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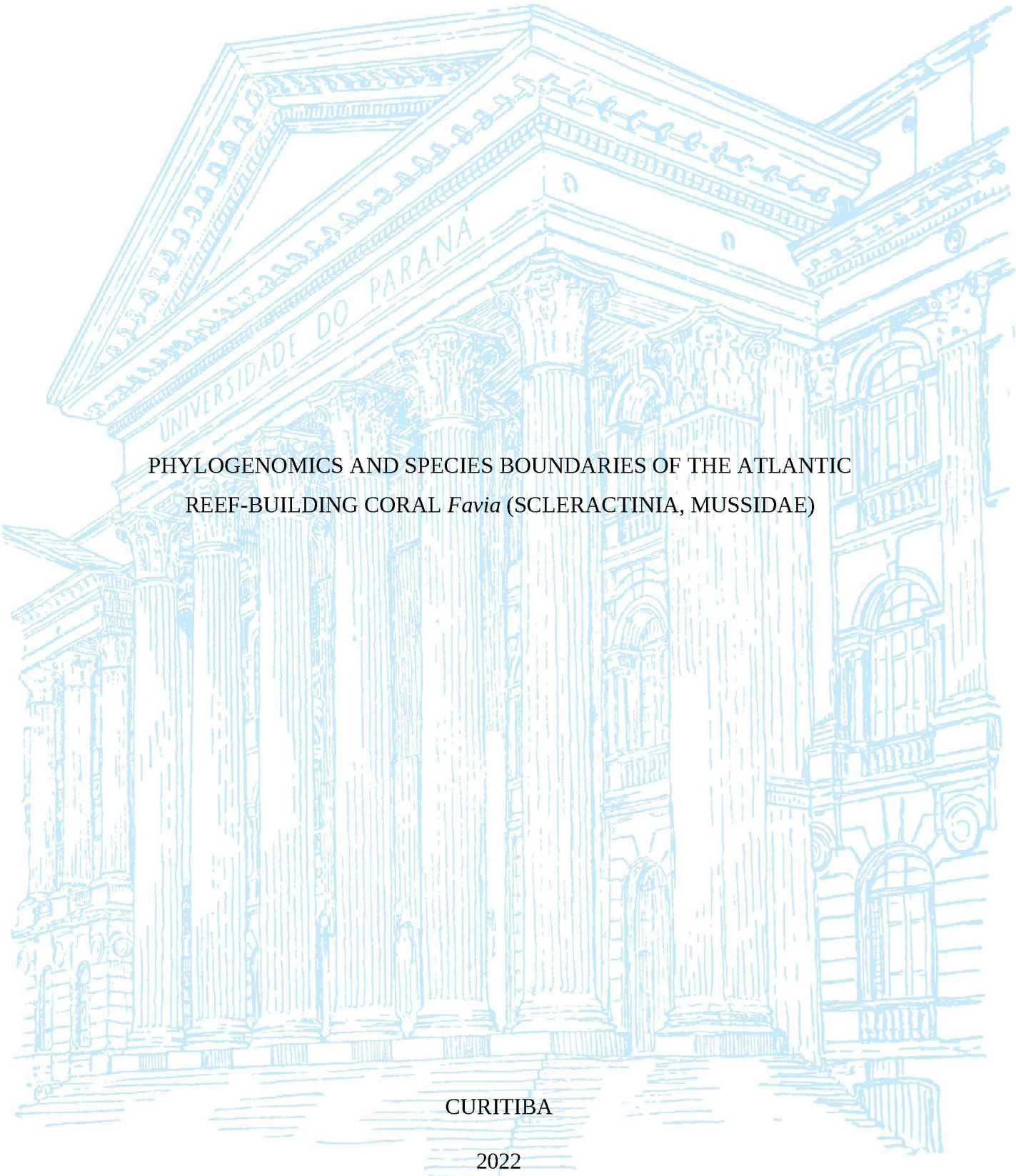

PHYLOGENOMICS AND SPECIES BOUNDARIES OF THE ATLANTIC REEF-BUILDING CORAL *Favia* (SCLERACTINIA, MUSSIDAE)

CURITIBA

2022

CAROLINA DE LIMA ADAM

PHYLOGENOMICS AND SPECIES BOUNDARIES OF THE ATLANTIC REEF-BUILDING CORAL *FAVIA* (SCLERACTINIA, MUSSIDAE)

Tese submetida ao curso de Pós-Graduação em Zoologia, Setor de Ciências Biológicas, Universidade Federal do Paraná para obtenção do grau de Doutora em Zoologia

Orientador: Prof. Dr. Marcos Soares Barbeitos

CURITIBA

2022

DADOS INTERNACIONAIS DE CATALOGAÇÃO NA PUBLICAÇÃO (CIP)
UNIVERSIDADE FEDERAL DO PARANÁ
SISTEMA DE BIBLIOTECAS – BIBLIOTECA DE CIÊNCIAS BIOLÓGICAS

Adam, Carolina de Lima
Phylogenomics and species boundaries of the atlantic reef-building coral *Favia* (Scleractina, Mussiidae) / Carolina de Lima Adam. – Curitiba, 2022.
1 recurso on-line : PDF.

Tese (Doutorado) – Universidade Federal do Paraná, Setor de Ciências Biológicas, Programa de Pós-Graduação em Zoologia.
Orientador: Prof. Dr. Marcos Soares Barbeitos.

1. Recifes e ilhas de coral. 2. Variação genética. 3. Ecologia dos recifes de coral. I. Barbeitos, Marcos Soares, 1975-. II. Universidade Federal do Paraná. Setor de Ciências Biológicas. Programa de Pós-Graduação em Zoologia. III. Título.

Bibliotecária: Giana Mara Seniski Silva CRB-9/1406

TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação ZOOLOGIA da Universidade Federal do Paraná foram convocados para realizar a arguição da tese de Doutorado de **CAROLINA DE LIMA ADAM** intitulada: **PHYLOGENOMICS AND SPECIES BOUNDARIES OF THE ATLANTIC REEF-BUILDING CORAL *Favia* (SCLERACTINIA, MUSSIDAE)**, que após terem inquirido a aluna e realizada a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de doutora está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

CURITIBA, 31 de Janeiro de 2022.

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Agradecimentos

Agradeço ao meu orientador, Dr. Marcos Soares Barbeitos, por aceitar me orientar e me receber no LEOM de braços abertos. A fama de mestre mal humorado e exigente é real, mas as portas (e o *inbox*) sempre estiveram abertas pra receber seus padawans. Obrigada por estender a mão pra uma *noob* que mal sabia o que era uma linha de comando, confiar nela e acreditar que seria capaz. Agradeço também a todos os colegas do LEOM, especialmente Ana e Julian, que dividiram esse projeto desafiador junto comigo. Juli, obrigada por todos os litros de café compartilhados enquanto discutíamos artigos e desvendávamos novas análises.

Agradeço à Coordenação de Aperfeiçoamento de Pessoal de Ensino Superior (CAPES) pela bolsa de doutorado e ao seu Programa de Internacionalização (PRINT) pela bolsa de doutoramento sanduíche. À Universidade Federal do Paraná, ao Programa de Pós-Graduação em Zoologia da UFPR e a todos os professores que fizeram parte da minha formação durante estes dois anos de mestrado e quase cinco anos de doutorado. Agradeço também aos técnicos e funcionários terceirizados do Departamento, que sempre foram solícitos e dispostos a ajudar. Especialmente, agradeço ao "Seu Luiz" pelo carinho diário e o sorriso fácil que nos recebia todos os dias. Você nos deixou cedo demais.

Ao meu comitê de acompanhamento, Dra. Carla Zilberberg, Dr. David Carlon e Dr. Eduardo Carneiro. Obrigada pelas discussões produtivas e sugestões tão essenciais. Vocês foram o norte necessário para me guiar durante todo esse processo. Em especial ao Dave, agradeço por ter sido a ponte que me levou até o ToBo e garantiu a finalização desta tese.

Agradeço ao Dr. Robert Toonen por ter aceitado me orientar durante o estágio sanduíche e aos colegas do ToBo Lab por terem me recebido com tanto carinho desde o primeiro dia, em especial 'A'lea, Derek, Leah e Paolo. Trabalhar em um ambiente tão diverso, acolhedor e cientificamente produtivo foi uma das melhores experiências que tive no doutorado.

Agradeço à companhia de todas as mulheres do "Time to Work" durante esta pandemia. Obrigada por estarem virtualmente presentes tanto nos dias em que o trabalho era feito por amor quanto nos dias em que era feito na força do ódio! É um prazer fazer parte de um grupo de mulheres cientistas tão resilientes e companheiras.

Agradeço à todas as pessoas que foram o suporte emocional necessário que me auxiliou a chegar aqui. À minha familinha curitibana, Mari, Eder, Steh, Pedro, Julian e Thay por compartilharem boas risadas, cervejas e conversas agradáveis, tornando a vida mais leve. Agradeço especialmente ao Sean pelo companheirismo durante minha estadia em terras

havaianas, por ter aceitado explorar a ilha ao meu lado e por ter se mantido tão presente mesmo estando milhares de quilômetros distante daqui. Mahalo nui loa!

Ao Pedro, agradeço por ter estado ao meu lado durante todo esse processo e me carregado (as vezes literalmente!) durante todos os momentos difíceis e desafiadores. Obrigada pelas as longas conversas, sejam elas científicas, políticas, amorosas ou até mesmo pra passar horas discutindo sobre quais produtos podem ser considerados sorvete. Você e a Lola foram os melhores *housemates* que eu poderia ter. Agradeço também ao Muris, por ter sido um amigo de tanta confiança e um exemplo tão valioso do que é ser um cientista. Que nossa *brotheragem* viva por muitos anos dentro e fora da academia, e que um dia a gente possa viver o sonho de fazer pesquisa, cultivar cogus, produzir cerveja e ter um bar de bêbado.

Finalmente, agradeço aos meus pais, Gisele e Ivan, por terem me dado suporte incondicional durante todos esses anos. Vocês me criaram num ambiente de muito carinho, estímulo e companheirismo. Apesar de me darem muita liberdade, sempre mostraram na prática a importância de trabalhar muito e dedicar 100% de si ao que faz. Vocês me mostraram que coragem não é ausência de medo, mas o ato de levantar a cabeça frente aos desafios e ir com medo mesmo!

“Do the best you can until you know better. Then when you know better, do better.”

Maya Angelou

RESUMO

Corais escleractíneos são os principais engenheiros de um dos ecossistemas mais diversos do planeta, os recifes de coral. Estas espécies são sensíveis às variações ambientais e estão diretamente ameaçadas por impactos antrópicos locais, sobrepesca, poluição e doenças, cujos efeitos são intensificados pela pressão gerada pelas mudanças climáticas. Para reverter os efeitos negativos destes estresses ambientais é essencial identificar as unidades taxonômicas que constituem o ecossistema recifal e compreender de forma completa suas dinâmicas populacionais, fornecendo conhecimento básico para a elaboração de planos de conservação efetivos. Nesta tese, nós utilizamos polimorfismos de nucleotídeo único (da sigla em inglês SNPs) obtidos a partir da técnica ezRAD, baseada em representação reduzida do genoma (da sigla em ingles RADseq) para responder a estas questões a respeito do coral do gênero *Favia* do Atlântico. No Capítulo I nós avaliamos os limites taxonômicos entre duas espécies de coral de águas rasas distribuídas ao longo das Províncias Caribenha, Brasileira e meio-Atlântica, *Favia fragum* e *F. gravida*, utilizando um total de 19,648 SNPs. Recuperamos topologias conflitantes utilizando reconstruções baseadas em concatenação e coalescência. Análises de máxima verossimilhança utilizando SNPs concatenados fornecem posicionamentos alternativos para *F. fragum* em relação à *F. gravida* do Brasil e Ilha de Ascenção, na Província Meio-Atlântica, dependendo da estratégia de filtragem e do número de sítios parcimoniosamente informativos utilizados, o que atribuímos à segregação incompleta de linhagens. Análises baseadas em coalescência forneceram estimativas mais consistentes, recuperando *F. gravida* do Brasil como grupo irmão de *F. fragum* do Caribe, sendo a Ilha de Ascenção o clado mais basal, resultando em *F. gravida* como parafilética em relação à segunda espécie. No Capítulo II nós avaliamos a estrutura populacional, recuperando quatro agrupamentos genéticos principais independente do nível de dados faltantes: *F. fragum* do Caribe, *F. gravida* da Ilha de Ascenção e duas populações de *F. gravida* no Brasil, dividindo a costa em população Norte e Sul. AMOVA revelou variação genética entre Caribe, Brasil e Ascenção, com diferenças significativas também obtidas entre populações dentro destas províncias. Apesar dos loci se mostrarem regionalmente bem definidos, todas as populações mostraram sinais de introgressão gênica com outras populações. Análise de estruturação hierárquica revelou resolução adicional ao longo da costa brasileira e filtragem menos restritiva recuperou subpopulações geograficamente coerentes dentro dos grupos principais. Estas subpopulações também formaram clados bem suportados em nossas reconstruções filogenéticas. No Brasil, a riqueza alélica se mostrou mais alta na população sul, a qual contém o Banco de Abrolhos, uma estrutura recifal que possivelmente serviu como refúgio

para corais escleractíneos durante o último máximo glacial. Em um período de transgressões e regressões oceânicas, o banco manteve, hipoteticamente, sua diversidade e talvez tenha posteriormente recolonizado outras populações. Nossos resultados revelaram três linhagens bem definidas em *Favia* do Atlântico, demonstrando a necessidade de reavaliação da única espécie atualmente reconhecida pela Lista Vermelha da IUCN. Também identificamos estruturação genética significativa dentro da linhagem brasileira, recuperando de forma consistente nossos locais de coleta em clados bem suportados e como agrupamentos bem definidos de acordo com coeficientes ancestrais. Apesar de forte estruturação geográfica, as populações mostraram sinais de fluxo gênico, sendo que algumas delas podem ter servido como fontes de diversidade genética no passado.

