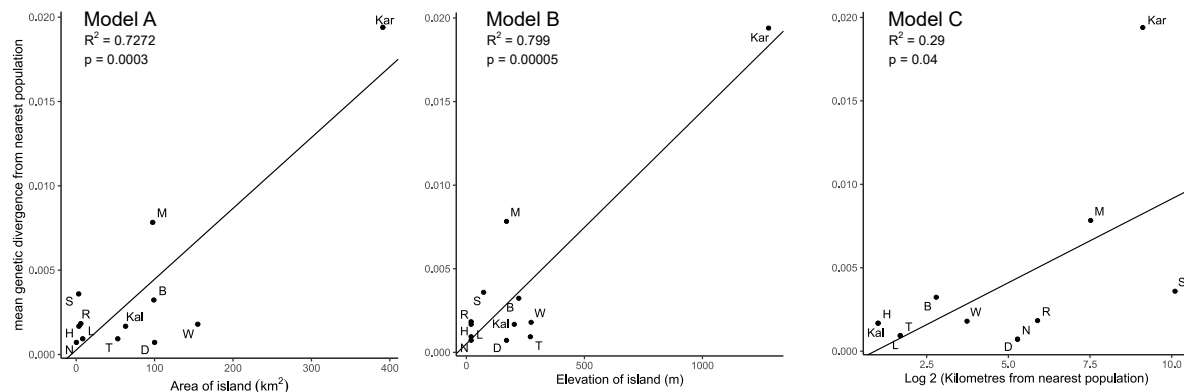


Figure 5. Linear regressions of genetic divergence between neighbouring island monarch populations fit to three island biogeographic models. These are genetic divergence by (A) island area, (B) island elevation, and (C) geographic isolation. Genetic divergence is the mean proportion of varying nucleotides (uncorrected p-distance) in concatenated ND2-ND3 sequences. Each data point represents an island in Wallacea or Melanesia: (M)enui, (W)angi-wangi, (Kal)edupa, (T)omia, (B)inongko, (H)oga, (R)unduma, (L)intea Selatan, (N)usalaman, (D)jaul, (S)ulei, and (Kar)kar.

