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Exploring the role of Micronesian islands in the maintenance of coral genetic diversity in the Pacific Ocean

S. W. DAVIES,* E. A. TREML,† C. D. KENKEL* and M. V. MATZ*

*Department of Integrative Biology, The University of Texas at Austin, 1 University Station C0990, Austin, TX 78712, USA, †Department of Zoology, University of Melbourne, Melbourne, Vic. 3010, Australia

Abstract

Understanding how genetic diversity is maintained across patchy marine environments remains a fundamental problem in marine biology. The Coral Triangle, located in the Indo-West Pacific, is the centre of marine biodiversity and has been proposed as an important source of genetic diversity for remote Pacific reefs. Several studies highlight Micronesia, a scattering of hundreds of small islands situated within the North Equatorial Counter Current, as a potentially important migration corridor. To test this hypothesis, we characterized the population genetic structure of two ecologically important congeneric species of reef-building corals across greater Micronesia, from Palau to the Marshall Islands. Genetic divergences between islands followed an isolation-by-distance pattern, with *Acropora hyacinthus* exhibiting greater genetic divergences than *A. digitifera*, suggesting different migration capabilities or different effective population sizes for these closely related species. We inferred dispersal distance using a biophysical larval transport model, which explained an additional 15–21% of the observed genetic variation compared to between-island geographical distance alone. For both species, genetic divergence accumulates and genetic diversity diminishes with distance from the Coral Triangle, supporting the hypothesis that Micronesian islands act as important stepping stones connecting the central Pacific with the species-rich Coral Triangle. However, for *A. hyacinthus*, the species with lower genetic connectivity, immigration from the subequatorial Pacific begins to play a larger role in shaping diversity than input from the Coral Triangle. This work highlights the enormous dispersal potential of broadcast-spawning corals and identifies the biological and physical drivers that influence coral genetic diversity on a regional scale.

Keywords: *Acropora*, biophysical model, dispersal, genetic diversity, isolation by distance, stepping stone

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Introduction

Waters of the Indo-West Pacific (also termed 'The Coral Triangle') support the greatest tropical marine biodiversity on the planet (Briggs 1987; Vernon 1995; Veron *et al.* 2009). The processes responsible for generating and redistributing this diversity have significant consequences for the persistence, speciation and extinction of numerous marine taxa. Understanding the limitations to gene flow to and from the Coral Triangle will improve predictions of how marine biodiversity patterns might be affected by global climate change (Burrows *et al.* 2011), which is invaluable both for prioritization of management efforts and basic understanding of evolution in the ocean.

Several models of seascape connectivity between the Coral Triangle and its surrounding oceans have been

Correspondence: Sarah W. Davies, Fax:512 471 3878; E-mail: daviessw@gmail.com

developed (Treml *et al.* 2008; Kool *et al.* 2011; Wood *et al.* 2014). Most recently, Wood *et al.* (2014) inferred little direct migration from the Coral Triangle to the central Pacific, but instead proposed that the Coral Triangle supplies larvae to Micronesia, which in turn serves as a source for the central Pacific via the North Equatorial Counter Current (NECC, Fig. 1). Micronesia is therefore hypothesized to serve as a series of stepping stones connecting the Coral Triangle to the central Pacific. If species from the Coral Triangle are incapable of dispersing the expanse of Micronesia within one generation, differentiation in gene frequencies should build up across Micronesia as distances between populations increase (i.e. an 'isolation-by-distance (IBD)' pattern should be observed) (Wright 1943; Kimura & Weiss 1964; Slatkin 1993). This prediction can be explicitly tested through population genetic methods.

Few studies have explored genetic connectivity within Micronesia and between Micronesia and the rest of the Pacific, and thus far dispersal patterns remain unresolved. A study of the yellow tang fish (*Zebrasoma flavescens*) found support for westward migration from Hawaii to the Central Pacific (Pohnpei) (Eble *et al.* 2011), contrasting with the eastward migration patterns suggested in studies of other marine species (Priest *et al.* 2012; Timmers *et al.* 2012). This lack of consistency in dispersal patterns among taxa might be due to variations in species life history, dispersal capabilities or spawning characteristics. Importantly, the group of organisms that serve as the foundation for these ecosystems, reef-building corals (phylum Cnidaria, class Anthozoa, order Scleractinia), remain understudied in the Pacific (Keyse *et al.* 2014).

Coral dispersal is potentially extensive because most major reef-building species reproduce by releasing gametes into the water column, resulting in pelagic larvae that disperse broadly with ocean currents (Baird *et al.* 2009). Many larvae can survive for months in the absence of settlement cues (Graham *et al.* 2008, 2013), and different species appear to be flexible in the length of their pelagic larval duration (PLD) (Connolly & Baird 2010). Coral population genetic studies have revealed gene flow on scales ranging from tens to hundreds of kilometres (Ayre & Hughes 2000, 2004; Underwood *et al.* 2009; Torda *et al.* 2013), with evidence for long-distance dispersal (Baums *et al.* 2005; Severance & Karl 2006; van Oppen *et al.* 2011), resulting in high genetic connectivity and large geographical ranges for many coral species. However, recent work suggests that dispersal distances for many taxa are less than previously assumed. There is high potential for local retention, where individuals remain in the same population from which they originated (Figueiredo *et al.* 2013), suggesting that wide-ranging species may rely on stepping stones for long-distance gene flow. Given the extensive ranges for most coral species, it is