Palavras-chave: corais escleractíneos, SNP, coalescência, estruturação genética, segregação incompleta de linhagens, introgressão gênica

ABSTRACT

Scleractinian corals are the main builders of one of the most diverse ecosystems in the world, the coral reefs. These species are sensitive to environmental variation and directly threatened by disease, local anthropic impact climate change. To reverse the negative effects of global warming, it is essential to identify the taxonomic units that make up the reef ecosystem and fully understand their population dynamics, which provide basic knowledge for effective conservation plans. In this dissertation, we employed single nucleotide polymorphisms (SNPs) discovered via ezRAD, a flavor of reduced representations sequencing (RADseq) strategy, to assess these questions regarding the Atlantic stony coral *Favia*. In the First Chapter, we evaluated the taxonomic boundaries between too broadly distributed species, *Favia fragum* and *F. gravida*, using up to 19,648 SNPs. We recovered conflicting topologies based on concatenation and coalescent-based reconstructions. Maximum likelihood analysis of concatenated SNPs provided alternative placements of *F. fragum* in respect to *F. gravida* from Brazil and Ascension Island depending on the filtering strategy and number of parsimony informative sites (PIS) used, which we attributed to incomplete lineage sorting (ILS). Coalescent-based analysis provided more consistent estimates, recovering the Brazilian *F. gravida* as sister to Caribbean *F. fragum*, and the Ascension Island *F. gravida* as the most basal lineage, rendering *F. gravida* paraphyletic. In the Second Chapter, we assessed the population structuring of the genus. We recovered four main genetic clusters regardless of varying levels of missing data: *F. fragum* from the Caribbean, *F. gravida* from Ascension Island, and two populations from the Brazilian *F. gravida*, diving the coast into Northeast and East populations. AMOVA revealed genetic variation among the Caribbean, Brazil, and Ascension, with significant differences observed in all analyzed geographic scales. Although the loci are regionally well-defined, all populations showed signs of admixture. Hierarchical structuring analysis provided further resolution within the Brazilian coast and allowing loci with more missing data recovered geographically coherent subpopulations nested within the main groups, and these subpopulations formed well-supported clades in our phylogenetic reconstructions. Within Brazil, allelic richness was higher in the East population, which contains the Abrolhos Bank, a reef structure that potentially served as a refugium for Scleractinian corals after the Last Glacial Maximum. During a period of oceanic transgressions and regressions, the bank held its range and diversity and later may have recolonized other populations. Our results revealed three well-defined lineages within the Atlantic *Favia*, calling for the re-evaluation of the current single species recognized by the IUCN's Red List. Furthermore, we identify significant genetic structure within the Brazilian

lineage, with datasets with moderate amounts of missing data consistently recovering our sampling sites in well-supported clades and as well-defined clusters based on their ancestral coefficients. Despite strong geographic structuring, the populations showed signs of genetic exchange and some populations might have served as sources of genetic diversity in the past.

Key-words: scleractinian corals, SNPs, coalescent, genetic structure, incomplete lineage sorting, admixture

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LISTA DE SIGLAS

ASC - Ascension Island / Ilha de Ascenção
BC - Brazil current / corrente do Brasil
BIC - bayesian information criterion / critério de informação bayesiana
BLAST - Basic local alignment search tool
BS - bootstrap support
CI - confidence interval / intervalo de confiança
DAPC - discriminant analysis of principal components / análise discriminante de componentes principais
ILS - incomplete lineage sorting / segregação incompleta de linhagens
LBA - long-branch attraction / atração de ramo longo
LD - linkage disequilibrium / desiquilíbrio de ligação
LL - lower limit / limite inferior
MAC - minor allele count
MAF - minor allele frequency
mtDNA - mitochondrial DNA / DNA mitocondrial
NCBC - North coastal Brazilian current / corrente norte do Brasil
PCA - principal components analysis / análise de componentes principais
PCR – polymerase chain reaction / reação em cadeia da polimerase
RADseq - restriction-site associated DNA sequecing / sequenciamento de DNA associado a sítios de restrição
sCF - site concordance factor / fator de concordância de sítios
sDF - site discordance factor / fator de discordância de sítios
SEC - South Equatorial current / corrent Sul Equatorial
sNMF - sparce non-negative matrix factorization / fatoração esparsa de matrizes não-negativas
SNP - single nucleotide polymorphism / polimorfismos de nucleotídeo único
UCE - ultraconserved elements / elementos ultraconservados
UFboot - ultrafast bootstrap support
UL - upper limit / limite superior

SUMÁRIO

Introdução geral

Os recifes de coral são grandes estruturas formadas a partir do esqueleto de corais escleractíneos, um grupo atualmente representado por mais de 1,600 espécies (Hoeksema and Cairns, 2021). Estimativas de riqueza apontam que pouco mais de 30% das espécies marinhas estão associadas ao ecossistema recifal (Fisher et al. 2015), constituindo um dos mais biodiversos do planeta. Sua alta produtividade está intimamente atrelada à simbiose que ocorre entre o coral e as zooxantelas, algas unicelulares que fornecem nutrientes ao coral na forma de produtos fotossintéticos (Hoegh-Guldberg, 1999). Também oferecem indispensáveis serviços ecológicos e retorno econômico, como proteção costeira, atividades turísticas e exploração farmacológica e pesqueira (Moberg e Folk, 1999). Infelizmente, fatores antrópicos locais e mudanças climáticas globais estão elevando a mortalidade de espécies de corais formadores de recife, essenciais para a manutenção da biodiversidade deste ecossistema (Carpenter et al. 2008; Doney et al. 2012). Com a redução da cobertura coralina, a biodiversidade que os recifes acomodam também será perdida. Com isso, os serviços ecossistêmicos prestados pelos recifes entrarão em declínio, afetando a sociedade direta e indiretamente, especialmente comunidades indígenas costeiras (Eddy et al. 2021). Para nos assegurarmos de que a totalidade dos ecossistemas recifais seja preservada, é essencial que tenhamos uma boa compreensão de suas dinâmicas populacionais e história demográfica. A conectividade genética, em especial, tem um papel central na resiliência das populações (Van Oppen e Gates, 2006). Portanto, entender os padrões de conectividade ao longo da distribuição de uma espécie é fundamental para identificar quais populações precisam ser priorizadas, a fim de elaborar planos de manejo eficientes que contemplem a continuidade dos processos ecossistêmicos (Margules e Pressey, 2000; Cowen e Sponaugle, 2009).

Ademais, é necessário entendermos também as relações evolutivas entre os organismos que compõe os recifes. O conceito de espécie é um tema de acalorado debate na comunidade científica, especialmente dada a existência de diferentes definições de espécie que frequentemente apresentam incompatibilidades conceituais (de Queiroz, 2007). Isso leva ao questionamento de que, em última análise, delimitar espécies é uma decisão muito mais filosófica do que prática (Zachos, 2018). Porém, a descrição de unidades taxonômicas delimitadas permanece necessária para a implementação de planos de conservação (Agapow et al. 2004; Mace, 2004), tornando a delimitação de espécies uma necessidade. Dentre os cerca de 24 diferentes conceitos de espécie (de Queiroz, 2007) algumas definições guarda-chuva são amplamente utilizadas: conceito biológico, definido como populações naturais de indivíduos que se reproduzem entre si e são reprodutivamente isolados de outras

populações naturais (Mayr, 1942; Dobzhansky, 1970); conceito ecológico, que considera grupos de indivíduos ocupando uma zona adaptativa que evoluem de maneira independente de outros grupos de indivíduos fora desta zona (van Valen, 1976); e conceito filogenético, que leva em consideração a monofilia recíproca entre diferentes grupos de indivíduos (Donoghue, 1985). Todos estes conceitos apresentam incongruências associadas, como a possível permeabilidade de algumas barreiras reprodutivas ao fluxo gêncio e o fato de que o processo de especiação pode ocorrer mesmo na presença de fluxo gênico (Feder, Egan e Nosil, 2012; Harrison e Larson, 2014). Como ambos fenômenos podem ocorrer em corais (Carlon e Budd, 2002; van Oppen et al. 2002; Vollmer e Palumbi, 2002), uma alternativa seria adotar um conceito unificado de espécies (de Queiroz, 2005, 2007), que incorpora uma definição mais abrangente e define espécies como metapopulações, ou parcelas de uma metapopulação, que evoluem de maneira independente.

Historicamente, a taxonomia de corais escleractíneos é fundamentada na morfologia de seus esqueletos. No entanto, corais pétreos apresentam ampla variação morfológica intraespecífica, incluindo variabilidade nos caracteres utilizados em sua identificação (Muko et al., 2000; Gittenberg e Hoeksema, 2006; Todd et al., 2008). Em alguns casos a variabilidade é observada em diferentes populações de uma mesma espécie ao longo de sua distribuição geográfica, e em outras é tão extensa que caracteres taxonomicamente relevantes divergem em uma mesma colônia (Veron, 2013). A falta de confiança na utilização destes caracteres para a identificação de corais foi comprovada a partir dos primeiros estudos utilizando marcadores moleculares, demonstrando que muitas das famílias eram na realidade parafiléticas (Fukami et al. 2004; Budd et al. 2010; Kitahara et al. 2016). O gênero *Favia*, por exemplo, compreendia espécies distribuídas ao longo do Atlântico e Indo-Pacífico. Porém, dados moleculares revelaram que favídeos do Atlântico são filogeneticamente mais próximos a espécies da família Mussidae do Atlântico do que de seus congêneres do Pacífico (Fukami et al. 2004). Estes dados levaram a uma ampla revisão taxonômica dos corais escleractíneos, separando indivíduos que anteriormente formavam a família Faviidae em duas sub-famílias: Mussinae, correspondente às espécies do Indo-Pacífico, e Faviinae, correspondente às espécies do Atlântico. O gênero *Favia* do Atlântico, portanto, é formado pela espécie-tipo *F. fragum* e sua espécie irmã *F. gravida* (Budd et al. 2012; Baron-Szabo, 2018). Apesar da ampla sobreposição de caracteres diagnósticos na macromorfologia de corais, estudos detalhados de sua micromorfologia e a utilização de microestruturas têm se mostrado altamente informativos para a taxonomia de Scleractinia (Kitahara et al. 2016). Muito progresso foi feito na determinação destes novos caracteres morfológicos, especialmente no

nível microestrutural, que apresentam menor plasticidade e corroboram os resultados moleculares, mostrando-se robustos para a diagnose ao nível de família (Budd e Stolarski, 2011; Janiszewska et al. 2011; Kitahara et al. 2013; Arrigoni et al. 2014).

Porém, as controvérsias taxonômicas se estendem além do nível de família, e *F. fragum* e *F. gravida*, por exemplo, já foram consideradas morfotipos de uma mesma espécie (Veron e Stafford-Smith, 2000). A supracitada plasticidade fenotípica presente em corais dificulta ainda mais sua identificação e ampla variabilidade morfológica já foi documentada nas duas espécies, partindo de variação entre colônias de diferentes localidades (Laborel, 1969; Amaral e Ramos, 2007) até variações morfológicas observadas em um gradiente de profundidade, que apresentaram também uma contraparte molecular revelada através de alozimas (Carlon e Budd, 2002; Figura 1). Análises filogenéticas utilizando o marcador nuclear β-tubulina não identificaram haplótipos compartilhados entre *F. fragum* e *F. gravida*, além de recuperar divergência haplotípica entre populações da costa brasileira e do Golfo da Guiné, revelando estruturação populacional (Nunes et al. 2008). Um recente estudo baseado em um marcador nuclear e um ribossomal demonstrou ampla divergência genética entre *F. fragum* e *F. gravida*, e também entre amostras de *F. gravida* do Brasil, ilhas meio-Atlânticas e Golfo da Guiné, sendo que a ilha de Ascenção se mostrou a mais divergente (Taschima et al. 2021). Este provável isolamento entre províncias não é inesperado, dada a estratégia reprodutiva empregada por ambas as espécies. *Favia fragum* e *F. gravida* são corais hermafroditas que possuem fecundação interna, incubam suas larvas e apresentam transferência vertical de suas algas endossimbiontes, liberando larvas capazes de assentarem poucas horas após sua liberação (Calderon et al. 2000; Goodbody-Gringley, 2010). Considerando que os recrutas assentam muito próximos das colônias-mãe, a dispersão destas espécies é presumivelmente muito limitada, indo de acordo com os dados moleculares (Goodbody-Gringley et al. 2010; Carlon e Lippé, 2011). Ademais, estima-se que *F. fragum* apresente altas taxas de auto-fecundação, chegando a quase 50% em colônias obtidas em Florida Keys (Brazeau et al. 1998; Carlon and Lippé, 2011), e dada a proximidade filogenética é possível que taxas similares também possam ocorrer em *F. gravida*. Altas taxas de auto-fertilização e clonalidade, outro fenômeno que também pode ocorrer em corais escleractíneos (Ayre and Hughes, 2000), podem enviesar estimativas de diversidade genética e heterozigosidade, influenciando análises de genética de populações (Charlesworth, 2003; Jullien et al. 2019).

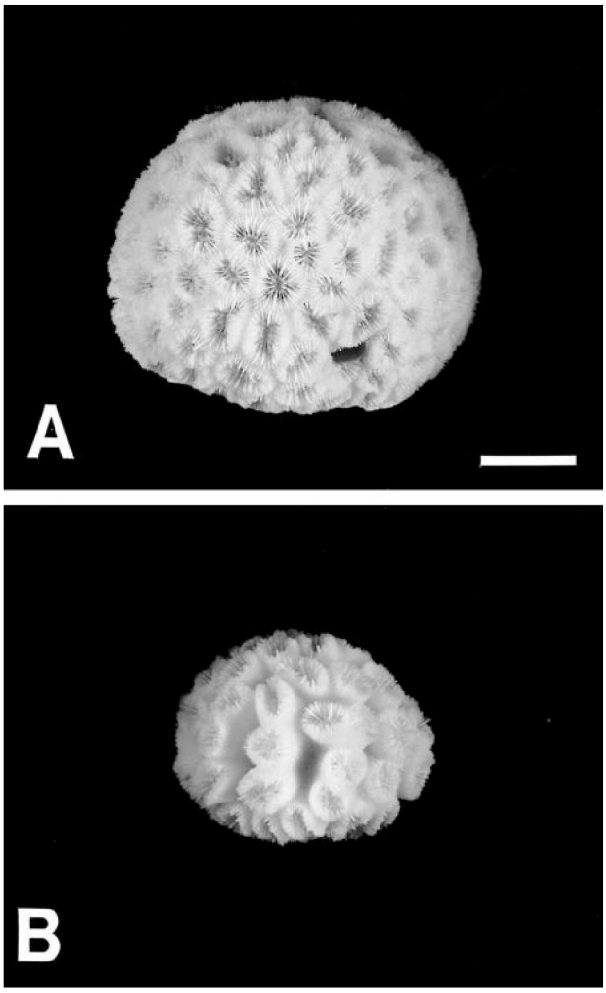

Figura 1 - Fotografias dos esqueletos dos dois morfotipos de *Favia fragum* encontrados no Panamá. (A) - morfotipo encontrado em maior densidade entre 3.0 e 5.0 m; (B) - morfotipo encontrado exclusivamente em águas rasas (1.0 m ou menos). Barra de escala representa 1 cm. Fonte: Carlon e Budd (2002).