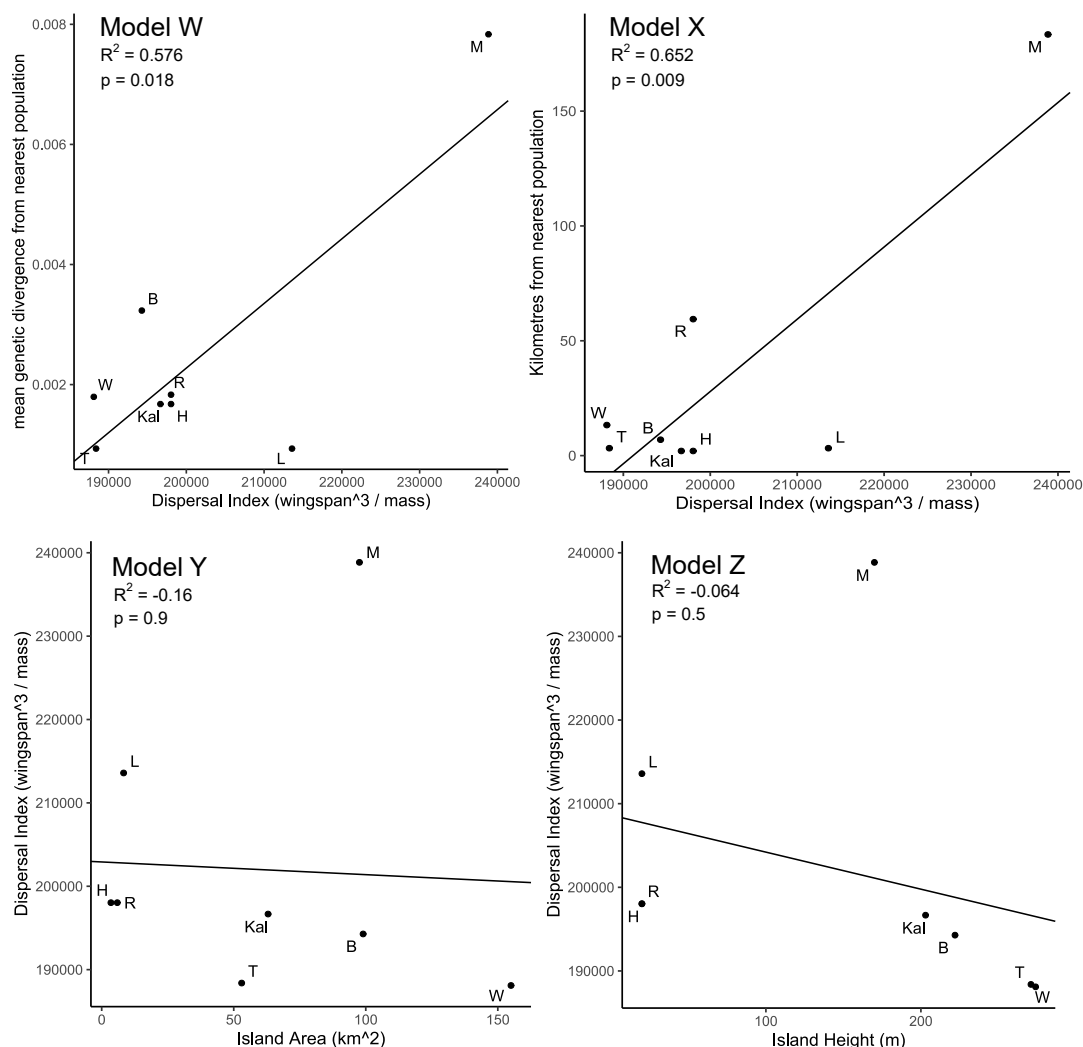


Figure 6. Linear regressions of genetic divergence and dispersal ability of island monarch populations fit to four island biogeographic models. These are W) genetic divergence as a function of dispersal ability, X) dispersal ability as a function of geographic isolation, Y) dispersal ability as a function of island area, and Z) dispersal ability as a function of island elevation (permanence). Genetic divergence is the mean proportion of varying nucleotides (uncorrected p-distance) in concatenated ND2-ND3 sequences. Each data point represents an island in Wallacea: (M)enui, (W)angi-wangi, (Kal)edupa, (T)omia, (B)inongko, (H)oga, (R)unduma, (L)intea Selatan.

Table 2. Sample sizes for populations included in study. A full list of birds used in analyses is available in Supplementary Table S1.

Island	Archipelago	Region	Species	Genetic Sample Size	Morphological Sample Size
Buton	Sulawesi	Wallacea	<i>Hypothymis puella</i>	2	5
Kabaena	Sulawesi	Wallacea	<i>Hypothymis puella</i>	3	4
Muna	Sulawesi	Wallacea	<i>Hypothymis puella</i>	3	3
Southeast Sulawesi	Sulawesi	Wallacea	<i>Hypothymis puella</i>	6	11
Djaul	Bismarck	Melanesia	<i>Monarcha cinerascens</i>	1	-
Karkar	Bismarck	Melanesia	<i>Monarcha cinerascens</i>	1	-
Nusalaman	Bismarck	Melanesia	<i>Monarcha cinerascens</i>	1	-
Sulei	Solomon	Melanesia	<i>Monarcha cinerascens</i>	1	-
Menui	Sulawesi	Wallacea	<i>Monarcha cinerascens</i>	9	4
Binongko	Wakatobi	Wallacea	<i>Monarcha cinerascens</i>	5	5
Hoga	Wakatobi	Wallacea	<i>Monarcha cinerascens</i>	4	4
Kaledupa	Wakatobi	Wallacea	<i>Monarcha cinerascens</i>	6	19
Lintea Selatan	Wakatobi	Wallacea	<i>Monarcha cinerascens</i>	2	1
Runduma	Wakatobi	Wallacea	<i>Monarcha cinerascens</i>	4	3
Tomia	Wakatobi	Wallacea	<i>Monarcha cinerascens</i>	5	13
Wangi-wangi	Wakatobi	Wallacea	<i>Monarcha cinerascens</i>	7	33