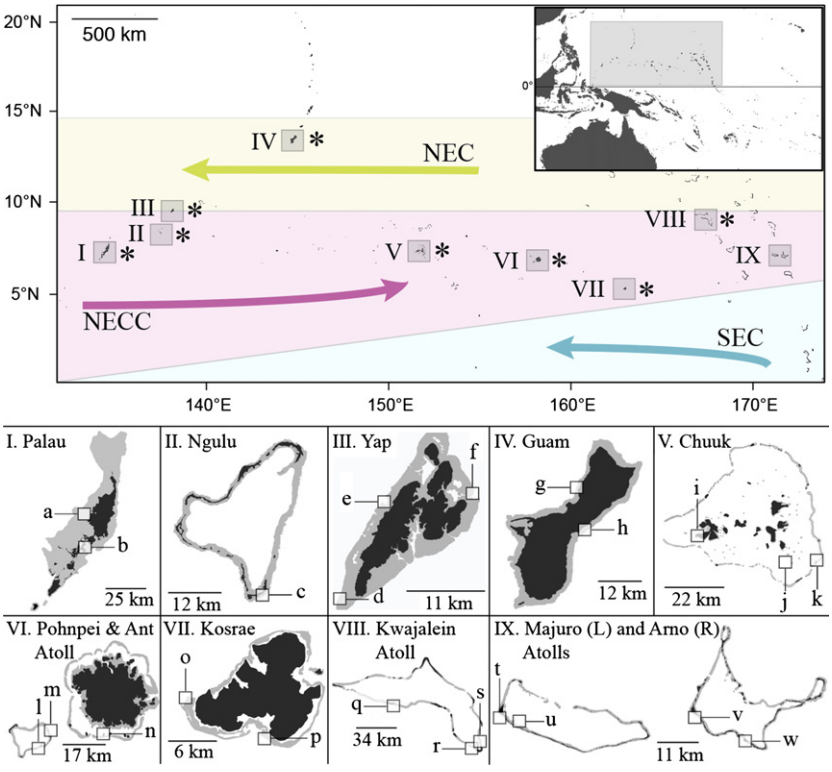

Fig. 1 Geographic locations of the Micronesian islands where *A. hyacinthus* and *A. digitifera* corals were collected. Top: map of the Micronesian Pacific with an inset of the Pacific Ocean for reference. Islands where samples were collected are designated with grey boxes. The subset of islands included in the biophysical model are marked with an (*). Coloured blocks are estimates of dominant current patterns (Bonjean & Lagerloef 2002). Yellow designates the North Equatorial Current (NEC). Pink designates the North Equatorial Counter Current (NECC). Blue represents the South Equatorial Current (SEC). Arrows in each quadrant represent current direction. Bottom: enlarged regional maps for each island with sampling sites shown in boxes. Detailed information on each sampling site is located in Table 1.

reasonable to predict that Micronesian islands serve as effective stepping stones, even though these islands are small, remote and separated by large expanses of open ocean.

Here, we implemented a seascape genetics study of two Pacific coral species of the genus *Acropora*, the most species-rich and ecologically important genus with some of the largest geographical ranges [i.e. *A. digitifera* range >100 000 km^2 (Veron 2000)]. We sampled *A. digitifera* and *A. hyacinthus* over the entire range of greater Micronesia, in addition to one subequatorial Pacific location to test (i) what are the dispersal limits for a coral with a long PLD and a large geographical range; (ii) whether the distribution of regional genetic diversity is consistent with a stepping stone model; (iii) to which extent biophysical models of larval dispersal can explain observed genetic differentiation patterns; (iv) whether two closely related species sharing the same reproductive strategy exhibit similar genetic structures; and (v) whether Micronesia serves as a dispersal corridor between the Coral Triangle and the central Pacific.

Materials and methods

Detailed materials and methods can be found in Appendix S1 (Supporting information).

Sampling locations and methodology

From 2009 to 2011, snorkelling or scuba (3–7 m depth) was used to sample 23 reef sites on ten islands throughout Micronesia (Fig. 1, Table 1). Fifty colonies (>2 m apart) of each coral species (*Acropora hyacinthus* and *A. digitifera*) were sampled per reef. Both species were collected at the same GPS coordinates and depth was maintained constant within a sampling site whenever possible. Colonies were photographed for confirmation of species identification, and one small (~2 cm), randomly chosen branch tip was collected, preserved in 96% ethanol and stored at −20 °C. A total of 2095 specimens were collected. An additional site south of the equator (Phoenix Islands $N = 19$ collected in 2008) was included post hoc to test specific dispersal hypotheses for *A. hyacinthus*.

Table 1 Reef Site Collections. GPS coordinates, main island group, and number of *A. digitifera* and *A. hyacinthus* genotyped. Site letter corresponds to Fig. 1 island insets

Site	Island	GPS	*A. digitifera*	*A. hyacinthus*
a. West Channel Reef	Palau	7°31′55.7 N, 134°29′42.8 E	39	44
b. Lighthouse Reef	Palau	7°16′62.4 N, 134°27′61.9 E	49	50
c. Ngulu	Ngulu Atoll	8°18′12.0 N, 137°29′18.7 E	0[2]	46
d. South Tip Reef	Yap	9°26′05.4 N, 138°02′10.4 E	45	48
e. West Outer Reef	Yap	9°33′47.3 N, 138°05′71.5 E	46	50
f. Goofnuw Channel	Yap	9°34′26.4 N, 138°12′19.2 E	49	37
g. Pago Bay	Guam	13°25′66.6 N, 144°47′94.3 E	45	0*
h. Tanguisson	Guam	13°32′61.1 N, 144°48′52.6 E	50	0*
i. West Polle	Chuuk	7°19′69.7 N, 151°33′21.1E	45[1]	39
j. Aroch Patch Reef	Chuuk	7°14′42.0 N, 151°53′95.4 E	0[2]	49
k. South East Pass	Chuuk	7°14′60.3 N, 152°01′29.1 E	0[2]	49
l. Ant Atoll (South)	Pohnpei	6°45′05.9 N, 157°59′23.3 E	0[2]	48
m. Ant Atoll (East)	Pohnpei	6°47′42.3 N, 158°01′20.7 E	47	47
n. Roj	Pohnpei	6°46′37.7 N, 158°12′24.1 E	50	43
o. Coral Garden	Kosrae	5°18′47.2 N, 162°53′01.8 E	46	44
p. Hiroshi Point	Kosrae	5°15′88.0 N, 162°59′01.8 E	41	46
q. Nell Pass	Kwajalein	9°6′58.9 N, 167°18′71.7 E	21	0*
r. Carlson Reef	Kwajalein	8°44′95.7 N, 167°40′70.0 E	47	0*
s. North Point	Kwajalein	8°44′63.4 N, 167°44′11.5 E	48	0*
t. Laura Cove	Majuro	7°07′92.8 N, 171°02′64.7 E	46	16[1]
u. Army School	Majuro	7°07′40.5 N, 171°03′10.3 E	47	0*
v. Arno	Arno Atoll	7°2′96.7 N, 171°33′92.2 E	45	0*
w. Ine	Arno Atoll	6°58′98.1 N, 171°41′84.5 E	40	0*
Kiribati	Phoenix Islands	4°27′18.6 S, 171°14′36.3 W	0[2]	17
TOTAL			846	673

*indicates that no individuals of this species were found.
[1]indicates all individuals from this island group were pooled for analyses.
[2]indicates that individuals were not collected from this site but are likely present.