Estudos sobre padrões de conectividade entre populações coralinas dos recifes brasileiros são escassos e apresentam resultados contrastantes para diferentes espécies. *Mussismilia hispida*, uma espécie que apresenta um único evento de liberação massiva de gametas por ano, demonstrou estruturação genética entre populações da costa do Brasil e três ilhas oceânicas utilizando microssatélites (Peluso et al. 2018). *Montastrea cavernosa* e *Siderastrea siderea* não mostraram níveis significativos de diferenciação genética utilizando dois marcadores nucleares (Nunes et al. 2011). O mesmo estudo reportou estruturação entre populações de *F. gravida* separadas por ~1,000 km. Porém, este estudo avaliou apenas duas populações, omitindo padrões de isolamento por distância que poderiam ser revelados com uma amostragem mais completa. Por outro lado, o estudo de Teschima et al. (2021), que avaliou a estruturação populacional e conectividade genética em toda a distribuição de *F. gravida* no Brasil, reportou panmixia ao longo da costa, contrariando a ideia de reduzido fluxo gênico

para a espécie. No entanto, este resultado pode ser consequência do baixo poder de resolução dos marcadores utilizados para resolver este nível de estruturação. Utilizando um grande número de marcadores altamente informativos nós esperamos fornecer ampla resolução para as relações de *Favia* no Atlântico, finalmente estabelecendo o status taxonômico de *F. gravida* e determinando sua posição em relação à *F. fragum*, além de possibilitar uma análise mais detalhada da conectividade ao longo da costa do Brasil.

O uso de tecnologias de sequenciamento de alta capacidade e a crescente acessibilidade a inúmeros protocolos de laboratório reduziram significativamente o custo do preparo e sequenciamento de amostras de DNA, permitindo que pesquisadores gerem grandes conjuntos de dados para inferências filogenéticas e filogeográficas (Mardis, 2017). Atualmente, métodos que se baseiam em representação reduzida do genoma são os mais utilizados em estudos filogenômicos, sendo o sequenciamento de fragmentos de DNA associados a sítios de restrição, da sigla em inglês RADseq, um dos mais populares (Andrews et al. 2016). RADseq é uma definição guarda-chuva que engloba todos os métodos que utilizam enzimas de restrição para digerir DNA genômico, gerando pequenos fragmentos aos quais adaptadores são ligados. Posteriormente, estes fragmentos passam por seleção de tamanho para então serem sequenciados em plataformas de alto rendimento (Davey and Blaxter, 2010; Van Dijk et al., 2014). A cada dia um número maior de organismos tem seu genoma completo disponível, porém, isto não é universal. Uma das grandes vantagens dos métodos de representação reduzida é o fato de não exigirem um genoma de referência, permitindo que pesquisas de qualidade sejam conduzidas em organismos não-modelo (Ellegren, 2014; Fonseca et al. 2016).

O pós-sequenciamento de dados RADseq compreende a demultiplexação dos dados, filtragem por qualidade, montagem *de novo* (na ausência de um genoma referência), mapeamento, detecção e filtragem dos SNPs de acordo com a porcentagem de dados faltantes e a exclusão de inserções e deleções. Estes passos são essenciais para assegurar que apenas marcadores informativos e de alta qualidade serão inclusos nas análises subsequentes (McCormack et al. 2013; O'Leary et al., 2016). Como no método RADseq apenas um subconjunto do genoma alvo é analisado, é possível sequenciar centenas de amostras e milhares de marcadores simultaneamente, aumentando a abrangência de questões a serem respondidas e possibilitando transitar entre análises de escala local e global em um único estudo (Edwards, Schultz and Campbell-Staton, 2015; Pellens, Faith and Grandcolas, 2016).

A presente tese teve como objetivo utilizar marcadores moleculares de alta resolução para investigar as relações filogenéticas no gênero *Favia* do Atlântico e examinar os padrões de

conectividade e a diversidade genética de populações ao longo de sua distribuição. No primeiro capítulo utilizamos métodos baseados em concatenação e coalescência, além de diferentes estratégias de filtragem de loci para reconstruir a topologia de *Favia* utilizando amostras de *F. fragum* do Caribe, e populações de *F. gravida* distribuídas ao longo de toda a costa brasileira e na ilha meio-Atlântica de Ascenção. No segundo capítulo investigamos a estruturação populacional entre e dentro das províncias. A alta resolução oferecida pelos SNPs revelou marcada diferenciação entre as três províncias, e nossa ampla amostragem na costa do Brasil identificou ampla estruturação genética de *F. gavida* ao longo da costa brasileira. Estes dados podem ser usados por entidades governamentais e órgãos ambientais para elaborar planos de manejo e estratégias de conservação que considerem estas áreas como unidades independentes, o que irá auxiliar na manutenção dos ecossistemas recifais do Atlântico Sul.

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Chapter I: Conflicting signals in the phylogeny of the Atlantic coral genus *Favia* (Scleractinia, Faviidae) evidenced by concatenation versus coalescent-based methods

Abstract

Scleractinian corals are well-known for the high levels of variation in the skeletal traits traditionally used in their taxonomy, which may lead to unreliable diagnostic characters and discordance between morphological and molecular data when it comes to species delimitation. Here, we employed reduced-representation sequencing (ezRAD) to evaluate taxonomic boundaries between two Atlantic faviids, *Favia fragum* and *F. gravida*, for which species limits are still controversial. Analyses based on concatenation and coalescent-based methods of up to 19,648 single nucleotide polymorphisms (SNPs) recovered conflicting topologies. Clade placement of *F. fragum* with respect to *F. gravida* from Brazil and Ascension Island varied with filtering levels when phylogenies were estimated via standard maximum likelihood analysis, possibly due to incomplete lineage sorting (ILS). Inconsistencies were overcome by coalescent-based analyses that placed Ascension Island *F. gravida* as sister group of a highly supported clade formed by Brazilian *F. gravida* and Caribbean *F. fragum*, therefore challenging the monophyly of the former species. Currently, *F. fragum* and *F. gravida* are considered a single species in the IUCN's Red List, whose distribution encompasses the Caribbean and South Atlantic, but our results show that the Atlantic *Favia* is made up of at least three different lineages, calling for a re-evaluation of name validity and their conservation threat status.

Keys words: coral phylogenetics, coalescent-based methods, RAD-Seq, SNPs, ILS, IQ-TREE

Introduction

Molecular and morphological approaches to species delimitation come into conflict when genetically distinct lineages have no identifiable phenotypes (i.e. cryptic species) or have high morphological disparity but no significant genetic structure (Bickford et al., 2007; Fišer, Robinson, & Malard, 2018). Both scenarios are rife among hard coral species, responsible for building one of the most diverse and productive ecosystems on the planet (Moberg & Folke, 1999). The taxonomy of Scleractinia is traditionally rooted in skeletal traits, which present a high degree of inter- and intraspecific variation (Todd, 2008). In closely related taxa with overlapping quantitative traits, the selection of diagnostic characters may have a subjective component (Budd & Klaus, 2001; Fujita et al., 2012) and environmentally mediated plasticity of those traits complicates the matter even further (Ow & Todd, 2010; Dubé et al., 2017; Johnston et al., 2017).

Conversely, plasticity may lead to considerable convergence among distantly related taxa: phylogenetic reconstructions using mitochondrial and nuclear markers have shown that many zooxanthellate coral families are not monophyletic. For instance, some of these reconstructions have recovered type species of the families Faviidae and Mussidae in the same clade (Fukami et al., 2008; Kitahara et al., 2010; Huang et al., 2011). The discordance between molecular and morphological characters raised concerns about the frequency of convergent morphological characters and homoplasy obscuring taxonomic relationships (Forsman et al., 2009; Flot et al., 2011; Arrigoni et al., 2012; Schmidt-Roach et al., 2013; Arrigoni et al., 2016; Terraneo et al., 2016), but molecular systematics of corals can be equally problematic. The "handful of markers" approach has often led to weakly-supported phylogenetic hypotheses clouded by incomplete lineage sorting, especially when analyzing complexes of closely related species (Maddison & Knowles, 2006). This situation in corals calls for approaches capable of yielding broader and representative sampling of genomes. Whole-genome sequencing (e.g. Shinzato et al., 2021), targeted sequence capture (e.g. Cowman et al., 2020), restriction site-associated DNA sequencing (RADseq- e.g. Toonen et al., 2013; Bongaerts et al., 2021), are greatly improving phylogenetic resolution at the species level, and in some cases, uncovering reticulate evolution in scleractinian corals (e.g. Mao, Economo, & Satoh, 2018; Mao et al. 2018). Processes such as recombination and hybridization cause the evolutionary history of some species to be better explained by a network (reticulated tree) rather than a typical tree (Linder and Riesenberg, 2004; Edwards et al. 2016). Stress on coral populations due to climate change (Hughes et al., 2017, 2019) brings urgency to a more comprehensive understanding of scleractinian systematics and implications for their conservation status.

The Atlantic species *Favia fragum* (Esper, 1797) and *F. gravida* (Verrill, 1868) are good examples of controversy in coral taxonomy. They are currently recognized by some taxonomists as separate species (Nunes et al. 2008; Hoeksema, 2012), but previously *F. gravida* was considered an ecomorph of *F. fragum* (Veron, 2000), despite their very distinct geographic distributions. *Favia fragum* is commonly found across the Caribbean Sea, the Gulf of Mexico, and the Florida Keys and it is also described for Bermuda and Cape Verde, whereas *F. gravida* is found along the Brazilian coast and in several mid-Atlantic islands (Hoeksema, Roos, & Cadée, 2012). The International Union for Conservation of Nature (IUCN) Red List does not include *F. gravida*: the distribution of *F. fragum* encompasses the range of both species, its threat status is listed as "least concerned" and its population trend is considered stable (Aronson et al., 2008), which means that the species is assumed to be

abundant, although no specific information on population dynamics was used in this classification. Colonies from the two species can be distinguished based on the number of septa, with *F. gravida* presenting four complete septal cycles. But many diagnostic morphological characters used to differentiate them are highly variable, and some qualitative traits are subjective, e.g. "[...] somewhat longer series [...], more widely spaced septal teeth" (Budd et al., 2012). Nevertheless, molecular data suggest that *F. fragum* and *F. gravida* are separate species and have also uncovered contrasting patterns of connectivity within *F. gravida*, i.e. restricted gene flow between coastal populations in Brazil, but introgression between Brazilian and mid-Atlantic Island populations (Nunes et al., 2008; Nunes, Norris & Knowlton, 2011). Furthermore, the mating system (Carlon & Lippe, 2011) and larval biology (Carlon & Olson, 1993) of *F. fragum* are likely to limit gene flow by gametes or larvae to small spatial scales. Previous studies have shown strong genetic structuring among populations in the Caribbean Sea (Goodbody-Gringley et al., 2010) and along a depth gradient within a sampling site (Carlon & Budd, 2002). Assuming similar biological traits in *F. gravida*, these studies suggest a high potential for isolation by geographic distance and perhaps cryptic speciation. Hence, expanded sampling of southern specimens is crucial to better understand the evolution of the genus across the Atlantic Ocean.

The boost in genomic and computational resources over the past decades has enabled biologists to gather and analyze larger numbers of markers with more sophisticated tools, leading to more realistic demographic reconstructions (Hey et al., 2018) and improved phylogenetic inferences (Mardis, 2008). RADseq has quickly become one of the most popular and widely used approaches of reduced representation sequencing (Puritz, Hollenbeck & Gold, 2014; Andrews et al., 2016; Campbell et al., 2018; Hohenlohe et al., 2018). Since a reference genome is not required, this technique allows researchers to apply it to non-model organisms (Andrews et al., 2016), as is the case of *Favia* spp. However, estimating reliable species phylogenies remains an obstacle, since the hundreds to thousands of loci that may now be easily sequenced have unique genealogical histories, leading to pervasive discordance among trees derived from different markers (Maddison, 1997; Degnan and Rosenberg, 2009). Hence, methods that incorporate the underlying coalescent process into tree inference are arguably the most appropriate way to bypass the gene tree vs. species tree conflict (Maddison and Knowles, 2006).

In this study, we used high-resolution markers discovered through ezRAD sequencing (Toonen et al., 2013), an accessible and cost-effective technique that also makes it possible to assemble long contigs, such as complete or nearly complete mitogenomes (Tisthammer et al.,

2016). We also recovered hundreds of ultraconserved (UCE) loci from our assemblies using a previously published baitset for Hexacorallia (Cowman et al. 2020), in an effort to incorporate sequence-based markers in our analyses. We employed a broad sampling strategy, including Ascension Island and the entire distribution of *F. gravida* in Brazil, plus Caribbean *F. fragum* specimens, to estimate the phylogeny of *Favia* in the Atlantic and also assess how coalescent versus concatenated methods influence the support for the current taxonomy of the genus.

Methods

Sampling

We selected one individual from each of seven populations of *Favia gravida*, six from the Brazilian coast and one from Ascension Island, located at the mid-Atlantic ridge between Brazil and Africa, and two Panamanian specimens of *Favia fragum*, each corresponding to the two different morphotypes identified by Carlon and Budd (2002). A specimen of the endemic Brazilian mussid *Mussismilia hispida* (MH_CE_352) was used as an outgroup in all analyses (Figure 1; Table S1). Colonies were collected by snorkeling and/or SCUBA under the Chico Mendes Institute for Biodiversity Conservation (ICMBio) permit number 50095-1, and coral tissue samples were preserved in DMSO saturated-salt buffer (Gaither et al., 2011) or 90% ethanol and stored at -20°C until extraction.

