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Evolutionarily labile dispersal behavior and discontinuous habitats enhance population differentiation in island versus continentally distributed swallows

Grant G. Broyles[1], Brian M. Myers[1,2], Nicholas R. Friedman[3,4], Dency F. Gawin[5], Farah S. Mohd-Taib[6], Penigran G.M. Sahlan[7], Sampath S. Seneviratne[8], N. Chamalka G. de Silva[8,9], Thilini T.M. Lekamlage[8,10], Amanda K. Hund[11,12], Elizabeth S.C. Scordato[1,]

[1]Department of Biological Sciences, California State Polytechnic University, Pomona, CA, United States
[2]Department of Biology, Eastern Oregon University, La Grande, OR, United States
[3]Biodiversity and Biocomplexity Unit, Okinawa Institute of Science and Technology Graduate University, Onna, Japan
[4]Centre for Taxonomy and Morphology, Museum of Nature Hamburg, Leibniz Institute for the Analysis of Biodiversity Change (LIB), Hamburg, Germany
[5]Faculty of Resource Science and Technology, Universiti Malaysia Sarawak, Kota Samarahan, Sarawak, Malaysia
[6]Department of Biological Sciences and Biotechnology, Faculty of Science and Technology, Universiti Kebangsaan Malaysia, Selangor, Malaysia
[7]Sabah Forestry Department, Forest Research Centre, Sandakan, Sabah, Malaysia
[8]Avian Sciences and Conservation, Department of Zoology and Environment Sciences, The University of Colombo, Colombo, Sri Lanka
[9]Department of Physiology and Neurobiology, College of Liberal Arts and Sciences, University of Connecticut, Storrs, CT, United States
[10]Department of Biological Sciences, University of Lethbridge, Lethbridge, AB, Canada
[11]Department of Ecology and Evolution, The University of Colorado, Boulder, CO, United States
[12]Department of Biology, Carleton College, Northfield, MN, United States

Corresponding author: Department of Biological Sciences, California State Polytechnic University, 3801 W. Temple Ave, Pomona, CA 91768, United States.
Email: escordato@cpp.edu
G.G.B and B.M.M. contributed equally to this study.

Abstract

The causes of population divergence in vagile groups remain a paradox in evolutionary biology: dispersive species should be able to colonize new areas, a prerequisite for allopatric speciation, but dispersal also facilitates gene flow, which erodes population differentiation. Strong dispersal ability has been suggested to enhance divergence in patchy habitats and inhibit divergence in continuous landscapes, but empirical support for this hypothesis is lacking. Here we compared patterns of population divergence in a dispersive clade of swallows distributed across both patchy and continuous habitats. The Pacific Swallow (*Hirundo tahitica*) has an insular distribution throughout Southeast Asia and the Pacific, while its sister species, the Welcome Swallow (*H. neoxena*), has a continental distribution in Australia. We used whole-genome data to demonstrate strong genetic structure and limited introgression among insular populations, but not among continental populations. Demographic models show that historic changes in habitat connectivity have contributed to population structure within the clade. Swallows appear to exhibit evolutionarily labile dispersal behavior in which they reduce dispersal propensity after island colonization despite retaining strong flight ability. Our data support the hypothesis that fragmented habitats enhance population differentiation in vagile groups, and suggest that labile dispersal behavior is a key mechanism underlying this pattern.

Keywords: dispersal, speciation, introgression, island biogeography

Introduction

The relationship between population divergence and dispersal ability has long been debated in evolutionary biology (Claramunt et al., 2012; Diamond et al., 1976; Mayr et al., 2001; Slatkin, 1987; Yamaguchi, 2022). Strong dispersal ability allows species to colonize new areas, which is a prerequisite for subsequent population divergence, but dispersal also maintains gene flow between populations, which slows divergence and inhibits speciation (Diamond et al., 1976; Kennedy et al., 2016; Kisel & Barraclough, 2010; Price, 2008). Birds have been particularly well-studied in efforts to resolve this conflict because wing shape is an easily measurable proxy for dispersal ability (Sheard et al., 2020). However, associations between dispersal ability and speciation in birds are complex: while Diamond et al. (1976) proposed speciation rate might be highest at intermediate dispersal abilities, some comparative studies find a negative relationship between dispersal ability and diversification rates (Claramunt et al., 2012; Weeks & Claramunt, 2014) while others find higher diversification rates (Phillimore et al., 2006) and more rapid transitions to sympatry (Pigot & Tobias, 2015) in dispersive clades. One hypothesized cause of these discrepancies is that the

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Table 1. Currently recognized Oceanic Swallow species and subspecies with geographic ranges and phenotypic descriptors. *H. t. tahitica* and *H. t. domicola* have been proposed to be elevated to species status, with remaining Pacific Swallow subspecies renamed *H. javanica;* proposed revisions are indicated in parentheses. Asterisks indicate subspecies not sampled in this study.

Species	Subspecies	Geographic range	Phenotypic description
Pacific Swallow	*H. t. javanica (H. j. javanica)*	Coastal Southeast Asia, Malay Archipelago, Philippines, Andaman Islands	Pale, streaky ventral coloration, large white tail spots
	H. t. namiyei (H. j. namieyei)	Taiwan and Ryukyu Islands	Pale, streaky ventral coloration, large white tail spots
	H. t. albescens (H. j. albescens)	Eastern New Guinea	Pale, streaky ventral coloration, large white tail spots
	H. t. frontalis (H. j. frontalis)*	Western and Central New Guinea	Pale, streaky ventral coloration, large white tail spots
	H. t. ambiens (H. j. ambiens)*	New Britain (hybrid of *frontalis* and *subfusca*)	Intermediate/variable ventral coloration, intermediate/variable tail spots
	H. t. subfusca (H. j. subfusca)	New Ireland, Solomon Islands to Fiji and Tonga	Sooty gray ventral color, no tail spots, large body size
Hill Swallow (proposed)	*H. t. domicola (H. domicola)*	Sri Lanka and the Western Ghats	Pale ventral color, large white tail spots, small body size
Tahiti Swallow (proposed)	*H. t. tahitica (H. tahitica)*	Society Islands (Tahiti and Mo'orea)	Nearly black ventral color, no tail spots, small body size
Welcome Swallow	*H. n. neoxena*	Eastern Australia and Tasmania	Pale ventral coloration, white tail spots, clearly forked tail
	H. n. carteri	Southwestern Australia	Pale ventral coloration, white tail spots, forked tail

relationship between dispersal ability and population divergence depends in part on habitat connectivity: strong dispersal ability may impede divergence in continuously distributed habitats, but facilitate divergence in fragmented landscapes such as island archipelagos or mountain ranges (Claramunt et al., 2012; Diamond et al., 1976; White, 2016). However, this hypothesis lacks clear empirical support.

A key mechanism by which fragmented or patchy habitats may accelerate divergence in dispersive species is evolutionary lability of dispersal propensity (Diamond et al., 1976; Moyle et al., 2009; Wilson, 1961). This mechanism has been invoked to explain explosively diverse avian radiations in which phenotypically and genetically differentiated allospecies have rapidly arisen on nearby islands (Andersen et al., 2015; Diamond et al., 1976; Jønsson et al., 2014; Moyle et al., 2009). In a scenario of labile dispersal propensity, species go through evolutionary phases in which a dispersive ancestor colonizes new islands, sometimes during periods of higher habitat connectivity such as low sea levels. There is then selection for reduced dispersal following island colonization because the benefits of dispersal decrease as available islands become saturated. Island populations subsequently diverge in allopatry, with some species even evolving flightlessness (Wright et al., 2016).

Although loss of dispersal ability may explain the origin of clades that are widely distributed but genetically differentiated among nearby islands (e.g., "great speciators," Andersen et al., 2015; Jønsson et al., 2014; Manthey et al., 2020; Moyle et al., 2009; Pedersen et al., 2018; Pepke et al., 2019), less clear are the drivers of population divergence in clades that retain robust flight ability after island colonization, for example due to ecological selection on foraging strategy. In these groups, population differentiation may arise despite strong flight ability if overwater dispersal is costly. This would result in reduced dispersal propensity if not reduced dispersal ability on islands, and support the hypothesis that patchy habitats (and consequent allopatry) can accelerate population divergence in putatively dispersive groups (Claramunt et al., 2012). By contrast, if overwater dispersal is not a significant barrier for vagile species, then gene flow can persist between island populations, similar to expectations for continuous habitats on continents. Variables such as philopatry, breeding phenology, competitive exclusion, historic changes in the distribution of suitable habitat, and ecological selection may then better predict whether population structure ultimately emerges in the absence of physical barriers to gene flow (Friesen, 2015; Lombal et al., 2020; Sexton et al., 2009; Taylor et al., 2019). One way to disentangle these potential drivers of population divergence is to compare population genetic structure and gene flow in closely related dispersive groups that inhabit patchy vs. continuous habitats. Comparing island vs. continental systems offers an ideal test case.

