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Title: Congruent patterns of connectivity can inform management for broadcast spawning corals on the Great Barrier Reef

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Abstract

Connectivity underpins the persistence and recovery of marine ecosystems. The Great Barrier Reef (GBR) is the world's largest coral reef ecosystem and managed by an extensive network of no-take zones, however information about connectivity was not available to optimise the network's configuration. We use multivariate analyses, Bayesian clustering algorithms and assignment tests of the largest population genetic dataset for any organism on the GBR to date (*Acropora tenuis,* >2500 colonies; >50 reefs, genotyped for ten microsatellite loci) to demonstrate highly congruent patterns of

connectivity between this common broadcast spawning reef-building coral and its congener A*cropora millepora* (~950 colonies; 20 reefs, genotyped for 12 microsatellite loci). For both species there is a genetic divide at around 19°S latitude, most probably reflecting allopatric differentiation during the Pleistocene. GBR reefs north of 19°S are essentially panmictic whereas southern reefs are genetically distinct with higher levels of genetic diversity and population structure, most notably genetic subdivision between inshore and offshore reefs south of 19°S. These broadly congruent patterns of higher genetic diversities found on southern GBR reefs most likely represent the accumulation of alleles via the southward flowing East Australia Current. In addition, signatures of genetic admixture between the Coral Sea and outer shelf reefs in the northern, central and southern GBR provide evidence of recent gene flow. Our connectivity results are consistent with predictions from recently published larval dispersal models for broadcast spawning corals on the GBR thereby providing robust connectivity information about the dominant reef-building genus *Acropora* for coral reef managers.

Introduction

The largest coral reef system in the world, the Great Barrier Reef (GBR), is located off the coast of East Australia. This world heritage area is ~350,000 km^2 in size and comprises ~2,900 reefs. While the GBR is in a relatively good condition compared to most other reef systems around the globe, an alarming ~50% decline in coral cover has been documented over the past three decades (De'ath *et al.* 2012), indicating that continued careful management is critical for its persistence. Rezoning of the GBR in 2004 resulted in an increase of no-take areas from ~4.5% to more than 33% of the GBR Marine Park (GBRMP) (Fernandes *et al.* 2005). The benefits of no-take zones in the GBRMP have been irrefutably demonstrated for fitness, biomass and 'spill-over' of fish species targeted by fisheries (Emslie *et al.* 2015; Harrison *et al.* 2012; McCook *et al.* 2010), and recent studies have demonstrated benefits for non-target species such as corals, including the lowered incidence of coral diseases in no-take zones (Lamb *et al.* 2015). Nonetheless, large-scale disturbances [thermal anomalies, cyclones, flood plumes, crown-of-thorn starfish (COTs) outbreaks] can rapidly negate the positive effects of no-take zones (Emslie *et al.* 2015). Indeed, thermal anomalies (and their associated impacts on marine organisms) in the period 1985-2009 equally affected areas inside and outside no-take zones in the GBRMP (Ban *et al.* 2012). Connectivity is a critical factor for improving the effectiveness of networks of no-take zones to respond to disturbances (Lagabrielle *et al.* 2014), as recruitment from external sources is essential for the recovery of reefs that have undergone high mortality (Lukoschek *et al.* 2013). However, lack of information about connectivity meant it was not used for the rezoning of the GBR (Fernandes *et al.* 2005) nor in the design of most other marine no-take networks around the world (Almany *et al.* 2009; Lagabrielle *et al.* 2014; Magris *et al.* 2014).

Reproductive connectivity (the dispersal of individuals among sub-populations that survive to reproduce (Burgess *et al.* 2013; Pineda *et al.* 2007)) underpins the persistence of populations by accelerating recovery following high mortality, maintaining genetic diversity, and introducing new gene variants, the substratum on which natural selection acts. Three pieces of empirical data are needed to evaluate the effectiveness of a network of no-take zones; the connectivity matrix, per capita fecundity of populations, and survival of recruits (Burgess *et al.* 2013). Connectivity has proved notoriously difficult to measure empirically due to the small size and high dispersal potential of larvae (Burgess *et al.* 2013; Jones *et al.* 2009; Kool *et al.* 2013; Pineda *et al.* 2007). On the GBR empirical estimates of larval retention and dispersal have been obtained for reef fish using larval tagging (Jones *et al.* 1999) and genetic parentage analysis (Harrison *et al.* 2012); however, these estimates are limited both spatially and temporally (Jones *et al.* 2009). Moreover, larval tagging is not possible for many marine organisms (such as corals) and parentage analysis necessitates species identification of recruits, which has not yet been achieved for broadcast spawning corals (Babcock *et al.* 2003). As a means of addressing these issues, considerable effort has focused on developing hydrodynamic models for the GBR (Brinkman *et al.* 2011; Condie *et al.* 2012; Lambrechts *et al.* 2008), which coupled with information about larval biology have been used to simulate larval dispersal and predict connectivity for corals (Andutta *et al.* 2012; Thomas *et al.* 2014), fish (Bode *et al.* 2006; James *et al.* 2002), and COTs (Hock *et al.* 2014). However, numerical models rely on many assumptions (Botsford *et al.* 2009), particularly in the complex hydrodynamics of shallow-water marine habitats of the GBR (Brinkman *et al.* 2011; Condie *et al.* 2012; Lambrechts *et al.* 2008). Moreover realised dispersal maybe quite different from the dispersal potential predicted from larval dispersal models, and the models do not account for post-settlement survival; thus empirical measures of connectivity are required to substantiate model predictions (Burgess *et al.* 2013).

Population genetics provides a means of assessing gene flow integrated over many generations from which realised dispersal and post settlement survival can be inferred (Jones *et al.* 2009; Kool *et al.* 2013). While traditional estimates of gene flow rely on theoretical models with assumptions that are often violated in natural populations (Hedgecock *et al.* 2007), recently developed individual-based genetic analyses, such as assignment tests, are less conditional and allow direct genetic estimation of contemporary connectivity (Hedgecock *et al.* 2007). Further, the ability to demonstrate congruent patterns of connectivity for multiple species with similar reproductive biology will be highly informative for optimising network designs of no-take areas, particularly when considered with information from larval dispersal models. Such data have, unfortunately, not been available for the GBR, as until recently, population genetic studies investigating connectivity in GBR corals have either been restricted to small geographic ranges (Souter *et al.* 2010) or had sparse sampling over larger

geographic ranges (Ayre & Hughes 2000, 2004). Population genetic studies on the GBR with higher intensity sampling over large spatial scales on the GBR are rare for any organism, and only one has been conducted for a broadcast spawning coral (van Oppen *et al.* 2011).

