1. TITLE: Genetic signatures through space, time and multiple disturbances in a ubiquitous brooding coral

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ABSTRACT

The predominance of self-recruitment in many reef-building corals has fundamental and complex consequences for their genetic diversity, population persistence and responses to climate change. Knowledge of genetic structure over local scales needs to be placed within a broad spatial context, and also integrated with genetic monitoring through time to disentangle these consequences. Here, we examined patterns of genetic diversity over multiple spatio-temporal scales across tropical Australia in the ubiquitous brooding coral, *Seriatopora hystrix*. We also analysed complimentary environmental and demographic data to elucidate the seascape drivers of these patterns. Large genetic differences was detected between the east versus west coasts of Australia. In northwest Australia, geographic differentiation dominated genetic structure over multiple scales. However, three sympatric lineages were detected at the largest offshore reef system (Scott Reef). Similar to the differences observed among putative species in eastern Australia, these lineages were associated with different levels of wave exposure. Local genetic structure within the Scott Reef system was relatively stable over ten years, but temporal differences were observed that reflected small but important genetic changes over a few generations during recovery after severe bleaching. These results highlight the importance of self-recruitment together with occasional longer distance connectivity for the persistence of a metapopulation across spatially and temporally variable environments. Our multidimensional research provides a foundation for further long-term genetic monitoring to inform conservation strategies and highlights that sampling scales, ecological effects and cryptic diversity are important considerations to develop realistic understanding of the evolutionary resilience of corals.

KEYWORDS

Eco-evolutionary dynamics, seascape genetics, genetic diversity, metapopulation, *Seriatopora hystrix*, temporal genetic monitoring

INTRODUCTION

The capacity for populations to adapt to a changing environment depends on sufficient standing stock of genetic diversity (Frankel 1974; Moritz 2002; Sgro *et al.* 2011). It is now well recognised that adaptation can occur rapidly, and the reciprocal and ongoing interplay between ecological and evolutionary dynamics often leads to demographic and genetic change over a few generations (Hendry 2016; Schoener 2011). It follows that high levels of intra-specific diversity reduce the vulnerability of populations over time scales relevant to management; a consideration that is supported by ecological and genetic studies (Bolnick *et al.* 2011; Forsman & Wennersten 2015; Hughes *et al.* 2008; Reusch *et al.* 2005; Spielman *et al.* 2004). In spatially structured metapopulations however, local patterns of connectivity and ecological factors such as population size and habitat heterogeneity interact in complex ways to influence the maintenance and distribution of intra-specific genetic diversity (Gaggiotti 2017; Hanski & Simberloff 1997). Therefore, to effectively conserve local populations, communities and ecosystems threatened by rapid climate change, it is important to understand eco-evolutionary dynamics and this involves establishing how local patterns of connectivity and demography link with observed patterns of genetic diversity and population persistence (Calosi *et al.* 2016; Haig *et al.* 2016).

Reef-building corals are not only ideal model taxa for exploring eco-evolutionary dynamics, but this research is also much needed. They are the principal structural engineers of coral reef ecosystems, but are under serious threat from warming oceans, acidification and other anthropogenic disturbances (Hoegh-Guldberg *et al.* 2007; Hoey *et al.* 2016; Hughes *et al.* 2017). In particular, extreme heating events causing widespread coral bleaching have increased in both intensity and frequency, and now tend to re-occur on timeframes that are shorter than the time required for recovery (Hughes *et al.* 2018). Corals can be phenotypically plastic or morphologically conserved, but either way a growing number of genetic studies show much greater inter- and intra-specific diversity (or cryptic diversity) are present than was previously recognised (e.g. Forsman *et al.* 2009; Ladner & Palumbi 2012; Pinzon *et al.* 2013; Richards *et al.* 2016; Schmidt-Roach *et al.* 2013; Thomas *et al.* 2014).

48 In some cases, cryptic lineages or putative species are associated with specific habitats (e.g. Warner
49 *et al.* 2015), temperature regimes (Barshis *et al.* 2013; Dixon *et al.* 2015; Kenkel *et al.* 2015; Palumbi *et*
50 *al.* 2014), or life history traits such as reproductive timing (e.g. Gilmour *et al.* 2016b; Rosser 2015,
51 2016; Rosser *et al.* 2017). Hence, understanding how patterns of inter-individual, inter-specific and
52 intra-specific genetic diversity are created, maintained and distributed in corals is essential for
53 conservation decision-making (Beger *et al.* 2014; van Oppen & Gates 2006).

54 Many ecological, genetic and oceanographic studies indicate that self–recruitment (recruitment into a
55 population from itself) at the reef scale or finer dominates the population replenishment of corals
56 (e.g. Andutta *et al.* 2012; Figueiredo *et al.* 2013; Gilmour *et al.* 2009; Underwood *et al.* 2009). Routine
57 dispersal distances have been estimated at less than 20 – 30 kilometres (McLeod *et al.* 2009; Mora *et*
58 *al.* 2006; Underwood *et al.* 2013) and as little as a few hundred metres (Miller & Ayre 2008;
59 Underwood *et al.* 2007). High levels of self-recruitment can create two antagonistic influences on the
60 distribution of genetic diversity in a metapopulation. When local environments differ, adaptation and
61 genetic divergence is likely, resulting in increased overall diversity. However, in the absence of input
62 of exogenous genes, the standing stock of genetic diversity in local populations may be eroded by
63 processes such as clonality, inbreeding and disturbance and genetic drift (Frankham 1996; Uecker
64 2017).

65 In most cases, the relative importance of self-recruitment versus environmental heterogeneity for the
66 maintenance and distribution of genetic diversity in corals is unclear. Although a temporal
67 perspective is essential to disentangle these eco-evolutionary interactions (Eizaguirre & Baltazar-
68 Soares 2014; Habel *et al.* 2014; Schoener 2011), we are not aware of any coral studies that have
69 followed genetic structure and diversity through time. Previous genetic studies of corals used data
70 collected at a single point in time, preventing examination of the transgenerational effects of recent
71 environmental changes, disturbances and colonisation events on observed patterns. Considering the
72 dynamic and complex nature of coral population dynamics together with the increasing rate of

73 climate change, monitoring *in situ* genetic change over multiple generations is particularly important
74 for their effective conservation (Schwartz *et al.* 2007; van Oppen & Gates 2006).

75 Northwest Australia's shallow coral reefs provide a novel system to study eco-evolutionary
76 resilience because they are isolated and extremely heterogeneous (Wilson 2013). These reef systems
77 are separated by several hundred kilometres, and range from oceanic and platform reefs that occur
78 in exposed, clear waters on the continental shelf margin, to the fringing reefs that occur in turbid,
79 macrotidal, but relatively sheltered waters of the inshore Kimberley (Figure 1). There are few
80 chronic anthropogenic stressors in the region but corals growing on the offshore atolls have proven
81 vulnerable to climate impacts. In 1998, there was a major mass bleaching event at Scott Reef which
82 reduced live coral by around 80% and this was succeeded by another moderate bleaching event in
83 2010, tropical cyclones in 2005, 2007 and 2012 (Gilmour *et al.* 2013), and another very recent severe
84 bleaching in 2017 (Hughes *et al.* 2017). While some progress has been made in understanding the
85 scale and strength of population connectivity among the northwest Australian reefs (reviewed in
86 Underwood *et al.* 2013), the finer-scale patterns of genetic differentiation, and the influence that
87 climatic disturbances have had on the distribution of genetic diversity through time are not known.

88 Here, we address these knowledge gaps by investigating the genetic relationships within and among
89 reef systems and the effects of extreme climatic events on population trajectories of the ubiquitous
90 coral *Seriatopora hystrix* corals in Australia. *Seriatopora hystrix* is a widely distributed brooding coral
91 that is vulnerable to temperature anomalies (bleaching) as well as physical disturbance by cyclones. It
92 is therefore a particularly 'weedy" coral (see Darling *et al.* 2012), being fast growing with rapid
93 recovery after disturbance, high population turnover, high reproductive output and philopatric
94 dispersal. The internally fertilised, predominantly outcrossed larvae (> 97%; Warner et al. 2016, but
95 see Sherman 2008) are brooded within the polyp and released at an advanced developmental stage
96 (Atoda 1951). In northwest Australia, planulation is prolonged with larvae released over many
97 months from October through to April (Gilmour *et al.* 2016a). These larvae settle within hours if
98 suitable substrata are available (Prasetia *et al.* 2017), and genetic studies on Australia's west

(Underwood *et al.* 2007, 2009; van Oppen *et al.* 2011) and east (Ayre & Dufty 1994; Ayre & Hughes 2000; Bongaerts *et al.* 2010; Bongaerts *et al.* 2011; Noreen *et al.* 2009; van Oppen *et al.* 2008; Warner *et al.* 2015; Warner *et al.* 2016) coasts supports dominance of philopatry. However, several lines of evidence indicate larval dispersal of *S. hystrix* may be bimodal. Because seriatopora larvae contain maternal zooxanthellae (Harrison & Wallace 1990), they can settle after many weeks when deprived of substrata in the laboratory (Harii *et al.* 2002; Nishikawa *et al.* 2003; Richmond 1987). Thus, long-distance dispersal may supplement self-recruitment under appropriate conditions (Underwood *et al.* 2007; van Oppen *et al.* 2008). However, a recent study of *S. hystrix* on the Great Barrier Reef (GBR) detected putative species that are not clearly distinguishable by morphology (Warner *et al.* 2015), complicating earlier connectivity conclusions. Therefore, a similar re-assessment in the light of this cryptic diversity is needed in northwest Australia (*sensu* Pante *et al.* 2015).