Laboratory procedures

DNA was isolated from 1762 coral samples following (Davies *et al.* 2013). An assay of twelve microsatellite loci [Table S1, supporting information modified from (Wang *et al.* 2009)] was established and loci were amplified using polymerase chain reaction (PCR). Locus *WGS153* failed to consistently amplify in *A. digitifera* samples, and therefore, only 11 of 12 loci were maintained in downstream analyses for this species. Individuals failing to amplify at ≥4 loci were excluded from analyses yielding a total of 1744 DNA samples genotyped.

Genetic data analysis

Morphological species identification is difficult for acroporid corals, so an objective approach using the Bayesian method implemented in STRUCTURE v2.3.3 (Pritchard *et al.* 2000) was used to identify and filter out incorrect collections (Fig. S1, Supporting information). Briefly, all data for 11 SSR loci shared between two species were pooled ($N = 1744$), STRUCTURE was run with $K = 3$ and no priors, and all individuals with a $q > 0.5$ for an incorrect species cluster were removed ($N = 225$). The final data set consisted of 1519 total individuals of which 846 were *A. digitifera* and 673 were *A. hyacinthus* (Table 1). Detailed methods can be found in Appendix S1 (Supporting information). GENEPOP v4.2 (Raymond & Rousset 1995) tested for heterozygote deficits (5000 dememorizations, 1000 batches and 5000 iterations) and GENALEX version 6.5 (Peakall & Smouse 2006) determined observed (H_o) and expected (H_e) heterozygosities, number of alleles (N_a), number of private alleles and Shannon's diversity index (sHa), and these were regressed against both Euclidean and biophysically modelled distances (see detailed description below). Heterozygote deficits and linkage disequilibrium information are summarized in Appendix S1. Pairwise F_{ST}, Jost's D and unbiased Nei's genetic distances were calculated in GENALEX v6.5 (Peakall & Smouse 2006) to describe genetic differentiation between all islands. F_{ST} values were chosen to test for isolation by distance (IBD), however, IBD with Jost's D values were also tested and the same patterns emerged (Fig. S2, Supporting information). As allelic diversities and the frequencies of the most common allele for each locus were similar between the two species (Fig. S3, Supporting information), pairwise F_{ST} values were chosen as the test statistic for comparative IBD analysis to facilitate relating our data to earlier coral connectivity studies. Nei's unbiased genetic distances were applied to create two-dimensional principle coordinate analysis (PCoA) plots for each species (Fig. S4, Supporting information). Mantel's tests (Mantel 1967) tested for IBD significance (negative correlation between geographical and rescaled genetic distance ($F_{ST}/(1–F_{ST})$) using the Mantel test function in the *ecodist* package in R (Goslee & Urban 2007) with 10 000 permutations. Slopes of these relationships were compared using linear models and likelihood ratio tests determined if slopes were significantly different between species.

Log-likelihood values for each K (number of inferred populations: 1–5) were computed by running an admixture model with location prior in STRUCTURE (10 replicates, 10^6 iterations, burnin = 300 000) for *A. hyacinthus* (12 loci) and *A. digitifera* (11 loci) data separately. Following the recommendations of (Evanno *et al.* 2005), ΔK was calculated using STRUCTURE Harvester (Earl & Vonholdt 2012), then CLUMPP (Jakobsson & Rosenberg 2007) and DISTRUCT (Rosenberg 2004) produced graphics. Additional hierarchical analyses were completed on data subsets to investigate potential within-cluster structure.

Biophysical model

A spatially explicit biophysical modelling framework was used to predict dispersal potential between coral reefs/islands of Micronesia (Starred islands in Fig. 1), thereby revealing the location, strength and structure of a species' potential population connectivity (Treml *et al.* 2012). Modelling resulted in two types of matrices (Table S5, Supporting information): the connectivity probability matrix (P) quantifying the likelihood that a larva released from each habitat patch survives to settle on another patch (natal or downstream sites) in any year (diagonal of this matrix is the probability of local retention) and the migration matrix (M) representing the proportion of settlers at a reef patch that came from a particular larval source (the diagonal of this matrix is proportion of self-recruitment). The migration matrices were converted to biophysical distance matrix (D) using log (M^{-1}) transform, so that one unit of biophysical distance corresponds to 10-fold decrease in proportion of immigrant settlers (Table S5). The details on the model are described in Appendix S1 and Table S4 (Supporting information). Biophysical distances were then correlated with genetic divergences to test for isolation by resistance (geographical distance and current patterns), the PLD that best fit each species' divergence (45, 65 and 90 days) and the directionality of migration across the seascape.

Results

Genetic diversity within populations

Within-island Shannon diversity estimates (sHa) were negatively correlated with island distance from Palau

for both *A. hyacinthus* (r^2_{adj} = 0.79, P = 0.005) and *A. digitifera* (r^2_{adj} = 0.82, P < 0.001) (Fig. 2B, Tables S2, S3). The diversity decline with distance for *A. digitifera* was significantly greater than for *A. hyacinthus* (P_{LRT} = 0.017). For *A. digitifera*, private allele number per island ranged from 0.09 to 1.27 and a significant decrease with distance from Palau was observed (r^2_{adj} = 0.55, P = 0.013). Private allele number for *A. hyacinthus* ranged from 0.08 to 0.42 and no effect of distance was observed (Fig. S5, Supporting information).