Here we conduct such a comparison using a clade of swallows in Southeast Asia and Oceania. There are two recognized species in this clade: the Pacific Swallow (*Hirundo tahitica*), which has a primarily insular distribution throughout Southeast Asia and the Pacific, and the Welcome Swallow (*H. neoxena*), which has a primarily continental distribution in Australia. Pacific Swallows inhabit both oceanic and continental islands and have therefore experienced historic variation in habitat connectivity due to sea level change. While there are only two described subspecies of Welcome Swallow, there are eight subspecies of Pacific Swallow, two of which have been proposed to be elevated to species status (Table 1, Del Hoyo et al., 2014; Limparungpatthanakij et al., 2020; Sibley & Monroe, 1990). These are the Sri Lankan and Indian subspecies (*H. t. domicola*), proposed to be renamed the Hill Swallow (*H. domicola*), and the Tahitian subspecies (*H. t. tahitica*), proposed to be renamed the Tahiti Swallow (*H. tahitica*; Table 1). Together, we refer to the Hill, Pacific, Welcome, and Tahiti Swallows as the "Oceanic" clade. Oceanic Swallows are a relatively young clade: phylogenies show that Pacific and Welcome Swallows are sister taxa

separated by 5.8% mitochondrial sequence divergence (Dor et al., 2010; Sheldon et al., 2005), while genetic analysis has never been conducted on Hill and Tahiti Swallows.

Swallows in the family Hirundinidae are highly vagile and have one of the highest average hand-wing indices (HWI), a measure of wing shape commonly used as a proxy for flight ability, among passerines (Kipp, 1959; Lockwood et al., 1998; Sheard et al., 2020). HWI varies little across the genus *Hirundo* (Tobias et al., 2022), suggesting conservation of wing shape associated with an aerial insectivorous foraging niche. However, there is likely considerable variation among species in dispersal behavior despite similar HWI. While some species in the family, such as the Barn Swallow (*H. rustica*), cross large water gaps on migration and show limited population genetic structure across continent-wide distributions (Safran et al., 2016; Scordato et al., 2017, 2020), many others are African endemics with small ranges and presumably short dispersal distances (Turner & Rose, 2010). In reconstructing phylogenetic relationships in the Hirundinidae, Sheldon et al. (2005) observed that geographic neighbors were frequently close relatives, suggesting swallows may disperse shorter distances than expected given their high HWI, although the reason for this pattern is not clear. Within the Oceanic clade, Pacific Swallows and western populations of Welcome Swallows are primarily sedentary, while eastern Welcome Swallows are partial migrants along the Australian coast and cross the Bass Strait into Tasmania (Turner, 2020). This variation in migratory behavior among closely related populations suggests dispersal propensity could be quite labile despite little variation in HWI.

The large geographic ranges of Pacific and Welcome Swallows, high HWI, and both island and continental distributions make this an ideal system in which to test the hypothesis that patchy landscapes such as islands facilitate population divergence in species with strong dispersal ability relative to continuous landscapes. To test this hypothesis, we sampled widely across the ranges of Oceanic swallows and compared population genetic structure and introgression in island vs. continentally distributed species. We assessed the association between water gap size (a proxy for habitat connectivity) and extent of population differentiation, and used demographic models to determine whether the timing of population divergence coincided with periods of enhanced habitat patchiness, such as high sea levels. If water gaps do not represent a significant barrier to dispersal and swallows retain high dispersal propensity following island colonization, we expected to find little population structure and evidence for ongoing gene flow in both Pacific and Welcome Swallows. By contrast, if the patchy habitats created by island distributions represent a significant barrier to dispersal, or if swallows exhibit evolutionary lability in dispersal propensity following island colonization, we expected to find strong population genetic structure and limited gene flow among insular Pacific Swallows, but not in continental Welcome Swallows. Finally, if dispersal distances are generally short in swallows due to factors unrelated to flight ability, such as philopatry, nest site limitation, competitive exclusion, or habitat patchiness on continents as well as islands, we expected to find limited gene flow and isolation-by-distance in both Pacific and Welcome Swallows.

Materials and methods

Sample collection

We sampled six of the eight subspecies of Pacific Swallow and the two subspecies of Welcome Swallow (Figure 1, Table 1). We found strong genetic differentiation that supports the distinctiveness of the Hill and Tahiti lineages (see Results, Figure 2), and therefore refer to them by their proposed species names in the following analyses.

To assess dispersal and gene flow across land vs. water, we sampled Pacific Swallow populations across the large island of Borneo, on large land masses separated by narrow seas in the central part of the species range (Peninsular Malaysia, Borneo, Papua New Guinea), and on isolated islands on the extremities of the range (Okinawa and Fiji, Figure 1, Table 1, Supplementary Table S1). In 2018 we collected blood samples from Pacific Swallows in Peninsular Malaysia (*H. t. javanica*; $N = 14$), at four sites in Malaysian Borneo (*H. t. javanica*; $N = 49$), in Okinawa (*H. t. namiyei*; $N = 15$), and on Viti Levu in Fiji (*H. t. subfusca*; $N = 15$). We sampled Hill Swallows ($N = 15$) from Sri Lanka in 2019 and Tahiti Swallows ($N = 2$) from Tahiti in 2021, which provided additional island samples. All birds were caught in mist nets, and we collected a small (~100 ul) blood sample via brachial vein puncture. We stored samples in lysis buffer treated with 2% SDS. We supplemented our field samples with museum tissue (heart and liver) of Pacific Swallows from the Oro Province of eastern Papua New Guinea (*H. t. albescens*; $N = 4$; collected in 1987), leaving only two unsampled subspecies of Pacific Swallow: *H. t. frontalis* from central and western Papua New Guinea, and *H. t. ambiens* from New Britain.

Welcome Swallows are native throughout Australia and self-colonized New Zealand and New Caledonia within the last 60 years (de Naurois, 1979; Mason, 2013, Figure 1). To ensure we sampled broadly from a large continental range, we obtained museum tissues (heart and liver) of both subspecies of Welcome Swallow from across five regions of Australia: *H. n. neoxena* ($N = 22$) in Queensland, New South Wales, and Tasmania, and *H. n. carteri* ($N = 8$) in South and Western Australia (collected between 1989 and 2017, Supplementary Table S1). Samples from Tasmania allowed us to assess the impact of a small water gap on population structure in Welcome Swallows. We used samples of three Barn Swallows (*H. rustica*) and four Tree Martins (*Petrochelidon nigricans*) as outgroups in our analyses.

Library preparation, sequencing, and bioinformatics

We extracted DNA using either a salt extraction (Aljanabi & Martinez, 1997) or Qiagen DNEasy extraction kits (Qiagen, Valencia, California, USA). Extractions followed the manufacturer's protocol except that we incubated samples with 30ul of Proteinase K for 24 hours at 56 °C. We estimated DNA concentration using a Qubit fluorometer. DNA concentrations ranged from 14 to 150 ng/ul. Genomic libraries were prepared at the University of Colorado BioFrontiers Sequencing Core (2018 samples) and at Medgenome Inc (2019 and 2021) using Illumina Nextera XT kits. We conducted whole-genome paired-end 150bp sequencing on an Illumina HiSeq platform at Novogene (Malaysia, Fiji, Okinawa samples) and Medgenome Inc (Australia, Sri Lanka, Papua New Guinea, Fiji, Okinawa, and Tahiti samples). Samples were sequenced to 6–11× coverage, and a subset of samples were resequenced at both facilities to control for lane effects. A subset of samples ($N = 5$ each from Peninsular Malaysia, Borneo, Fiji, Okinawa, Australia, and Sri Lanka, $N = 4$ from Papua New Guinea, and $N = 2$ from Tahiti) were sequenced to higher coverage (19–50× coverage) at Medgenome (Supplementary Table S1).