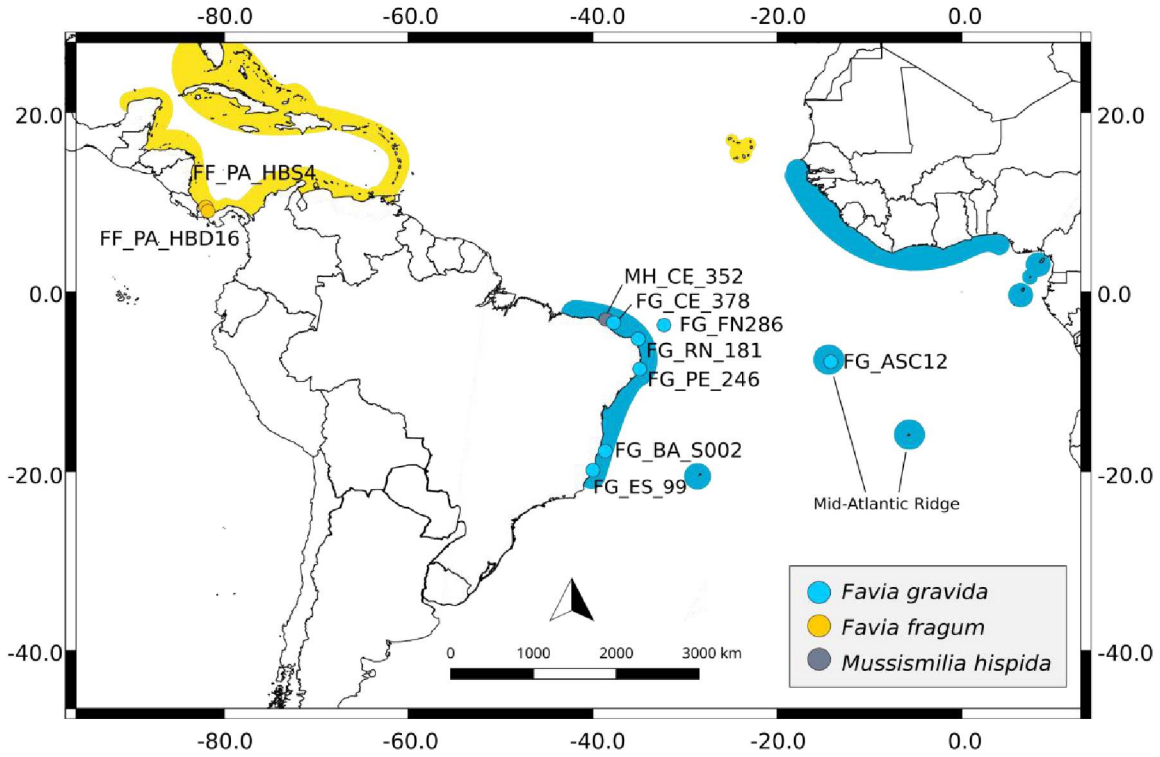

Figure 1 - Known geographic distribution of *Favia fragum* (FF) and *F. gravida* (FG) modified from Aronson et al. (2008) and circles representing samples used in this study. A specimen of *Mussismilia hispida* (MH) was used as outgroup. Circles corresponding to sampling sites are color coded according to species. FF_PA_HBS4 and FF_PA_HBD16 - Panamá (9.307 N; 82.142 W); MH_CE_352 and FG_CE_378 - Ceará, Brazil (3.598 S; 38.392 W); FG_FN286 - Fernando de Noronha, Brazil (3.854 S; 32.444 W); FG_RN_181 - Rio Grande do Norte, Brazil (5.393 S; 35.254 W); FG_PE_246 - Pernambuco, Brazil (8.736 S; 35.085 W); FG_BA_S002 - Bahia, Brazil (17.896 S; 38.827 W); FG_ES_99 - Espirito Santo, Brazil (20.012 S; 32.444 W); FG_ASC12 - Ascension Island, Brazil (7.933 S; 14.366 W).

Molecular analysis

We extracted DNA from tissue samples of *F. fragum* using the Omega E.Z.N.A Tissue DNA kit, and Invitrogen PureLink Genomic DNA kit in the case of *F. gravida*, following the manufacturers' instructions. Extractions were purified using 1.8X AmPureXP magnetic beads. DNA quality was assessed via electrophoresis in 1.5% agarose gel, ensuring that only high molecular weight DNA was carried over to the digestion step. Quantification was performed with Qubit 2 Fluorometer and the dsDNA High Sensitivity Assay kit.

Libraries were prepared following the ezRAD protocol (Toonen et al., 2013). Briefly, samples were digested using the enzyme DpnII (New England Biolabs), in 50µL reactions containing 5µL DpnII NEB 10X Buffer, 2 units of DpnII, and 200-1000ng of high molecular weight genomic DNA. Digestions were incubated at 37°C for 3 hours, then heat-inactivated for 20 minutes at 65°C, purified using 1.8X AMPureXP beads, and considered successful if

their electrophoretic pattern in UV transilluminated 1.5% agarose gels changed from a clear band to a broad smear. Libraries were constructed using the KAPA HyperPrep Library kit (Roche Sequencing Store) following the updated ezRAD protocol (Knapp et al., 2016). After A-tailing, end-repair and adapter ligation (KAPA unique dual index), size selection was performed with Mag-Bind Magnetic Beads (Omega Bio-Tek) by targeting fragments in a 350-700bp range in two steps with DNA:bead ratios of 1:0.5 and 1:0.2, respectively. Libraries were amplified using six PCR cycles with KAPA HiFi Hotstart Ready-mix (Omega Bio-Tek), purified using 1:1 DNA:AMPure XP beads, validated using Qubit dsDNA HS kit, Agilent 2100 Bioanalyzer and qPCR, and sequenced (V3 2x300bp PE) on the Illumina MiSeq platform at the Advanced Genomics Core Facility (ASGPB), University of Hawai‘i at Mānoa.

SNP bioinformatics

We assessed raw read quality with FASTQC (Andrews, 2010) and subsequent processing was performed with the bioinformatic pipeline dDocent (Puritz, Hollenbeck and Gold, 2014). Comparisons among four different pipelines using both simulated and empirical data show that dDocent is faster, has a smaller memory footprint and results in loci with better taxon coverage than the remainder pipelines (Jungwirth, 2017). The first step within dDocent is the removal of universal adapters and reads with Phred <30. The *de novo* assembly was conducted using default parameters (minimum within individual coverage value to include a read for assembly (k1) = 3; and minimum number of individuals a read must be present in to include for assembly (k2) = 2) and a contig clustering threshold of 0.90 (i.e. 90% similarity among sequences in the same cluster). This assembly contains the coral DNA plus all genetic material from associated biota that may have been sequenced, including DNA from the endosymbiont algae (Rohwer et al., 2002; Stat et al., 2012). In order to detect endosymbiont contamination, we performed a local BLAST against complete genomes of *Breviolum*, *Cladocopium*, and *Symbiodinium* species using an expectation (e-value) cutoff of e^{-5}. The contigs that blasted against endosymbiont genomes were removed, creating what we called *holobiont* dataset. We also BLASTed these reference contigs against a local scleractinian database assembled from 29 nuclear and 12 complete mitochondrial genomes (listed in Table S2), keeping only contigs that successfully blasted against the scleractinian genomes, thus producing the *coral* dataset. SNPs were called using FreeBayes from within dDocent and the resulting variant call file (VCF) was filtered using VCFtools (Danecek et al. 2011). Loci with allele balance (defined as the proportion of reads covering the alternative allele, considering only the heterozygous calls) below 0.15 or above 0.75 were excluded as potential false

heterozygotes or paralogs. We also filtered out loci with a minor allele frequency <5% (--maf 0.05). To test the influence of different filtering strategies in the reconstructions we partitioned the *holobiont* and *coral* datasets into alignments containing 30%, 20%, 10% and 0% missing data (g7, g8, g9, and g10, respectively). We also assessed the influence of the parameters minor allele count (--mac 2 and 3) and minimum mean coverage (--min-meanDP 10 and 20, hereafter denominated "mDP"). Finally, we filtered out indels and kept only a single random SNP per locus. We used the python script *vcf2phylip* (available at https://github.com/edgardomortiz/vcf2phylip) to convert the VCF file into PHYLIP and NEXUS formats to perform the subsequent phylogenetic analyses. Heterozygous calls were encoded with IUPAC ambiguity codes in the alignments.

UCE bioinformatics

We used the UCE bait set redesigned by Cowman et al. (2020) to target specific Hexacorallia loci in our RAD-seq reads using the PHYLUCE pipeline (Faircloth 2016). The bait set consists of 16,114 baits designed to capture 2,474 Hexacorallia loci (1,127 loci from coral genomic data and 1,347 exon loci from coral transcriptomic data). Briefly, we used Velvet (Zerbino and Birney, 2008) with default parameters to perform the assembly of each sample, and matched the UCE bait set to our assembled contigs at 70% identity and 70% coverage, following Cowman et al. (2020). Loci were extracted into FASTA files. Alignment and edge trimming of each file were performed with MAFFT (Katoh et al. 2002), using default parameters. Loci recovered from a minimum of 75%, 90%, and 100% of the sequenced specimens were concatenated, generating three alignments (UCE75, UCE90, and UCE100) with equivalent taxon occupancy.

Phylogenetic analyses

SNP data were employed in maximum likelihood (ML) tree search using IQ-TREE v.2.1.2 (Minh et al., 2020). Best-fit substitution model selection was conducted in ModelFinder (Kalyaanamoorthy et al., 2017) via Bayesian information criterion (BIC). Branch support in IQ-TREE was assessed by 1,000 ultra-fast bootstrap (UFboot) replicates, a less biased and fast alternative to other nonparametric bootstrap approaches (Mihn et al. 2013). The interpretation is slightly different from the standard bootstrap and the branch is considered well supported with UFboot values >95. We also computed the site concordance factors (sCF), defined as the average proportion of parsimony-informative sites that support a given branch in the reference tree when 100 random quartets of taxa are sampled around each

internal node. Two values of site discordance factors (sDF) i.e, the support for the two other quartets not present in the reference tree, are also reported by IQ-TREE hence by definition, the sum of sCF, sDF_1, and sDF_2 always adds up to 1 (Mihn, Hahn, & Lanfear, 2020). Alignment sizes, percentage of parsimony informative sites (PIS), ambiguous calls in the alignment and branch support values (UFboot and sCF) for the topologies produced by each alignment dataset employed in the concatenation analysis were used as sample units to perform a principal components analysis (PCA). To increase discrimination between the two competing topologies (*F. gravida* monophyletic vs. *F. gravida* paraphyletic, see Results), branch support was re-coded as negative values whenever *F. gravida* was not recovered as monophyletic (see Results). This was done in order to better visualize the distribution of datasets based on their resulting topology.

In order to integrate the genealogical history of individual loci, we also estimated the topology under a coalescent framework using the quartet sampling method SVDquartets (Chifman and Kubatko, 2014), implemented in PAUP* 4.0 (Swofford, 2001), with exhaustive quartet sampling and 1,000 bootstrap replicates to assess branch support. SVDQuartets is a site-based method that uses biallelic SNP markers, assumed to be unlinked, to infer the splits in quartets of taxa.

ABBA-BABA analysis

We used the software Dsuite (Malinsky, Matschiner and Svardal, 2021) to calculate Patterson's D statistic, commonly denominated ABBA-BABA, based on biallelic SNPs across quartets of populations/species (Green et al. 2010; Durand et al. 2011). Considering no gene flow between these populations, ABBA and BABA allelic patterns are expected to have equal frequencies, while deviations from this ideal ratio indicate admixture or incomplete lineage sorting (ILS) between any given pair of populations. We calculated ABBA-BABA statistics for four clades, as recovered in the phylogenetic reconstructions (see Results): *F. fragum*, *F. gravida* from Ascension Island, and two subgroups within the Brazilian samples of *F. gravida*, namely the Northeast and East clades. To assess significance, the algorithm *Dtrios* calculates Z-scores and their respective *p*-values (we chose $\alpha = 0.01$).

Results

Bioinformatics

FASTQ files had an average of 4.28 million reads of 301bp per library (ranging from 2,942,294 to 5,830,097 reads). After quality control, an average of 4.08 million reads (~95%) was retained for further analyses, with the overall average depth of 13X, and an average depth per sample varying from 8X to 18X (Table S3). A total of 94,345 contigs were retained in the resulting holobiont reference assembly, and only 53 unique contigs were successfully BLASTed against the endosymbiont database. These contigs were removed from further analysis. In contrast to the endosymbiont search, BLAST alignment against the host database yielded a reference assembly with 58,452 (e^{-5}) contigs. We obtained a total of 1,126,868 raw SNPs, but the number of SNPs effectively included in the alignments varied from 1,036 to 19,648 (Table 1). The number of parsimony informative sites (PIS) in the alignments varied drastically depending on the dataset and filtering strategy, with mDP 20 rendering datasets with the lowest PIS counts (Table 1).

We recovered a total of 1,867 UCE loci from our contigs (75.4% of the total bait set), ranging from 684 to 1,039 loci in individual samples. Loci were extremely conserved and presented low counts of PIS, possibly due to the short fragment sizes only matching the UCE cores and not reaching the highly informative flanking regions (Table S4).

Table 1 - Branch support values for Maximum Likelihood analysis performed in IQTREE (UFboot - ultrafast bootstrap value; sCF - site concordance factor, reported as percentages) for the phylogenetic reconstructions based on holobiont and coral SNP loci. Asc - *F. gravida* samples from Ascension Island; MAC - minor allele count; PIS - parsimony informative sites. Values in bold represent UFboot support >95.

Dataset	Min. meanDP	MAC	(%) Missing	Align. length	# PIS	Clade			
						F.fragum +Asc		*F. gravida*	
						UFboot	sCF	UFboot	sCF
Holobiont	10	2	0	3,567	913	**96**	38.6		
			10	10,542	4,451	**96**	39.3	-	
			20	16,230	6,133	94	42.7		
			30	17,448	6,442	92	44.8		
		3	0	6,316	3,315	**97**	40.8		
			10	15,213	8,980	**99**	42.7	-	
			20	18,846	11,345	**100**	44.9		
			30	19,648	11,769	**100**	46.3		
	20	2	0	1,894	41			88	36.7
			10	3,858	114	-		**96**	36.9
			20	4,243	141			87	37.1
			30	4,353	147			88	38.7
		3	0	2,114	81			89	37.2
			10	3,952	185	-		**99**	37.7
			20	4,287	225			**98**	37.8
			30	4,375	233			**98**	38.7
Coral	10	2	0	2,175	605	**97**	40.5		
			10	6,130	2,729	89	40.1	-	
			20	9,735	3,795	86	46.3		
			30	11,585	4,005	80	45.9		
		3	0	4,365	2,026	87	41.0		
			10	9,967	5,459	**95**	42.5	-	
			20	12,303	6,937	**96**	46.4		
			30	12,839	7,218	94	45.1		
	20	2	0	1,036	26			55	33.9
			10	1,962	76	-		38	34.8
			20	2,196	89			54	35.4
			30	3,107	95			83	36.8
		3	0	1,150	44			67	36.9
			10	1,960	114	-		89	36.8
			20	2,162	136			90	37.9
			30	3,137	151			**98**	37.7

Concatenation analysis

The best-fit model chosen by ModelFinder was TVM (transversion mode) for all SNP datasets. The concatenation approach in IQ-TREE recovered two competing topologies. Analyses of datasets with mDP 10 recovered *F. fragum* as sister group of the Ascension Island *F. gravida* with moderate to high UFboot support in the *holobiont* datasets and low to moderate support in the *coral* datasets, but with low sCF values (average sCF = 43) (Figure

2A; Figure S1; Table 1). Analyses of datasets with mDP 20 recovered *F. gravida* as a monophyletic clade with variable UFboot support values, ranging from 88 to 99 (average UFboot = 93) for the *holobiont* datasets and 38 to 98 (average UFboot = 72) for the *coral* datasets. sCF were lower than observed for the mDP 10 datasets (average sCF = 37) (Figure 2B; Table 1; Figure S2). HKY+F (Hasegawa, Kishino and Yano, 1985) was the best-fit model chosen by ModelFinder for all the UCE datasets.