Here we test the hypothesis that population genetics and larval dispersal models predict similar connectivity patterns for broadcast spawning corals on the GBR. We combine multivariate analyses with individual-based analyses of multi-locus genotypes of recent gene flow (assignment tests) and its effects on population structure (Bayesian clustering analyses) to evaluate patterns of genetic variation for two species of broadcast spawning corals, *Acropora tenuis* and *Acropora millepora,* on the GBR. These analyses are robust to non-equilibrium assumptions and deviations from Hardy-Weinberg Equilibrium (HWE) and Linkage Disequilibrium (LD) (Hedgecock *et al.* 2007; Hellberg 2007), commonly found in corals (Hellberg 2007). Specifically, we compare results from analyses of new data for *A. tenuis* (2544 colonies from 54 sites across 12° latitude) with new analyses of a previously published dataset for the congener *A. millepora* (947 colonies from 20 sites across the same geographic range) (van Oppen *et al.* 2011). Both *A. tenuis* and *A. millepora* are common broadcast spawning species on the GBR and typically spawn within a few days of each other and have similar pelagic larval durations, achieving settlement competency within 4-5 days and maximum settlement rates 7-10 days post-spawning (Connolly & Baird 2010; Nishikawa *et al.* 2003). Our results show highly congruent patterns of gene flow and genetic structure between the two coral species, and with recently published larval dispersal models (Hock *et al.* 2014; Thomas *et al.* 2014) strongly suggesting these patterns are representative for reef-building coral species with similar biological characteristics on the GBR. These findings can inform the design of networks of no-take areas and a range of other coral reef management and restoration approaches.

Materials and Methods

Sampling and spatial data

Samples for *A. tenuis* from the GBR were collected between 2009 and 2013 and samples from 68_MAG_CAY in the Coral Sea were collected in 2007. The aim was to sample 50 colonies per site (except for three sites in the Palm Islands sampled at high intensity, see below). The sample size mean and mode were 37 and 48, respectively. At each site sampling occurred on the reef flat, crest or upper slope between depths of 1 to 12 m. Each colony was sampled by snapping off a branch using a diving knife and samples fixed in absolute ethanol. The exact GPS coordinates were obtained for 753 colonies sampled in the Palms Islands plus 524 colonies sampled at 16 sites throughout the GBR using a floating GPS reader towed by SCUBA divers. Each sampled colony (n = 1277) was photographed and the time stamp on the picture was used to determine the exact GPS coordinates of the colony from

synchronised clocks in the GPS and underwater camera. The remaining 1267 sampled colonies were assigned approximate GPS coordinates of the 32 sites where they were collected (Table S1).

High-intensity sampling for *A. tenuis* was conducted at three of the six Palm Island sites sampled, comprising two sheltered sites (38_OI_CB, 41_OI_SH) and one exposed site (37_OI_EX). At each site 50 m transect tapes were deployed along the reef crest and samples were collected from colonies of *A. tenuis* on the reef flat, crest and slope 10-20 m on either side of the transect tapes. The aim was to sample all colonies of *A. tenuis* in a given area of fringing reef at each site. Sampling was undertaken by a team of two divers who swum in a zigzag pattern along the transect tape with one diver collecting a sample of each *A. tenuis* colony encountered.

Microsatellite genotyping of Acropora tenuis

Although species-specific microsatellites have not been developed for *A. tenuis,* previous research successfully used seven microsatellite loci developed for the congener *A. millepora* (van Oppen *et al.* 2007) to evaluate genetic connectivity amongst *A. tenuis* populations in Western Australia (Underwood *et al.* 2009). Additional microsatellite loci subsequently developed for *A. millepora* have also been shown to have within-genus transferability (to *A. hyacinthus*) (Wang *et al.* 2009), as have microsatellites developed for other species of *Acropora* (Baums *et al.* 2009; Tang *et al.* 2010). We tested primer pairs for 50 microsatellite loci developed for *A. millepora* (van Oppen *et al.* 2007; Wang *et al.* 2009), *A. muricata* (Tang *et al.* 2010) and *A. palmata* (Baums *et al.* 2009; Baums *et al.* 2005) for transferability to *A. tenuis*. PCR amplifications were conducted using Qiagen Type-IT in 10 µL reactions following manufacturers instructions. Cycling conditions for testing primer pairs and subsequent multiplex genotyping of 12 loci selected for screening all samples were as follows: 95°C for 5 min, followed by 30 cycles of 95°C for 30 s, 50°C for 90 s, and 72°C for 30 s, then 30 min at 60°C. Other annealing temperatures (55°C and 60°C) were also tested in the preliminary screening phase. Twelve loci yielded polymorphic inserts that amplified reliably and consistently. These loci were PCR amplified in two multiplex reactions (Table S2), which were diluted 1:10 and dehydrated before being sent to Georgia Genomics Facility (http://dna.uga.edu) for fragment analysis on an Applied Biosystems 3730xl DNA Analyzer with the GGF500ROX internal size standard (http://dna.uga.edu/services/dye-labeled-size-standard/) added to each well. Fragment sizes (alleles) were determined using GeneMarker®, SoftGenetics LLC (www.softgenetics.com). All alleles were scored automatically and checked manually. Samples with ambiguous alleles were reamplified and genotyped. Two loci (Amil2_010 and Amil2_011) had considerable amounts of missing data (mainly because genotypes could not be scored consistently) and were removed prior to analyses.

Genetic Analyses for Acropora tenuis

Identical MLGs were identified using all ten loci in GenAlEx ver. 6.5 (Peakall & Smouse 2012). The probability of identity, $P_{(ID)}$, was used to evaluate whether repeat MLGs were the result of sexual or asexual reproduction (Waits *et al.* 2001). Repeat MLGs occurred both within and among sites. Based on the magnitude of $P_{(ID)}$ and the spatial distribution of MLGs within and among sites (see ESM), the most parsimonious conclusion was that within-site repeat MLGs (n = 59) and among-site repeat MLGs within the Palm Islands (n = 19) were produced asexually, and all but one copy of these 78 repeat MLGs were removed prior to analyses. The remaining among-site repeat MLGs (n = 88), separated by 10's to 100's of kilometers and unlikely to have been produced asexually, were retained (ESM). The resulting dataset (2454 colonies, including 708 colonies from the Palm Islands) was further reduced to achieve approximately equal sample sizes (n = 50) for large-scale analyses, by removing 440 of 590 samples collected from three sites in the Palm Island. The final dataset comprised 2014 samples (Table S1).

HWE, LD and F_{IS}

Tests of LD were conducted for pairs of loci among sites and for pairs of loci across all sites in GenePop (ver. 4.3: (Rousset 2008) using 20 batches with 5000 iterations per batch and 10,000 dememorisation steps. Locus-by-site tests of HWE were undertaken in the R package adegenet (ver. 1.4-2: (Jombart 2008)) and a global test of HWE was implemented in GenePop (ver. 4.3: (Rousset 2008) using one-tailed tests for heterozygote deficiency, a common observation in corals (Baums 2008). Global F_{IS} values and observed (Ho) and expected (He) heterozygosities were estimated in GenePop (ver. 4.3: (Rousset 2008). P values for a significance of 0.05 were adjusted for multiple tests using both the Benjamini and Hochberg False Discovery Rate (B-H FDR: (Benjamini & Hochberg 1995) and the Benjamini and Yekutieli False Discovery Rate (B-Y FDR: (Benjamini & Yekutieli 2001).