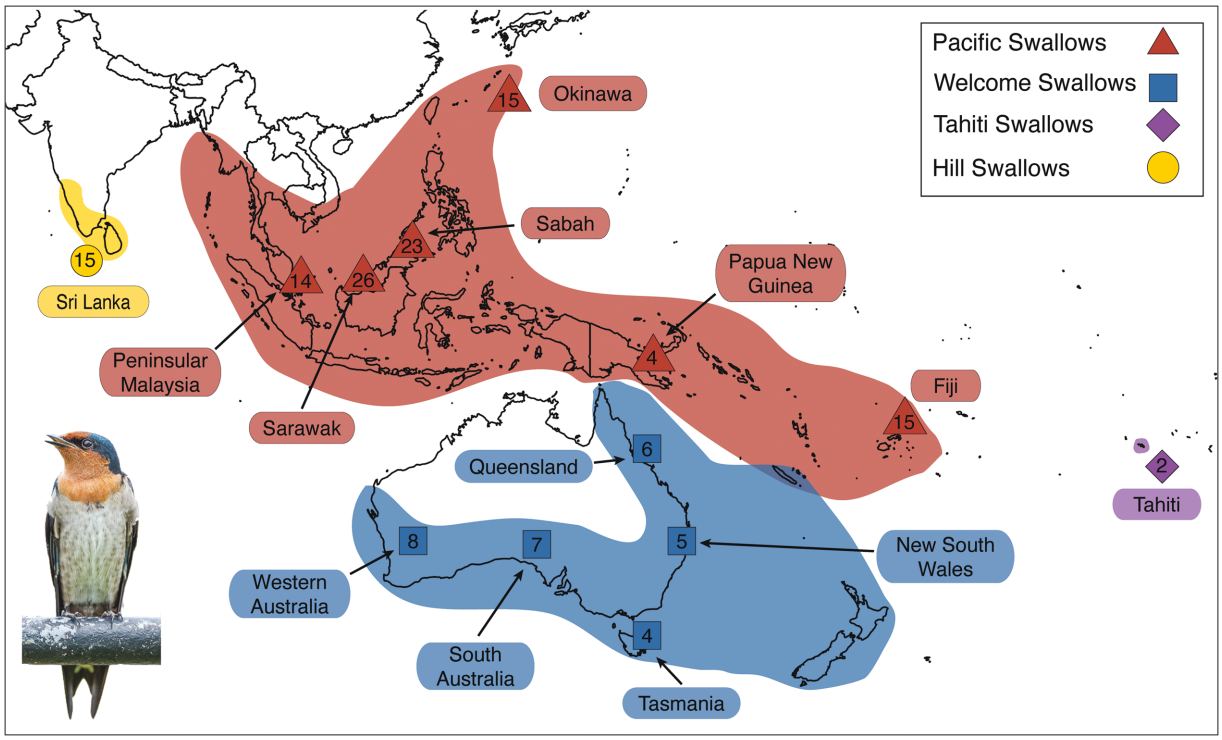

Figure 1. Range map of the Oceanic swallow clade. Pacific Swallows are distributed throughout Southeast Asia and Melanesia. Welcome Swallows inhabit Australia, New Zealand, and New Caledonia. Hill Swallows, a subspecies of Pacific Swallow proposed to be elevated to species status, are found in Sri Lanka and the Western Ghats. Tahiti Swallows, another Pacific Swallow subspecies proposed to be elevated to species status, occur only on the islands of Tahiti and Mo'orea. Sampling sites and sample sizes included in this study are indicated by the icons. Inset photo shows typical phenotype of the *H. t. javanica* subspecies of Pacific Swallow from Borneo. Photograph by A. K. Hund.

We trimmed adapters and low-quality reads using Trimmomatic (v. 0.32, Bolger et al., 2014) with the following options: Leading:3, Trailing:3, Slidingwindow:4:15, Minlen:36. We mapped reads to a high-quality chromosome-level Barn Swallow reference genome assembly consisting of 364 scaffolds (Vertebrate Genomes Project 2021; https://www.ncbi.nlm.nih.gov/assembly/GCA_003692655.1) using BWA-MEM v 0.6 (Li, 2013). Paired and unpaired reads were merged using SAMTOOLS (Li et al., 2009). We performed variant calling using the multiallelic caller in BCFtools mpileup version 1.11 (Li, 2011). Variants were filtered to have a minimum depth of 5, maximum depth of 50, minimum read quality of 30, minor allele frequency of 5%, and less than 15% missing data in VCFtools v. 0.1.16 (Danecek et al., 2011). Individuals with an average read depth below 5 were removed, indels were removed, and only biallelic sites were retained. Filtering and variant calling yielded 144 individuals plus 7 outgroup samples and 5,689,033 SNPs for analysis. We also generated an invariant sites VCF using the same filters but with minor allele frequency set to 0 for the high-coverage data; this VCF was used for analyses of nucleotide diversity, F_{ST}, and demography.

Population structure

We used multiple approaches to assess population genetic structure. First, we used the maximum likelihood-based model in ADMIXTURE version 1.3.0 (Alexander et al., 2009). We pruned the data in PLINK v.1.9 (Purcell et al., 2007) using 50kb sliding windows with 10bp steps and an r^2 value of 0.1, resulting in 434,966 unlinked SNPs. We had eight geographic sampling regions in our dataset (Australia, Borneo, Fiji, Okinawa, Papua New Guinea, Peninsular Malaysia, Sri Lanka, and Tahiti), with multiple sampling locations in Borneo and Australia. We therefore first ran ADMIXTURE on the whole dataset, excluding outgroups, for values of K from 1 to 12 with fivefold cross-validation. We recovered no structure within Welcome Swallows from this analysis, so we reran ADMIXTURE on Welcome Swallows alone with values of K from 1 to 7, corresponding to all unique sampling locations Australia, to assess finer-scale structure. We also ran ADMIXTURE on just Pacific and Hill swallows with values of K from 1 to 9, again corresponding to distinct sampling locations.

We next used principal components analysis (PCA) implemented in PLINK to further assess population structure using the same set of linkage-pruned SNPs. We explored relationships among principal components (PCs) one through four for the whole dataset, for Welcome Swallows alone, and for Pacific/Hill Swallows alone. Because PCA is sensitive to variation in sample sizes (Novembre & Stephens, 2008), we ran the analysis on both the whole dataset and on a subsampled dataset where we randomly selected four individuals per geographic sampling region. Finally, we used our invariant sites VCF and high-coverage individuals to calculate pairwise F_{ST} among all populations, and nucleotide diversity (π) within each population, using 50kb windows in pixy v1.1.1 (Korunes & Samuk, 2021).

Phylogenetics

Analyses of population structure revealed unexpectedly strong divergence, and we therefore reconstructed evolutionary relationships within the clade. We randomly pruned our

dataset to $N = 3$ individuals from each genetically distinct population identified in ADMIXTURE at $K = 8$, as this was the highest value of K for which we recovered clear population clusters corresponding to geographic sampling regions. Because we found no evidence of population structure within Welcome Swallows or within Borneo in the ADMIXTURE analysis, we randomly chose three samples from each region to include in the phylogenetic analysis. We included the Tree Martin and Barn Swallow as outgroups. We randomly subsampled the dataset to 498,873 SNPs to reduce computational time. Maximum likelihood tree construction was performed using RaxML version 8.2.12 (Stamatakis, 2014) with 1,000 bootstraps using the GTR-GAMMA model with no binary backbone. We also generated a species tree using SVDquartets in PAUP* version 4.0a (Chifman & Kubatko, 2014) with default settings and 1,000 bootstraps. In both RaxML and PAUP*, the Tree Swallow was designated as the outgroup a priori.

Introgression

If Oceanic swallows maintain high dispersal propensity after island colonization, we might expect frequent instances of gene flow among island populations. To investigate evidence for gene flow, we used TreeMix v1.13 (Pickrell & Pritchard, 2012) to infer migration events on a maximum likelihood tree using our linkage-pruned SNP dataset. We generated six trees with up to five introgression events ("migration edges") for the eight geographically distinct populations identified by ADMIXTURE plus the outgroups. We ran TreeMix with default parameters and 1,000 bootstraps. TreeMix guidelines suggest that no additional migration edges be added to a tree once at least 99.8% of the variation is explained (Pickrell & Pritchard, 2012). To determine the percent variance explained by additional migration edges we used the get_f() script that accompanies TreeMix.

To corroborate our TreeMix results, we generated D statistics in Dsuite using the Dtrios program (Malinsky et al., 2021). Dsuite runs ABBA/BABA tests on all potential four-taxon pectinate trees in a dataset with the format ((P1,P2),P3),O), with the outgroup, O, having the ancestral allele (A), the derived allele denoted as B, and the species tree expected to have the form BBAA. Dsuite arranges P1 and P2 so that the D statistic is always positive (i.e., introgression occurs between P2 and P3 and ABBA > BABA). We used Barn Swallows as our outgroup and assessed introgression between all possible combinations of the eight populations used in our phylogenies. We used a Bonferroni correction to control for multiple testing and retained comparisons with corrected p-values < .05 and D statistics > .05. D statistics calculated for many lineages can be difficult to interpret because introgression may have occurred between ancestral lineages that have subsequently diverged into multiple terminal taxa. We therefore followed the parsimony principle outlined in Pulido-Santacruz et al. (2020) and assumed that if all terminal taxa in a clade showed evidence of introgression with a lineage in a different clade, this represented a single gene flow event between ancestral populations.

We next used fastsimcoal2 (Excoffier et al., 2021) to determine if instances of gene flow identified by TreeMix and Dsuite were ancient (>5,000 generations ago), recent (<5,000 generations ago), constant over time, or nonexistent (null hypothesis). We used our invariant site VCF of high-coverage individuals to generate a site frequency spectrum using easySFS (https://github.com/isaacovercast/easySFS). We then ran fastsimcoal2 for each gene flow event with 1,000,000 coalescent simulations and 100 optimization cycles 100 times to find the global optimum of the best combination of parameter estimates for each model. We chose the best model based on likelihood and AIC scores. We assumed a mutation rate of 0.23×10^{-8} based on an estimate for the collared flycatcher (*Ficedula albicollis*; Smeds et al., 2016).