In this study, we use mitochondrial and microsatellite markers to measure the genetic structure and diversity in *S. hystrix* through space and time across tropical Australia. We complement this genetic dataset with environmental and demographic data to explore the ecological factors that underpin metapopulation persistence. First, we compare the genetic relationships among the coral populations of northwest Australia and the GBR to test whether cryptic lineages identified on the east coast exist in the northwest. In so doing we eliminate the potentially confounding influence that unidentified cryptic species might have on connectivity estimates. Second, we characterise the broad-scale metapopulation structure of *S. hystrix* across most of its range in northwest Australia to test for the relative dominance of geographic differentiation and the relative importance of self-recruitment versus long distance dispersal for population maintenance. Third, we monitored the genetic structure and diversity over a decade at sites with different histories of disturbance and environmental conditions to investigate the seascape drivers of genetic composition. Specifically, we test whether reductions in coral cover brought about by bleaching either reduced genetic diversity and increase differentiation through impacts on population sizes (see Frankham 1996), or increased genetic diversity and reduce differentiation by facilitating the successful recruitment of long distance

125 immigrants (see Miller *et al.* 2009; Underwood *et al.* 2007). We also test whether genotypes and
126 differentiation of local populations are influenced by different levels of wave exposure at these sites.
127 Overall our seascape genetic analysis provides an extensive examination of eco-evolutionary
128 resilience in a keystone species at a globally significant location to inform conservation strategies.

129 MATERIALS AND METHODS

130 *Coral samples*

131 To assess the broad-scale spatial distribution of genetic diversity in *Seriatopora hystrix*, we collated
132 existing and new data from reefs across inshore and offshore locations in northwest Australia (Figure
133 1). Additionally, within the offshore region, multiple sites and several reefs were sampled at Scott
134 Reef and Rowley Shoals, which we refer to as "systems". We avoided clone-mates by sampling
135 colonies separated by at least 1.5 metres and not collecting from loose fragments. Between 17 and
136 49 adult colonies were sampled at each site from transects that were consistently 200 to 300 metres
137 in length. A total of 275 new samples were collected from Ashmore Reef and the inshore Kimberley
138 region (Figure 1) and combined with previous data from Browse Island (n = 74), the Rowley Shoals
139 (n =115) and Scott Reef systems (n = 281; Underwood *et al.* 2009), and from the Great Barrier Reef
140 (GBR) on the east coast of Australia (n = 876; Warner *et al.* 2015; data reference
141 doi:10.5061/dryad.).

142 To assess temporal changes in genetic structure and diversity over local spatial scales, we compared
143 samples from the largest offshore reef system in northwest Australia (Scott Reef) at three times
144 spanning ten years (Figure1). In 2004 , 281 colonies were sampled from five sites; SL1, SL2, SL4, SL5,
145 SS1, SS3 (previously analysed in Underwood *et al.* 2007). Here, we analyse additional collections: in
146 2009, 91colonies were collected from three of these sites (SL1, SL2 and SS1) and in 2014, 214
147 colonies were sampled from seven sites (SL1, SL2, SL3, SL4, SS1, SS2 and SS3). Collections through
148 time at the Scott Reef system were conducted along permanent transects at each site. All sites were
149 located in the reef slope habitat at 6-9 m depth, but varied in relative exposure to the open ocean
150 (see wave exposure analysis below).

Phylogeographic relationships between east and west Australia

We used two approaches to determine the genetic relationships between east and west coast populations of *S. hystrix* in northern Australia. First, we sequenced a 1372-bp segment of the mitochondrial putative control region using the primers and PCR conditions in Chen *et al.* (2008) to infer the evolutionary history of *S. hystrix* in northern Australia and test whether mtDNA lineages on the GBR (Warner *et al.* 2015) exist in northwest Australia (details of mtDNA sequencing and analysis given in Appendix S1). Second, genotypes of *S. hystrix* at seven microsatellite loci (Underwood *et al.* 2006) were used to compare genetic structure and diversity on each side of Australia, and whether any of the four putative species identified by Warner *et al.* (2015) on the GBR have affinities with northwest Australian corals (see Appendix S2: Genetic protocol, quality control and summary statistics of northwest Australian microsatellite data). To assess genetic relationships among all coral samples, Principal Coordinate Analyses (PCoA) were conducted in GenAlEx v6.5 (Peakall & Smouse 2006) based on codominant genotypic distance among pairs of individuals from: i) the combined data set of northwest Australia and the GBR, ii) within the GBR and iii) within northwest Australia. Additionally, to estimate the relative level of differentiation among populations across northern Australia, we calculated average F_{ST} and G''_{ST} between northwest Australia and the GBR, and among putative species on the GBR, in GenAlEx, and tested for significant differences with 1000 random permutations. To assess the amount of genetic diversity within *S. hystrix* across tropical Australia, we measured the gene diversity (H_{SK}) calculated per locus and site with FSTAT v2.9.3 (Goudet 2001). This measure is an unbiased estimate of expected heterozygosity and adjusts for unequal sample sizes. Average H_{SK} was calculated across sites where n ≥ 15 within northwest Australia and within the putative species groups on the GBR. We compared average H_{SK} between northwest Australia and the GBR with 1000 permutations of a randomised data using sites within each group as replicates in FSTAT.

Population genetic clustering within northwest Australia

We delimited the major genetic clusters in microsatellite data of northwest Australia with the Bayesian software STRUCTURE v2.3 (Pritchard *et al.* 2000; see Appendix S3). Specifically, we utilised the 'genotypic cluster' species definition (Mallet 1995) to test whether genetically distinct groups living in sympatry exhibit cohesion among geographically distant populations as per Warner *et al.* (2015). This analysis included all the temporal collections at Scott Reef. In the primary clustering analysis, we first identified the optimal number of genetic clusters (*K)* in the entire data set without prior information on sampling location of colonies. From this, mean and variance of log likelihoods and posterior probabilities of the number of clusters from K = 1 to 12 were inferred. The independent allele frequency model was employed because initial explorations indicated differentiation among clusters was large. We tested the accuracy of assignments by running STRUCTURE with the LOCPRIOR model in a second analysis at K = 2 and 7 (identified as optimal *K's)*.

This primary clustering analysis identified two main genetic clusters linked to inshore and offshore regions. We assessed a finer level of structure within the inshore and offshore regions in a secondary clustering analysis. We used the NOPRIOR model to first assess the optimal number of genetic clusters by running STRUCTURE from K = 1 to 9, and the correlated allele frequencies to improve clustering of corals living in sympatry. To test the robustness of the assignments of the small number of individuals that appeared to have strong genetic affinities among geographically separate systems, we also applied the LOCPRIOR model.

To further assess the spatial distribution of microsatellite variation over broad-scales within and among the geographic regions of northwest Australia, we conducted an hierarchical Analysis of Molecular Variance (AMOVA; Excoffier *et al.* 1992) in GenAlEx. We calculated the proportion of variation measured with F_{ST} between the offshore and inshore regions (F_{RT}), among sites within regions (F_{SR}) and among all sites (F_{ST}) relative to overall variance within the entire data set. Here, we also used standardised measures of F - statistics denoted by F'_{RT}, F'_{SR} and F'_{ST} which are analogous to

G''_{ST} but calculated with AMOVA (Meirmans & Hedrick 2011). Tests for statistical significance were based on 1000 random permutations.

To assess the amount of genetic diversity within *S. hystrix* populations of northwest Australia, we measured gene diversity (H_{SK}) at each site with FSTAT (as per the analysis between east and west Australia) within the Scott Reef system, the Rowley Shoals system, Browse Island, and the inshore Kimberley region. We compared average H_{SK} among these four groups with 1000 permutations of a randomised data which used sites within groups as replicates in FSTAT.

Local spatio-temporal genetic patterns at Scott Reef

To validate membership of individual *S. hystrix* colonies to three sympatric clusters revealed in the secondary clustering analysis at the Scott Reef system, we employed a tertiary clustering analysis in STRUCTURE with samples from the Scott Reef system at $K = 3$. We included all temporal collections at Scott Reef, and also the corals from Ashmore Reef because of their affinities with one of the Scott Reef clusters. To place these STRUCTURE-defined clusters in context of the overall variation in northwest Australia, we also constructed an UPGMA dendogram using the three Scott Reef clusters defined by STRUCTURE (for individuals with $q > 0.70$) and all other sites in the entire northwest Australia data set based on D_A distances (Nei *et al.* 1983) and 10, 000 bootstraps in POPTREE2 (Takezaki *et al.* 2010). In addition, we used a PCoA to assess segregation of clusters defined by STRUCTURE (for individuals with $q > 0.70$) using a standardised genotypic distance matrix in GenAlEx. To quantify the degree of genetic differentiation among the sympatric clusters within the Scott Reef system and compare this with differentiation to the Ashmore Reef samples, we calculated pairwise F_{ST} and G''_{ST} between the three STRUCTURE-defined clusters from Scott Reef and the samples collected from Ashmore Reef in GenAlEx. To compare the amount of genetic diversity among clusters, we also estimated unbiased gene diversity (H_{SK}) within each cluster, and tested for significant differences among collections in FSTAT using 1000 permutations of a randomised data and sites (with $n \geq 15$) as replicates.