Menui. The bootstrap value supporting Clade W was 68, but the Bayesian probability was robust at 0.96. The other eight birds netted on Menui made up a separate clade, M, supported by a strong bootstrap value of 98 and a Bayesian probability of 1. The mean distance between the M and W clades was 1%. In Melanesia, the bird from Sulei in the Solomon Islands grouped with the two birds from the central Bismarcks (Djaul and Nusalaman) in a well-supported Clade B, which had a bootstrap value of 99 and a Bayesian probability of 1. The Karkar bird had a distinct haplotype (MOCI_K03) with a mean distance of 1.9% from Clade B. Within-group variability was 0.2% in Clade W, 0.08% in Clade M, and 0.3% in Clade B. Branch support for monophyletic *M. cinerascens* was comparatively low (bootstrap value of 60, Bayesian probability of 0.84).

The genetic distance we found between island monarchs of Wallacea and Melanesia (2.7%) is closely equivalent to that between well-differentiated monarch species, as *Monarcha castaneiventris* (MOCA_H01) had a mean distance of 2.6% from our Wallacean samples and 2.8% from the Melanesian birds. The ABGD analysis separated our island monarch haplotypes into either three or four molecular “species” depending on the prior intraspecific divergence. At the more conservative end, it calculated 1.6% as the barcode gap distance, which is in line with interspecific ND2 barcode gaps found by other studies on birds (Pellegrino et al. 2017, O’Connell et al. 2019d), and with this it divided the haplotypes into three groups. Pairwise distances between all haplotypes are available in the Supplementary Material (Table S4).

We found that the patterns of pairwise p-distances between islands and ABGD analyses of island monarch haplotypes aligned with geographic divisions (Figure 3).

At levels of interspecific divergence similar to those seen in other birds (Pellegrino et al. 2017, O’Connell et al. 2019d), ABGD divided the island monarch into three species: one on Karkar (MOCI_K03), one on the other Bismarck and Solomon islands (MOCI_B01, B02, and B04), and one in Wallacea (MOCI_W05-M21). Species-level divergence between Wallacea and Melanesia is well-supported, matching the divergence between *M. cinerascens* and *M. castaneiventris*. Additionally, there is evidence of weaker divergence (likely below species level) within the Wallacean birds. With a smaller barcode gap of 0.7%, the ABGD produces a fourth group composed of haplotypes found exclusively in birds from Menui (MOCI_M18-21). These Menui-exclusive haplotypes represent eight of the nine birds caught on Menui (Figure 3a). One bird from Menui carried a haplotype (MOCI_W09) common to four of the Wakatobi islands. The (W)akatobi, (M)enui, (K)arkar, and (B)ismarck groups can all be seen as distinct clusters on the haplotype network (Figure 3b) and monophyletic groupings on the phylogenetic tree (Figure 3c). Together, this evidence supported Divergence Pattern 3: a species-level division between Wallacean and Melanesian populations, and population structure within both regions.

Between the islands inhabited by the pale-blue monarch, which were connected by land bridges in recent geological history, there was no geographic population structure evident (Figure 4), and no two haplotypes of this species were more than 0.6% different from one another (Table S3).