Effects of geographic distance and water gaps on population differentiation

To test the relationship between population differentiation (pairwise F_{ST}) and overwater dispersal, we contrasted the shortest "as the crow flies" geographic distance between pairs of populations with the size of water gaps between those populations. We grouped our samples into three categories: within Pacific Swallow comparisons, within Welcome Swallow comparisons, and interspecific comparisons (Pacific, Welcome, Hill and Tahiti Swallows). Since our goal was to assess the effects of water vs. land on population differentiation, we included the four sampling sites on Borneo as separate populations in the within- Pacific Swallow comparison. We grouped samples from Australia into populations from Western Australia, South Australia, New South Wales, Queensland, and Tasmania in the within- Welcome Swallow comparison. However, since pairwise F_{ST} was very small within Borneo and within Australia, we lumped these populations for the interspecific comparisons. We therefore calculated pairwise F_{ST} values between, for example, all of Australia and other populations, and estimated straight-line distances to the closest sampled Australian population.

We next classified each population pair as being separated by land, by small water gaps, or by large water gaps. Populations were separated by small water gaps if birds could move between them without having to cross a gap of >600 km at present-day sea levels. Thus, even though Okinawa and Papua New Guinea are separated by ~4,500 km as the crow flies, they are separated by small water gaps because swallows could disperse through nearby islands in the Philippines. Conversely, Fiji is ~2,700 km from Australia, but is separated by a large water gap. We chose 600 km as the cutoff because there was a clearly bimodal distribution in our dataset, with several gaps between 150 and 500 km, and several gaps > 1,500 km (Supplementary Figure S1).

If swallows disperse readily over water, we expected to find a pattern of increasing F_{ST} with increasing straight-line distance between populations (isolation-by-distance (IBD), Wright, 1943). By contrast, if water acts as a significant barrier, we expected to see greater genetic differentiation with increasing water gap size, even if the straight-line distance between populations was shorter. To test this hypothesis, we first used Mantel tests implemented in the "vegan" package in R (Oksanen et al., 2013) to assess correlations between F_{ST} and straight-line distance across our whole dataset, as well as within Pacific and Welcome Swallows and in our interspecific comparisons. We then built linear mixed models with pairwise F_{ST} as the response variable and geographic distance and water gap size as explanatory variables. We included "species contrast" as a random effect, indicating whether comparisons were within Pacific Swallows, within Welcome Swallows, or interspecific. We included species contrast as a random effect rather than a main effect because of nonindependence in the relationship between species contrast and

water gap size ($\chi^2 = 21.4$, $p = .0003$) and because we were focused on isolating the impact of water gap size on population genomic differentiation. Mixed models were built using the "lmer" package (Bates et al., 2014) and *p*-values calculated using Satterthwaite's method in the "lmerTest" package (Kuznetsova et al., 2015) in R.

Changes in historic effective population size

To assess whether island colonization is associated with reduced dispersal propensity and if population divergence coincides with periods of increased habitat patchiness, we inferred changes in effective population size (Ne) of Oceanic swallow populations using PSMC (Pairwise Sequentially Markovian Coalescent, Li & Durbin, 2011) with our subset of high-coverage individuals. We ran PSMC using 64 atomic time intervals and 28 free intervals with the *–p* parameter set to "4 + 25 × 2 + 4 + 6," corresponding to four time intervals spanned by the first population size parameter, two time intervals spanned by the next 25 population size parameters, four time intervals for the third population size parameter, and six time intervals for the fourth population size parameter (Li & Durbin, 2011). We set the upper limit of the TMRCA (the *–t* parameter) to 5,000,000 generations, and the theta/rho ratio (the –r option) to 1. Because PSMC is sensitive to population structure, we analyzed the eight genetically distinct populations identified in ADMIXTURE and our phylogenies separately. We ran PSMC for five individuals from each population (except for Papua New Guinea and Tahiti, which only had $N = 4$ and $N = 2$ samples respectively). We ran 25 bootstrap replicates for each population using the "splitfa" function and a modified version of the script provided with PSMC.

PSMC generates plots of changes in N_e over time, with the x-axis scaled by generation time and the y-axis scaled by mutation rate (Nadachowska-Brzyska et al., 2016). Since these parameters have not been measured in Oceanic Swallows (although age of first breeding for Welcome Swallows in New Zealand is 8–14 months, Mason, 2013), we generated PSMC plots with a range of values to produce upper and lower bounds for the timing of island colonization and population divergence (Mather et al., 2020). We used a 1-year generation time based on previous demographic studies of the Barn Swallow (Smith et al., 2018; Zink et al., 2006) as well as 2- and 2.5-year generation times, which are often used for small-bodied passerine birds (Brommer et al., 2004; Nadachowska-Bryzka et al., 2016 , 2021). We scaled mutation rates to 1.8×10^{-9}, 2.3×10^{-9}, and 3.18×10^{-9}, representing the range of values reported for passerine birds in the literature (Nadachowska-Brzyska et al., 2015). PSMC is most reliable for timescales ranging 20,000–3,000,000 generations before present (gbp, Li & Durbin, 2011; Schiffels & Durbin, 2014), and we therefore only report results within this range.

Results

Population structure and phylogenetics

Cross validation of our ADMIXTURE analysis gave $K = 5$ as the best supported number of clusters (Figure 2B). At $K = 5$, there were clear clusters corresponding to (a) Welcome Swallows; (b) Sri Lankan Hill Swallows; (c) Southeast Asian Pacific Swallows from Peninsular Malaysia, Borneo, and Papua New Guinea; (d) Pacific Swallows on Okinawa; and (e) Pacific Swallows on Fiji. We found little evidence for mixed ancestry within the Pacific Swallow group. Tahiti Swallows did not form a distinct cluster at $K = 5$, and instead exhibited roughly half their ancestry from Welcome Swallows and half their ancestry from Pacific Swallow populations, but this may be due in part to small sample size. Larger values of K revealed finer-scale population structure: at $K = 8$, there were distinct clusters corresponding to each geographic region we sampled, including Tahiti. There was little evidence of mixing between groups, with the exception of potential admixture between Peninsular Malaysia and the Sarawak region of Borneo (Figure 2B). Values of K larger than 8 did not reveal additional clustering on the large land masses of Borneo and Australia. ADMIXTURE analysis of just Pacific and Hill swallows recovered the same clusters found in the whole dataset, with $K = 4$ and $K = 5$ having similarly low cross-validation scores (0.371 and 0.375) and clusters corresponding to (a) Hill Swallows; (b) Fiji; (c) Okinawa; and (d) the Peninsular Malaysia/Borneo/Papua New Guinea group. Borneo separated from Peninsular Malaysia and Papua New Guinea at $K = 5$. ADMIXTURE analysis of just Welcome Swallows showed $K = 1$ as the best supported value, indicating very little structure across the entire continent.

The PCA showed similar results to ADMIXTURE (Figure 2C, Supplementary Figure S2). In the PCA of all samples, PC1 (34% of the variation) separated most Pacific Swallows from Welcome Swallows and revealed strong differentiation in the insular Fijian and Sri Lankan Hill Swallow populations. Surprisingly, Tahiti Swallows grouped closely with Welcome Swallows in PC space, suggesting shared ancestry between these lineages. The PCA using a subsampled dataset showed the same patterns, and plots of PCs 3 and 4 did not yield additional insight into geographic structure and are therefore not shown. PCA of only Pacific and Hill Swallows showed the same clustering patterns as in the whole dataset (Supplementary Figure S2A). PCA of only Welcome Swallows explained comparatively little genetic variation and showed populations distributed along PC1 according to geographic proximity (Supplementary Figure S2B). The exception was two birds from Queensland that clustered with Tasmania, suggesting they may have been caught while overwintering.

All populations of Pacific Swallows were clearly differentiated in F_{ST} (Table 2, mean $F_{ST} = 0.36$), supporting the ADMIXTURE and PCA results. In particular, there were very high F_{ST} values between the Fijian population of Pacific Swallows and all other populations (Table 2). By contrast, divergence among Welcome Swallow populations within Australia was shallow (mean $F_{ST} = 0.025$), with the most differentiation occurring between Tasmania and Western Australia ($F_{ST} = 0.06$; Table 2). Nucleotide diversity was low overall in small island populations (Fiji, Tahiti, and Okinawa), consistent with little gene flow after island colonization (Table 2).