Once we ascertained that the clusters at the Scott Reef system were not completely reproductively isolated (i.e. conspecific; see results), we measured the changes in spatial genetic structure through time at the Scott Reef sites which were re-sampled (SL1, SL2, SL4, SS1 and SS3). We first calculated F_{ST} and G''_{ST} (± *SE* across loci) among temporal collections at each site, and among sites within each time, in GenAlEx. Tests for significant differentiation were based on F_{ST} with 1000 random permutations, and significance was adjusted after sequential Bonferroni correction for multiple tests when $P < 0.05$. Pairwise F_{ST} estimates were also calculated among all sites and temporal collections and utilised to visualise genetic relationships among sites and temporal collections with a PCoA using a standardised distance matrix in GenAlEx. To track temporal changes in the amount of genetic diversity at each site, we estimated unbiased gene diversity (H_{SK}) across sites within the 2004, 2009 and 2014 collections, and tested for significant differences among them in FSTAT with 1000 permutations of a randomised data set using sites as replicates.

Quantifying seascape genetics at Scott Reef

To investigate links between genetics and environmental heterogeneity on local populations of *S. hystrix*, we quantified the responses in coral cover to environmental disturbances at each study site and their routine exposure to wave energy. The percent cover of *Seriatopora* spp. was measured annually from 1994 to 1999, and then biannually from 2001 to 2014 (excluding 2006), along five permanent 50m transects at each site, from digital images using a point intercept method (Smith *et al.* 2008). *Seriatopora hystrix* is by far the dominant species of *Seriatopora* at these reefs, so the percent cover at the level of genus provides a suitable surrogate for changes in the cover of *S. hystrix*. We also generated quantitative estimates of relative wave exposure at each site using a 'Generic model for estimating relative wave exposure' (GREMO, Hill *et al.* 2010; Pepper & Puotinen 2009 and details in Appendix S5).

Using these estimates of wave exposure and coral cover, we performed several node-based analyses to test the relative influence of these environmental factors on site-specific genetic metrics. These methods are appropriate and effective for measuring environmental influence on genetic structure

and diversity because they account for the non-independence inherent in multiple pairwise comparisons (Riginos *et al.* 2016; Selkoe *et al.* 2016). First, we measured the effect of wave exposure and/or coral cover on local F_{ST} at each site with the software GESTE v2.0 (Foll & Gaggiotti 2006). Local F_{ST} quantifies genetic differentiation between the local population and the whole metapopulation. We used a burn-in of 5×10^6, a thinning interval of 50 and a sample size of 10000, 10 pilot runs with a length of 5000. Second, to augment this GESTE analysis with a simple and illustrative analysis, we performed several linear regressions to test whether genetic composition co-varied with wave exposure. Specifically, we tested whether wave exposure predicted: the relative abundance of *S. hystrix* genotypes assigned to the 'sheltered' genetic cluster (see Results), genetic differentiation (local F_{ST}), and gene diversity (H_{SK}) at each site at the Scott Reef system. Third, to examine the relationship between coral cover and genetic structure and diversity, we performed linear regressions of local F_{ST} with coral cover, as well as gene diversity with coral cover. Finally, to provide context for these genetic results, we tested whether wave exposure had a direct influence on coral cover.

RESULTS

Phylogeographic relationships between east and west Australia

In contrast to an absence of phylogeographic structure of mtDNA sequences (Appendix S1, Figure S1), the microsatellites revealed large and significant genetic structure across tropical Australia. The northwest Australian samples were clearly differentiated from the GBR samples, and there was no affinity with any of the putative cryptic lineages identified by Warner *et al.* (2015) in east Australia (Figure 2A). Genetic differentiation in the GBR samples was dominated by wave exposure (i.e. sheltered versus exposed sites; Figure 2B). However, no such pattern of clustering associated with wave exposure was evident across northwest Australia. Moreover the PCoA showed structuring based on shelf position (i.e. inshore versus offshore). Clusters were not discrete however, and genotypes from different regions and systems overlapped (Figure 2C). The differentiation between northwest Australia and the GBR was large and significant (F_{ST} = 0.200 and G''_{ST} = 0.797; $P < 0.001$)

278 and comparable to differentiation among putative species groups on the GBR (F_{ST} = 0.284 and G''_{ST} =
279 0.615; P < 0.001). No differences were detected in the overall amount of genetic diversity within the
280 GBR (H_{SK} = 0.406) compared with northwest Australia (H_{SK} = 0.414: P = 0.809; for gene diversity
281 estimates at all sites and across systems/regions see Figure S2).

282 *Population genetic clustering within northwest Australia*

283 Geographic differentiation dominated the structure of microsatellite data of *S. hystrix* in northwest
284 Australia, with STRUCTURE revealing distinct clusters between the inshore and offshore samples.
285 The primary clustering analysis indicated the uppermost level of structure as indicated by Δ*K* was *K* =
286 2 (Figure S3). Geographic differentiation between the inshore and offshore regions was completely
287 resolved with the LOCPRIOR model, with all genotypes correctly assigned (q > 0.6) to sampling
288 region (Figure 3A). Importantly, clusters continued to segregate almost exclusively according to
289 sampling location up to *K* = 7, and this finer level of structure was supported as optimal *K* with the
290 Pritchard *et al.* (2000) method (Figure S3).

291 The secondary clustering analysis, which focused within the offshore and inshore regions of
292 northwest Australia, reinforced the pattern of geographic differentiation. Within the offshore region,
293 *K* = 5 was the optimal number of clusters based on the Evanno *et. al.* (2005) method and there were
294 strong membership coefficients across most individuals (Figure S4). All individuals from Rowley
295 Shoals, Browse Island and Ashmore Reef were confidently assigned to sampling reef (q > 0.7) with
296 the LOCPRIOR model (Figure 3B). In the Scott Reef system however, three sympatric clusters were
297 identified; two of these were endemic to the Scott Reef system, while the third clustered with the
298 Ashmore Reef samples (Figure 3C). Within the inshore region, clusters consistently segregated
299 according to location (Figure 3D), with optimal *K* = 2 estimated by the Evanno *et. al.* (2005) and 6 by
300 the Pritchard *et al.* (2000) method (Figure S5). Importantly, at *K* = 6, all individuals were correctly
301 assigned (q > 0.62) to their sampling site with the LOCPRIOR model (Figure 3D).

Consistent with the strong signal of geographic differentiation revealed by the clustering analysis, the AMOVA revealed significant ($P < 0.001$) and large spatial differences in allele frequencies between offshore and inshore regions of northwest Australia ($F_{RT} = 0.145$, $F'_{RT} = 0.311$). Differences among sites within regions were also significant ($P < 0.001$) and large ($F_{SR} = 0.164$, $F'_{SR} = 0.299$), leading to very large overall significance ($P < 0.001$) and very large differentiation among all sites ($F_{ST} = 0.293$ and $G''_{ST} = 0.398$). The amount of genetic diversity (H_{SK}) showed no obvious geographic pattern across northwest Australia, and did not vary significantly among the Scott Reef system, the Rowley Shoals system, Browse Island and the inshore Kimberley ($P = 0.423$), due to the considerable variation among sites within these areas (Figure S2).

Local spatio-temporal genetic patterns at Scott Reef

The presence of three sympatric clusters at Scott Reef system was clearly evident in the tertiary clustering analysis. Of the 566 individuals examined, 472 were assigned ($q > 0.7$) to one of two clusters endemic to Scott Reef, while 42 individuals were assigned ($q > 0.7$) to a third cluster that included all the corals from Ashmore Reef (Figure 3C). The remaining 52 individuals from the Scott Reef system were not assigned ($q > 0.70$) to any cluster, and many of these were clearly admixed ($q \sim 0.5$) to one of the two clusters endemic to Scott Reef. These admixed individuals were particularly prevalent at one site (SL5; Figure 3C). Relative abundances of the two lineages endemic to Scott Reef were associated with wave exposure, with most individuals from the more sheltered (SL1, SL2) versus exposed (SL4, SS1, SS2 and SS3) sites assigned to different lineages (Figure 3C and see also results below). Lastly, a proportion of colonies at the moderately sheltered site of SL3 (50%) and the exposed site of SL4 (25%) were assigned to the 'ashmore' lineage (Figure 3C). From here on, we refer to these three clusters at Scott Reef as the 'ashmore', 'sheltered' and 'exposed' lineages.

Segregation and membership of the three STRUCTURE-defined lineages at the Scott Reef and Ashmore Reef systems were well supported by the UPGMA and PCoA (Figure S6). Differentiation between the corals from Scott Reef assigned to the 'ashmore' lineage and those from Ashmore Reef was moderate ($F_{ST} = 0.07$), but less than that among the three lineages (ashmore, exposed and

328 sheltered) within the Scott Reef system (average pairwise F_{ST} = 0.12 ± 0.033SE: Table 1). There were
329 also significant differences (P = 0.015) in the amount of genetic diversity among each lineage, with
330 lower diversity in the 'exposed' lineage (H_{SK} = 0.320), compared to the 'sheltered' (H_{SK} = 0.483) and
331 'ashmore' (H_{SK} = 0.496) lineages.