Population differentiation

Significant global F_{ST} values were observed for both *A. digitifera* (0.023) and *A. hyacinthus* (0.042); however, differentiation was nearly two times greater in *A. hyacinthus*. All *A. digitifera* pairwise between-island F_{ST} values were significant; however, they were low and ranged from 0.003 (Majuro–Arno) to 0.042 (Kosrae–Palau) (Table 2A). For *A. hyacinthus*, one between-island pairwise F_{ST} value was not significant (Yap–Ngulu). However, all other between-island pairwise F_{ST} values for *A. hyacinthus* were significant and ranged from 0.009 (Chuuk–Pohnpei) to 0.127 (Pohnpei–Phoenix) (Table 2B). Both species showed strong patterns of IBD (*A. digitifera* Mantel's r^2 = 0.616, P = 0.007; *A. hyacinthus* Mantel's r^2 = 0.740, P = 0.047), supporting a stepping stone model. Notably, *A. hyacinthus*' IBD slope was significantly different (2.73 times steeper) from *A. digitifera's* (P_{LRT} = 0.021, Fig. 2A). Principal coordinate analyses (PCoA) based on Nei's unbiased genetic

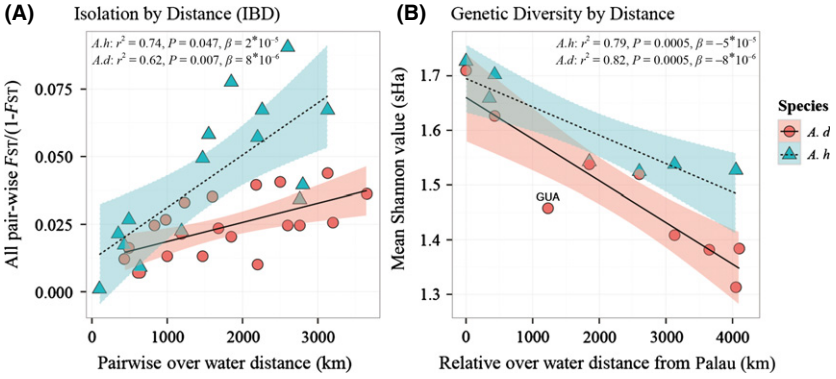

Fig. 2 Isolation by distance (IBD) and genetic diversity observed for *A. digitifera (A. d)* and *A. hyacinthus (A. h)*. (A) Pairwise genetic differentiation [(F_{ST}/(1–F_{ST})] of two coral species as a function of geographical distance between islands (km). (B) Mean Shannon diversity estimates (sHa) for each sampled island relative to geographical distance from the island closest to the Coral Triangle (Palau). GUA: Guam.

Table 2 Pairwise F_{ST} values between all island pairs. All significant comparisons are shaded in grey and nonsignificant comparisons are in bold text. *** =<0.001

A. *A. digitifera*

	Palau	Yap	Guam	Chuuk	Pohnpei	Kosrae	Kwajalein	Majuro	Arno
Palau	0.000	***	***	***	***	***	***	***	***
Yap	0.012	0.000	***	***	***	***	***	***	***
Guam	0.032	0.024	0.000	***	***	***	***	***	***
Chuuk	0.020	0.013	0.026	0.000	***	***	***	***	***
Pohnpei	0.024	0.010	0.034	0.007	0.000	***	***	***	***
Kosrae	0.042	0.024	0.038	0.021	0.016	0.000	***	***	***
Kwajalein	0.035	0.025	0.039	0.023	0.013	0.007	0.000	***	***
Majuro	0.038	0.025	0.034	0.026	0.024	0.015	0.014	0.000	***
Arno	0.036	0.019	0.038	0.027	0.019	0.011	0.012	0.003	0.000

B. *A. hyacinthus*

	Palau	Ngulu	Yap	Chuuk	Pohnpei	Kosrae	Majuro	Phoenix
Palau	0.000	***	***	***	***	***	***	***
Ngulu	0.021	0.000	**0.177**	***	***	***	***	***
Yap	0.017	**0.001**	0.000	***	***	***	***	***
Chuuk	0.072	0.055	0.047	0.000	***	***	***	***
Pohnpei	0.083	0.063	0.054	0.009	0.000	***	***	***
Kosrae	0.063	0.038	0.033	0.022	0.026	0.000	***	***
Majuro	0.051	0.036	0.030	0.062	0.066	0.054	0.000	***
Phoenix	0.072	0.085	0.075	0.115	0.127	0.104	0.086	0.000

distances nearly recapitulate island geographical configurations and explained 58% of the variation for *A. digitifera* and 79% for *A. hyacinthus* (Fig. S4).

Bayesian analysis of genetic structure

A. digitifera. STRUCTURE analysis corroborated F_{ST} values and demonstrated that populations increasingly diverged with distance (Fig. 2A). STRUCTURE uses a Monte Carlo Markov chain (MCMC) clustering algorithm to assign individuals with similar multilocus genotypes to distinct populations. For *A. digitifera* ($n = 846$), an optimal solution of $K = 3$ clusters was used based on ΔK. Individuals from Guam assigned strongly to its own independent cluster (Fig. 3A). All data except Guam were then divided into two clusters, the western cluster (from Palau to Pohnpei, orange assignments) and the eastern cluster (from Kosrae to Arno, burgundy assignments). All islands other than Guam followed IBD predictions with the eastern cluster gradually replacing the western cluster. Further STRUCTURE analyses were performed on the western and eastern clusters independently. Within the western cluster ($n = 370$), $K = 2$ optimal subclusters were identified (Fig. 3A), and within the eastern cluster ($n = 381$), $K = 4$ was the optimal solution. Individual membership assignments for both east and west island clusters supported IBD, as expected under a stepping stone migration model.