The two approaches to constructing phylogenetic trees (RAxML and SVDquartets) resulted in the same tree topology, with all nodes at or near 100% bootstrap support (Figure 2A). This topology showed two major clades: one comprising Pacific and Hill Swallows, and one comprising Tahiti and Welcome Swallows. Within the Pacific/Hill clade, the Sri Lankan Hill Swallows were sister to all other populations. Within the remaining Pacific Swallows, the Fijian population was sister to all other populations, supporting an early east–west split between subspecies that corresponds to differences in phenotype (Figure 2A, Table 1). Okinawa

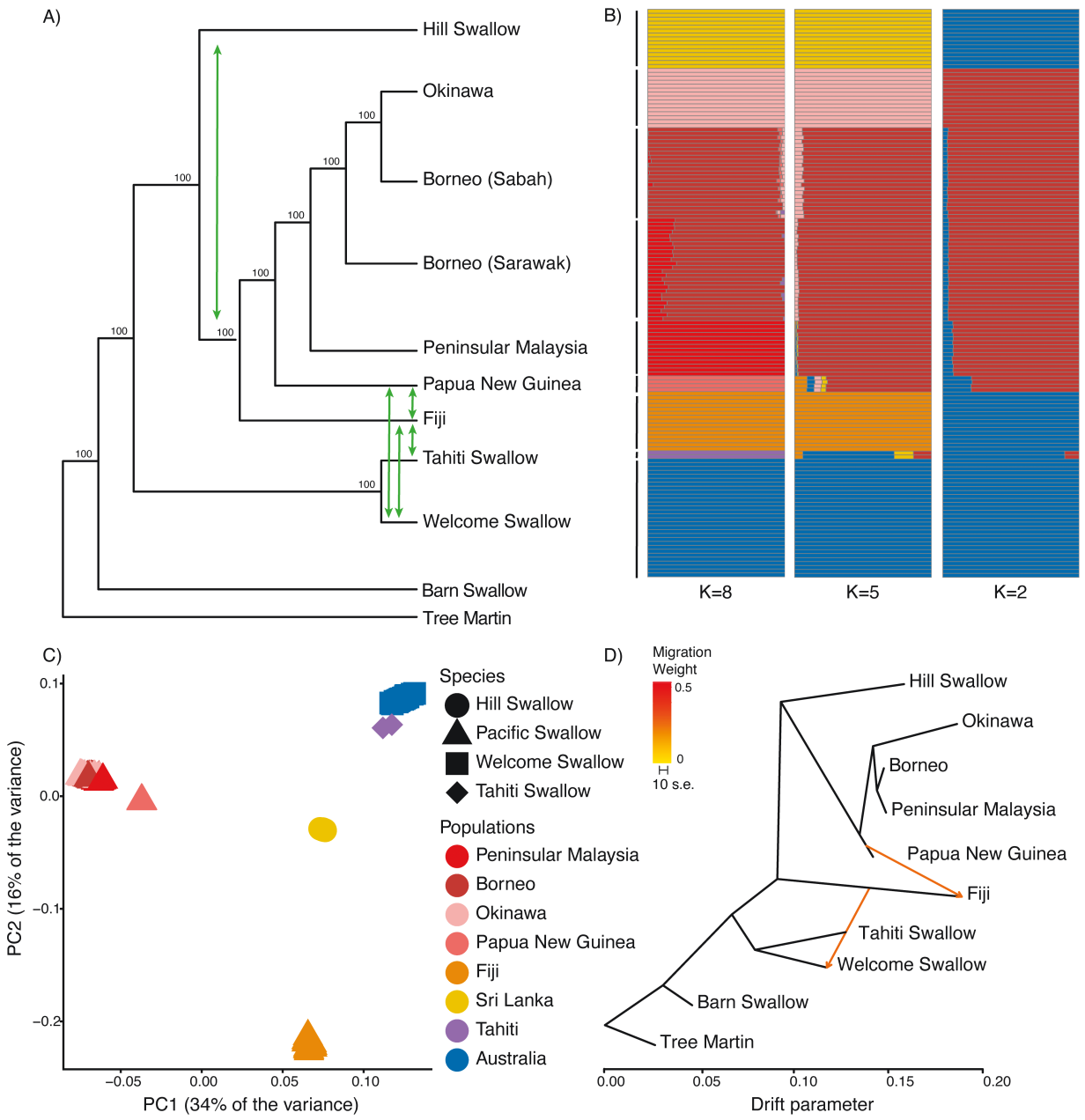

Figure 2. Summary of phylogenetic relationships, population structure, and introgression in the Oceanic Swallow complex. (A) Consensus tree from RAxML and SVDquartets shows Pacific and Welcome Swallows form sister clades. Hill Swallows are sister to all other Pacific Swallow populations, and Tahiti Swallows are sister to Welcome Swallows. Okinawa is nested within populations from Borneo. Arrows indicate introgression identified using ABBA/BABA tests in Dsuite. (B) ADMIXTURE plots ($K = 8$, $K = 5$, and $K = 2$) for all Oceanic swallows. Black vertical lines indicate which samples correspond to the tips of the phylogenetic tree. Cross validation showed $K = 5$ to be the best number of clusters. At $K = 8$ all geographic sampling regions occur as distinct clusters (C) PCA is consistent with ADMIXTURE. PC1 (34% of the variance) separates most Pacific Swallow populations (triangles) on the left hand side of the plot from Welcome and Tahiti Swallows (squares and diamonds) on the right. The Fijian population of Pacific Swallows (orange triangles) and the Sri Lankan Hill Swallows (circles) form discrete clusters in the middle of PC1 and are further separated on PC2 (16% of the variance). Pacific Swallows from Okinawa, Peninsular Malaysia, and Borneo all cluster tightly at the lowest values of PC1, while Papua New Guinea (PNG) had slightly larger values of PC1. (D) TreeMix maximum likelihood tree with two migration edges. TreeMix identified introgression between Pacific Swallow populations in PNG and Fiji, and between the Fijian population and Welcome Swallows in Australia. The drift parameter is particularly long in Fijian swallows, indicating substantial genetic drift after divergence.

was nested within samples from Borneo. Phylogenetic analysis confirmed that Tahiti Swallows are sister to Welcome Swallows; this is a surprising result, as Tahiti Swallows were previously considered to be a subspecies of Pacific Swallow (Limparungpatthanakij et al, 2020). Overall, our analyses of population genetic structure showed strong differentiation among Pacific Swallow populations and little evidence of ADMIXTURE between islands, but weak differentiation among continentally distributed Welcome Swallows. Our results support proposals (Sibley & Monroe, 1990, del Hoyo et al., 2014) to elevate Hill and Tahiti Swallows to species status, although a full taxonomic revision is warranted.

Introgression

TreeMix produced a maximum likelihood tree that generally matched the topology of the phylogenetic tree, with

Table 2. Pairwise F_{ST} of all sampled Oceanic swallow populations (lower triangle) and values of π for each population (diagonal). Top: There is strong differentiation between all populations, with the exception of Borneo, Peninsular Malaysia, and Papua New Guinea (PNG). Estimates of π (diagonal) show that nucleotide diversity is much lower in small island populations (Fiji, Okinawa, Tahiti) than large island and continental populations. Bottom: Pairwise F_{ST} between Welcome Swallow populations in Australia (NSW = New South Wales). Differentiation between these populations is weak. F_{ST} results are presented as mean ± SD.

All populations	Borneo	Fiji	Hill	Malaysia	Okinawa	PNG	Tahiti	Welcome
Borneo	0.0061							
Fiji	0.55 ± 0.18	0.0031						
Hill	0.56 ± 0.18	0.85 ± 0.24	0.0066					
Malaysia	0.04 ± 0.03	0.64 ± 0.20	0.63 ± 0.20	0.0061				
Okinawa	0.19 ± 0.10	0.69 ± 0.21	0.69 ± 0.21	0.24 ± 0.12	0.0048			
PNG	0.09 ± 0.06	0.74 ± 0.24	0.72 ± 0.23	0.10 ± 0.07	0.28 ± 0.16	0.0066		
Tahiti	0.46 ± 0.17	0.86 ± 0.26	0.81 ± 0.25	0.49 ± 0.17	0.59 ± 0.20	0.56 ± 0.20	0.0032	
Welcome	0.57 ± 0.17	0.67 ± 0.21	0.67 ± 0.21	0.54 ± 0.18	0.65 ± 0.19	0.52 ± 0.19	0.42 ± 0.20	0.0106
Welcome Swallows	**Western Australia**	**South Australia**	**NSW**	**QLD**	**Tasmania**			
Western Australia	–							
South Australia	0.02 ± 0.04	–						
NSW	0.03 ± 0.04	0.01 ± 0.02	–					
Queensland	0.04 ± 0.10	0.02 ± 0.04	0.01 ± 0.02	–				
Tasmania	0.06 ± 0.07	0.03 ± 0.05	0.02 ± 0.03	0.01 ± 0.06	–			

the exception of Okinawa emerging as sister to Borneo and Peninsular Malaysia, rather than nested within Borneo. TreeMix calculates a drift parameter for each population that measures genetic drift after differentiation. Consistent with measures of nucleotide diversity, the Fijian Pacific Swallow population and the Hill Swallows had large drift parameters (Figure 2D), likely due to founder effects and reductions in gene flow after island colonization.