Genetic Diversity, Population Structure and Isolation-by-Distance

Genetic diversity was assessed using mean numbers of alleles per locus (Na), allelic richness (Ar) and allelic evenness (Ae) using the gstudio package (ver. 1.3: (Dyer 2014) in R. Rarefaction to the smallest sample size (n = 9) was used to account for the influence of sample sizes on estimates of Ar and Ae, with the harmonic mean taken across 99 permutations. Population structure was estimated using global and population pairwise F_{ST} values calculated using an AMOVA approach (Excoffier *et al.* 1992) and G'_{ST} (Hedrick 2005), which is not biased by allelic variability. Both global and population pairwise F_{ST} values were calculated in GenAlEx ver. 6.5 (Peakall & Smouse 2012) with significance tested using 999 permutations. Global and pairwise G'_{ST} measures were estimated in the

mmod package (Winter 2012) in R. Principal component analysis (PCA) was used to evaluate patterns of spatial genetic structure among colony-MLGs. PCA was conducted in R (R_Core_Team 2013), with missing data for each locus replaced with mean genotypes for the respective site. Multidimensional scaling (MDS), based on pairwise G'_{ST} values, was used to visualize the genetic relationships among populations. Isolation-by-distance (IBD) was tested by regressing pairwise G'_{ST} and pairwise $F_{ST}/(1 - F_{ST})$ values onto the Euclidean distance between sites, with significance tested using a Mantel permutation test. MDS and IBD analyses were conducted using the vegan package (Dixon 2003) in R and including and excluding 68_MAG_CAY in the Coral Sea, which lies outside the GBR reef matrix and would not be expected to conform to the assumptions of the analyses.

Acropora millepora genetic data

The *A. millepora* dataset (van Oppen *et al.* 2011) comprised 922 colonies with identical MLGs from 20 reefs in the GBR. Seven reefs were identical to those sampled for *A. tenuis*, comprising three northern (01_WAL_IS, 05_NIGHT, 07_WILKIE), three central (28_MYR, 41_OI_SH, 44_OI_WP) and one southern (52_KEPPEL), while four reefs (Darley, Ross, Boulton, Goble) were in very close proximity to four reefs sampled for *A. tenuis* (48_SEAGULL, 49_STUCCO, 50_Reef20-344, 51_BUGAT). The remaining nine reefs sampled for *A. millepora* covered similar geographical distribution to *A. tenuis*, with the exception that *A. millepora* was not sampled in the southern Swain and Capricorn Bunker reefs.

Bayesian clustering analysis:

Bayesian clustering algorithms, implemented in STRUCTURE ver. 2.3.3 (Pritchard *et al.* 2000) and TESS ver. 2.3 (Chen *et al.* 2007), were used to examine spatial genetic structure for the entire datasets for both *A. tenuis* and *A. millepora*. STRUCTURE analyses were conducted using the admixture and no-admixture models, with correlated allele frequencies, using sampling sites as prior (LOCPRIOR), which has been shown to better resolve genetic structure when there is low genetic divergence (Hubisz *et al.* 2009). MCMC chains used a burn-in of 50,000 chains followed by 500,000 of MCMC replications. Ten independent chains were run for each K (number of genetic clusters) from 1 to 12 (*A. tenuis)* and 1 to 9 (*A. millepora*) and the most likely value of K for each species was evaluated using the method of Evanno *et al.* (2005) as implemented in STRUCTURE HARVESTER (Earl & vonHoldt 2012). STRUCTURE implements a prior that emphasizes the existence of clusters, which may make it prone to errors when geographical sampling is discrete along clines (Chen *et al.* 2007), as in this study. TESS addresses this issue by using a spatially continuous prior based on the geographical coordinates of each individual sampled in the study. TESS was run using the CAR admixture model, which assumes spatial autocorrelation of the genomes of individuals in closer

geographical proximity compared with those further apart. The strength of this autocorrelation (ψ) was set to the default value of 0.6. TESS was run with a burn-in of 10,000 sweeps followed by 25,000 sweeps, with 100 independent runs conducted for each K. The average DIC for each value of K was used to evaluate the most likely number of genetic clusters. The coefficient of ancestry was calculated for each individual for the most likely value of K in CLUMPP version 1.1.2 (Jakobsson & Rosenberg 2007) and results visualized using DISTRUCT version 1.1 (Rosenberg 2004).

Assignment tests: A. tenuis *and* A. millepora

Assignment tests of movement are especially appropriate when populations are recently diverged, as is likely to be the case for GBR corals, due to the long generation times of corals and the relatively recent recolonization of the GBR following the most recent Pleistocene glaciation (< 20,000 years ago). GeneClass2 (Piry *et al.* 2004) was used to examine first generation migrants (FGMs) for *A. tenuis* and *A. millepora* on the GBR. This method performs better in assigning/excluding individuals to their correct population of origin than other likelihood and distance-based methods (Cornuet *et al.* 1999) and, unlike BayesAss , does not impose the unrealistic assumption of at least 70 % self-recruitment (Hellberg 2007), which clearly would be violated in both *Acropora* species in this study. In the first step of each analysis, migrants were identified using the criteria and computational algorithm of Rannala and Mountain (1997) with 10,000 simulated genotypes and an alpha of 0.01. For each species, FGMs were excluded from the relevant data set, which then served as the reference data to which migrants were assigned. Migrants were assigned to populations (sites) if their assignment probabilities were greater than 0.1.

Multiple Factor Analysis

Congruence in the spatial patterns of genetic variation for *A. tenuis* and *A. millepora* was further explored using multiple factor analysis (MFA) focusing on the 11 sites with genetic data available for both species. MFA is an ordination approach that describes correlations among matrices subjected to individual PCAs, whereby global canonical axes describing PC's across the matrices are inferred {Borcard, 2011 #87}. PCA based on population allele frequencies is a suitable approach for describing genetic variation {Jombart, 2008 #58}. For each species allele frequencies were scaled using scaleGen function in the R package adegenet {Jombart, 2011 #88}. A third matrix of latitude and longitude was included to explicitly account for the spatial location of each site {Jombart, 2008 #58}. Correlations among the three matrices were described using RV coefficients, the equivalent of multivariate Pearson correlation coefficients. The MFA among the three matrices and estimates of RV coefficients were conducted in FactoMineR {Husson, 2015 #89}.

Results

HWE, LD and F_{IS}

Among 2430 pairwise combinations of loci within sites, only 15 combinations showed significant LD after adjusting p values using B-H FDR: α_{CRIT} = 0.0003 (Benjamini & Hochberg 1995), whereas 46 combinations were significant using B-Y FDR: α_{CRIT} = 0.006 (Benjamini & Yekutieli 2001) (Table S3). In both cases, the same four loci (Amil2_002, Amil2_012, EST014 and EST121) contributed to > 70 % of cases with significant LD (Table S3), with each locus contributing from 16 to 20 %. Pairwise combinations of loci with significant LD were geographically clustered (Table S3). Eight of the 15 pairs of loci significant under B-H FDR occurred on the exposed sides of two adjacent Ribbon Reefs (12_NN_FR, 6 pairs; 10_YONG_FR, 2 pairs), while the remaining seven pairs were clustered in the southern GBR (six pairs on five Swain Reefs, and one in the Heron Island group) (Fig. 2). Similarly, 15 of the 46 pairs of loci significant under B-Y FDR occurred on the Ribbon Reefs (12_NN_FR, 10_YONG_FR, 22_SN_PIT) while 28 pairs occurred in the southern GBR (all seven Swain Reefs sampled, 61_HI_CCAS, 63_HI_WIST1, and 51_BUGAT). Two of the other three pairs occurred on 68_MAG_CAY, while only one pair of loci in LD occurred the central GBR (33_JBR) (Fig. 2). Among the 45 pairwise combinations conducted across all sites, 12 pairs of loci had significant LD using both the B-H FDR (p = 0.0133) and B-Y FDR (p = 0.0114) (Table S3).