A. hyacinthus. STRUCTURE analysis of *A. hyacinthus* ($n = 656$) indicated an optimal solution of $K = 2$ clusters. The IBD signature in *A. hyacinthus* STRUCTURE data (Fig. 3B) was not as visually apparent as it was for *A. digitifera*, although Mantel's test was highly significant (Fig. 2A). Instead, a strong break between western Micronesia (Palau, Ngulu and Yap) and eastern Micronesia (Chuuk, Pohnpei and Kosrae) was observed (Fig. 3B). Data were split into western (Palau–Yap) and eastern (Chuuk–Majuro) clusters and additional STRUCTURE analyses were independently performed. The western cluster ($n = 275$) had $K = 4$ optimal subclusters and the eastern cluster ($n = 381$) had $K = 2$ subclusters. Within the western cluster, structure was observed between Palau and Ngulu–Yap; however, no structure was observed between Ngulu and Yap, which corroborated their nonsignificant F_{ST} values (Table 1B). Within the eastern cluster, Chuuk and Pohnpei were assigned to the same cluster ($F_{ST} = 0.009$), while Kosrae and the Marshall Islands exhibited more structure ($F_{ST} = 0.054$). Upon closer inspection of the first STRUCTURE analysis for *A. hyacinthus*, we observed that Majuro individuals clustered more closely with western individuals when compared to the more proximate central Micronesia cluster. An additional analysis was completed to determine whether the Marshall Islands and western Micronesia might be receiving *A. hyacinthus* immigrants from subequatorial locations via the South Equatorial Current (SEC, Fig. 1). This STRUCTURE analysis included samples from the Phoenix Islands and confirmed that Phoenix Island *A. hyacinthus* were more similar to both the Marshall Islands and western Micronesia populations compared to other central Micronesian populations (Fig. 4).

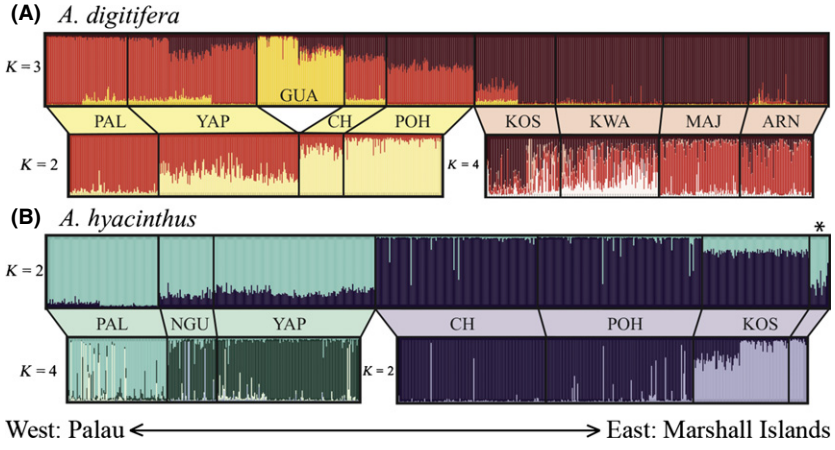

Fig. 3 STRUCTURE population assignments for two species of *Acropora* across greater Micronesia. (A) The top panel shows results for all *A. digitifera* individuals at an optimal population number (K) of 3. The bottom panels show population assignments obtained separately for the western cluster (Palau–Pohnpei except Guam, $K = 2$) and the eastern cluster (Kosrae–Arno, $K = 4$). (B) The top panel shows results for all *A. hyacinthus* individuals at an optimal population number (K) of 2. The bottom panels show population assignments obtained separately for the western cluster (Palau–Yap, $K = 4$) and the eastern cluster (Chuuk–Marshall Islands, $K = 2$). The asterisk (*) identifies pooled Marshall Islands samples.

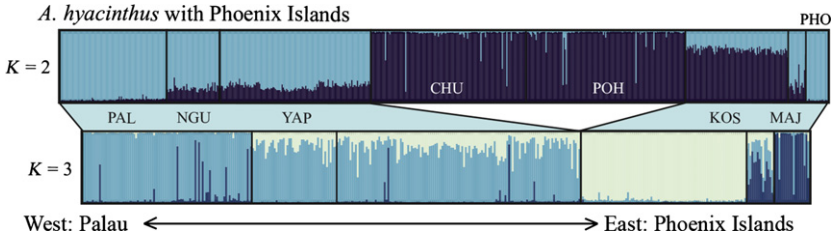

Fig. 4 STRUCTURE population assignment for *Acropora hyacinthus* in Micronesia with the addition of the Phoenix Islands (a subequatorial Central Pacific location). The top panel shows results for all individuals at an optimal population number (*K*) of 2. The bottom panel shows population assignments for all individuals when Chuuk and Pohnpei were removed using a *K* of 3.

Biophysical modelling

Biophysical distances (negative logarithm of the proportion of immigrant settlers) were more strongly correlated with genetic divergences when compared to Euclidean distances, and when best-fit dispersal distance matrices were used for each species, an additional 15–21% more genetic variation was explained. *Acropora hyacinthus*' best-fit model was 65 day PLD with minimum biophysical distance (comparing both directions of migration) between all pairs of sampled islands (Fig. 5B, Mantel's $r^2 = 0.89$, $P = 0.014$). For *A. digitifera*, 90-day PLD with maximum biophysical distance between island pairs showed the strongest correlation