332 Spatial variation among sites was greater than the temporal variation within a given site for the Scott
333 Reef system. The majority of temporal collections were consistently distinguished by their location
334 with PCoA of pairwise genetic differences (Figure 4A). Congruently, genetic differentiation among
335 sites measured by F_{ST} at each time was greater than differentiation through time at each site, while
336 global F_{ST} across all sites remained relatively constant through time (Figure 4B). Similar patterns were
337 observed with G''_{ST} (Table S5). Low but significant differences in allele frequencies were detected
338 through time at SL1, SL2 and SS1, but not at SL4 and SS3 where only two temporal collections were
339 undertaken (Figure 4B). By far the largest changes in allele frequencies were observed at SL1, which
340 switched from a population characterised by the 'sheltered' lineage to one dominated by the
341 'exposed' lineage between 2009 and 2014 (Figure 3C, 4A and 4B). The amount of genetic diversity
342 within each site significantly changed through time (P = 0.042, Figure 4C); gene diversity across sites
343 increased from the 2004 collection (mean H_{SK} = 0.459) to the 2009 collection (mean H_{SK} = 0.564),
344 and then decreased to the lowest level in the 2014 collections (mean H_{SK} = 0.40).

345 *Quantifying seascape genetics at Scott Reef*

346 The mean cover of *Seriatopora* at sites across the reef system ranged from 1 to 6%, with variation
347 closely linked to physical disturbances (Figure 5). By far the largest drop in cover resulted from
348 extreme temperature anomalies in 1998 (Gilmour *et al.* 2013), which caused coral bleaching and a
349 subsequent reduction in cover of *Seriatopora* to 0% at most sites, except SL3 and SL4 where there
350 was a relative decrease in cover of 80% and 50%, respectively. Recovery rates from the mass
351 bleaching also varied considerably, but were fastest at the two sites (SL3, SL4) with the highest
352 remaining cover. Six years later, at the time of the first genetic collection (2004), cover at SL3 and
353 SL4 was higher than prior to the mass-bleaching, half (50-60%) the pre-bleaching levels at SL2 and

354 SS3, and far lower (<10%) than the pre-bleaching levels at SS1, SS2, and SL1. Over the next five
355 years, populations were differentially affected by cyclones and a moderate bleaching event (Figure 5).
356 In 2010, shortly after the second genetic collection, cover was similar or greater than that prior to
357 the mass-bleaching in 1998 at most sites, but for SL2 (44%) and particularly SL1 (12%) and SS2 (3%).
358 Over the next four years, the most significant disturbance was a severe cyclone (2012) that caused a
359 relative decrease in cover at the exposed sites (SL3, SL4) of > 95%, and 29% at SL1 (Figure 5). The
360 cover at most other sites had increased during this time (2010-2014), but for SS2 where there had
361 again been no detectable increase in cover (Figure 5). At the time of the third genetic sample (2014),
362 cover was a little lower (<25%) than that prior to the mass-bleaching in 1998 at four sites (SL1, SL2,
363 SS2, SS3), similar (75%) at SL2, and far higher (>400%) at SS1.

364 Exposure to wave energy varied across sites within the Scott Reef system, being greatest at sites on
365 the outer-slope and/or with a westerly aspect (Figure 5). From 2010 to 2017, wave energy
366 approached the Scott Reef system frequently (77%) from the SW (Figure S7). However, the largest
367 waves (significant wave height > 2m) approached from the W, WNW and NW directions (Figure
368 S8), reflecting the influence of seasonal storms and tropical cyclones. Therefore, the relative
369 exposure to wave energy was highest (0.34) on the western flank of North Reef adjacent to the
370 channel (SL4), and lowest at the inner-slope sites (SL1, SL3 and SL5 < 0.18), particularly (0.01) at the
371 southern end of South Reef (SL2; Figure 5 and Table S6).

372 Results from the environmental association analysis showed that wave exposure had a more
373 important influence than coral cover on the relative abundance of lineages, genetic differentiation,
374 and genetic diversity at each site in the Scott Reef system. Results from the GESTE analysis revealed
375 that wave exposure ($p = 0.361$) explained the variation in local F_{ST} better than coral cover ($p = 0.070$)
376 or the interaction between the two parameters ($p = 0.001$). The linear regressions showed that with
377 increasing wave exposure, the relative abundance of the sheltered lineage decreased ($R^2 = 0.72$;
378 Figure 6A), the local F_{ST} increased ($R^2 = 0.031$; Figure 6B), and gene diversity decreased ($R^2 = 0.41$;
379 Figure 6C) at each site across the Scott Reef system. Conversely, coral cover accounted for little of

variation in local F_{ST} (R^2 = 0.077; Figure S9A), a small proportion of the variation in gene diversity (R^2 = 0.14; Figure S9B), and there was no relationship between coral cover and exposure (R^2 = 0.001; Figure S9C).

DISCUSSION

Evolutionary patterns on GBR versus northwest Australia

This study identified genetic signatures in *Seriatopora hystrix* from northwest Australia that are clearly distinct from those at the Great Barrier Reef (GBR), but also revealed common evolutionary patterns on both coasts of Australia. Warner et al.'s (2015) data from the GBR showed that discrete genetic clusters were putative species associated with different microhabitats on the same reef, and were cohesive between regions separated by several hundred kilometres. Conversely, the major genetic clusters within northwest Australia segregated geographically (Figure 3) and we consider them conspecific, based on the lower overall subdivision compared with that observed on the GBR.

Despite the dominance of geographic differentiation in northwest Australia, at Scott Reef, the genetic structure showed similar, but less well developed, patterns to the habitat-based differentiation on the GBR. The three sympatric lineages from Scott Reef approached, but did not meet, Mallet's (1995) and Good and Wake's (1992) operational definition of species in which genetically distinct groups exhibit cohesion among distant populations and are separated from others in sympatry. Specifically, one lineage had affinities with the Ashmore Reef corals 180km to the north, but was strongly differentiated from sympatric Scott Reef lineages (Figure 3 and Table 1). The two endemic Scott Reef lineages also differed in their composition (G''_{ST} = 0.257) and amount (H_{SK}; 'exposed' lineage = 0.32 versus H_{SK}; 'sheltered' lineage = 0.48) of genetic diversity. However, the presence of admixture between lineages within some individuals at the Scott Reef system, and the lower levels of differentiation among sympatric lineages compared with the putative species on the GBR, indicate that barriers to reproduction between these three lineages within the Scott Reef system are incomplete. For example, at one site (SL5), many individuals had a similar probability of belonging to either lineage (Figure 3C), did not exhibit significant heterozygote deficits indicative of admixture at

406 the site level (Table S3), and this admixture within individuals remained even for K > 3 (Figure S4).
407 Therefore, we consider the three sympatric lineages at the Scott Reef system form a conspecific
408 metapopulation that occasionally interbreed.

409 *Eco-evolutionary dynamics in northwest Australia*

410 Our results revealed large and significant genetic structure over multiple spatial scales, including:
411 between the GBR and northwest Australia, between the inshore and offshore regions within
412 northwest Australia, and among sites within both of these northwest Australian regions. High levels
413 of spatial structuring have been reported in *S. hystrix* at numerous locations including east Australia
414 (Ayre & Dufty 1994; Ayre & Hughes 2000; Bongaerts *et al.* 2010; Noreen *et al.* 2009; van Oppen *et al.*
415 2008), Indonesia (Starger *et al.* 2010; Starger *et al.* 2015), Japan (Prasetia *et al.* 2017) and in the Red
416 Sea (Maier *et al.* 2005). These previous studies utilised data from a single time, but it is difficult to
417 distinguish how much genetic differentiation is due to ephemeral or chaotic genetic patchiness that is
418 common in marine organisms (Hedgecock & Pudovkin 2011; Johnson & Black 1984; Larson & Julian
419 1999; Selkoe *et al.* 2006). Here, we showed that spatial genetic structure remained relatively stable
420 over ten years through significant changes in population sizes across the Scott Reef system; despite
421 small (but significant) site-specific temporal changes, this temporal genetic variation was considerably
422 less than the spatial variation within each time (Figure 4B). This result supports the conclusion that
423 most larvae self-recruit, because the temporal differences reflect changes through just a few
424 generations, whereas spatial differences will have accumulated over many generations. This
425 conclusion is further supported by earlier fine-scale analysis at the Scott Reef and Rowley Shoals
426 systems that showed most *S. hystrix* larvae disperse over distances of hundreds of metres
427 (Underwood *et al.* 2007, 2009). More importantly however, we provide the first temporal evidence
428 that self-recruitment drives population persistence, and that spatial genetic structure measured at a
429 single point in time is not ephemeral in corals.