In 540 individual tests of HWE in locus by site combinations, >80 % of sites had at least one locus that significantly deviated from HWE (B-H FDR, 43 of 54 sites, α_{CRIT} = 0.0071; B-Y FDR, 47 of 54 sites, α_{CRIT} = 0.0073) (Table S4). Given that Amil2_018 and Amil2_022 had a disproportionate number of significant deviations (for 19 and 29 of 54 populations respectively), a subset of analyses (PCA, MDS, AMOVA, STRUCTURE, TESS) were conducted for the GBR data (n = 2014) excluding these two loci. There were no differences in the overall results for these analyses using the eight-locus dataset compared with the ten-locus dataset. There was a consistent pattern of observed homozygote excess in MLGs for nearly all sites with moderate ($F_{IS} \leq 0.27$) but significant F_{IS} values most sites (B-H FDR, 50 of 54 sites, α_{CRIT} = 0.046; B-Y FDR, 47 of 54 sites, α_{CRIT} = 0.011) (Table S4).

Genetic diversity, population structure and IBD

Number of alleles per locus ranged from 3 to 17 (average Na = 9.2 across all loci) for the entire GBR (Table S4). Rarefacted Ar across all loci within populations ranged from 2.3 to 3.1 (average = 2.65 for entire GBR); rarefacted Ae ranged from 1.6 to 2.2; and Ho ranged from 0.22 to 0.40, while He ranged from 0.28 to 0.47 (Table S4). Ar, Ae and He (Table S4) were positively correlated with latitude ($r \geq 0.44$; $P < 0.001$), with a strong trend of higher diversities occurring in the southern GBR and the Coral Sea (Fig. 2, *Inset*; Table S4). AMOVA partitioned 3.4 % of the genetic variation among populations

(F_{ST} = 0.034, $p < 0.001$). Pairwise F_{ST} values ranged from -0.010 to 0.152 with most significant differences occurring between southern GBR reefs and the rest of the GBR, and among southern-GBR reefs (Fig. S1). The first two components of the PCA of individual MLGs across the GBR plus Coral Sea accounted for 24% of genotypic variation in the data. PC1 partially delineated southern GBR sites from the remaining GBR and MLGs from southern GBR sites had higher variance in PC1 compared with other GBR regions (Fig. 3A). MDS for the GBR alone showed that most far northern, northern and central GBR sites strongly clustered together (Fig. 3B). Two exceptions to this pattern were 12_NN_FR and 22_SN_PIT in the Ribbon Reefs, which did not cluster with other reefs (Fig. 3B) and had significantly different F_{ST} values from most other reefs in the GBR (Fig. S1). Southern sites clustered less strongly (Fig. 3B); nonetheless there was a geographic signal in the data with one cluster comprising all six mid-shelf southern GBR sites (Fig. 1: sites 60-67) while a second cluster comprised six of seven sites in the offshore Swain Reefs (Fig. 1: sites 54-59) plus 51_BUGAT. MDS of pairwise G'_{ST} values differentiated the 53 GBR sites from the Coral Sea but otherwise did not provide much resolution (Fig. S2). There was significant but not strong support for IBD among the 53 sites sampled within the GBR (G'_{ST}; $R = 0.45$; $p < 0.001$) (Fig. S3A) and, although still significant, the correlation between genetic and geographic distance decreased for the GBR plus Coral Sea (68_MAG_CAY) (G'_{ST}; $R = 0.29$; $p < 0.001$) (Fig. S3B). Results using $F_{ST}/(1 - F_{ST})$ were virtually identical (not shown).

Bayesian clustering analysis: A. tenuis *and* A. millepora

STRUCTURE analysis for *A. tenuis* using the admixture model indicated that two ($\Delta K = 280$) or three ($\Delta K = 240$) genetic clusters best explained the genetic patterns in the data, whereas the no-admixture model had highest support for two clusters ($\Delta K = 1155$) but also a large peak at four clusters ($\Delta K = 453$) (Figs. S4A-B). DIC scores from TESS analyses declined steeply between K = 2 and K = 4 and then plateaued, providing strongest support for four genetic clusters (Fig. S4C), so results for four clusters were presented. STRUCTURE analysis for *A. millepora* using the admixture and no-admixture models indicated that two ($\Delta K = 1150$) genetic clusters best explained the genetic patterns in the data (Figs. S4D-E). DIC scores from TESS analyses for *A. millepora* declined steeply between K = 2 and 4 (although not to the same extent as for *A. tenuis*) and then plateaued, providing stronger support for four genetic clusters (Fig. S4F). In order to best compare genetic patterns between the two species we focused on the results for K = 4.

TESS (Fig. 2) and STRUCTURE (Figs. S5A-C) returned very similar patterns with most colonies of *A. tenuis* from the 35 GBR sites sampled north of 19°S comprising one genetic cluster (Fig. 2 A-D). The only exceptions to this pattern were four sites (10_YONG_FR, 12_NN_FR, 22_SN_PIT,

26_PITH), which had some colonies that belonged to the ubiquitous genetic cluster (Fig. 2; light green), and some colonies that belonged to one of the other three genetic clusters. Specifically, 10_YONG_FR and 12_NN_FR (exposed sites facing the Coral Sea on two ribbon reefs) had colonies from a second genetic cluster (Fig. 2; pink) that also occurred at two outer Swain Reefs (53_EAST_CAY and 56_FRIG), and the Coral Sea (68_MAG_CAY). Importantly, 11_YONG_LAG and 13_NN_LAG (sheltered sites facing the GBR lagoon on these same two ribbon reefs) did not have colonies from this second cluster (Fig. 2). In addition, 26_PITH, an outer shelf reef in the central GBR had colonies from a third genetic cluster (Fig. 2; orange) that was abundant on the Swain Reefs and 68_MAG_CAY, Coral Sea; and 22_SN_PIT, a submerged reef in the northern GBR lagoon, had colonies from a fourth genetic cluster (Fig. 2; blue). 68_MAG_CAY, Coral Sea, essentially comprised two genetic clusters (Fig. 2; pink and orange) that were abundant in the Swain Reefs, plus the three northern outer shelf sites already mentioned.

TESS (Fig. 4) and STRUCTURE (Figs. S5D-F) for *A. millepora* showed similar patterns, with most colonies from the GBR sites sampled north of 19°S (n = 11) comprising one genetic cluster (Fig. 4A,B). Offshore GBR reefs south of 19°S were dominated by a second genetic cluster (Fig. 4C, orange) admixed to a greater or lesser extent with the ubiquitous cluster, while inshore reefs comprised admixtures of the ubiquitous cluster and the other two genetic clusters (Fig. 4D, pink, blue).