Morphological Results

Of the five birds measured in order to compare measurements by both DOC and NMM (Table 1), the

same wing length was recorded in two cases (including the only island monarch measured by both recorders), while DOC measured the wing length as 0.5–1mm longer than NMM in the others. Our paired two-sample *t*-test found a mean difference of 0.5 between the two recorders, which was not statistically significant ($p = 0.08$). This allowed us to include both recorders' data. Bird SUL2219, the one island monarch caught on Menui with a Wakatobi haplotype (MOCI_W09), had to be excluded from morphological analyses as it was immature. The M clade has a higher dispersal index than the W clade (*t*-test, $p < 0.0001$).

Biogeographic Results

We found support in our data for the three models (Figure 5) proposed by Linck et al. (2016). There was a strong positive correlation between the area of an island and the genetic divergence of its island monarchs (Model A, $p < 0.001$, $R^2 = 0.73$). There was also a positive relationship between the elevation of an island and the genetic divergence of its monarch population (Model B, $p < 0.0001$, $R^2 = 0.8$). Like Linck et al. (2016), we found a relatively weaker positive relationship between genetic divergence and geographic isolation. While this relationship was statistically significant, it explained less of the variation (Model C, $p < 0.05$, $R^2 = 0.29$). This was consistent whether Model C used the logarithm in base 2, base 10, or the natural log of geographic isolation. When not using a log scale, Model C found a relationship in Wallacea, where geographic coverage was complete ($p < 0.01$), but not when including Melanesia, where the sampling was incomplete ($p > 0.1$). This supports the hypothesis that the gap in sampling between Sulei and Djaul in Melanesia turns Sulei into an outlier artificially, and that the log scale counters this outlier.

To these we added models (Figure 6) exploring the relationship between dispersal ability and both genetic differentiation and island parameters in Wallacea. We found dispersal ability to be related positively to both genetic divergence (Model W, $p < 0.05$, $R^2 = 0.58$) and geographic isolation (Model X, $p < 0.01$, $R^2 = 0.65$). But we found no correlation between dispersal ability and island size (Model Y, $p = 0.5$) or island elevation (Model Z, $p = 0.48$).

Discussion

Phylogenetics and biogeography

Islands in the “natural laboratory” of Wallacea (Whittaker et al. 2017), where the fauna of Asia transitions into that of Australo-Papua and the Pacific (Ali and Heaney 2021), have been colonised by monarch flycatchers (Monarchidae) with contrasting life history strategies. The pale-blue monarch is a sedentary resident species from an Asian lineage, while the island monarch is one of Melanesia's original supertramps (Diamond 1974). Despite their different origins and inferred differences in dispersal ability, we find that the natural experiment has resulted in both island and pale-blue monarchs diverging significantly

from their closest relatives outside Wallacea, implying that the deep water barriers around this region have cut off gene flow from outside.

The pale-blue monarch's split from the black-naped monarch demonstrates that even a bird with a range from India to Borneo has difficulty crossing to Sulawesi across a deep water barrier. Within the pale-blue monarch, however, we have found no population structure at the scale of this study (Figure 4). The pale-blue monarch shares this pattern with the region's relatively dispersive birds like the white-eyes (O'Connell et al. 2019d) and sunbirds (O'Connell et al. 2019b), a pattern that contrasts with non-dispersive birds like the red-backed thrush (Robinson-Dean et al. 2002) and Sulawesi babbler (Ó Marcaigh et al. 2021b), which do exhibit divergence on this same scale. Thus the pale-blue monarch does not provide evidence for a link between competition, *r* -/K-selection, and dispersiveness.