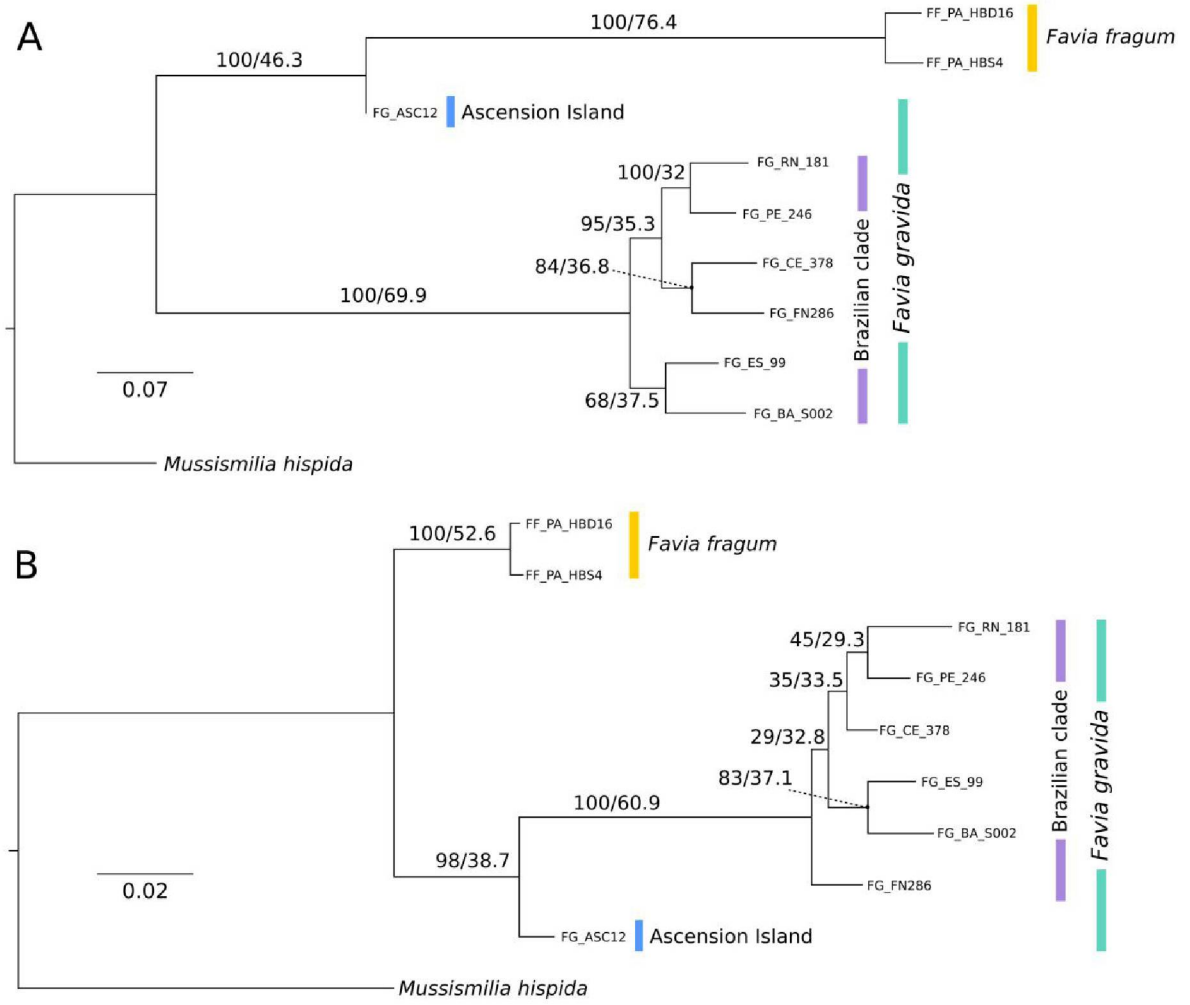

Figure 2 - Maximum likelihood (ML) tree of Atlantic *Favia* generated in IQ-TREE. Phylogenies based on the *holobiont* dataset with 30% missing data (SNPs) and minor allele count = 3.(A) minimum mean depth = 10 and (B) minimum mean depth = 20. Scale bar represents substitutions per site. Values on branches represent ultrafast bootstrap (UFboot) support and site concordance factor (sCF), respectively.

Principal components analysis (PCA) shows that the topologies were most strongly influenced by the mDP value, with mDP 20 presenting low counts of PIS (average 4%) and high percentages of ambiguities in the alignment (average 52%), while mDP 10 had a higher

PIS count (average 45%) and fewer ambiguities (average 31%) (Figure 3 and S3; Table 1). For both *holobiont* and *coral* datasets sCF values for the internal nodes were lower than 50% i.e., lower than the sum of sDF values for the competing quartets, particularly in the case of mDP 20 datasets (Figure 4).

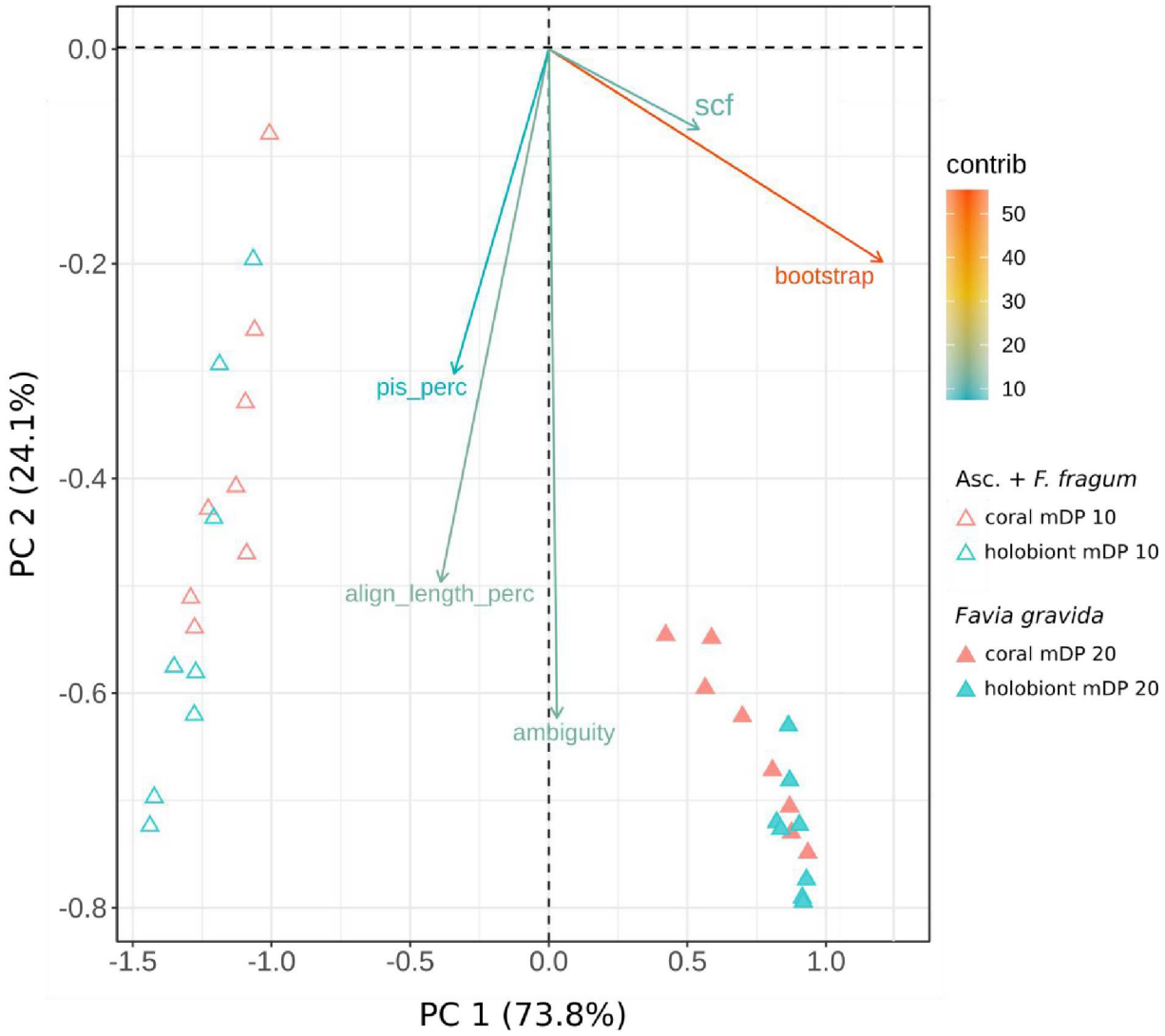

Figure 3 - Principal components analysis (PCA) biplot of SNP alignment datasets and explanatory variables showing the loading of each variable and their summed contribution to both PCs. Contrib - contribution of variables to the principal components; mDP - minimum mean depth; PIS - parsimony informative sites; sCF - site concordance factors.

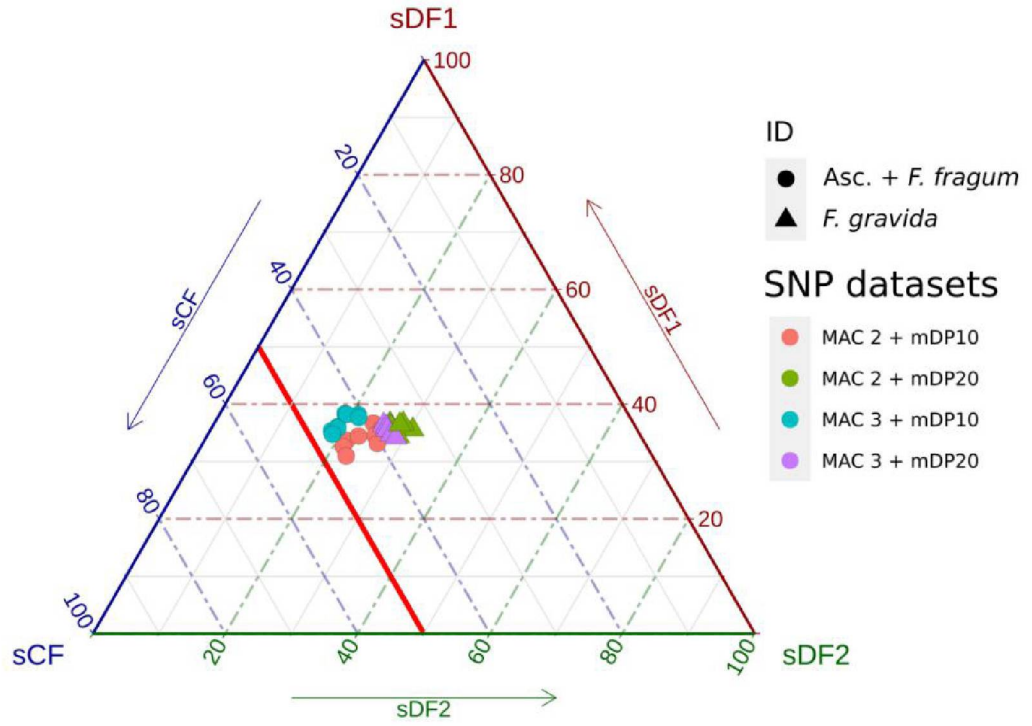

Figure 4 - Ternary plot showing the distribution of site concordance (sCF) and the two site discordance factors (sDF1 and sDF2) for competing topologies based on maximum likelihood analysis of SNP data performed in IQTREE. The red line indicates the threshold of 50%, below which the dataset favors the two other quartets not represented in the species tree. ASC - Ascension Island samples; MAC - minor allele count; mDP - minimum mean depth.

ABBA-BABA analysis

We used the main branches recovered in the concatenation analysis to perform an ABBA-BABA analysis. The highest D values and Z-scores were found between Ascension Island and the East Brazilian clade and between Ascension Island and *F. fragum*. Weak admixture/ILS was detected between Ascension Island and the Northeast Brazilian clade, and between the latter and *F. fragum* (Table 2).

Table 2 - Patterson's D statistic (ABBA-BABA statistic) for trios of populations of Atlantic *Favia*. ASC - *F. gravida* from Ascension Island; BRA1 - Northeast Brazilian populations of *F. gravida* (all except Abrolhos e Aracruz) *;* BRA2 - East Brazilian *F. gravida;* FRA - *F. fragum*. *Mussismilia hispida* was used as an outgroup.

P1	P2	P3	D-statistic	Z-score	p-value	BBAA	ABBA	BABA
BRA1	BRA2	ASC	0.02	3.92	<0.001	5671.87	3047.13	2910.57
FRA	ASC	BRA1	0.15	20.19	0	4201.61	4149.57	3051.28
BRA2	ASC	FRA	0.14	17.56	0	4143.19	4062.19	3047.25
BRA1	BRA2	FRA	0.02	4.49	<0.001	6757.51	2953.28	2816.04

Coalescent-based analysis

SVDQuartets recovered the same topology across all datasets and filtering strategies. Ascension Island was recovered as sister to a clade that included *F. fragum* and the Brazilian samples of *F. gravida* (Figure 5; Figs. S4 and S5; Table 3), but with low support. This clade was well supported in the *holobiont* and *coral* mDP 10 datasets (average BS = 98.9) and in the more restricted mDP 20 datasets (overall average BS = 75.3), although support was lower in the *coral* alignments (average BS = 63.3).

The Brazilian samples formed a clade with maximum support in all coalescent-based reconstructions regardless of dataset and filtering strategy (Figure 5; Figs. S4 and S5). This clade received maximum UFboot support in the concatenated analyses of mDP 10, and ranged from 78 to 100 in the mDP 20 datasets (Figure 2; Figs. S1 and S2). The majority of mDP10 datasets split the Brazilian coast samples into two (East and Northeast) clades (Figs. S1 and S4).

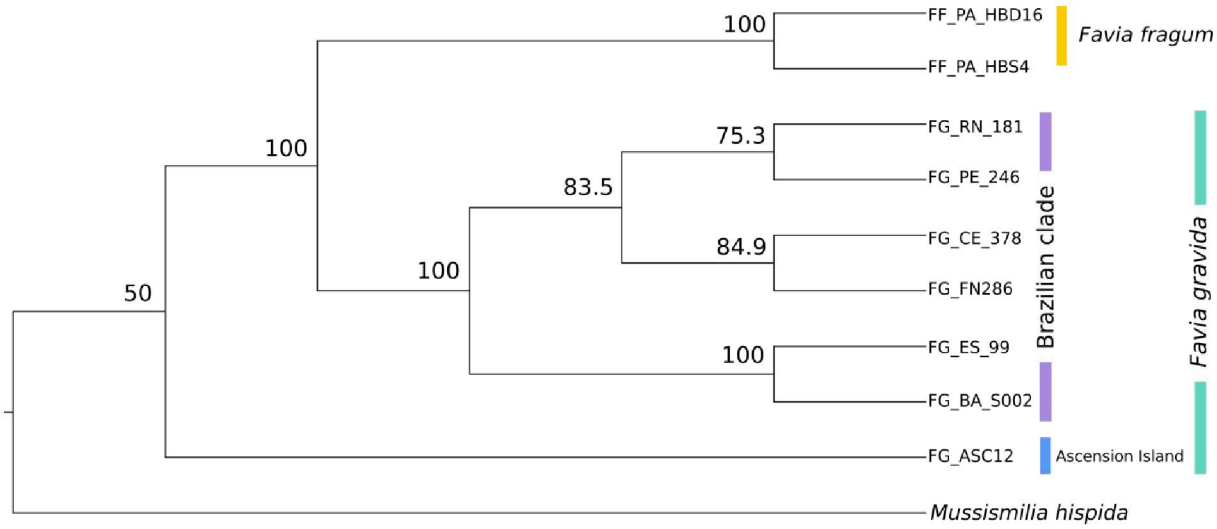

Figure 5 - Phylogenetic tree inferred with the SVDQuartets method in PAUP* based on the *holobiont* dataset with 30% missing data, minor allele count = 3, and minimum mean depth = 10. Values on branches represent bootstrap support.