Assignment tests: A. tenuis *and* A. millepora

For *A. tenuis,* 189 of 2014 colonies (9.4 %) were identified as FGMs based on the GeneClass2 analysis. FGMs were identified at all 54 sites sampled, with frequencies ranging from one to seven per site (Fig. S6A). Of these 189 FGMs, 107 could not be assigned to any of the 53 other sites sampled. Twenty-one of the remaining 82 FGMs were assigned to just one of the sampled sites; 16 to two sites; five to four sites, four to five sites, four to six sites; while the remaining 32 FGMs were assigned to between seven and forty-three sites (Fig. S6B). This issue of multiple, and potentially inaccurate, assignments per FGM has previously been documented in high gene flow systems (Saenz-Agudelo *et al.* 2009). The numbers of FGMs assigned to each site ranged from one to thirty-three, except for two sites with small sample sizes [36_DAVIES (n = 9) and 40_OI_RP (n = 21)] to which no FGMs were assigned. Based on these data there were no clear patterns to the distribution of putative source reefs for the 82 FGMs. A filtered set of assignment probabilities was created that included the 37 FGMs assigned to just one or two reefs and, for the remaining 45 FGMs (assigned to four or more reefs), the three source reefs with highest assignment probabilities for each FGM (Fig. S6C). These filtered assignment probabilities showed that, although putative source reefs (Fig. 5, columns) for FGMs of *A. tenuis* (Fig. 5, rows) were located throughout the GBR, 16 sampled sites were never identified as

being among the most likely putative source reefs (Fig. 5). These 16 sites were almost exclusively located in the northern Ribbon Reefs (five sites) and central GBR (eight sites), plus 68_MAG_CAY, Coral Sea.

For *A. millepora,* 54 of 922 colonies (5.9 %) were identified as FGMs and, as with *A. tenuis,* FGMs were identified at all 20 reefs sampled, with frequencies ranging from one to five per reef (Fig. S7A). However, 44 of these 54 FGMs were not assigned to one of the other 19 sampled sites (Fig. S7A). Of the remaining ten putative FGMs, three were assigned to one site, two to two sites, three to five sites, and one each to six and seven sampled sites. Using filtered assignment probabilities (as for *A. tenuis*) 11 of the 20 sampled sites were not identified as being among the most likely putative source reefs, and were predominantly located in the northern and inshore southern and central GBR (Fig. S7B).

Multiple Factor Analysis

The first two axes of the MFA explained 46% of the variance among the three PCAs describing allele frequencies for *A. tenuis*, *A. millepora* and latitude/longitude for the 11 co-sampled sites (Fig. 6) and allele frequencies across sites were highly correlated between the two species (RV coefficient = 0.69), although marginally above a 5% significance threshold ($p = 0.056$), but with only 11 sites the power to test significance is low. The first dimension of the MFA differentiated northern and central sites in the GBR from southern sites, while the second dimension differentiated the southern inshore 52_KEPPEL from the other ten sites (Fig. 6). The congruent strength and direction of the partial PCA axes for *A. tenuis* and *A. millepora* for dimension 1 (and to a lesser extent dimension 2) of the MFA highlights their shared patterns in genetic variation (Fig. 6, Inset A). Both species showed moderate but non-significant correlation between allele frequencies and spatial location (*A. tenuis*: RV = 0.32, $p = 0.163$; *A. millepora*: RV = 0.40, $p = 0.059$) indicating that the correlation in allele frequencies between the two species exceeds any correlation arising directly from geographic distance (Fig. 6, Inset A).

Discussion

Major genetic structure in east Australian A. tenuis

The analyses presented here identified geographic structure for *A. tenuis* on the GBR that broadly grouped into: 1) the southern inshore (52_KEPPEL) and midshelf Heron/One Tree Islands; 2) the southern offshore reefs (i.e. the Swains and 52_BUGAT); and 3) the remaining reefs in the far northern, northern and central GBR. The Coral Sea reef (68_MAG_CAY) is genetically distinct from those on the GBR. As discussed previously (van Oppen *et al.* 2011), recolonization of the GBR by shallow-water biota after the Pleistocene glaciations is believed to have occurred from three distinct

refugia: the Queensland Plateau in the north, the Marion Plateau in the south, and the far southern Moreton Bay area (~27.5°S). We hypothesise allopatric differentiation during the Pleistocene is still observable and is reflected in the main genetic clusters identified on the GBR. Coral Sea reefs are isolated from the GBR by large spans of ocean devoid of reefs, thus gene flow between the Coral Sea and the GBR is restricted. Nonetheless, signatures of genetic admixture between the Coral Sea and outer shelf reefs in the northern, central and southern GBR provide evidence of recent gene flow.

Congruent patterns of genetic diversity and population structure between Acropora *species*

Bayesian clustering analyses revealed highly congruent patterns of genetic structure for two broadcast spawning corals, *A. tenuis* and *A. millepora*, throughout the GBR. Although the geographic distribution of sampling was not identical, both species had shared a pattern of almost complete genetic uniformity among GBR reefs north of 19°S GBR (with the exception of a few admixed sites for *A. tenuis* in the northern GBR). Reefs in the southern GBR were genetically distinct, with each site comprising varying degrees of admixture between the ubiquitous genetic cluster and one or more of three other genetic clusters. For both species, outer shelf reefs had higher levels of admixture than inshore reefs, however the latitude of outer reefs where marked admixture first occurred was somewhat further south for *A. tenuis* (20°S, 51_BUGAT) than for *A. millepora* (19.1°S, Darley) but both species showed a general pattern of increasing admixture at higher latitudes (*A. millepora* was not sampled in the southern Swain Reefs). Broadly congruent patterns of higher genetic diversities found on southern GBR reefs for *A. tenuis* (Fig. 2) and *A. millepora* (van Oppen *et al.* 2015) reflect this pattern of admixture and may represent the accumulation of alleles via the southward flowing East Australia Current. The hypothesis that the southern GBR represents an accumulation of genetic diversity is further supported by the PCA of *A. tenuis* (Fig. 3A), which showed that MLGs in the northern GBR represent a subset of those in the south. One exception to the pattern of higher diversity in the southern GBR was the somewhat lower genetic diversities for *A. millepora* in the Keppel Islands (van Oppen *et al.* 2015), most likely the result of intense repetitive disturbances over the past 25 years. Both species shared a genetic divide between inshore and offshore southern GBR reefs, while *A. tenuis* had a further genetic divide between the outer Swain Reefs and midshelf Heron/One Tree Islands (unfortunately these were not sampled for *A. millepora*). Further sampling of southern GBR reefs for *A. millepora* and other broadcast spawning corals is needed to confirm these finer-scale genetic divides.