In the island monarch, we found that Melanesian and Wallacean birds were as genetically distant from one another (mean 2.7%) as they were from the unambiguously different species *M. castaneiventris* (2.8% and 2.6% mean distance from Melanesia and Wallacea, respectively). We also identified population structure within both Wallacea and Melanesia, supporting Divergence Pattern 3. In Melanesia, ABGD identified the Karkar population (a single sample) as a potential species. Although Karkar is geologically part of the Bismarck volcanic arc (Silver et al. 2009), its proximity to the New Guinea mainland has a strong influence on its native fauna, to the point that biogeographers consider it part of the New Guinea region rather than the Bismarck region (Mayr 1941, Beehler and Pratt 2016). Diamond and Lecroy (1979) noted the peculiarity of Karkar's birds, describing it and neighbouring Bagabag Island as “a zoogeographically interesting mixing zone” between New Guinea and the Bismarck Archipelago. Although the Solomon Islands are quite distant from the Bismarcks and their monarchs are named as a separate subspecies (*Monarcha cinerascens impediens*), our ABGD analysis assigned the Sulei haplotype to the same population as haplotypes from Nusalaman and Djaul in the Bismarcks. This may support the hypothesis of Mayr and Diamond (2001) that the species originated in the Bismarcks and only colonised the Solomons recently.

A Menui population was found to be distinct based on a larger sample size. Of the nine birds netted on Menui, eight of them (88.9%) formed “Clade M”, with haplotypes unique to Menui and a mean distance of 1% from the other Wallacean birds in Clade W (Figure 3). These birds also exhibited higher dispersal indices than those from the Wakatobi. Menui is 183km from the Wakatobi, a relatively short distance for a supposed dispersal specialist which, according to current taxonomy, maintains a range across more than 4000 kilometres of deep water. That the island monarch population of Menui remained undocumented until so recently (Monkhouse et al. 2018) demonstrates how our lack of knowledge of little-explored areas of bird endemism still hampers our understanding

(Rheindt et al. 2020). Inadequate species distribution data (the “Wallacean shortfall”) often complicate conservation efforts (Whittaker et al. 2005). One immature bird netted on Menui (ID SUL2547) carried a “W” haplotype common to the Wakatobi islands (MOCI_W09), also found in birds from Wangi-wangi, Lintea Selatan, Hoga, and Tomia (Figure 3). This may be evidence of natal dispersal from the Wakatobi to Menui, without enough gene flow to prevent genetic divergence, in keeping with the “occasional wandering” of island monarchs from one differentiated population to another described by Mayr (1944). Alternatively, it may not have been a natural movement: birds are regularly translocated around Indonesia in a highly active bird trade, giving rise to an “Asian Songbird Crisis” (Marshall et al. 2020). Birds from Wangi-wangi are known targets (O’Connell et al. 2021). This trade has existed for centuries and even Wallace’s biogeographic studies were sometimes complicated by it, as he noted of the region’s parrots that “The greatest confusion exists as to their distribution, owing to their being carried from island to island by the native traders” (Sclater 1859).

Implications for the supertramp strategy

Evolutionary biology and biogeography owe many of their most important insights to the diversity and distribution patterns of island bird communities (Darwin 1859, Wallace 1863, MacArthur and Wilson 1967, Mayr and Diamond 2001). Modern techniques, applied to previously little-explored areas, allow these foundational frameworks to be continually updated. Recent work on distributions (mapped in Eaton et al. 2021) has made it clear that the island monarch exhibits the same “supertramp” distribution in Wallacea as it does in Melanesia, being restricted to small islands while the pale-blue monarch occupies the larger islands. This pattern of island occupancy is thus reinforced as a predictable phenomenon that warrants an ecological or evolutionary explanation. It may be the invisibility of communities present on larger islands, rather than the incidence of island arrival events alone, that explain the absence of the island monarch, but precise causes are far from being understood. Further, the island monarch has diverged most strongly on larger, higher, and more distant islands (Models A, B, and C), in keeping with predictions based on previous work with the supertramp Louisiade white-eye (Linck et al. 2016). The supertramp strategy was initially envisioned as an adaptive response to the *r*-selective environments of small islands (Diamond 1974). If such adaptation were ongoing, our study system of small islands would be subject to “continuous swamping”, and thus hold an unstructured population “without noticeable geographic variation” (Mayr 1942). Instead, we found substantial divergence between Wallacea and Melanesia, and lesser divergence within each region (Divergence Pattern 3). It is possible that what we call supertramp species simply correspond to lineages with high colonising potential, with island populations tending to differentiate as a result of a

reduced propensity to disperse after they establish on islands.