The best fit TreeMix tree included two migration edges (Figure 2D). The first was between Pacific Swallows in Papua New Guinea and Fiji. The second migration edge was between Fijian Pacific Swallows and Welcome Swallows. The largest D statistics from the ABBA/BABA tests also occurred between Fiji and Welcome Swallows (Figure 2A; Table 3). Dsuite identified several additional instances of introgression (Figure 2A; Table 3). Although these were significant, the values of the D statistic were lower, likely reflecting old or limited introgression not detected by TreeMix. First, there was introgression between Pacific Swallows in Papua New Guinea and Welcome Swallows. Second, there was introgression between Tahiti Swallows and Fijian Pacific Swallows. Finally, introgression occurred between Hill Swallows and all Pacific Swallow populations except Fiji. This likely reflects introgression between ancestral lineages that occurred after divergence of the Fijian population but prior to divergence of other Pacific Swallow populations in Southeast Asia (Figure 2A).

Simulations in fastsimcoal2 showed that models of ancient gene flow (>5,000 generations ago) had the highest likelihood scores, with two exceptions. First, we found evidence of recent gene flow between Borneo and Peninsular Malaysia, consistent with ADMIXTURE plots indicating potential introgression between these populations. Second, a model of constant gene flow had the highest likelihood score for the Tahiti Swallow and the Welcome Swallow, although, like the ADMIXTURE analysis, this may be influenced by the small sample size for Tahiti (Supplementary Figure S3). Overall, gene flow between Oceanic swallow populations was generally limited and old.

Geographic distance and water gaps

We found a positive but nonsignificant relationship between F_{ST} and straight-line geographic distance across the entire dataset (Mantel test, $r = 0.37$, $p = .07$). However, when we treated intra- and inter-specific comparisons separately, we found very different patterns: within insular Pacific Swallows, there was a strong positive correlation between F_{ST} and straight-line distance between populations ($r = 0.83$, $p = .02$, Figure 3A). Within Welcome Swallows, this relationship was much weaker ($r = 0.56$, $p = .09$, Figure 3A), reflecting greater genetic homogenization in Australia. In interspecific comparisons, we found no evidence for increasing genetic differentiation with increasing geographic distance between populations ($r = 0.15$, $p = .35$, Figure 3A).

Our linear mixed model including geographic distance and gap type as main effects and species contrast as a random effect showed significantly greater values of F_{ST} among populations separated by both small (0.48 ± 0.18, $t = 2.65$, $p = .012$) and large (1.40 ± 0.26, $t = 5.35$, $p = 4.03e\text{-}06$) water gaps compared to land gaps, but found no significant effect of straight-line geographic distance (0.034 ± 0.10, $t = 0.34$, $p = .73$) on F_{ST}, and no significant interaction between gap type and distance (Figure 3B). Species contrast accounted for 53% of the variance. Together, these results indicate that the size of water gaps- our measure of habitat patchiness- better explains population differentiation than does straight-line geographic distance (Figure 3).

Change in historic effective population size

We used different mutation rates and generation times to explore ranges of divergence times and estimates of N_e in our PSMC models. Varying generation time and mutation rate has predictable scaling effects on PSMC plots: increasing generation time pushes demographic events further into the past and increasing mutation rate decreases estimates of N_e (Nadachowska-Brzyska et al., 2016). Divergence time can be inferred from PSMC plots as the time at which the N_e traces for different populations separate from each other.

Table 3. ABBA/BABA tests showing population trios with D statistic values of 0.05 or greater using Barn Swallows as the outgroup. The table is arranged from highest D statistic to lowest. The expectation from the species tree is a BBAA pattern (P1 and P2 sharing the derived allele), and introgression is always between P2 and P3 (P2 and P3 sharing the derived allele). All D statistics are significant at p-values < 10^{-20}. Patterns of introgression fall into several categories that are alternately shaded in the table. First, there is introgression between Fiji and Welcome Swallows regardless of which population is in the P1 position, indicating gene flow after Fiji split from the rest of Pacific Swallow clade. Second, there is introgression between all western Pacific Swallow populations and Hill Swallows when Fiji is in the P1 position. This likely indicates gene flow between ancestral Pacific and Hill Swallows after Fiji diverged but before the other Pacific Swallow populations split. Third, there is introgression between Papua New Guinea (PNG) and Fiji when other Pacific Swallow populations are in the P1 position. Fourth, there is introgression between Fiji and Tahiti, and finally, there is introgression between PNG and Welcome Swallows when various other Pacific Swallow populations are in the P1 position.

P1	P2	P3	*D*	*Z*	BBAA	ABBA	BABA
Okinawa	Fiji	Welcome	0.227	17.657	427605	196749	124043
Borneo	Fiji	Welcome	0.225	17.981	428330	196754	124532
Malaysia	Fiji	Welcome	0.223	18.083	428070	196244	124600
Hill	Fiji	Welcome	0.216	15.408	322666	234398	151212
PNG	Fiji	Welcome	0.192	15.476	450881	183429	124245
Fiji	Malaysia	Hill	0.151	17.854	299618	211398	156078
Fiji	Borneo	Hill	0.147	17.928	299980	210854	156690
Fiji	Okinawa	Hill	0.145	17.806	299462	209919	156894
Fiji	PNG	Hill	0.142	18.545	328613	198794	149281
Okinawa	PNG	Fiji	0.122	16.977	355153	170509	133514
Borneo	PNG	Fiji	0.118	17.111	350081	171911	135614
Malaysia	PNG	Fiji	0.116	17.826	344792	172870	136828
Tahiti	Welcome	Fiji	0.108	15.805	234911	217690	175081
Hill	Fiji	Tahiti	0.079	9.637	315168	184934	157878
Okinawa	Fiji	Tahiti	0.076	11.711	420956	149242	128217
Borneo	Fiji	Tahiti	0.074	12.197	421634	149220	128636
Malaysia	Fiji	Tahiti	0.073	12.695	421480	148813	128476
Hill	PNG	Welcome	0.072	10.519	373406	176602	152744
PNG	Fiji	Tahiti	0.067	11.264	448141	140098	122495
Okinawa	PNG	Welcome	0.065	18.005	620901	109611	96165.7
Borneo	PNG	Welcome	0.062	21.661	615356	110539	97572.4
Malaysia	PNG	Welcome	0.059	21.037	609424	110855	98466.8

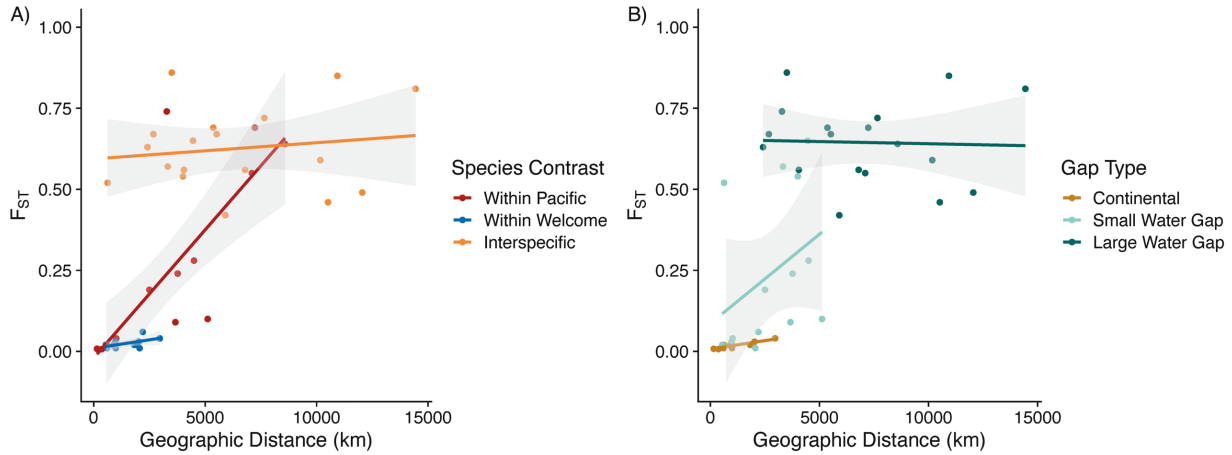

Figure 3. Relationship between F_{ST} and geographic distance among different species contrasts and water gap sizes. (A) There is a weak effect of isolation-by-distance within Welcome Swallows and no effect of isolation-by-distance in interspecific comparisons, but F_{ST} increases dramatically with increasing geographic distance within Pacific Swallows. (B) F_{ST} is greater among populations separated by water gaps than among continental populations, and greatest among populations separated by large water gaps. Plots show raw data with separate linear models and 95% confidence intervals fitted to each group; Mantel tests and linear mixed models are reported in the main text.