Congruence between genetic connectivity and larval dispersal models

To date, just one larval dispersal model (LDM) has been published that encompasses the entire GBR (Hock *et al.* 2014). Larvae were characterized as passive, neutrally buoyant particles, with a pre-

competency period of 24 hours, competency period of 28 days, and larvae were regarded as 'settled' as soon as arriving within 1 km of a reef-polygon (Hock *et al.* 2014). These characteristics are broadly comparable to those of broadcast spawning corals (Connolly & Baird 2010). This LDM found that many source reefs (reefs with most out-components, Fig. S3B in Hock et al. (2014)) were located in the far northern GBR and southern outer GBR (Swain Reefs), while the central and southern inshore GBR had very few source reefs. These findings are consistent with the distribution of source reefs of FGMs of *A. tenuis* (Fig. 5) and *A. millepora* (Fig. S7B). However, the LDM also identified a high concentration of source reefs in the northern GBR (Fig. S3B in (2014)), whereas few reefs in this region were identified as sources of FGMs for either species. The LDM identified reefs receiving the most larvae from elsewhere in the GBR (in-components, Fig. S3A in (2014)) were concentrated in the southern and far northern GBR, whereas reefs in the northern sector received few larvae. By contrast, average numbers of FGMs within regions were distributed relatively evenly throughout the GBR for both *A. tenuis* (Fig. 5) and *A. millepora* (Fig. S7B). Among the various factors that might account for these discrepancies, perhaps the most important is that the LDM was based on hydrodynamic data from just one spawning event (December 2008), thereby not accounting for annual variation in hydrodynamic conditions, whereas genetically identified FGMs represent multiple generations of larval dispersal. In addition, larval dispersal was modeled for COTs (2014), which spawned one month later than corals on the GBR in 2008 (Baird *et al.* 2009).

Thomas *et al.* (2014) modeled larval dispersal for four broadcast spawning coral species (including *A. millepora* but not *A. tenuis)* in the central GBR (~1000 reefs) using larval characteristics identified experimentally (2010) and hydrodynamic data from one spawning event (December 2007), and larvae were tracked for 28 days. A graph theoretical approach was used to identify communities (strongly connected clusters of reefs that are weakly connected to other reefs in the network) and showed that broadcast spawning corals with larval characteristics of *A. millepora* comprise six communities in the central GBR (Fig. 10D in (2014)). Eleven sites sampled for *A. tenuis* and eight sites sampled for *A. millepora* occurred within the area of the LDM (2014), and there is broad (but not complete) agreement between the communities identified by graph theory analyses and genetic clusters identified by Bayesian clustering analyses. Graph theory identified two large outer-shelf communities: 1) a northern community comprising outer-shelf reefs from ~18°S to ~20°S (Fig. 10D green in (2014)); and 2) a southern community comprising reefs between ~18.5°S and ~21.5°S (Fig. 10D orange in (2014)). The two communities overlapped between ~19°S and ~20°S, which corresponds to latitudes where genetic admixture appears for both species. Moreover, the northern community (Thomas *et al.* 2014) encompassed seven sites identified as genetically homogenous for *A. tenuis* (Fig. 2C: 28_MYR, 29_DIP, 30_CHICK, 33_JBR, 34_KEEPER, 35_WHEEL, 36_DAVIES), while the southern community (Thomas *et al.* 2014) encompassed four sites with increasing admixture for *A. tenuis* (Fig.

2E: 48_SEAGULL, 49_STUCCO, 50_Reef20344 and 51_BUGAT) and four sites with varying degrees of admixture for *A. millepora* (Fig. 4C: Ross, Boulton, Goble and Darley). Graph theory also identified four inshore communities, one of which (Fig. 10D pink in (2014)) included inshore Holbourne and Calder Reefs identified as genetically distinct from adjacent outer-shelf reefs for *A. millepora* by Bayesian clustering analyses (Fig. 4). Nonetheless, a second inshore community (Fig. 10D blue in (2014)) included Magnetic Island, whereas there was no cross-shelf genetic divide for *A. millepora* between inshore Magnetic Is. and adjacent outer-shelf Myrmidon (Fig.3). Unfortunately, the Palms Islands, which were the only inshore central GBR reefs sampled for *A. tenuis* (and sampled for *A. millepora*), lay north of the boundary of the LDM precluding additional cross-shelf comparisons between predictions from graph theory and the genetic data.

Relevance for management of the GBR

Not withstanding some differences in geographic sampling, the strong similarity in patterns of genetic diversity and structure between two important broadcast spawning reef-building coral species, *A. tenuis* and *A. millepora,* combined with broad congruence between genetic data and recently published larval dispersal models, provide confidence that such patterns likely exist for other broadcast spawning coral species and can usefully be incorporated into future rezoning efforts and active management options such as reef restoration and assisted translocation. The high levels of connectivity in broadcast spawning acroporid corals north of 19°S latitude suggests that the present distribution of no-take zones in this part of the GBRMP is sufficient for maintaining connectivity. Conversely, the configuration of no-take zones in the southern GBR may not be best suited to ensure sufficient connectivity into the future given the spatially restricted levels of gene flow inferred from our analyses, as well as the predicted increases in severity and frequency of environmental disturbances. Further, the genetic break at 19°- 20° S needs to be considered in translocation initiatives. If the goal of translocation is to restore damaged reefs while maintaining genetic purity, best practice may be not to translocate across this break. However, if the aim is to introduce new genetic variants and maximise genetic diversity, translocation across the break should be contemplated. Our findings highlight the value of combining information across species and comparing results from empirical and modelling approaches to inform management.

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Data Accessibility

Genetic data and GPS co-ordinates for *A. tenuis* are available in at datadryad.org/resource/doi:10.5061/dryad.h8gh3

Genetic data for *A. millepora* are available at datadryad.org/resource/doi:10.5061/dryad.q0834p71

Author Contributions

VL, MvO conceived and designed the study, conducted fieldwork and collected samples; VL provided materials and conducted all laboratory work; VL, CR, MvO performed statistical analyses and interpreted the results; VL, MvO, CR wrote and approved the final manuscript.

Figure Legends

Figure 1. Map of Great Barrier Reef showing locations of 54 sites sampled for *Acropora tenuis*.

Figure 2. *Acropora tenuis* TESS results for four genetic clusters. Each bar represents a colony and colours represent the proportional contribution of each genetic cluster. Asterisks above names of sites