Across the Wallacean transition zone and into Melanesia, the island monarch appears to be making a transition of its own: from a widespread supertramp to a number of differentiated populations, each of them effectively sedentary and resident in a small area. Our findings support those of Linck et al. (2016) in showing that another of the classic supertramp species exhibits population structure on a relatively fine geographic scale. Like Linck et al. (2016) and Le Pepke et al. (2019), our results indicate that the supertramp condition appears to be temporary, and the populations in question are in fact incipient species which will differentiate over time. Our findings support Le Pepke et al. (2019) in integrating the supertramp condition into the well-established concept of the taxon cycle (Wilson 1959, 1961). Originally devised for ants, this cycle describes a series of stages that taxa pass through as they expand their ranges by colonising islands, then evolve into differentiated lineages and then undergo range contraction. Based on our findings, this seems to describe the history of monarch flycatchers in these regions quite well, with different *Hypothymis* and *Monarcha* populations occupying different points on the cycle.

Our dispersal index analysis let us probe deeper and explicitly examine the biogeographic underpinnings of dispersal ability. Our findings in this regard were contrary to the prediction of Linck et al. (2016) that conditions on larger, more permanent islands would select against dispersal ability. Our data suggest that the most dispersive birds were able to colonise the most isolated islands (Model X), where they diverged due to isolation by distance (Model C), as even their strong dispersal ability did not cause enough gene flow to prevent differentiation (Model W). Most divergence took place on larger and higher islands (Models A and B), but there is no evidence of reduction in dispersal ability under these stable conditions (Models Y and Z). In fact, it is to be expected that more permanent islands should hold the most differentiated populations, regardless of selective pressures. In their discussion of radiation, MacArthur and Wilson (1967) noted that more stable islands simply provide more time in which evolution can take place. Outside the supertramp debate, sedentary Wallacean residents like the *Ninox* owls have been shown to have diverged most on larger, higher islands (Gwee et al. 2017). Rather than losing their physical dispersal ability, the divergent island monarch populations could have evolved “behavioural flightlessness” (Diamond 1981, Komdeur et al. 2004, Bertrand et al. 2014). This is known to occur in other birds which are physically well adapted to dispersal, like *Zosterops* white-eyes (Moyle et al. 2009). Taken together, these studies suggest that similar processes govern genetic divergence in both highly dispersive and less dispersive species. In other words, between the speciation of supertramps and that of sedentary species there are differences “of degree and not of kind” (Darwin 1871).

Our findings illustrate that supertramp status can be viewed more accurately as an ecological rather than an evolutionary condition, or as the instigator of biogeographic patterns rather than the outcome. After colonising islands, the supertramp appears to “settle down” and transition to a resident species. The size, permanence, and isolation of the islands shape the population structure that emerges. Even if the supertramp lifestyle is a temporary phase within the taxon cycle, it is nevertheless an important factor in the region’s biodiversity as it regularly produces new island communities, which seed new evolutionary processes. As our study sampled a single supertramp species, we recommend that more of the original supertramps should be studied genetically, as the Louisiade white-eye and now the island monarch have been. This will allow scientists to continue building a complete picture of this fascinating mosaic of distribution and divergence.

Taxonomy

Our work has several implications for taxonomy, but further work is needed before new taxa can be described. Based on the genetic divergence we have found, the “island monarch” studied by Mayr and Diamond (2001) in Melanesia may be a cryptic species absent from Wallacea. The island monarch was described by Temminck (1827) from a specimen collected on Timor in Wallacea, an island it is now known to visit only in the monsoon (Eaton et al. 2021). Additional sampling in southern and eastern Wallacea, or sequencing of existing museum specimens, would therefore help to clarify whatever taxonomic divisions exist within the currently described island monarch. We also found variation within each region, divided by smaller genetic distances. Geographically circumscribed clades which are genetically and morphologically distinct, but are not reproductively isolated, may warrant subspecies status (Patten 2015). In Melanesia, the genetically distinct island monarchs of the Karkar area are already named as a subspecies, *Monarcha cinerascens nigrirostris* (Andersen et al. 2015a). In Wallacea, we recommend that the monarchs of Menui and the Banggai and Sula islands to its north be examined further, as they may reveal undocumented subspecies.