Depending on the generation time used, divergence between the Pacific and Welcome Swallow clades occurred from ~1.5 mya (one-year generation time) to more than 3.8 mya (2.5 year generation time; Figure 4, Supplementary Figure S4). A two-year generation time indicates divergence between Pacific and Welcome Swallows approximately 3.05 mya (Figure 4, Supplementary Figure S5). Phylogenies based on mtDNA show 5.8% sequence divergence between these two

species (Sheldon et al., 2005), which is approximately 2.7 mya using a standard avian molecular clock for cytochrome *b* (Weir & Schluter, 2008). Because the estimated mtDNA divergence time is closest to the two-year generation model in PSMC, we show results for a two-year generation time and an intermediate mutation rate in Figure 4, with other generation time and mutation rate results shown in Supplementary Figure S4. PSMC runs were generally consistent across multiple individuals within the same population and across bootstraps, even among individuals sampled from across broad geographic regions in Australia and Borneo (Supplementary Figures S6 and S7). We therefore present results from a single individual from each population in Figure 4.

Under a two-year generation time, the Sri Lankan population of Hill Swallows split relatively early from other Pacific Swallow populations, close to 3 mya. The Tahiti population diverged from Welcome Swallows over 2.1 mya, and the Fijian population of Pacific Swallows diverged at least 1.1 mya. Populations in Okinawa, Papua New Guinea, Borneo, and Peninsular Malaysia all began diverging around 300 kya (Figure 4, Supplementary Figures S4 and S5). However, divergence times for the island populations in Fiji, Tahiti, and Sri Lanka are somewhat uncertain. This is because PSMC has limited ability to project N_e far into the past in populations with low nucleotide diversity (Armstrong et al., 2020; Kumar et al., 2017), so the exact point at which these lineages diverged from their common ancestor was not detected in our models.

Patterns of N_e show that swallow populations in Australia and the large land masses of Southeast Asia all increased for much of the last 700,000–1,000,000 years (Figure 4). These populations then declined substantially 50,000–80,000 years ago, although the magnitude of these declines should be interpreted with caution, as they occur near the boundary of PSMC's sensitivity and our bootstraps show more variation in N_e within this timespan than for earlier events (Supplementary Figure S7). Nonetheless, the data consistently show population declines on all large land masses in the late Pleistocene.

In contrast to the larger land masses, all four small island populations (Fiji, Okinawa, Sri Lanka, and Tahiti) declined over time, suggesting little gene flow after island colonization (Figure 4). This pattern persisted regardless of generation time or mutation rate. The Tahiti, Fijian, and Sri Lankan populations all showed brief periods of expansion after divergence before declining steadily into the present, consistent with phases of colonization followed by declines (Liu et al., 2020).

Discussion

In this study we tested the hypothesis that fragmented habitats—specifically island systems—contribute to population divergence in a vagile clade of birds. We found that island-distributed populations exhibited strong population genetic structure and limited inter-island gene flow, whereas continentally distributed populations had little genetic structure and weak IBD. Our data suggest that water gaps represent a significant barrier even in this putatively dispersive group, and indicate that Oceanic Swallows likely reduce their dispersal propensity following island colonization despite the maintenance of flight ability. Our results support the hypothesis that the likelihood of population divergence in dispersive species depends on habitat connectivity (Claramunt et al., 2012), and particularly overwater dispersal propensity.

Evidence for lability of dispersal propensity in insular swallows

Strong population structure among insular but not continental populations of Oceanic Swallows supports the hypothesis

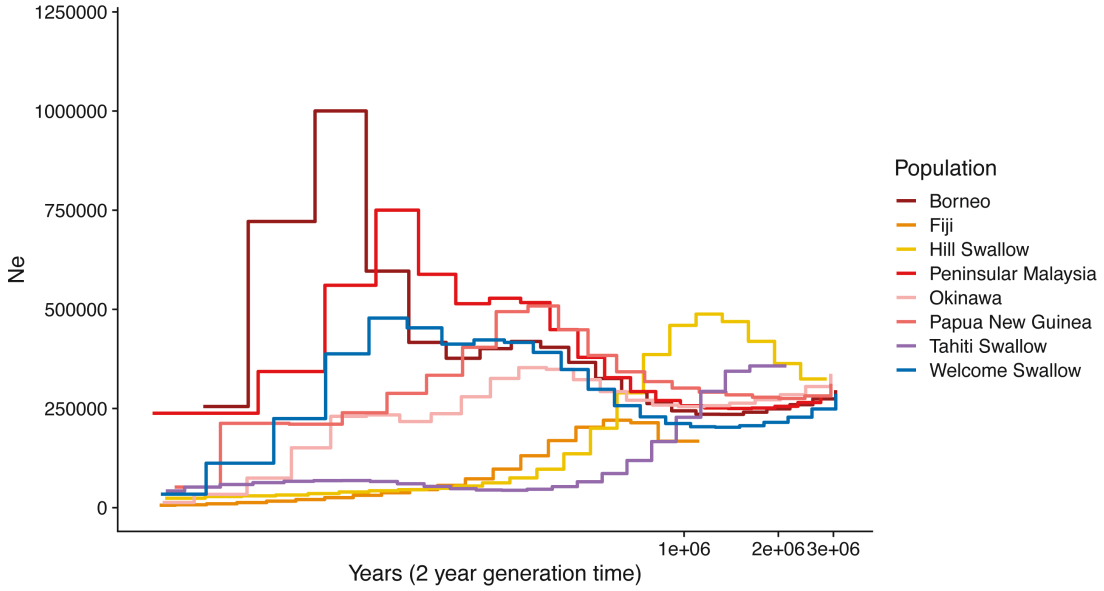

Figure 4. PSMC results for each population, scaled to a two-year generation time and mutation rate of 2.8×10^{-9}. The x-axis is on a log scale and ranges from 20,000 kya to 3 mya. Under this model, Welcome Swallows (blue line) diverged from the Pacific Swallow lineage ~3.05 mya. Hill Swallows (yellow) diverged at least 3 mya, and Tahiti Swallows (purple) split at least 2 mya. The Fijian population (orange) diverged approximately 1 mya. The island of Okinawa was likely colonized approximately 300 kya, the point at which this population begins to decline. Populations on the large land masses (Australia, Borneo, Peninsular Malaysia, and Papua New Guinea) increased over most of the last million years before declining in the late Pleistocene, while smaller island populations (Sri Lanka, Fiji, Okinawa, and Tahiti) declined fairly rapidly after divergence, consistent with limited gene flow after island colonization.

that water gaps are a substantial barrier to dispersal. There are two nonmutually exclusive explanations for this observation. First, successful overwater dispersal could be rare because swallows disperse short distances overall (Sheldon et al., 2005), due to factors like philopatry or nest site limitation (Lombal et al., 2020). In this scenario, island populations would be the result of rare long-distance dispersal events (Gillespie et al., 2012). However, if dispersal distances are generally short across the clade, we expected to observe isolation-by-distance among continental Welcome Swallow populations as well as insular Pacific Swallows. Instead, we observed weak differentiation and very little evidence of IBD in Welcome Swallows. Although the presence of unsampled continental populations means that IBD is expected to be weaker in continental vs. island comparisons (Meirmans, 2012), the absence of significant IBD in Welcome Swallows suggests dispersal distances are large enough to homogenize swallow populations across most of Australia.

A second possible explanation for strong population structure in insular but not continental populations is evolutionary lability of dispersal propensity in fragmented landscapes. Several lines of evidence support this scenario in Oceanic Swallows. We found that populations separated by both small and large water gaps were more genetically differentiated than those separated by land when controlling for straight-line geographic distance. Furthermore, our analyses showed clear declines in effective population size after divergence in all small island populations and little evidence for recent introgression, indicating that gene flow does not continue following establishment on islands. This is the pattern expected if dispersal behavior is reduced following island colonization (Gillespie et al., 2012; Liu et al., 2020). Added support for the evolutionary lability of dispersal propensity in the clade comes from Welcome Swallows: our results indicate that Tahiti was colonized by ancestral Welcome Swallows, giving rise to a sedentary population that is now phenotypically and genetically differentiated from its source. Additionally, Welcome Swallows, which exhibit seasonal migration in eastern Australia, were occasional vagrants in New Zealand before successfully establishing large breeding populations in the 1960s (Mason, 2013). New Zealand populations have since either become residents or exhibit limited within-island seasonal movements (Turner, 2020). Together, these observations indicate a history of rapid transitions in dispersal behavior in response to island colonization across the Oceanic clade and suggest that evolutionary lability of dispersal behavior has contributed to the current population structure in insular groups.