430 Underlying the relative temporal stability in spatial structure brought about by the dominance of self-
431 recruitment, our results show that genetic structure and diversity within the Scott Reef system are

also influenced by environment and disturbance history. The amount of genetic diversity across the Scott Reef system significantly changed through time following periods of impact and recovery from disturbances, particularly the mass-bleaching in 1998. There was a short and relatively small increase in gene diversity from 2004 to 2009, when coral cover remained low across the reef system, after which the system-wide gene diversity declined to the lowest levels in 2014, following a rapid increase in coral cover and the recovery of the reef system (Gilmour *et al.* 2013, Figure 4C and Figure 5). Furthermore, there was an indication of lower diversity within sites and temporal collections that had higher coral cover, although this relationship at the individual site level was clearly influenced by many undetermined factors (Figure S9B). Such a pattern is consistent with the hypothesis that the severe disturbance opened up large areas of substrata with a range of suitable environmental conditions, which were colonised by an unusually high proportion of immigrant larvae relative to self-recruits. As the coral cover increased and the available substrata decreased, the best adapted colonies and the proliferation of locally produced larvae then excluded immigrants, resulting in increased local differentiation and reduced genetic diversity. Congruently, an earlier study of *S. hystrix* at Scott Reef suggested that spatial differences in disturbance among sites in 2004 influenced long-distance dispersal patterns, with least disturbed sites providing the sources, and most disturbed sites providing the sinks for longer distance migrants (Underwood *et al.* 2007). Beyond the overriding effects of the mass-bleaching, we also show that wave exposure influenced genetic structure and diversity, with more exposed sites characterised by fewer corals from the 'sheltered lineage', greater local differentiation and reduced genetic diversity (Figure 6). This result suggests that local hydrodynamics also play a role in distribution of genetic diversity, whereby exposed sites exchange fewer migrants or only need to respond to relatively small environmental fluctuations, compared with sheltered sites.

The exceptions to the general temporal stability in spatial structure at the Scott Reef system highlights the eco-evolutionary interactions between disturbance, environment and genetic connectivity. At one site (SL1), the relative abundance of lineages changed over a five-years after

458 2009, with a switch from a population dominated by the 'sheltered' lineage to one dominated by the
459 'exposed' lineage. This switch was linked to the slow recovery of *S. hystrix* at the site, which had not
460 commenced until more than 15 years after the mass-bleaching (Figure 5). The site is located within
461 an eddy system at the eastern flank of south Scott Reef, and we hypothesis that its recovery was
462 facilitated by the infrequent supply of migrant larvae, sourced from adjacent exposed reef sites that
463 were either not severely affected by the mass-bleaching (e.g. SL4) or which had recovered rapidly
464 after 2005 (e.g. SS1; Figure 5). Once these migrant larvae had established, then they proliferated
465 locally and were responsible for the switch in lineage abundance. Among all the sheltered sites, SL1
466 has the highest wave exposure, further suggesting the likely recovery of it population to be facilitated
467 by the migrant larvae originating from both exposed populations. This hypothesis is well supported
468 by earlier assignment tests (Underwood *et al.* 2007). Irrespective of the precise origin of recruits, our
469 investigation shows that disturbances and subsequent recovery have not only facilitated shifts in the
470 relative abundance of different lineages, but have also been accompanied by the maintenance of high
471 levels of genetic diversity in the form of distinct lineages and heterozygosity (relative to the GBR and
472 inshore northwest Australia) across the Scott Reef metapopulation.

473 The differences among all three sympatric lineages persisted over ten years and several generations,
474 despite occasional connectivity among, and admixture within, some sites. These differences were
475 large, occurring across all microsatellite loci; G''_{ST} among lineages ranged from 0.185 to 0.942 at each
476 locus (data not shown). Although further exploration is required to elucidate whether this
477 divergence originated in allopatry, parapatry or sympatry, these patterns do mirror findings from
478 studies elsewhere that propose a role of localised adaptation in structuring coral populations.
479 *Seriatopora hystrix* has a recognised propensity for physiological adaptation to habitat (Bongaerts *et al.*
480 2011; Pantos *et al.* 2015), and this likely underpins the divergence into the putative species groups
481 observed on the GBR (Warner *et al.* 2015). Here, the two lineages endemic to the Scott Reef system
482 each dominated sites with different levels of wave exposure, and this association was accompanied by
483 correlations between exposure and site-specific levels of genetic differentiation and diversity; also

484 indicating an important role of ecological diversification in northwest Australia in which particular
485 genotypes are better adapted to sheltered or exposed conditions. Flushing of reef waters driven by
486 waves, tides and wind forcing often reduce temperature fluctuations and thus strongly influence coral
487 survival (Lowe & Falter 2015; Shedrawi *et al.* 2017), and is the most plausible mechanism creating
488 strong selective pressures. Corals that inhabit variable thermal environments exhibit greater thermal
489 tolerance than corals that have evolved in stable environments (Thomas *et al.* 2017), and these
490 differences are often heritable and can occur either among inshore and offshore habitats (Kenkel &
491 Matz 2016), or at local scales due to habitat variability within the same reef (Schoepf *et al.* 2015).
492 Habitat also appears to influence the composition of the symbiotic microbiome living within the coral
493 host (Bongaerts *et al.* 2011; Pantos *et al.* 2015; Sinniger *et al.* 2017). In particular, microbes living in
494 colonies from thermally variable or relatively warm environments may well confer heat tolerance
495 (Howells *et al.* 2012; Ziegler *et al.* 2017). Such ecological selection at the level of the holobiont likely
496 influences the genotypic structure of the host (Torda *et al.* 2017). Differentiation between lineages
497 may also be linked to differences in the timing of gametogenesis and planulation caused by differences
498 among sites in water temperature (e.g. Crowder *et al.* 2017; Crowder *et al.* 2014; Prasetia *et al.*
499 2017). Finally, the differentiation among *S. hystrix* lineages now living in sympatry is likely maintained
500 not only by extrinsic barriers (either geographic isolation, ecological diversification, or reproductive
501 timing), but also by intrinsic barriers such as pre- or post-zygotic incompatibilities (Bierne *et al.* 2011;
502 Kulmuni & Westram 2017).

503 *Conclusions*

504 Managing the evolutionary resilience of corals requires preserving the potential for future adaptation
505 and establishment of nascent species (Huang & Roy 2015). Our multidisciplinary study revealed that
506 although the evolutionary forces acting on *S. hystrix* on either side of the Australian continent are
507 independent, some commonalities exist. Specifically, the differentiation among putative species
508 observed on the GBR appears to be present, but less advanced, within the Scott Reef system. Our
509 study also showed that local genetic structure was relatively stable at the Scott Reef system, with the

major exception of a single site where almost complete genetic turn-over from the 'sheltered' to 'exposed' lineages was apparent in the decade following a severe bleaching event. Further, we showed the amount of genetic diversity within most populations in northwest Australia in the form of divergent lineages and high heterozygosity's is equivalent to the geographically continuous GBR (Figure S2B). This suggests that neither geographic isolation nor disturbance history has compromised standing stock of genetic diversity in northwest Australia in this species. These results not only highlight the importance of self-recruitment for the maintenance of these geographically isolated populations, but also that occasional longer distance connectivity redistributes genetic diversity across the metapopulation and facilitates persistence of local populations across spatially and temporally variable environments. Our multidimensional research provides a foundation for further long-term genetic monitoring to inform conservation strategies of coral reefs and highlights that sampling scales, ecological effects and cryptic diversity are important considerations to develop understanding of the evolutionary resilience of corals and their capacity to adapt to climate change. However, the effects on genetic diversity of sustained reductions in population sizes and altered connectivity patterns resulting from more severe and frequent coral bleaching and cyclones in the coming decades remains to be determined.

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Data accessibility

All data has been lodged in Dryad Digital Repository (doi:10.5061/dryad.8bk0rf3) and available via the following link: https://apac01.safelinks.protection.outlook.com/?url=https%3A%2F%2Fdoi.org%2F10.5061%2Fdryad.8bk0rf3&data=02%7C01%7Cj.underwood%40aims.gov.au%7C80bf19ccc2a944c5906008d574acb710%7Ce054a73b40dc4ae39fce60c537aa6fac%7C0%7C1%7C636543207519264205&sdata=YmrlP8ReZnUiD6%2Bs1PRiih4Y9OVuIu6LNba%2B5sR6RpY%3D&reserved=0

- DNA sequences: GenBank Accession Numbers for mitochondrial DNA haplotypes for new northwest Australia samples given in Table S1 and Dryad submission (FILE: Underwood_hystrix@NWA_DRYAD-DATA_mtDNA-haplotypes).
- Microsatellite genotypes: dryad master table of all northwest Australian *S. hystrix* genets with site name and microsatellite genotypes in GenAlEx format and including membership coefficients from the tertiary clustering analysis in STRUCTURE (FILE: Underwood_hystrix@NWA_DRYAD-DATA_genotypes)
- Coral cover data: dryad master table detailing data on % percentage coral cover of Seriatopora corals at each site at Scott Reef (FILE: Underwood_hystrix@NWA_DRYAD-DATA_coral-cover).
- Site coordinates: dryad master table detailing latitude and longitude in decimal degrees of each site, region, system and Reef of *S. hystrix* collections (FILE: Underwood_hystrix@NWA_DRYAD-DATA_site-coords).