Table 3 - Branch support values for coalescent-based analysis performed in SVDQuartets (BS - bootstrap value) for the phylogenetic reconstructions based on holobiont and coral SNP loci. Brazil - *F. gravida* samples from Brazil; MAC - minimum allele count. Values in bold represent bootstrap support >70.

Dataset	Min. meanDP	MAC	(%) Missing	Alignment length	*F.fragum* + Brazil (BS)
Holobiont	10	2	0	3,567	**100**
			10	10,542	**94.3**
			20	16,230	**98.9**
			30	17,448	**100**
		3	0	6,316	**100**
			10	15,213	**100**
			20	18,846	**100**
			30	19,648	**100**
	20	2	0	1,894	**70.4**
			10	3,858	**98.6**
			20	4,243	**97.4**
			30	4,353	**94.6**
		3	0	2,114	67.7
			10	3,952	**89.8**
			20	4,287	**89.2**
			30	4,375	**90**
Coral	10	2	0	2,175	**99.2**
			10	6,130	**98.7**
			20	9,735	**98.7**
			30	11,585	**93**
		3	0	4,365	**100**
			10	9,967	**100**
			20	12,303	**100**
			30	12,839	**100**
	20	2	0	1,036	56.1
			10	1,962	**73.1**
			20	2,196	**73.1**
			30	3,107	**74.9**
		3	0	1,150	63.9
			10	1,960	54.9
			20	2,162	54.9
			30	3,137	56.2

UCE phylogenetics

We recovered a total of 1,867 UCE loci from our contigs (75.4% of the total bait set), ranging from 684 to 1,039 loci in individual samples (Table S3). HKY+F (Hasegawa, Kishino and Yano, 1985) was the best-fit model chosen by ModelFinder for all UCE datasets. The UCE data recovered *F. gravida* and *F. fragum* as reciprocally monophyletic, with Ascension

Island as sister to the Brazilian *F. gravida* (Figure S). This is the same topology recovered by the mDP 20 datasets, which had the lowest PIS counts. Although we were able to successfully recover a significant percentage of bait-targeted UCE loci in our RAD-seq assemblies, our contigs only captured the core fraction of the UCEs, not reaching the highly informative flanking regions and leading to alignments with <1% of PIS (Table S3).

Discussion

This is the first study to use highly informative genome-wide data to examine the nominal species *Favia fragum* and *F. gravida* in the Tropical Atlantic. The analysis of thousands of SNPs and a sampling scheme that represented a significant portion of *F. gravida* range, recovered *F. gravida* as paraphyletic with respect to *F. fragum.* Standard ML analyses yielded conflicting topologies, as a possible consequence of statistical inconsistency. ABBA-BABA indicates the existence of incomplete lineage sorting (ILS), one of the main causes of topological incongruence in concatenation methods (Pollard et al. 2006). Furthermore, concatenation analyses are also more sensitive to long-branch attraction (LBA), another cause of phylogenetic inconsistency that might be present in our data due to the choice of a distant outgroup. Regardless of dataset and/or analytical framework, all our reconstructions strongly suggest the existence of cryptic lineages within the Atlantic *Favia*, and the taxonomic status of Ascension Island should be reconsidered.

Concatenation vs. Coalescent-based approach

Historically there was a long debate on the choice between concatenation and coalescent-based methods to resolve phylogenetic relationships, with the majority of authors favoring the latter (e.g., Kutschera et al. 2014; Xi et al. 2014; Davidson et al. 2015; Jiang, Edwards and Liu, 2020). One of the main arguments against using concatenation approaches in some cases is centered on how these methods deal with processes known to affect phylogenetic inferences, such as incomplete lineage sorting (ILS) and introgression. The presence of either may lead to topological incongruence and high support for the wrong tree in concatenation analysis, which combines multiple loci into a supermatrix and considers that they all share the same underlying evolutionary history, which is hardly realistic (Pollard et al. 2006; Kubatko and Degnan, 2007; Eckert and Carstens, 2008).

The ABBA-BABA results for *Favia* indicate the presence of ILS and/or introgression between Ascension Island and the Brazilian samples and also between Ascension Island and *F. fragum*. The causes of incongruent or unresolved phylogenies for corals are not always

distinguishable (Diekmann et al. 2001; Van Oppen et al. 2001), but studies suggest that introgression may play a major role in the evolutionary history of plants and animals (Mallet, 2005). Introgressive hybridization has been suggested for some Scleractinia genera (e.g. Van Oppen et al. 2003; Combosh and Vollmer, 2015; Cunha et al. 2019), but recent studies using integrative approaches point to misidentification as an alternative explanation for the topological incongruences (Arrigoni et al. 2020; Cowman et al. 2020; Ramírez-Portilla et al. 2022). Furthermore, the rapid larval settlement behavior in *Favia* spp. suggests limited dispersal (Carlon & Olson, 1993; Calderon, Castro, & Pires, 2000), which is incompatible with pervasive introgression across distances of at least 2,000km. Thus, we believe ILS to be the main source of the discordant ABBA-BABA patterns in our data, which calls for caution when analyzing the resulting topologies. These misleading effects can be minimized when trees are estimated under a coalescent framework since these methods are better at accommodating the discordance between gene trees and species trees (Carstens and Knowles, 2007; Alda et al. 2019; Wascher and Kubatko, 2021), as observed in RADseq generated SNP data (Hühn et al. 2021). Additionally, simulation analysis indicates that coalescent-based approaches consistently recovered the correct species tree even in scenarios where there is significant discordance between the underlying gene trees (e.g. Edwards, Liu and Pearl, 2007).

Positive misleading topologies can also be a result of the phenomenon of long-branch attraction (LBA), which is especially problematic in studies with sparse taxon sampling and might be caused due to fast-evolving species and/or distant outgroups (Felsenstein, 1978; Bergsten, 2005), which is the case of our study. Due to extensive back-mutations, sequences of distant outgroups may become spuriously similar to sequences of fast-evolving ingroup taxa, leading to LBA (Philippe and Laurent, 1998; Anderson and Swofford, 2004; Brinkmann et al. 2005, Rosenfeld, Payne and DeSalle, 2012). Since short internal and long external branches enhance the potential for discordance among gene trees and the species tree, this effect is particularly problematic in the presence of ILS, which is the case of our data (Degnan and Rosenberg, 2006; Liu, Xi and Davis, 2015). One way of resolving this problem might be including a closer outgroup, such as *Diploria* spp., which is suggested to be a sister clade of Atlantic *Favia* based on morphological and genetic data (Budd and Smith, 2005; Nunes et al. 2008). Furthermore, LBA can also be avoided by adding more than one outgroup taxa, which often helps break up the long branches and might lead to better phylogenetic estimations (Hendy and Penny, 1989, Lartillot, Brinkmann and Philippe, 2007; Ontano et al. 2021).

The topological inconsistency is observed in the bimodal distribution of branch support values in respect to the competing, dataset-dependent topologies recovered in the concatenation analyses (Figure 2). Under stricter filtering (mDP 20) that yielded lower PIS counts, *F. gravida* was recovered as monophyletic with variable bootstrap support values (38-98), but consistently low sCF values (average sCF = 35 - Figure 4; Table 1). Because sCF are calculated from quartets, meaning that a single site can only give support to one out of the three possible topologies among the four taxa, a ~33% sCF indicates that equal proportions of the informative sites provide support to each possible topology (Minh et al. 2020). The same topology was recovered by our sparse UCE data, which also had low numbers of PIS with respect to total alignment size, an additional cause of inaccuracy in gene tree estimation (Xi, Liu and Davis, 2015). As the alignment size and the PIS count increased in the mDP 10 datasets the branch support values for *F. fragum* + Ascension Island also increased (Table 1), a positive misleading effect that is typical of LBA (Delsuc, Brinkmann and Philippe, 2005; Kolaczkowski and Thornton, 2009) given that sCF values were low even with highest PIS counts and maximum bootstrap support (average sCF = 42.5 across different datasets), whereas the majority of sites support alternative topologies (average sDF = 57.5 - Table 1).

Besides ILS and introgression, coalescent-based methods are also less sensitive to long external branches and fast-evolving sites, minimizing the risk of statistical inconsistency due to LBA (Xi et al. 2014; Liu, Xi and Davis, 2015). Neither of the previous topologies was recovered by the coalescent site-based approach carried out in SVDQuartets, which returned a single consistent topology regardless of alignment size and PIS count (Figs. S1 and S2). Other than the listed advantages of using coalescent-based approaches, SVDQuartets have an additional asset in comparison to IQ-TREE. Our alignments presented a considerable percentage of IUPAC ambiguities, especially in the mDP 20 datasets. SVDQuartets correctly parses these residues as heterozygous sites, while IQ-TREE treats ambiguous calls as uncertain, splitting the tip likelihoods evenly among the two possible nucleotides (Minh et al. 2021).

Given these results, we suggest that the occurrence of ILS among *Favia* lineages, the influence of LBA due to an arguably distant outgroup, the loss of phylogenetic information in excessively filtered datasets, and the improper treatment of heterozygous sites given by IQ-TREE may have resulted in misleading support for the wrong tree. Coalescent-based analyses are seemingly a robust alternative for the inconsistent concatenation approach, yielding more consistent estimates of phylogenetic relationships. Hence, given the

aforementioned evidence, we believe that the topology recovered by SVDQuartets is a more reliable estimate of the phylogenetic relationship within the Atlantic *Favia*.

Coral vs. Holobiont datasets

In our reference assembly, only 53 contigs were BLAST-aligned to zooxanthellae algae genomes and ~57% of the contigs successfully aligned against coral genomes with an e-value $\leq e^{-5}$. Some of the remaining contigs that did not blast may belong to other organisms associated with the coral that are not represented in our sequence reference database. However, given that the genome of Symbiodiniaceae is larger than the coral genome (median sizes of 742Mb vs. 416Mb) and certainly the most commonly known contaminant in Scleractinian samples, and that symbiont contigs were removed from the *holobiont* dataset, we are confident that the remaining sequences were mostly coral DNA. This is reinforced by the assembly strategy used by dDocent, which requires sequences to be common to all species. Hence, these contigs are most likely genome fragments with high similarity shared among *F. fragum*, *F. gravida*, and *M. hispida*, but not with other species in the coral database assembled for this study. These results give us assurance that our *holobiont* SNP datasets were not influenced by alien sequences.

Within the different methods (concatenation vs coalescent-based) and filtering strategies the topologies were consistent in respect to whether the alignments belong to *holobiont* or *coral*. In the *coral* mDP10 datasets, the branch support values were slightly lower in concatenation analysis, and this difference was negligible in the coalescent-based analysis. On the other hand, there was a large reduction in branch support values for the mDP20 *coral* datasets in both concatenation and coalescent-based approaches (Figure S6). This result might be attributed to the low PIS count in the *coral* alignments when compared to *holobiont*, which is more evident in the mDP20 datasets (Table 1; Table S4).

Influence of missing data

High proportions of missing data coupled with pervasive ILS might lead to gene tree heterogeneity and conflicting topologies. Although they affect both concatenation and coalescent-based methods, the latter proved to be more robust to this particular factor and provided more consistent results, especially when a sufficient number of informative genes are sampled (Xi, Liu and Davis, 2016). Simulation studies also show that given a large number of genes, the performance of SVDQuartets under moderate levels of missing data is consistent even in high ILS scenarios (Nute et al. 2017). However, the proper threshold is a

fine line. Excessively filtering based on missing data percentages might actually increase species tree estimation error across multiple coalescent-based methods, particularly for datasets with high ILS (Molloy and Warnow, 2018). This is a trend in both concatenation and coalescent-based methods and might be explained by the fact that datasets with moderate percentages of missing data retain more phylogenetic information, increasing average branch support and accuracy (Huang & Knowles, 2016; Eaton et al., 2017; Crotti et al., 2019).

Here, we used four different missing data cut-offs, between 0% and 30%, to test their effect on our reconstructions. In the concatenation approach, tree backbones were dictated by the minimum mean depth and were consistent with respect to missing data proportions, but UFboot and sCFs were generally higher in datasets with moderate amounts of missing data (Figure S7 and S8). The same trend was observed in the coalescent-based approach: datasets with 0% missing data had the lowest bootstrap support values (Figure S8). Huang and Knowles (2016) point out that alignments with no missing data will probably lack highly informative loci and thus lose phylogenetic signal. They do not provide guidelines to select the optimal amount of missing data to be allowed in phylogenetic analyses, advocating for a thorough examination of each dataset. Eaton et al. (2017) recommend the use of site concordance factors as an additional measure to assess the support for problematic clades, an approach that we employed in our concatenation-based reconstructions. Our results showed that moderate amounts of missing data led to higher sCF values, presumably given the higher PIS count. Thus, although recovering the same backbone phylogeny and across different missing data thresholds, datasets with no missing data may be lacking informative markers yielding reduced support for the relationships within *Favia* spp.

Favia gravida paraphyly

Our preferred topology, based on the coalescent-based analysis, recovered *F. gravida* as paraphyletic in respect to *F. fragum*: Ascension Island was recovered as sister clade to a well-supported branch consisting of *F. fragum* and the Brazilian *F. gravida*. These species were first described based on their skeletal traits, which are known to be extremely plastic and variable (Amaral and Ramos, 2007), and the first studies investigating the phylogenetic relationships among Atlantic *Favia* using molecular markers either did not include samples from Ascension Island (Nunes et al. 2008; Nunes et al. 2011) or failed to amplify informative loci for Ascension samples (Zibrowius et al. 2017). Our results agree with a recent study based on two nuclear loci, which also recovered Ascension Island as sister clade to all other Atlantic *Favia* and the Caribbean *F. fragum* as sister to Brazilian and West African samples

of *F. gravida* (Teschima et al. 2021). Ascension is a young volcanic island (1-2 million years) 1,300km distant from the much older Saint Helena (14 million years) (Ashmole and Ashmole, 1997). These islands form the mid-Atlantic Ridge province, where a high degree of endemism of marine taxa has been described (Briggs and Bowen, 2012; Cowburn et al., 2021), and *Favia* is one of the few Scleractinian corals reported to occur on both of them (Hoeksema, 2012; Zibrowius et al. 2017). Phylogeographic studies suggest that the divergence between the Caribbean and the South Atlantic preceded the separation of East and West Atlantic populations for several marine fishes (Rocha et al. 2002; Carlin, Robertson and Bowen, 2003; Lastrucci et al. 2018), but our results suggest that the mid-Atlantic *Favia* sp. lineage was the first one to diverge from the rest. Discordant phylogeographic patterns can be explained by the contrasting life histories of distinct taxa, and features such as dispersal capacity and larval behavior might be significantly different among fishes and marine invertebrates (Carpenter et al. 2011). The mid-Atlantic Ridge is considered an important stepping-stone between the east and West Atlantic for multiple marine animals, and while a survey of reef fish species show that the province has an intermediate composition between these two regions (Floeter et al. 2007), it remains a poorly studied location (Briggs and Bowen, 2012; 2013; Soares, Tavares and Carneiro, 2018). Nonetheless, the geographic isolation and the genetic differentiation of the Ascension Island specimen compared to both Brazilian *F. gravida* and Caribbean *F. fragum* reinforces the hypothesis that the sample may belong to a distinct species.