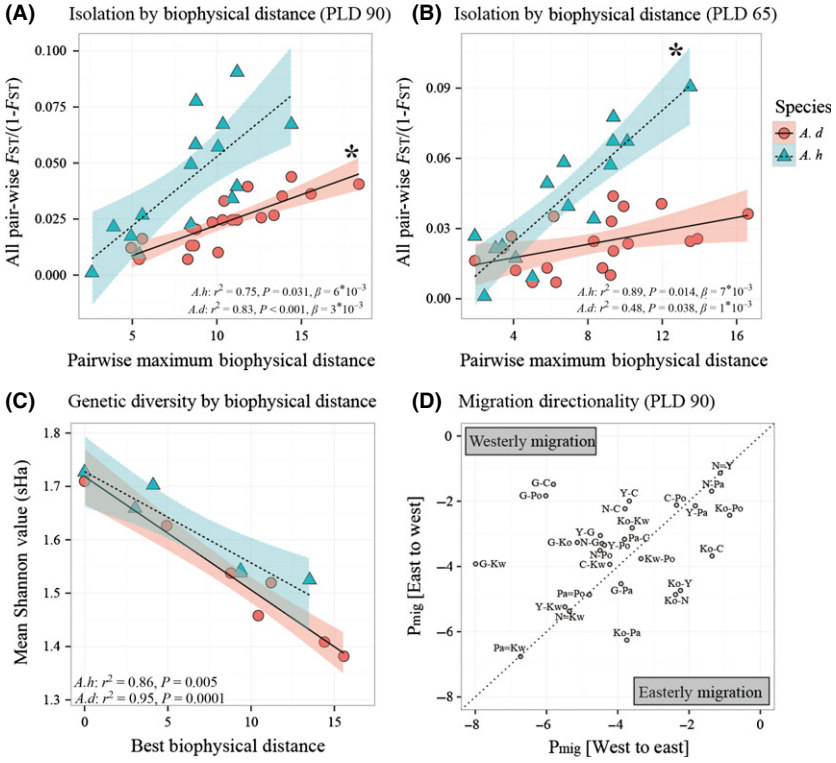

Fig. 5 Biophysical dispersal modelling results. On panels A–C, the *X*-axis shows biophysical distance: one unit corresponds to 10-fold decrease in the proportion of immigrant settlers. (A) Pairwise population divergences [$(F_{ST}/(1–F_{ST})$] for two *Acropora* species plotted against maximum pairwise biophysical distances (90-day maximum PLD). This model was the best fit for *A. digitifera* (model denoted by *) explaining 83% of the variation. (B) Pairwise population divergences plotted against minimum pairwise biophysical distances at a PLD of 65 days. This model was the best fit for *A. hyacinthus* (model denoted by *) explaining 89% of the variation. (C) Mean genetic diversity estimates (sHa) for each sampled island relative to the biophysical distance from Palau, using the best-fitting model for each species. (D) Migration directionality as estimated from the model. On this panel, both axes represent decimal logarithm of the probability of settlement but for different migration directions. Island pairs falling along the dashed 1:1 line are predicted to have equal migration in both directions. Islands falling above the line exhibit westerly migration preference and those falling below exhibit preferences towards easterly migration.

(Fig. 5A, Mantel's $r^2 = 0.83$, $P < 0.001$). Biophysical distance also explained more genetic diversity variation when best-fit models for each species were tested (Fig. 5C). *Acropora digitifera's* best-fit model explained an additional 13%, nearly all of the variation in genetic diversity (Mantel's $r^2 = 0.95$, $P < 0.001$). For *A. hyacinthus*, the best-fit model explained 7% more variation in genetic diversity (Fig. 5C, Mantel's $r^2 = 0.86$, $P = 0.005$). For all PLDs tested, biophysical distances in both directions were similar (near 1:1 line) for most islands; however, asymmetric migration was predicted for Guam and Kosrae. For island pairs involving Guam (except Guam–Palau pair), westerly migration was stronger, whereas for island pairs involving Kosrae (except Kosrae–Guam and Kosrae–Kwajalein), easterly migration was predicted (Fig. 5D). Large differences in reseeding capabilities were observed across islands regardless of PLD. Palau, Chuuk and Pohnpei exhibited strong reseeding with more than 89% of potential settlers coming from local sources. However, at Ngulu, Guam, Yap and especially at Kosrae, much lower reseeding values were predicted, ranging from 66% (Ngulu, 45-day PLD) to 29% (Kosrae, 90-day PLD) of potential settlers (Table S5).

Discussion

Stepping stone migration of Acropora

Theory predicts that under genetic equilibrium, differentiation in allele frequencies should correlate with between-population distances, yielding an isolation-by-distance (IBD) pattern, unless individuals can disperse across their entire range (Wright 1943; Slatkin 1993). Here, two acroporid corals show genetic divergences (F_{ST}) of only 0.023–0.042 across 4000 km of ocean, suggesting that gene flow throughout Micronesia is pervasive, although historical processes cannot be discounted, as populations may not be at equilibrium. Despite high genetic connectivity among populations, we find significant IBD, suggesting limitations to coral dispersal. There is strong evidence that island stepping stones are important for gene flow between remote Pacific reefs: between-island distances alone explain between 62% and 74% of estimated pairwise genetic divergences (F_{ST}) (Fig. 2A), and for *A. digitifera*, genetic distances closely recapitulate island configuration (Fig. S4). This pattern is especially noteworthy given that previous genetic studies on highly dispersive corals rarely find compelling geographical trends (Ayre & Hughes 2004; Baums *et al.* 2005, 2010; Magalon *et al.* 2005; Nakajima *et al.* 2009). Still, there are exceptions: *Porites lobata* in the Hawaiian islands [IBD = 37%, (Polato *et al.* 2010)], a Caribbean sea fan *Gorgonia ventali* [IBD = 17%, (Andras *et al.* 2013)] and *A. millepora* along the Great Barrier Reef [IBD = 54%, (van Oppen *et al.* 2011)] all exhibited significant IBD. This study reports the strongest evidence of IBD in broadcast-spawning corals to date, which might be due in part to the relatively less complex current systems in the area and the coarser grained sampling design.

The pattern of stepping stone dispersal (gradual accumulation of genetic divergence with distance) is evident in F_{ST} and STRUCTURE results for *A. digitifera* (Figs 2 and 3A). However, its congener *A. hyacinthus* exhibits stronger population breaks (Fig. 3B) similar to a study on rabbitfish (*Siganus sapidus*), where populations from eastern Micronesia diverge from western Micronesia (Priest *et al.* 2012). When dispersal distances derived from our biophysical model are considered instead of Euclidean distances, an even stronger IBD pattern emerges for *A. hyacinthus* (Fig. 5B). This strong linear IBD pattern for *A. hyacinthus* suggests that the apparent genetic break in STRUCTURE results between Yap and Chuuk might simply be due to the large unsampled distance between these islands (1470 km) rather than to specific barriers to migration.