Author contributions

- JU, JG, ZR and KM were all involved in design of research
- JU, JG ZR collected and curated genetic samples in the field and lab
- JU analysed the microsatellite genetic data, ZR analysed the mtDNA data, JG analysed the coral cover data, and MP analysed the wave exposure data
- All authors made substantial contributions to the writing and of the manuscript

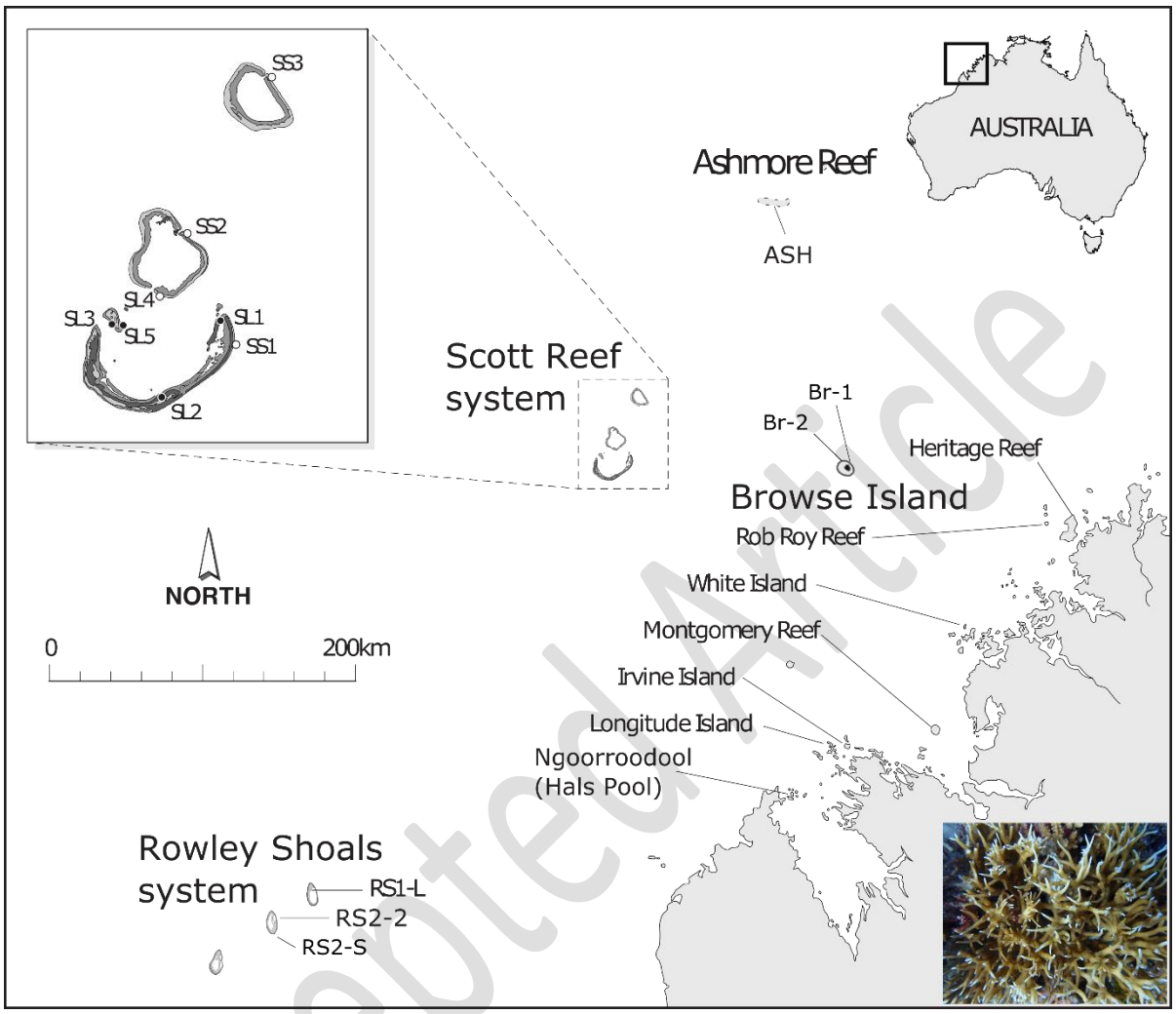
816 # TABLES

817 Table 1 Pairwise F_{ST} (above diagonal) and G''_{ST} (below diagonal) between the *S. hystrix* lineages defined by
818 STRUCTURE from the Scott Reef and Ashmore Reef systems for colonies with q > 0.70 to one of four
819 lineages.

	Scott (sheltered)	**Scott (exposed)**	**Scott (ashmore)**	**Ashmore**
Scott (sheltered)	-	0.076	0.101	0.115
Scott (exposed)	0.257	-	0.188	0.182
Scott (ashmore)	0.387	0.556	-	0.065
Ashmore	0.423	0.526	0.221	-

820

821 FIGURES



822

823 Figure 1. Map of genetic sampling sites of *S. hystrix* in northwest Australia, showing sites sampled from the
824 offshore region from Ashmore Reef, Browse Island and the systems of Scott Reef and Rowley Shoals, and from
825 the inshore region of the Kimberley. Top left inset shows the local-scale sites at the Scott Reef system which
826 were sampled in 2004, 2009 and/or 2014 (for details of spatial and temporal collections see Table S3 and Table
827 S4). Sites with solid symbols are more sheltered than sites with exposed symbols (but see also Figure 5).
828 Bottom right inset picture shows typical *S. hystrix* morphology in northwest Australia.

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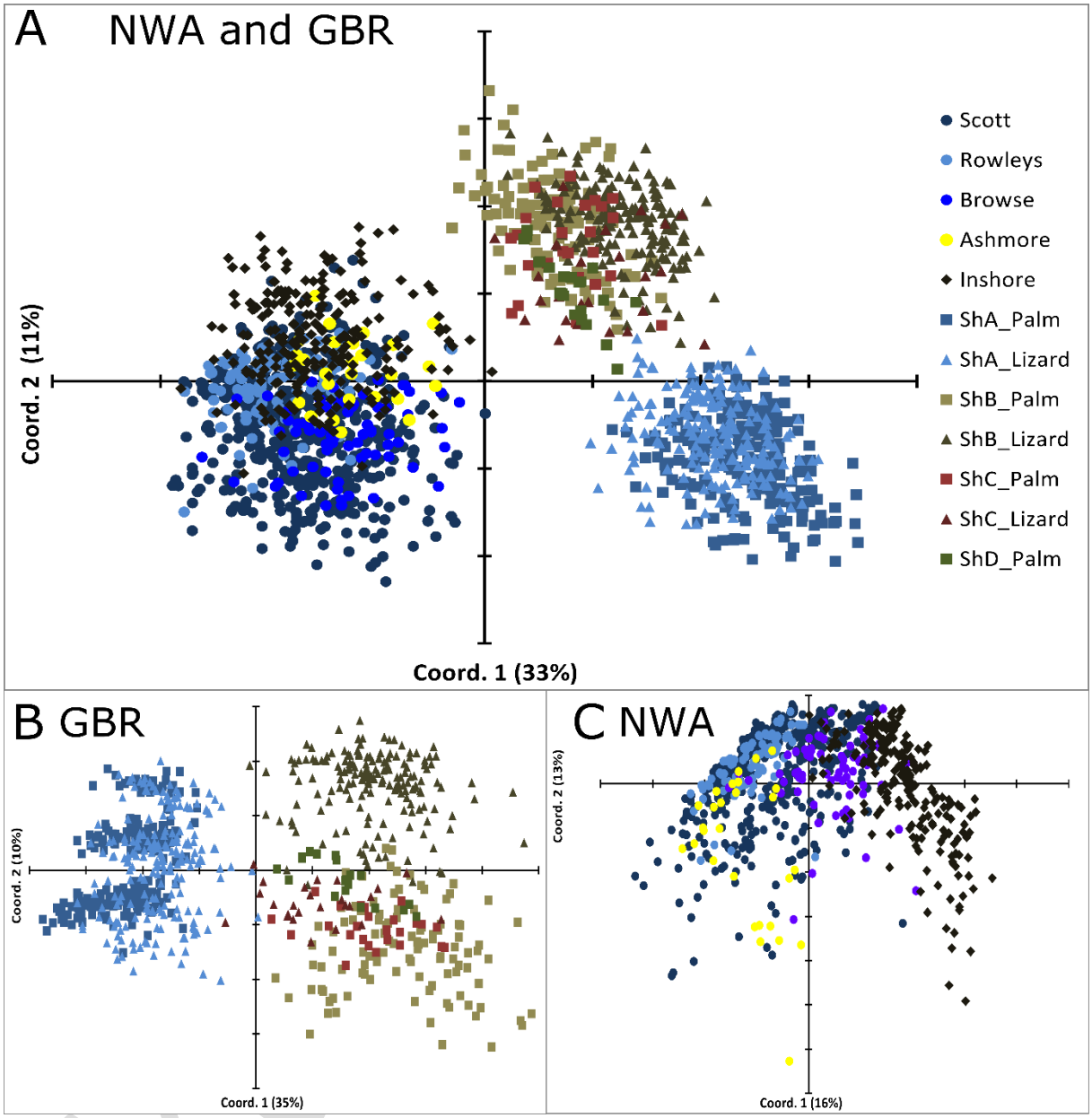
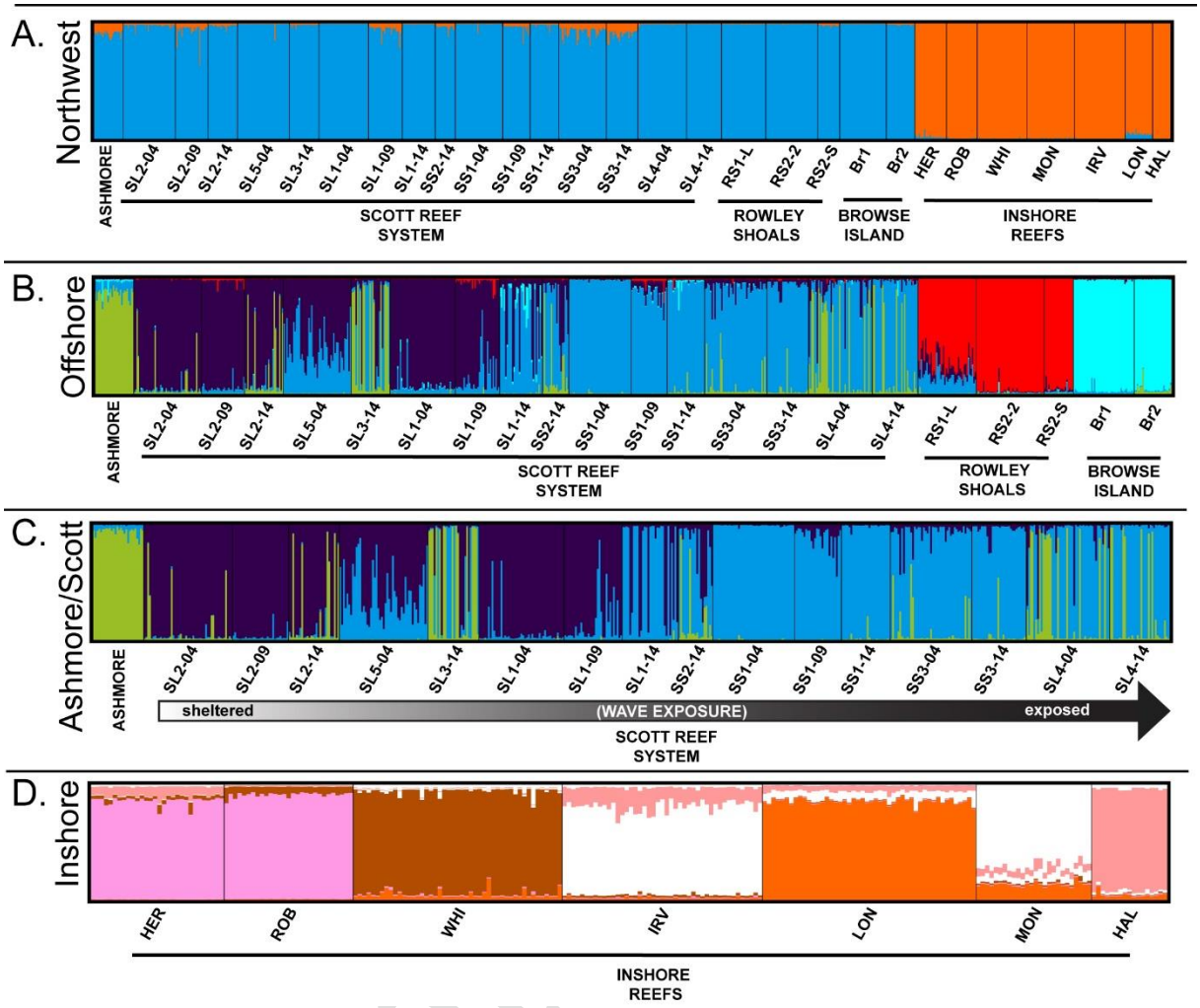