Caribbean and Brazilian samples

In all of our reconstructions, *F. fragum* and Brazilian *F. gravida* were recovered as well-supported clades, independent of the method, filtering strategy, and phylogenetic information content (Figs. 2 and 5; Figs. S1, S2,S4 and S5). Other than the geographic distance, the main geographic barrier separating the Caribbean *F. fragum* from the Southwestern and mid-Atlantic samples is the Amazon river, the largest drainage basin in the world (Latrubesse et al., 2010). High sediment deposition and freshwater discharge serve as a barrier for species distributions, and patterns of vicariance across the Amazon plume have been reported for multiple species (Briggs & Bowen, 2013). For example, fishes in the genus *Halichoeres* present contrasting patterns of connectivity according to cytochrome *b* data (Rocha et al., 2005). While the Caribbean and Brazilian populations of the generalist *H. bivitattus* and *H. poeyi* share haplotypes, the reef specialist *H. maculipinna* showed a clear phylogenetic split between populations along the Amazon/Orinocco barrier. The spiny lobster *Panulirus argus* presents strong differentiation between the Caribbean and Brazilian

metapopulations based on maximum likelihood analysis of mitochondrial (COI and 16S) and nuclear (ANT) markers, suggesting cryptic speciation (Tourinho, Solé-Cava, & Lazoski, 2012). Cruz et al., (2015) argue that the restriction in gene flow in *P. argus* is further intensified by biophysical retention generated by the North Brazilian Current, leading to high levels of self-recruitment in Brazilian populations. Using both mtDNA and SNP-based analyses, two distinct and reciprocally monophyletic lineages of the bridled goby *Coryphopterus glaucofraenum* were recovered separated by that barrier (Volk et al., 2020). Furthermore, based on three mtDNA gene regions and five nuclear loci, the split between the Brazilian populations of the seahorse *Hippocampus patagonicus* and the Caribbean *H. erectus* can also be linked to the Amazon barrier (Boehm et al., 2013). The freshwater discharge from the Amazon and Orinocco rivers can act as a permeable or strict barrier depending on the species biology (Tourinho et al., 2012; Liedke et al., 2020), but the latter seems to be the case in Scleractinian corals: population genetic analysis based on the nuclear markers β-*tubulin* and *Pax-C* from six species demonstrates differentiation between Brazilian and Caribbean populations, with the highest degrees of variation observed between *F. fragum* and *F. gravida* (Nunes et al., 2011), which was further confirmed by two additional markers (Teschima et al. 2021). Although presenting extensive variability in their macro and micromorphology, there is evidence of differentiation between the two regions, with *F. gravida* from Brazil presenting four complete septal cycles and taller callice elevation when compared to Caribbean *F. fragum* (Budd et al. 2012).

Within the Brazilian clade, which was recovered with maximum bootstrap support in both concatenated and coalescent-based approaches and yielded high sCF values (> 69%), we also recovered an East clade, represented by the ES and BA populations. This clade was recovered in most concatenated and coalescent-based analysis, although branch support was mostly moderate/low and sCF were consistently low in the IQ-TREE topologies (Figs. S1 and S2). Marine organisms present different patterns of phylogeographic structuring along the Brazilian coast. Some species have little to no genetic structure such as the penaeid shrimp *Litopenaeus schmitti* (Maggioni, Rogers, & Maclean, 2003) and the crabs *Armases angustipes* (Marochi, Masunari, & Schubart, 2017) and *Ucides cordatus* (Britto et al., 2018). Others, such as *Crassostrea* spp. oysters show evidence of isolation by distance (Lazoski et al., 2011), or divergence between coastal and oceanic reef populations of the bridled goby *Coryphopterus glaucofraenum* (Volk et al., 2020). In the stony coral *Mussismilia hispida,* principal coordinate analysis and Bayesian clustering analysis using 13 microsatellite loci also recovered a clear distinction in the eastern limit populations, which presented low levels of

genetic diversity and less admixture than the remaining populations (Leão, 1983). Low levels of admixture and partial isolation of peripheral populations are common in marine species, especially when populations present patterns of isolation-by-distance (Leão, Kikuchi, & Testa, 2003; Menezes, Sobral-Souza, & Solferini, 2020), which might be the case of *F. gravida*, given its presumed low dispersal capacity (Calderon et al., 2000). Taschima et al., (2021) failed to detect variation among the coastal sampling sites, but the employed markers may lack resolution to identify this differentiation. Our results were able to show a coherent phylogeographic pattern in the Brazilian clade in most datasets, suggesting genetic variation among coastal populations. More comprehensive sampling of individuals from each populations should clarify the patterns of connectivity, admixture, and the potential for clade-level divergence within the Brazilian coral *F. gravida*.

Conclusions

Coalescent-based analysis, which is less sensitive to the effects of LBA and ILS, and properly factors heterozygosity into phylogenetic inference, recovered *F. gravida* as paraphyletic with respect to its congener, *F. fragum* with high support. This paraphyly probably stems from misidentification of the Ascension clade caused by the variable morphology of the genus, which also led to *F. gravida* being previously recognized as a morphotype of *F. fragum*. Ascension and St. Helena Islands form the mid-Atlantic Province, a highly isolated region with high rates of endemism that probably have very reduced connectivity with the west Atlantic, especially for species with low dispersal potential. The recognition of three distinct *Favia* genetic lineages within the South Atlantic will upgrade the estimates of rates of endemism for these biogeographic regions. Also, our results highlight the need to update the status of the Atlantic *Favia* in the IUCN Red List, since a single species with an Amphi-Atlantic distribution and a threat status recorded as “least concern” is listed. If accepted as a separate species, the geographic range reduction for the Ascension Island may lead to this lineage being reassesed as “near threatened”, and population dynamic analyses are needed to improve estimates of demographic parameters that will give further support for this reassessment. At the very least, our results show that each of these regions requires an independent management strategy given the presumed genetic isolation among them.

Acknowledgements

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nivel Superior - Brasil (CAPES). Samples of *Favia gravida* were collected with support

from Fundação O Boticário de Proteção à Natureza's grant awarded to MSB (FBPN 1040-20151). Samples of *Favia fragum* were collected with support from National Science Foundation (DEB-05-43661) awarded to DBC. Lab work and sequencing was funded with support from National Science Foundation (NSF 1416889 & 1924604) awarded to RJT. We thank Carla Zilberberg and Mariane Teschima for providing Ascension Islands samples, and Ana Paula Winter and Julian Olaya Restrepo for field assistance. We also thank Zac Forsman for suggestions that improved the manuscript.

Supplemental data

Table S1 - Geographic distribution of specimens in this study

Species	Sample	Location	Coordinates
Favia fragum (Short morphotype)	HBD16	Hospital Bight, Panama	-9.30.-82.14
Favia fragum (Tall morphotype)	HBS4	Hospital Bight, Panama	-9.30.-82.14
Favia gravida	181	Rio Grande do Norte, Brazil	-5.39.-35.25
Favia gravida	246	Pernambuco, Brazil	-8.73.-35.08
Favia gravida	99	Espírito Santo, Brazil	-20.01.-40.15
Favia gravida	378	Ceará, Brazil	-3.71.-38.82
Favia gravida	FN286	Fernando de Noronha, Brazil	-3.85.-32.44
Favia gravida	S002	Bahia, Brazil	-17.89.-38.82
Favia gravida	ASC12	Ascension Island	-7.93.-14.36
Mussismilia hispida (outgroup)	352	Ceará, Brazil	-3.59.38.39

Table S2 - Assembly information for genomes used in the local Scleractinian BLAST database.

species	assembly	size_Mbp
acropora_acuminata	GCA_014633975.1	394
acropora_awi	GCA_014634005.1	428
acropora_digitifera	GCF_000222465.1	447
acropora_cytherea	GCA_014634045.1	426
acropora_millepora	GCA_004143615.1	386
astreopora_myriophthalma	GCA_014634185.1	373
montipora_capitata	GCA_006542545.1	614
montipora_cactus	GCA_014634245.1	652
acropora_echinata	GCA_014634105.1	401
acropora_florida	GCA_014634605.1	442
acropora_gemmifera	GCA_014634125.1	400
acropora_hyacinthus	GCA_014634145.1	447
acropora_intermedia	GCA_014634585.1	416
acropora_microphthalma	GCA_014634165.1	383
acropora_muricata	GCA_014634545.1	420
acropora_nasuta	GCA_014634205.1	416
acropora_selago	GCA_014634525.1	392
acropora_tenuis	GCA_014633955.1	403
acropora_yongei	GCA_014634225.1	438
montipora_efflorescens	GCA_014634505.1	643
orbicella_faveolata	GCA_002042975.1	485
pocillopora_damicornis	GCA_003704095.1	234
pocillopora_verrucosa	GCA_014529365.1	380
porites_rus	GCA_900290455.1	470
stylophora_pistillata	GCA_002571385.1	400
galaxea_fascicularis	gfas_v1.0	325
porites_lutea	plut_v1.1	536
fungia_spp	ffun_v1.0	588
goniastrea_aspera	gasp_v1.0	742
seriatopora_hystrix_mt	NC_010244	0.017
mussa_angulosa_mt	DQ643834	0.018
plesiastrea_versipora_mt	NC_042481.1	0.016
turbinaria_peltata_mt	NC_024671.1	0.019
echinophyllia_aspera_mt	NC_040169.1	0.018
alveopora_japonica_mt	NC_040136.1	0.019
pseudosiderastrea_formosa_mt	NC_026530.1	0.02
pavona_decussata_mt	NC_026527.1	0.019
euphyllia_ancora_mt	NC_015641.1	0.019
fungiacyathus_stephanus_mt	JF825138.1	0.02
astrangia_spp_mt	DQ643832.1	0.015
colpophyllia_natans_mt	DQ643833.1	0.017

Table S3 - Sequencing coverage for each sample.

Sample	Average depth	Standard deviation
FF_PA_HBD16	16.62	77.08
FF_PA_HBS4	17.11	66.21
GR_RN_181	12.47	72.67
GR_PE_246	13.64	52.86
GR_ES_99	18.17	71.16
GR_CE_378	10.81	43.22
GR_ASC12	15.94	77.25
GR_FN286	11.24	41
GR_BA_S002	8.69	41.64
MC_CE_352	8.2	39.22
Total	13.29	58.23

Table S4 - Number of ultraconserved element (UCE) loci retained in matrices according to minimum taxon occupancy. PIS - parsimony informative sites.

% Matrix	UCE loci count	Alignment length	Mean aligned locus length	PIS count
75	580	209,432	361	796
90	233	80,801	346	221
100	89	29,850	335	89

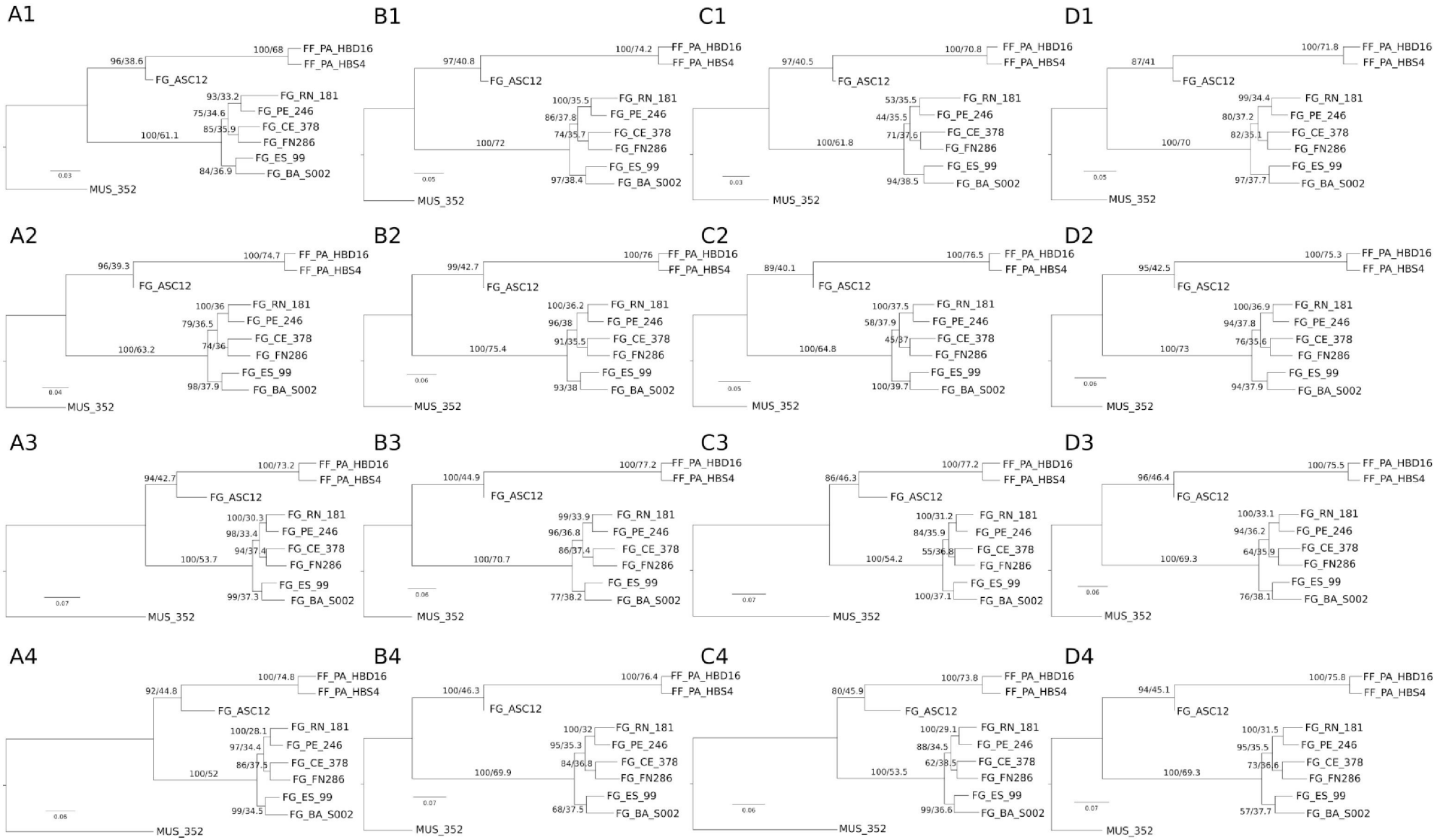

Figure S1 - Maximum likelihood (ML) tree of Atlantic *Favia* generated in IQTREE. Phylogeny based on datasets with minimum mean depth = 10. (A) *Holobiont* datasets with minor allele count = 2. (A1) 0% missing data; (A2) 10% missing data; (A3) 20% missing data; and (A4) 30% missing data. (B) *Holobiont* datasets with minor allele count = 3. (B1) 0% missing data; (B2) 10% missing data; (B3) 20% missing data; and (B4) 30% missing data. (C) *Coral* datasets with minor allele count = 2. (C1) 0% missing data; (C2) 10% missing data; (C3) 20% missing data; and (C4) 30% missing data. (D) *Coral* datasets with minor allele count = 3. (D1) 0% missing data; (D2) 10% missing data; (D3) 20% missing data; and (D4) 30% missing data. *Mussismilia hispida* was used as an outgroup.