Differences in population genetic structure among congeneric coral species

Scleractinian corals exhibit two sexual reproductive modes: broadcast spawning, where gametes are synchronously released into the water column for fertilization and development, and brooding, where eggs are fertilized internally and larvae develop within the colony and are competent to settle within hours of release (Harrison & Wallace 1990). Research has demonstrated contrasting pelagic larval durations (PLD) between brooding and broadcast-spawning corals, with some studies demonstrating more pronounced genetic structure in brooders (Hellberg 1996; Ayre & Hughes 2000; Underwood *et al.* 2009). Here, we observe strong differences in genetic divergence between two congeneric corals that share the same life history strategy (Fig. 2A) and exist in sympatry. Both species are hermaphroditic, broadcast-spawning corals that reproduce during annual spawning events (Baird *et al.* 2009) and would be expected, at least under most management regimes, to disperse similarly. However, *A. hyacinthus* was over two times more genetically structured than *A. digitifera* ($P_{LRT} = 0.021$), suggesting reduced dispersal potential. Comparative studies of closely related species both on land and in the ocean have also observed considerable variation among species in both the magnitude of genetic variation and in the size and strength of IBD (Zayed *et al.* 2005; Moyle 2006). While studies have explored variation in population genetics across

phylogenetically related coral species [e.g. (Ayre & Hughes 2000; Severance & Karl 2006)], our study is the first to demonstrate significantly different IBD strengths in congeneric corals.

Genetic connectivity differences between species could have several underlying causes, the most obvious being differences in effective population sizes (N_e): as between-population divergence (F_{ST}) depends on the absolute number of migrants, species could vary due to different N_e (Wright 1951). Unfortunately, no reliable data on species abundances in Micronesia are available to evaluate this possibility. *A. hyacinthus'* increased structure might be due to the presence of cryptic species, which have been described for this species (Ladner & Palumbi 2012). Given our strict approach to filtering incorrect species collections, encountering cryptic species is unlikely, especially given that there was evidence of admixture among major genotypic clusters identified by STRUCTURE (Figs 3B and 4). Alternatively, differences could be attributed to parameters of larval biology. Competency, defined as larval settlement responsiveness through time, has been shown to vary between closely related *Acropora* species (Ayre & Hughes 2000; Connolly & Baird 2010) and therefore might explain at least some of the variation we observe. Larvae of different species of *Acropora* have been shown to exhibit similar precompetency periods of 4–6 days (Harrison & Wallace 1990), so precompetency is unlikely to be the cause of between-species differences in differentiation. PLDs for these species have been previously estimated in the laboratory at >45 days for *A. digitifera* (Nishikawa & Sakai 2005; Graham *et al.* 2008) and >91 days for *A. hyacinthus* (Graham *et al.* 2008). Our study provides an opportunity to test which PLD is most compatible for each species, given the biophysical model of larval exchange at three PLDs, differentiation estimates and assuming equal effective population sizes. Results suggest that *A. digitifera* has a longer PLD than *A. hyacinthus*: 65-day PLD correlates best with divergences for *A. hyacinthus*, while 90-day PLD best correlates with *A. digitifera* (Fig. 5A, B). Disagreement with published PLD estimates is hardly surprising given that laboratory-based conditions are unlikely to mirror all aspects of larval life in the plankton.

Acropora digitifera is also known to inhabit a broader geographical range than *A. hyacinthus* (Veron 2000). Specifically within our study, Guam was outside of range for *A. hyacinthus*, but *A. digitifera* was prolific there. A larger geographical range for *A. digitifera* aligns well with its higher dispersal capability inferred here. Taken together, our results indicate that congeneric and supposedly ecologically equivalent coral species may have very different genetic connectivity patterns on a regional scale, generating challenging consequences for management.

Factors influencing genetic diversity of Acropora spp. across Micronesia

Genetic diversity (sHa) for both species and private allele number for *A. digitifera* were significantly correlated with island distance from Palau, with islands closer to the Coral Triangle exhibiting higher genetic diversities (Figs 2B and 5C). These results corroborate evidence of species diversity declines with longitudinal distance from the Coral Triangle (Veron *et al.* 2009). Diversity decrease could be a consequence of biased easterly dispersal out of the Coral Triangle (Jokiel & Martinelli 1992; Connolly *et al.* 2003; Treml *et al.* 2008; Wood *et al.* 2014), but may also reflect diminishing N_e because the combination of isolation and genetic drift associated with low N_e is expected to reduce genetic diversity, especially at the edges of species ranges (Hoffmann & Blows 1994). Lower diversities could also result from variations in reef age, with more diversity developing in older reefs. Island age, however, is unlikely to explain the observed genetic diversity gradient because Micronesian reefs are similar ages corresponding with the time since last glaciation. Experimentally estimated reef ages for Palau and the Marshall Islands are remarkably similar between islands [~6–8k years, (Montaggioni 2005)], contrary to our genetic diversity estimates (Tables S2 and S3). In agreement with a source/sink dynamic driven by the prevailing NECC, *A. digitifera* from the Marshall Islands, the farthest sampled island group from the Coral Triangle, had among the lowest values of genetic diversity (Tables S2 and S3; Fig. 2B) and this pattern held for private allelic richness (Fig. S5). In contrast, the less dispersive species, *A. hyacinthus*, had enriched private alleles in the eastern-most Micronesian islands (Kosrae and Marshall Islands) compared to central Micronesia (Chuuk and Pohnpei) (Table S3; Fig. S5). This paradoxical observation is explained by our STRUCTURE analysis involving *A. hyacinthus* from the Phoenix Islands (Fig. 4), which suggests that eastern populations of *A. hyacinthus* are more influenced by genetic exchange from south of the equator than by the diminishing immigration of Coral Triangle genotypes through Micronesia. A connection between the Marshall and Phoenix Islands through the Gilbert Islands and Tuvalu was hypothesized (Treml *et al.* 2008) for species exhibiting PLDs exceeding 30 days, which is likely the case for *A. hyacinthus* (Fig. 5B). The shared genetic influence of the subequatorial gene pool, possibly via the SEC, could also explain why eastern *A. hyacinthus* populations are more genetically similar to western Micronesian than to central Micronesian islands (Figs 3C and 4). The ages of Micronesian coral populations

(~6–8k years) prompts a cautionary note. Assuming mean age of reproductive maturity for *Acropora* species is 3–8 years (Wallace 1999), only about 1000 generations have passed since population establishment, considerably less time than needed for populations to reach genetic equilibrium. Therefore, we caution that genetic diversity patterns discussed here might, to some degree, reflect past bottlenecks and the history of initial island colonization. A comprehensive sampling scheme involving more coral species over broader geographical ranges would be required to rigorously investigate this possibility.