Contributions of habitat patchiness to population structure and dispersal behavior

Our analyses allowed us to ask how patchy landscapes, as well as nongeographic processes such as competition and breeding phenology, have shaped population structure and dispersal behavior in the Oceanic clade. We found that even comparatively short (<600 km) water gaps pose a greater barrier to swallows than land gaps. This is notable for species that regularly forage over rivers and along coastlines. Furthermore, suitable habitat for Welcome Swallows in Australia may have been historically patchy: Welcome Swallows are restricted to coastal areas with cliff faces where they can build nests, and are absent from the arid interior of the country. Weak population differentiation suggests that the potentially limited availability of nesting sites and large tracts of unsuitable land do not prevent gene flow among continental Australian populations. However, it is possible that shallow differentiation in Welcome Swallows is due in part to recent population expansions outside the sensitivity range of our demographic models. Since the arrival of Europeans, Welcome Swallows have nested on manmade structures (Turner, 2020). This increase in nesting habitat may have led to some genetic homogenization of previously differentiated populations. Thus, although our data suggest that water is the strongest barrier to dispersal, we cannot rule out a historic contribution of patchy continental landscapes.

Indeed, demographic reconstructions indicate that divergence within the Oceanic clade is relatively recent and has likely been shaped by interactions between biological traits like dispersal propensity and historic habitat connectivity. For example, we estimated that the Pacific and Welcome clades split approximately 3 mya. The collision of the Australian and Pacific plates during the early Pliocene (~5 mya) brought the faunas of Asia and Australia into closer proximity (Baldwin et al., 2012; Hall, 2002) and may have facilitated colonization of Australia from Asia by ancestral Oceanic Swallows. The Australian climate transitioned from a humid to an arid interval between 3.5 and 2.5 mya (Christensen et al., 2017; Sniderman et al., 2016), which may have pushed Welcome Swallows into wetter regions of southern Australia and restricted gene flow with Pacific Swallows through the creation of large areas of inhospitable habitat. Welcome Swallow populations declined through the late Pleistocene, but at some point, eastern populations developed partial migration, in which they overwinter in northern Queensland and breed in the south (Turner, 2020). Overwintering Welcome Swallows are now separated from Pacific Swallows by ~150 km across the Torres Strait and are sighted as vagrants in Papua New Guinea, although our data show no evidence of recent gene flow. Furthermore, both Pacific and Welcome Swallows occur in New Caledonia, although it is unclear if they breed in sympatry. At this stage of speciation, allochronic isolation, competitive exclusion by Pacific Swallows, or ecological selection, more than dispersal limitation, may maintain reproductive barriers between Pacific and Welcome Swallows. Study of sympatric populations in New Caledonia could shed light on the factors maintaining reproductive isolation between these species.

Changes in sea level and consequent habitat patchiness also likely contributed to population structure among Pacific Swallow populations on continental islands and islands separated by small water gaps, as has occurred in many less-vagile Southeast Asian taxa (reviewed in Lohman et al., 2011). For much of the Pleistocene, Borneo was connected to mainland Southeast Asia and water gaps between Okinawa and other islands were smaller than they are today (Bird et al., 2005). As in the Welcome Swallows, Pacific Swallow populations on the large Southeast Asian landmasses declined in the late Pleistocene, concurrent with rising sea levels (Cannon et al., 2009; Yang et al., 2021). The coincidence between population divergence and changes in effective population size in our demographic models, and climatic variation associated with sea level rise and reductions in suitable habitat, suggest that water barriers and other forms of habitat fragmentation have contributed to population structure in Oceanic Swallows despite their ability to disperse long distances.

Although Pleistocene sea level changes may have contributed to divergence among populations on continental islands,

swallow populations on distant oceanic islands such as Fiji and Tahiti can only be the result of long-distance dispersal. Our models suggest that there were at least two waves of colonization of the Pacific, first by ancestral Welcome Swallows and next by ancestral Pacific Swallows. Tahiti Swallows diverged from Welcome Swallows ~2 mya and likely made their way east from Australia, colonizing islands until they became established in Tahiti. Reductions in dispersal and localized extinctions likely followed, as swallows are now absent from all islands between Fiji and Tahiti, and Tahitian populations declined post divergence. Subfossil evidence supports this inference: swallow bones from 1,200 to 1,400 years ago were found in a cave on Henderson Island in the Pitcairn group (Wragg, 1995), even further east than Tahiti. The extirpation of this population coincided with the arrival of humans, suggesting the absence of swallows on smaller islands throughout the Pacific may be a recent phenomenon.

The Fijian population of Pacific Swallows diverged from its ancestor at least 1 mya and likely dispersed from Papua New Guinea. We found evidence of ancient (>5,000 years ago) interbreeding between Fijian swallows and both Tahiti and Welcome Swallows. We do not know if ancestral Tahiti or Welcome Swallows were present on Fiji when Pacific Swallows arrived and were subsequently displaced, if they were absent from Fiji and introgression occurred on other islands in the region, or if introgression occurred among extant populations > 5,000 years ago. However, the extremely low nucleotide diversity and the lack of recent gene flow on Fiji suggest a major reduction in dispersal behavior after island colonization.

Drivers of divergence in vagile clades

The great diversity of island bird radiations has been attributed in part to variation among species in their willingness to cross water gaps (Diamond, 1981) and to dispersive ancestors reducing dispersal propensity and often flight ability following phases of island colonization (Andersen et al., 2015; Cibois et al., 2011; Garcia-R & Trewick, 2015; Hosner et al, 2017; Jønsson et al., 2014; Kirchman, 2012; Manthey et al., 2020; Moyle et al., 2009; Pedersen et al., 2018; Pepke et al., 2019; Slikas et al., 2002). However, causes of diversification in species that maintain strong dispersal ability after island colonization have remained unclear (Linck et al., 2016; Lombal et al., 2020). Although the species and subspecies richness of the Oceanic Swallow clade is a fraction of that found in the great speciators, our analyses show that water is a substantial barrier to dispersal despite the retention of high HWI and strong flight ability. Swallows have thus not only reduced their dispersal behavior after arriving on islands, but populations on large land masses such as Borneo and Australia have not continued to send out successful island colonizers. This may be due to the loss of behavioral motivation, if not physical ability, to cross water barriers (Bertrand et al., 2014; Diamond, 1981; Komdeur et al., 2004), competitive exclusion of immigrants on islands with established swallow populations (Shaw & Gillespie, 2016; Waters et al., 2013), the loss of dispersive alleles from continental populations (Manthey et al., 2020), and/or the completion of evolutionary cycles of range expansions (Ricklefs & Bermingham, 2002). Together, our data suggest that even highly vagile taxa may exhibit rapid changes in dispersal propensity after island colonization, leading to population divergence.

Our results offer some insight into the complex relationship between dispersal ability and speciation. Comparative studies have found that high HWI values are associated with island distributions (Kennedy et al., 2016; Sheard et al., 2020) and the ability to expand ranges in topographically complex landscapes (White, 2016), indicating that strong flight ability can help navigate patchy habitats and establish new populations. However, larger values of HWI have been associated with slower diversification rates (Claramunt et al., 2012; Weeks & Claramunt, 2014), or not associated with diversification rates at all (Kennedy et al., 2016), regardless of habitat configuration. These seemingly nonintuitive results have been attributed to evolutionary lability of wing morphology, such that current measures of HWI may not reflect past dispersal ability (Hosner et al., 2017; Kennedy et al., 2016), and to HWI being an imperfect proxy for dispersal (Kennedy et al., 2016; Sheard et al., 2020; Weeks & Claramunt, 2014). Indeed, groups with uniformly high HWI due to foraging niche, such as seabirds and raptors, can exhibit cryptic and often unpredictable genetic structure due to past geographic barriers (Friesen, 2015; Lombal et al., 2020) and island distributions (Agudo et al., 2011). Our results indicate that at a microevolutionary scale, robust dispersal ability is associated with strong population differentiation in patchy habitats but weak differentiation in continuous habitats. This pattern is driven in part by behavioral changes in dispersal propensity, making HWI a poor proxy for patterns of within-clade differentiation. Our results may extend to other species with high HWI. For example, swiftlets of the genera *Aerodramus* and *Collocalia* are little studied but have diversified across islands in Oceania, with many examples of cryptic diversity and island endemism (Cibois et al., 2018; Rheindt et al., 2017) suggestive of labile dispersal behavior. Overall, our data support a key role for overwater dispersal specifically, and patchy habitats more generally, in the diversification of the Oceanic swallow clade. We suggest that evolutionarily labile dispersal behavior may be an important cause of population differentiation in vagile groups.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

Genotype data and metadata are available on Dryad DOI: 10.5061/dryad.18931zd3m. Blood samples are archived at California State Polytechnic University, Pomona, and are available upon reasonable request. Sequence data are available on GenBank PRJNA1021264.

Author contributions

E.S.C.S. conceived of the study with input from A.K.H. E.S.C.S. and A.K.H. collected the data with N.R.F., D.F.G., F.S.M.-T., P.G.M.S., S.S.S., N.C.G.d.S., and T.T.M.L.. E.S.C.S., G.G.B., and B.M.M. analyzed the data. G.G.B. wrote the first draft and E.S.C.S. wrote the final draft, with input from B.M.M. All authors contributed input on drafts of the manuscript.

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