Figure 2. PCoA illustrating genetic relationships from microsatellite genotypes of *S. hystrix* colonies sampled from the Great Barrier Reef (Palm Island and Lizard Island reefs), and from northwest Australia (the Scott Reef and Rowley Shoals systems, Browse Island, Ashmore Reef and the inshore Kimberley; see Figure 1 for map). Panel A shows the combined data set, Panel B shows the Great Barrier Reef samples only, and Panel C shows the northwest Australia samples only. Symbols are colour-coded according to geographic location of samples in northwest Australia, and by the putative species groups identified by Warner *et al.* (2015) on the Great Barrier Reef; ShA occurred in sheltered habitats, while ShB, ShC, and ShD occurred in exposed habitats. Percentage variation explained by each axis is given in brackets on axis labels.



840

841 Figure 3. Barplots from STRUCTURE clustering analyses with the LOCPRIOR model for *S. hystrix* corals from
842 each site and temporal collection from northwest Australia. Each coloured bar represents the statistical
843 assignment (q value) of each individual to a particular cluster. Panel A: results from analysis of entire data set
844 for *K* = 2 (CLUMPAK similarity score of 0.993 among major modes from 7/10 runs) showing the inshore and
845 offshore clusters. Panel B: results from analysis of offshore subset of data for *K* = 5 (CLUMPAK similarity score
846 of 0.973 from 9/10 runs). Panel C: results from analysis of the Ashmore Reef and Scott Reef subset of data for
847 *K* = 3 (CLUMPAK similarity score of 0.970 from 10/10 runs) with sites from the Scott Reef system shown in
848 increasing order of exposure from left to right. Panel D: results from analysis of the inshore subset of data for
849 *K* = 6 (CLUMPAK similarity score of 0.929 from 10/10 runs).