Conclusion

As both Melanesia and Wallacea are of global concern for the conservation of biodiversity (Myers et al. 2000, Brooks et al. 2006), as well as being foundational to the history of biogeography (Wallace 1860, Mayr and Diamond 2001), it is vital that we understand where and how these regions’ species are evolving. Better knowledge of their diversity, distributions, and evolutionary distinctness would allow conservationists to target the most relevant populations and biogeographers to fully develop the field’s most influential theories.

Wallace (1860) noted that “however narrow may be the strait separating an island from its continent, it

is still an impassable barrier against the passage of any considerable number and variety of land animals; and that in all cases in which such islands possess a tolerably rich and varied fauna of species mostly identical, or closely allied with those of the adjacent country, we are forced to the conclusion that a geologically recent disruption has taken place.” Our findings reinforce that this may even be true for dispersive birds: in both supertramp and sedentary monarchs, geologically recent land bridges allow islands to share populations, while even relatively narrow water barriers will cause genetic divergence as long as they are deep and, therefore, permanent. It is the number and diversity of such barriers around Wallacea that make it “a district *per se*, in the highest degree interesting” (Wallace 1860). Integrative taxonomy and comprehensive sampling are necessary to understand the diversity and distributions of species (Cicero et al. 2021) and, from there, the theoretical concepts these species have inspired.

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Author Contributions

FÓM, DOC, DJK, and NMM conceived this study. FÓM, DJK, and NMM led the writing of the manuscript. DJK, NMM, DOC, FÓM, AK, and KA carried out the fieldwork. FÓM, NL, and ND carried out the labwork. CM measured the geographic distances. FÓM analysed the data, with input from the other authors. All authors contributed to revising and improving the manuscript.

Data Accessibility

All new ND2 and ND3 DNA sequences from this study have been deposited in GenBank under accession numbers MZ604441 – MZ604552. The R code used in our analyses is available in Supplementary Appendix S1. The morphological and biogeographic data have been made available in Supplementary Appendices S2 and S3.

Ethics approval

Kementerian Riset Teknologi Dan Pendidikan Tinggi (RISTEKDIKTI) provided the necessary permits and approvals, under permit numbers 0143/SIP/FRP/SM/VII/2010, 278/SIP/FRP/SM/VII/2012, 279/SIP/FRP/

SM/VIII/2012, 174/SIP/FRP/E5/Dit. KI/V/2016, 159/SIP/FRP/E5/Fit. KIVII/2017, and 160/ SIP/FRP/E5/Fit. KIVII/2017. Handling of animals was also approved by the TCD Animal Research Ethics Committee, under reference number 060417.

Supplementary Material

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

Figure S1. Example PCR protocol used in this study

Figure S2. Diagram of the mitochondrial ND2 gene showing how we used internal primers to sequence the gene in two halves.

Figure S3. Full Bayesian tree showing all haplotypes.

Figure S4. Full Maximum Likelihood (ML) tree showing all haplotypes.

Table S1. DNA samples used in this study.

Table S2. PCR primers used in this study.

Table S3. Proportion difference (p-distance) between concatenated ND2-ND3 haplotypes in *Hypothymis*

Table S4. P-distances between concatenated ND2-ND3 haplotypes in *Monarcha*

Appendix S1. Expanded “Genetic Analyses” Section, with more detail on phylogenetic modelling, and R code used in analyses.

Appendix S2. Raw morphological data collected from monarchs.

Appendix S3. Biogeographic data used in our modelling.

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