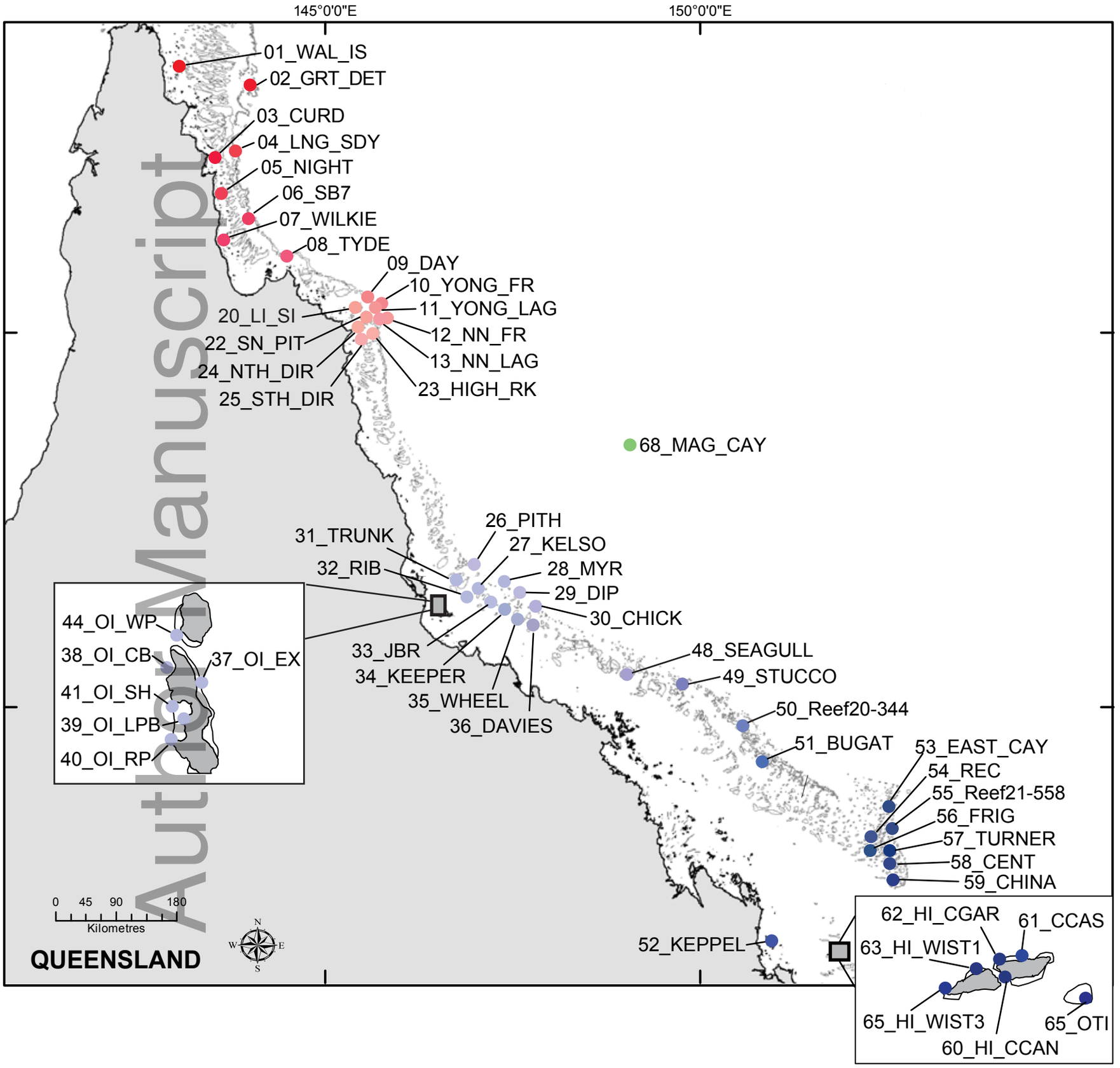
indicate the number of pairs of loci in linkage disequilibrium (LD). *Inset:* Patterns of genetic diversity as the difference between rarefacted allelic richness per site and overall mean for the GBR (2.65). Sites are in the same order as the TESS bar graphs.

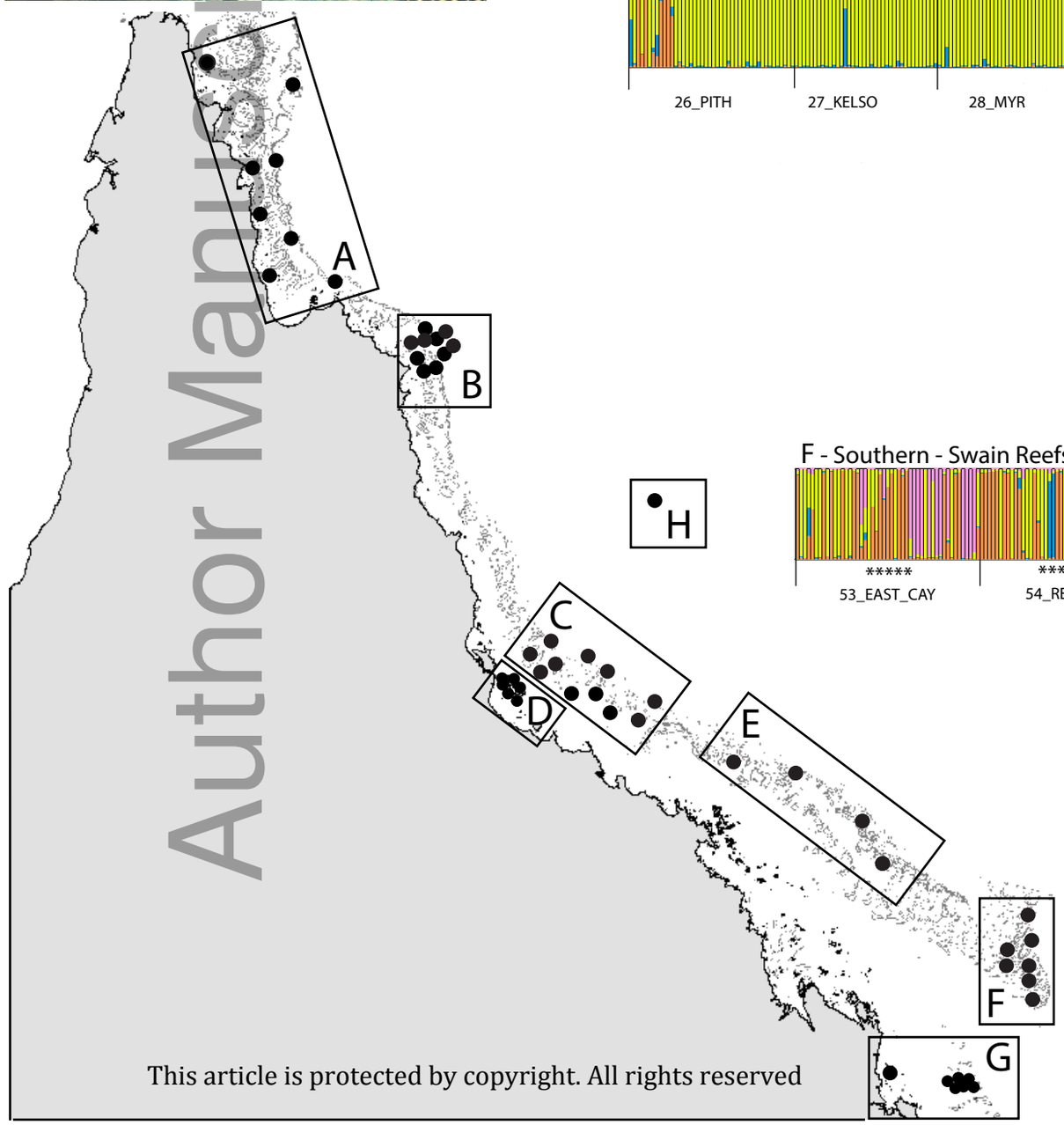
Figure 3. *A)* PCA for multilocus genotypes of 2014 colonies of *Acropora tenuis* for the entire GBR. Each dot represents a colony and colours correspond to sampling locations in Fig. 1. *B)* MDS of pairwise G'ST values for *A. tenuis* for 53 sites in the GBR sites (excluding 68_MAG_CAY in the Coral Sea) where each circle represents a site (colours and numbers correspond to Fig. 1).