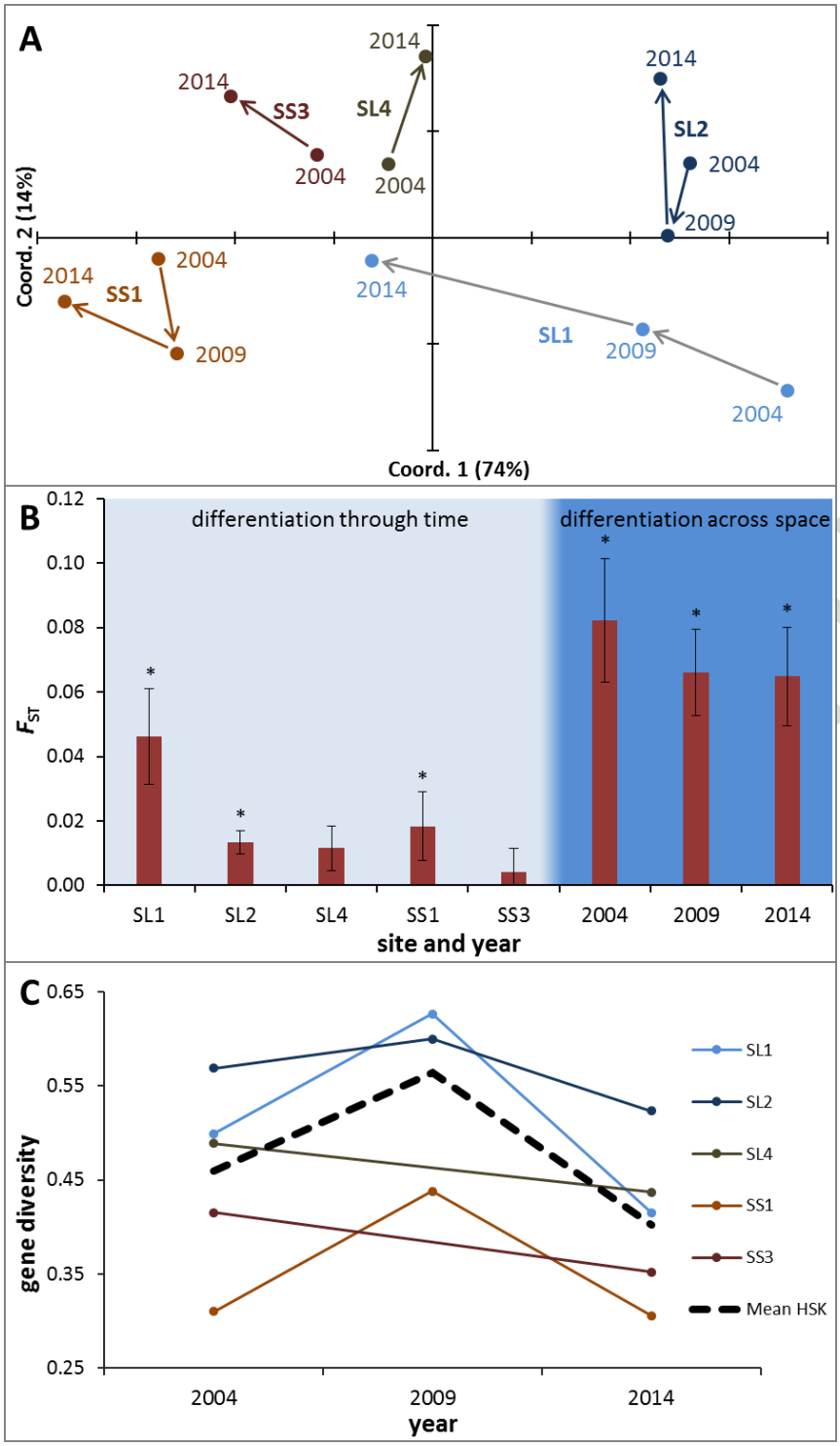
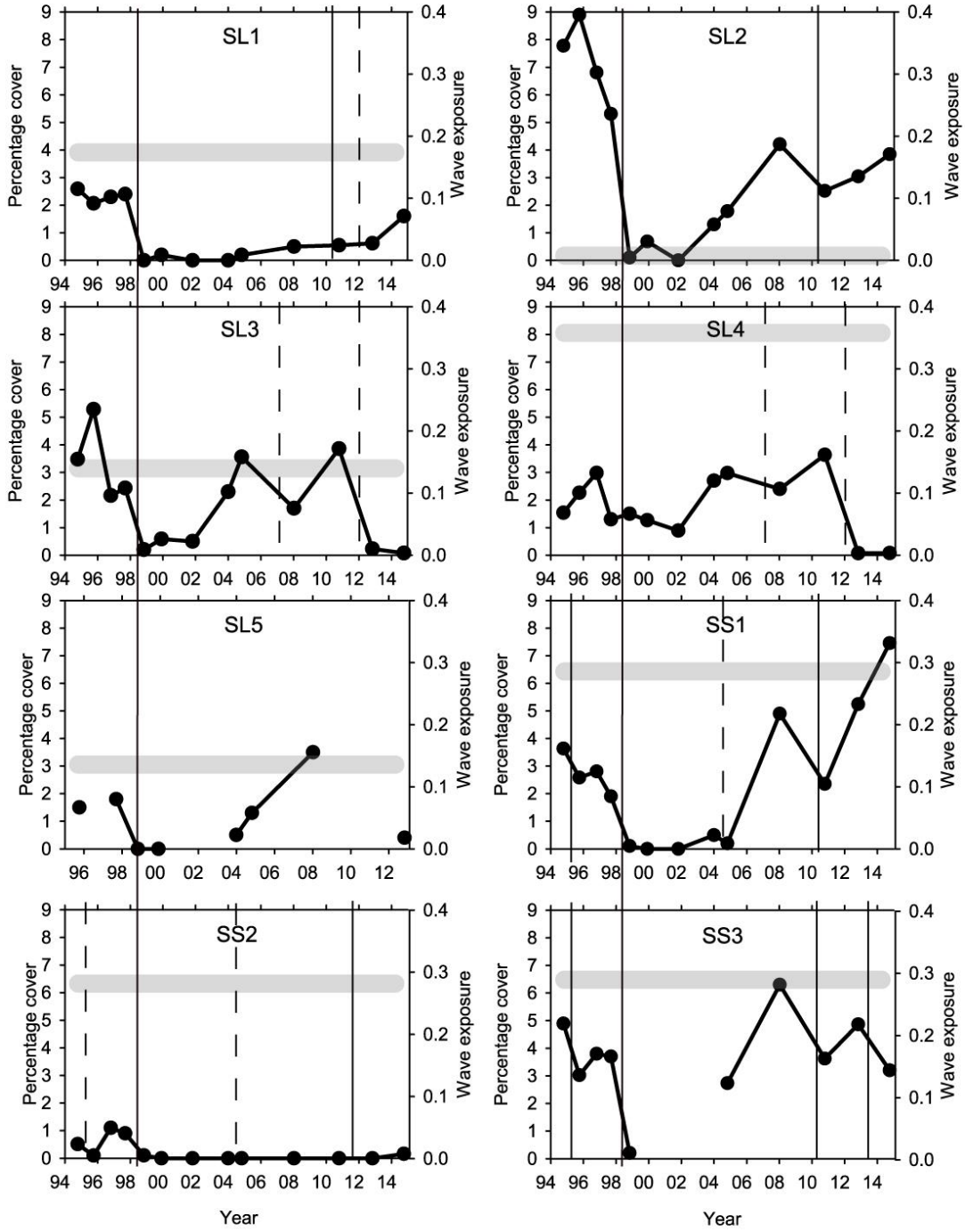
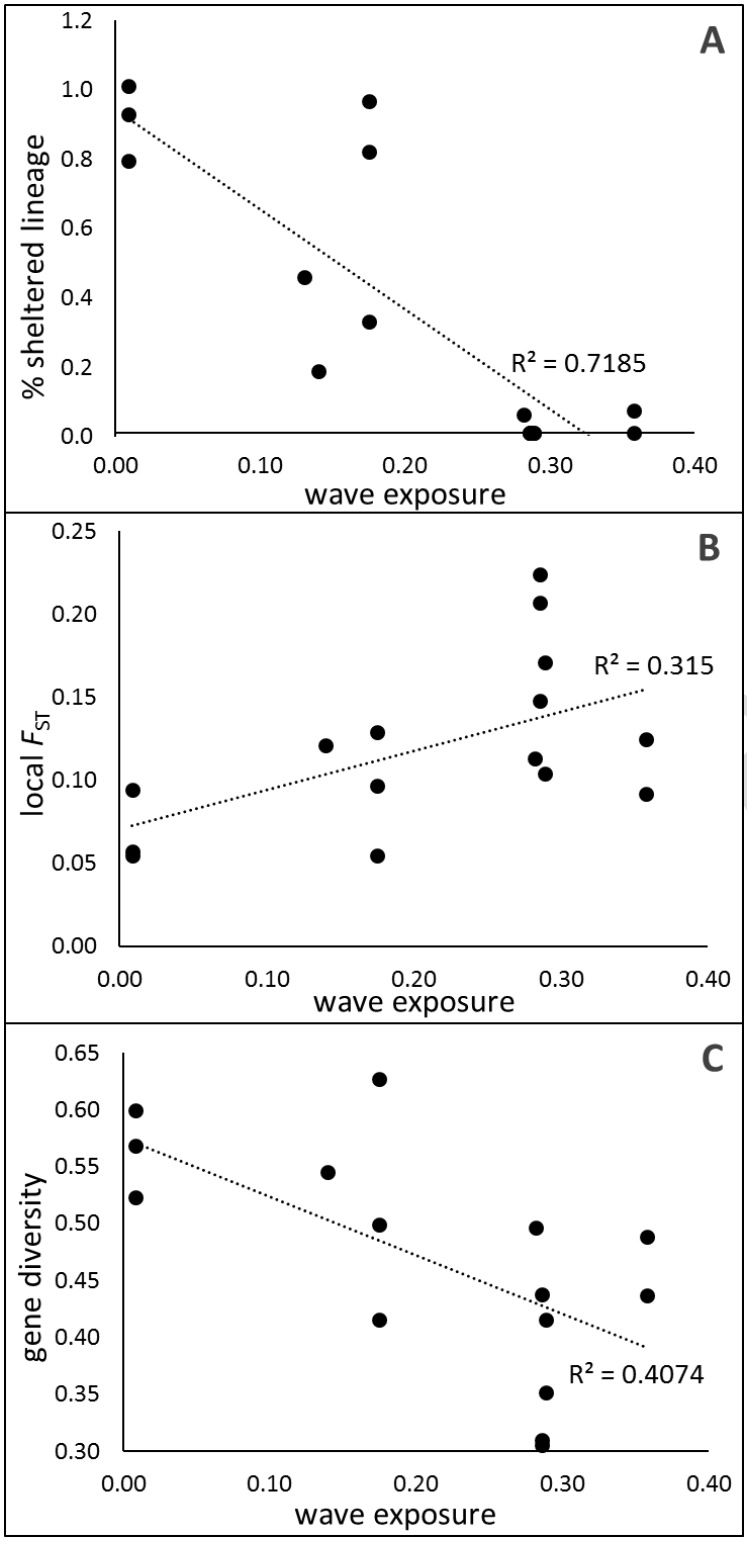


Figure 4. Spatio-temporal change in genetic structure and diversity for *S. hystrix* sampled from Scott Reef sites in 2004, 2009 and 2014. A: Principal Coordinates Analysis of pairwise genetic distances calculated with F_{ST} among sites and temporal collections. Arrows show direction of change in genetic composition between years. The percentage variation explained by each axis is given in brackets. B: Genetic differentiation calculated with F_{ST} among temporal collections at each site (light blue background) and across sites within each temporal collection (dark blue background). Error bars indicate ± *SE* calculated across loci, stars indicate significant differentiation adjusted with sequential Bonferroni correction for multiple tests when P< 0.05. C: Gene diversity (H_{SK}) at each site and time and averaged across each site at each time (mean H_{SK}).



859

860 Figure 5. Percentage cover (black line, primary y-axis) of *Seriatopora* at the Scott Reef system from 1994 to
861 2014. Major disturbance events are shown with vertical lines, including the severe bleaching in 1998 and a
862 milder bleaching in 2010 (solid lines), and cyclones in 2005, 2007 and 2012 (dashed line) which most adversely
863 affected SL4 and SL3. Normalised relative wave exposure based on wave directions and mean wave heights
864 from Wave Watch III data (NOAA – see text) from 2010-2017 at each site is also given (grey line, secondary y-
865 axis).



866

867 Figure 6. The correlation between local genetic composition and diversity of *Seriatopora hystrix* and wave
868 exposure at each site of the Scott Reef system. Plots show the linear regression of percentage membership to
869 the STRUCTURE-defined sheltered lineage with wave exposure (A), local F_{ST} with wave exposure (B), and
870 gene diversity (H_{SK}) with wave exposure (C).