Seascape resistance and connectivity in Micronesian corals

Ocean currents are important dispersal agents in marine environments, but determining the degree and directionality of migration remains a fundamental problem (Palumbi 1997; Warner & Cowen 2002; Botsford *et al.* 2009). Seascape genetic models have been employed on local and regional scales to elucidate spatial patterns of genetic differentiation. These models use empirical estimates of oceanographic features to predict spatial patterns of genetic differentiation. We find that differentiation in both coral species is considerably more correlated with modelled biophysical distances than Euclidean distances (compare Figs 2 and 5A, B), demonstrating that ocean currents play an important role in structuring coral populations, which has been previously shown in other marine systems ranging from corals (Galindo *et al.* 2006; Foster *et al.* 2012) to mussels (Gilg & Hilbish 2003). The increased correlation for *A. digitifera* was likely due to its presence in Guam, which is located within the North Equatorial Current (NEC Fig. 1) and exhibits strong bias towards westerly migration (Treml *et al.* 2008) that cannot be accounted for by Euclidean distance alone (Fig. 5D). Work on reef fish has also demonstrated strong subdivision between Guam and other Pacific islands (Priest *et al.* 2012).

Results from our dispersal model confirm that Micronesia can serve as a dispersal corridor between the Coral Triangle and central Pacific. However, we find evidence that dispersal in Micronesia is more complex than the predicted unidirectional easterly flow (Wood *et al.* 2014) and involves bidirectional exchange between most islands. Our model predicts predominant eastward migration for the island nearest the equator (Kosrae), while Guam, the northern-most site, shows a bias towards westerly migration (Fig. 5D). This complexity is likely due to latitudinal fluctuations of the NECC, variability of the NECC's strength during El Nino and La Nina years and its proximity to the westerly South Equatorial Current [SEC, Fig. 1; (Bonjean & Lagerloef 2002)].

These biophysical data also offered the opportunity to estimate the reseeding capabilities of each island, which are very useful metrics for conservation planning across the region. Here, we observed that some islands exhibited high reseeding (i.e. Palau with local settlers comprising >95% of total), while others reseeded at much lower rates (Table S5). Interestingly, at Kosrae, local settlers accounted for only 29–48% of the total (across PLDs modelled), suggesting that a tendency of genetic subdivision between the opposite sides of this small island (Fig. 3) could be due to influx of immigrants from opposing sources. Reseeding data are imperative for conservation planning as islands with high reseeding capabilities can focus on local measures, while strategies for islands receiving most of their settlers from elsewhere will need to plan conservation measures on wider scales.

Conclusions

Populations of two congeneric acroporid corals maintain genetic connectivity over thousands of kilometres using Micronesian islands as stepping stones. In addition to distance, current speed and direction clearly affect connectivity. Divergence patterns differ significantly between the two coral species despite phylogenetic relatedness, lack of obvious ecological niche differentiation and use of the same reproductive strategy, which may reflect differences in effective population sizes and/or larval biology. Generally, our results corroborate previous simulation models suggesting that Micronesia serves as a migration corridor from the Coral Triangle to remote islands of the central Pacific. However, this hypothesis is well supported only for the more dispersive of the two coral species, *A. digitifera*. Future work should aim to understand the biological factors differentiating potential connectivity from realized connectivity, as this study suggests that even small variations in life history traits can shape population dynamics on regional scales.

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S.W.D. and M.V.M. conceived and designed the experiment and sampling scheme. S.W.D., C.D.K. and M.V.M. acquired all of the permits and collected coral samples. S.W.D. developed microsatellite multiplex assays and completed all laboratory work. S.W.D. analysed the microsatellite data. E.A.T. completed biophysical modelling. All authors contributed to writing the manuscript.

Data accessibility

All genotyping data for both coral species, R code for data analyses and the matrix data from the biophysical models (PLD 45, 65 and 90) are publicly available on DRYAD dio:10.5061/dryad.90835.

Supporting information

Additional supporting information may be found in the online version of this article.

Fig. S1 STRUCTURE population assignment for all coral DNA samples that were isolated and amplified across the range of Micronesia sampled from Palau to the Phoenix Islands.

Fig. S2 Isolation By Distance (IBD) and isolation by biophysical distance observed for *A. digitifera (A. dig)* and *A. hyacinthus (A. hya)* based on a standardized pairwise genetic differentiation measure (Jost's D).

Fig. S3 Allelic comparisons between *Acropora digitifera* and *A. hyacinthus*.

Fig. S4 Principal Coordinate Analysis (PCoA) of genetic relationships (Nei's genetic distances) among Micronesian populations of *Acropora digitifera* and *Acropora hyacinthus*.

Fig. S5 Private allele richness for *A. digitifera (A. d)* and *A. hyacinthus (A. h)*.

Appendix S1 Detailed materials and methods.

Table S1 Summary of twelve microsatellite loci transferable from *A. millepora* SSR markers (Modified from (Wang *et al.* 2009)) and their corresponding multiplexing groups.

Table S2 Genetic summary statistics of eleven microsatellite loci from nine islands for *A. digitifera*.

Table S3 Genetic summary statistics of eleven microsatellite loci from seven islands for *A. hyacinthus*.

Table S4 A. Biophysical model information for reef data and release times. B. Biophysical model information for spawning time for Palau (left) and the rest of Micronesia (right). C. Details on the biological parameters specified in the biophysical model.

Table S5 Biophysical modeling results for three pelagic larval durations (PLD): 1) Migration matrices (M) represent the proportion of settlers at a reef patch that came from a particular larval source (the diagonal of this matrix is proportion of self-recruitment), 2) dispersal distance matrices (D) are derived from the migration matrices using $\log(M^{-1})$, which means that one unit of biophysical distance corresponds to 10-fold decrease in proportion of immigrant settlers, and 3) connectivity probability matrices (P), which quantifyies the likelihood that a larva released from each habitat patch survives to settle on another patch (natal or downstream sites) in any year (diagonal of this matrix is the probability of local retention). Source populations are rows and destination populations are columns.