Figure 4. *Acropora millepora* TESS results for four genetic clusters (as per Fig. 2).

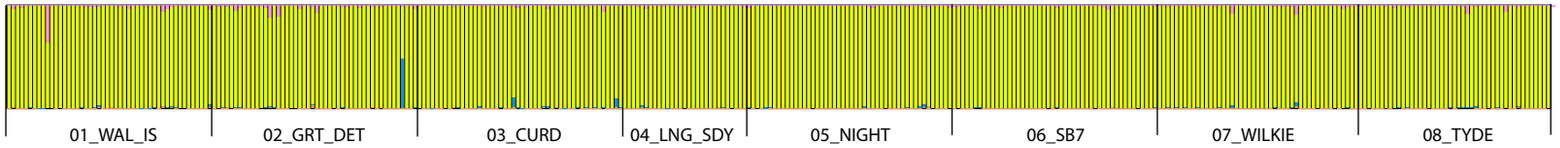
Figure 5. Distribution of source reefs (sites) for 82 *Acropora tenuis* FGMs based on filtered assignment probabilities. Rows indicate sites where one or more FGMs were identified and columns indicate putative source sites. *Total #FGM:* total number of FGMs per reef. *Assigned FGM:* numbers of FGMs assigned per site. Pale yellow squares = one FGM. Dark squares = two FGMs. Note that number of putative source sites are typically more than the number of assigned FGMs per site because up to three candidate source sites are shown per FGM (see text for details; Fig. S6C shows individual FGM assignment probabilities). All sites had FGMs but not all were assigned. Sites with no assignable FGMs (rows) are indicated by white zeros in grey shading. Sites to which no FGMs were assigned (columns) are indicated by zero below site name. Colours of sites match Fig. 1.

Figure 6. Multiple Factor Analysis (MFA) based on matrices of allele frequencies for *A. tenuis* and *A. millepora,* and spatial location (latitude and longitude) at 11 shared sites in the GBR. Large circles are MFA centroids for each site, with the number and colour of circle corresponding to the 11 sites shown on map in bottom left corner. Each MFA centroid is associated with individual PCA site scores for the three matrices (small circles with same colour as the corresponding MFA centroid). *Inset A*: The first two PCA axes for *A. tenuis*, *A. millepora,* and spatial location (latitude and longitude) projected on the first two MFA dimensions, which explained 46% of variance among PCAs. The circle (radius = 1) represents the maximum length of a partial standardized axis for individual PCAs.

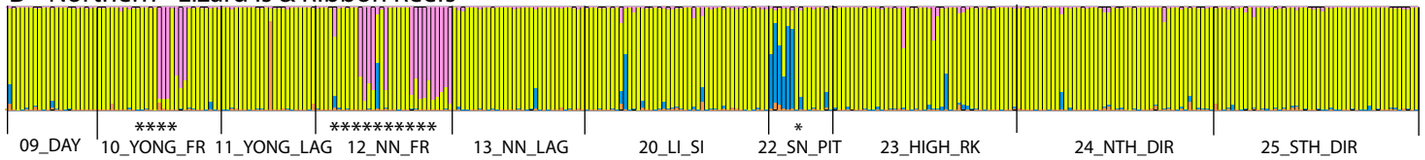




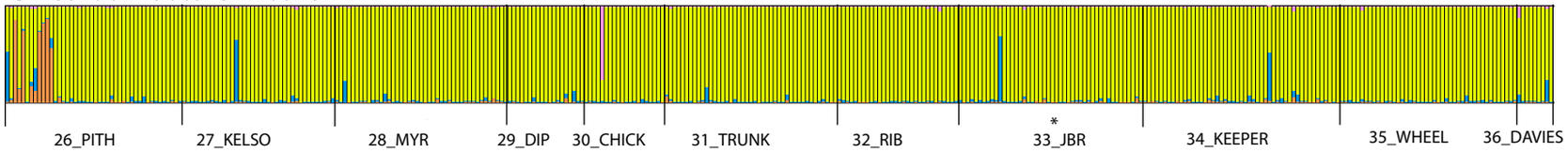
A - Far Northern



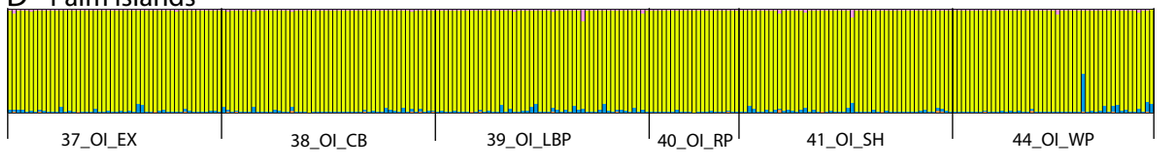
B - Northern - Lizard Is & Ribbon Reefs



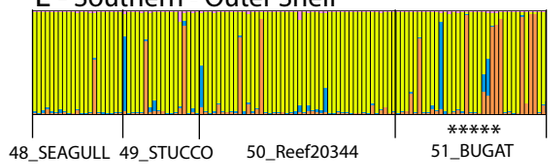
C - Central - Outer & Midshelf



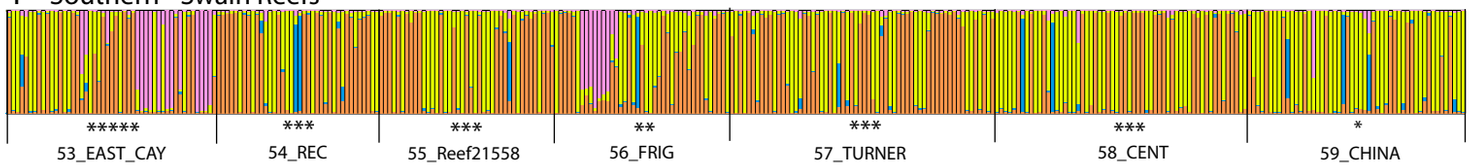
D - Palm Islands



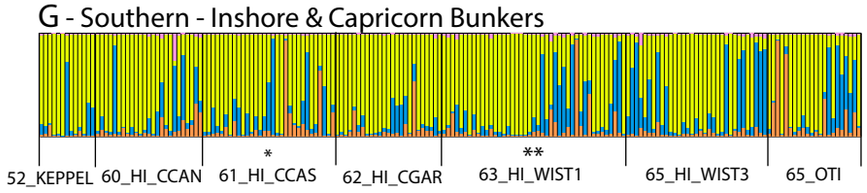
E - Southern - Outer Shelf



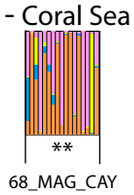
F - Southern - Swain Reefs



G - Southern - Inshore & Capricorn Bunkers



H - Coral Sea



Inset