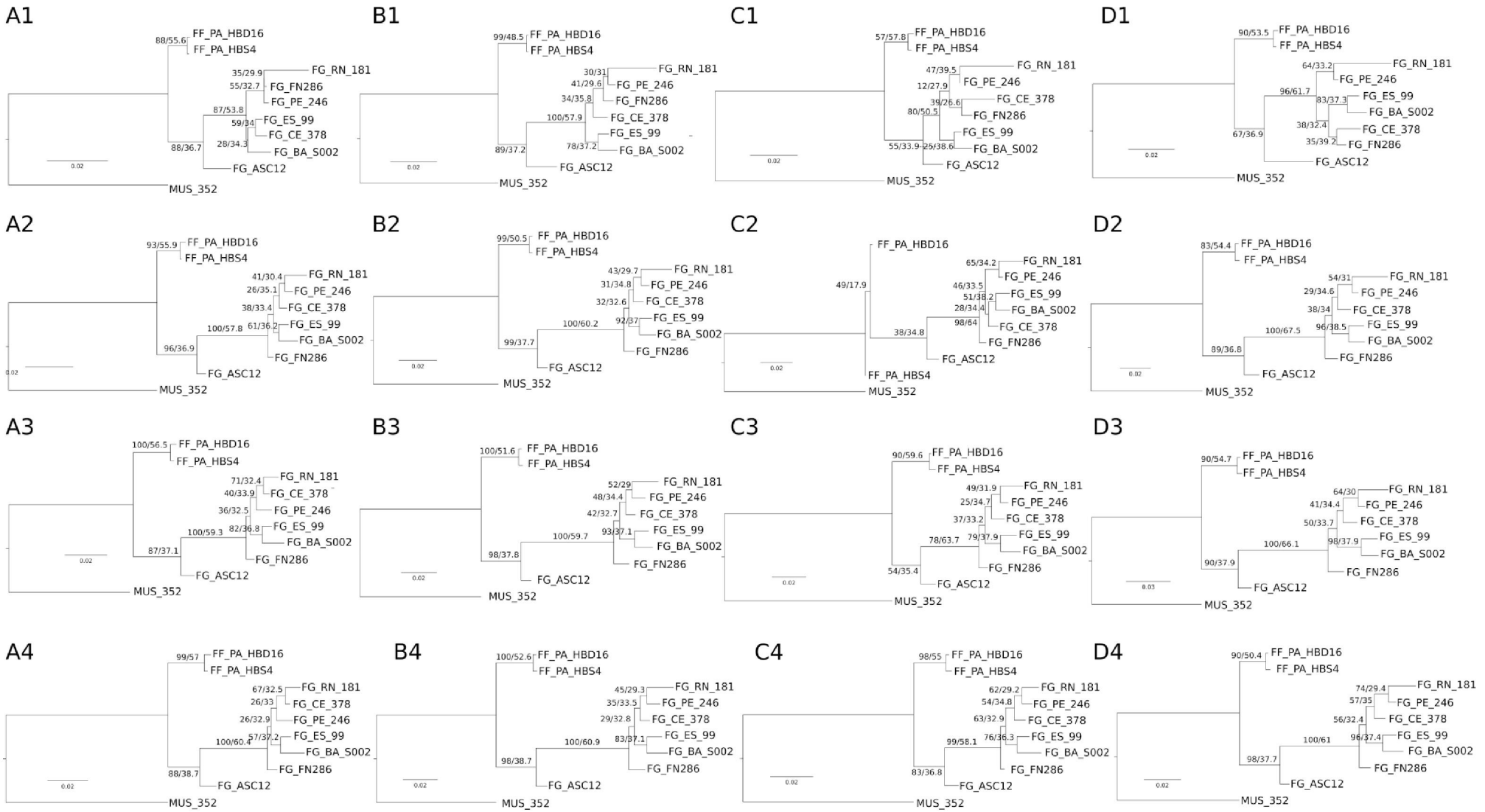

Figure S2 - Maximum likelihood (ML) tree of Atlantic *Favia* generated in IQTREE. Phylogeny based on datasets with minimum mean depth = 20. (A) *Holobiont* datasets with minor allele count = 2. (A1) 0% missing data; (A2) 10% missing data; (A3) 20% missing data; and (A4) 30% missing data. (B) *Holobiont* datasets with minor allele count = 3. (B1) 0% missing data; (B2) 10% missing data; (B3) 20% missing data; and (B4) 30% missing data. (C) *Coral* datasets with minor allele count = 2. (C1) 0% missing data; (C2) 10% missing data; (C3) 20% missing data; and (C4) 30% missing data. (D) *Coral* datasets with minor allele count = 3. (D1) 0% missing data; (D2) 10% missing data; (D3) 20% missing data; and (D4) 30% missing data. *Mussismilia hispida* was used as an outgroup.

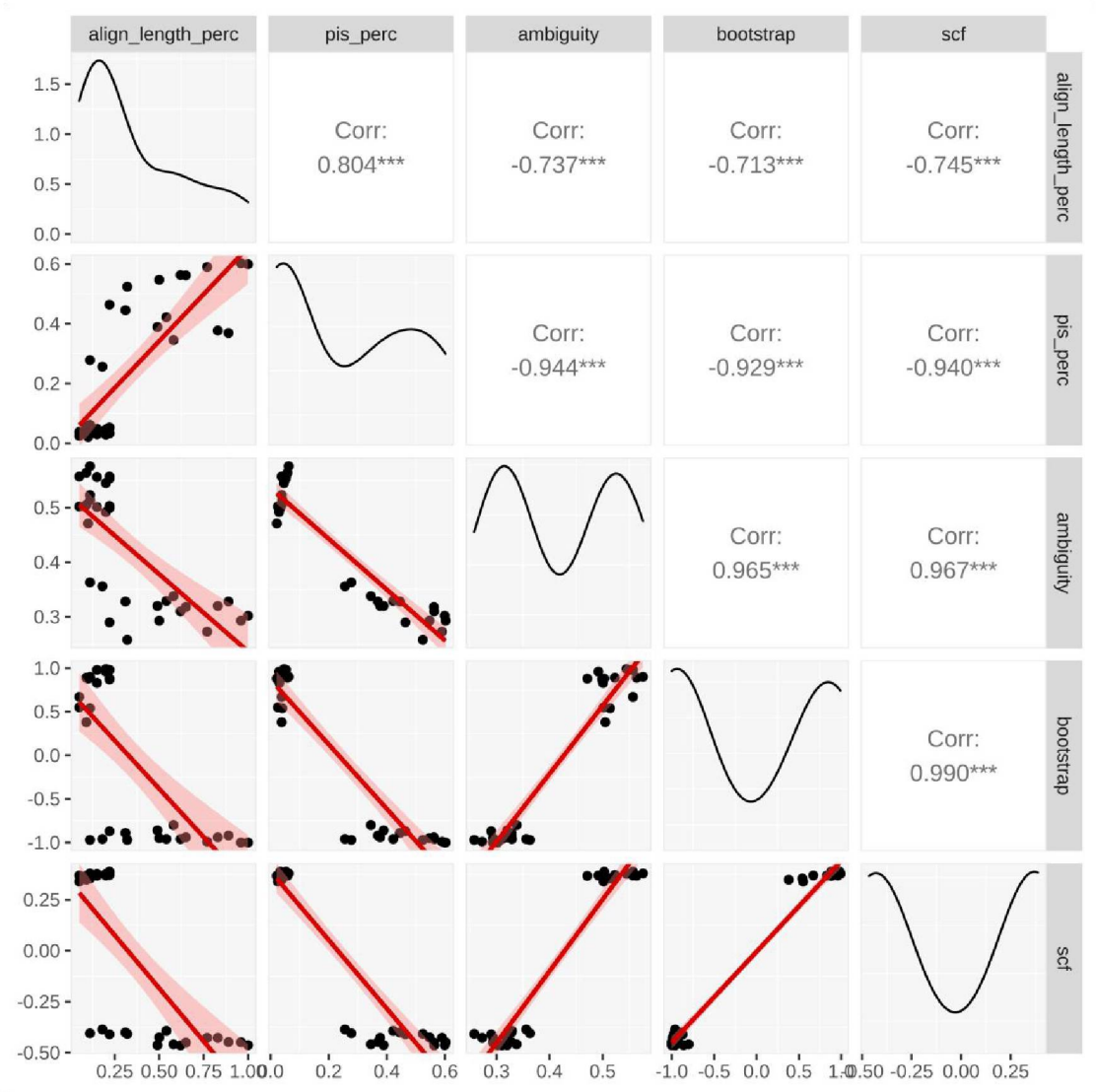

Figure S3 - Correlation analysis between variables influencing concatenation-based phylogenetic reconstructions. Lower triangle with scatter plots, upper triangle with correlation coefficients, and diagonal shows histograms of the data. All values were scaled to 1. Ultrafast bootstrap and site concordance factors (sCF) for the *F. fragum* + Ascension clade are coded as negative values.

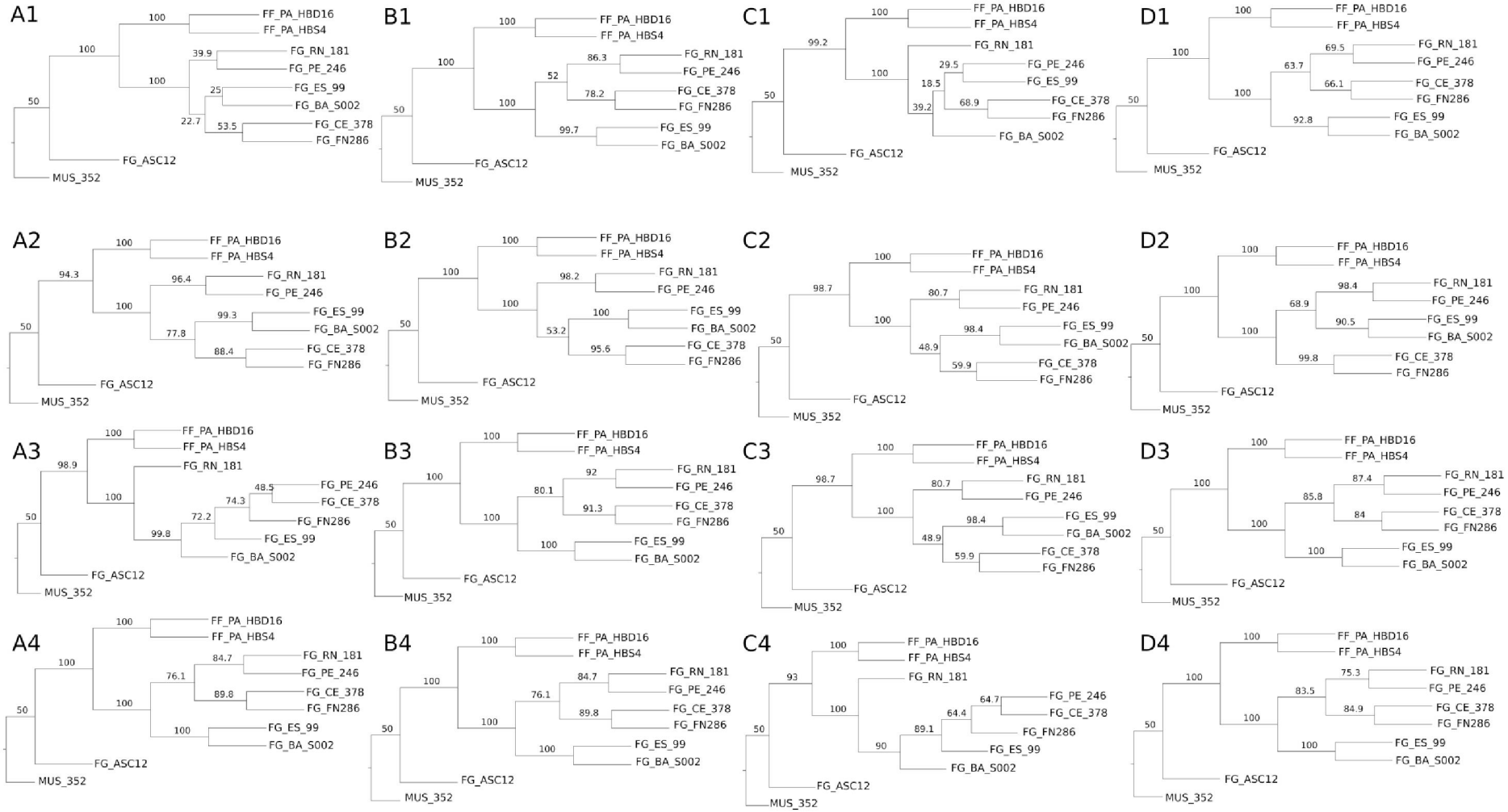

Figure S4 - Lineage tree of Atlantic *Favia* generated in SVDQuartets. Phylogeny based on datasets with minimum mean depth = 10. (A) *Holobiont* datasets with minor allele count = 2. (A1) 0% missing data; (A2) 10% missing data; (A3) 20% missing data; and (A4) 30% missing data. (B) *Holobiont* datasets with minor allele count = 3. (B1) 0% missing data; (B2) 10% missing data; (B3) 20% missing data; and (B4) 30% missing data. (C) *Coral* datasets with minor allele count = 2. (C1) 0% missing data; (C2) 10% missing data; (C3) 20% missing data; and (C4) 30% missing data. (D) *Coral* datasets with minor allele count = 3. (D1) 0% missing data; (D2) 10% missing data; (D3) 20% missing data; and (D4) 30% missing data. *Mussismilia hispida* was used as an outgroup.

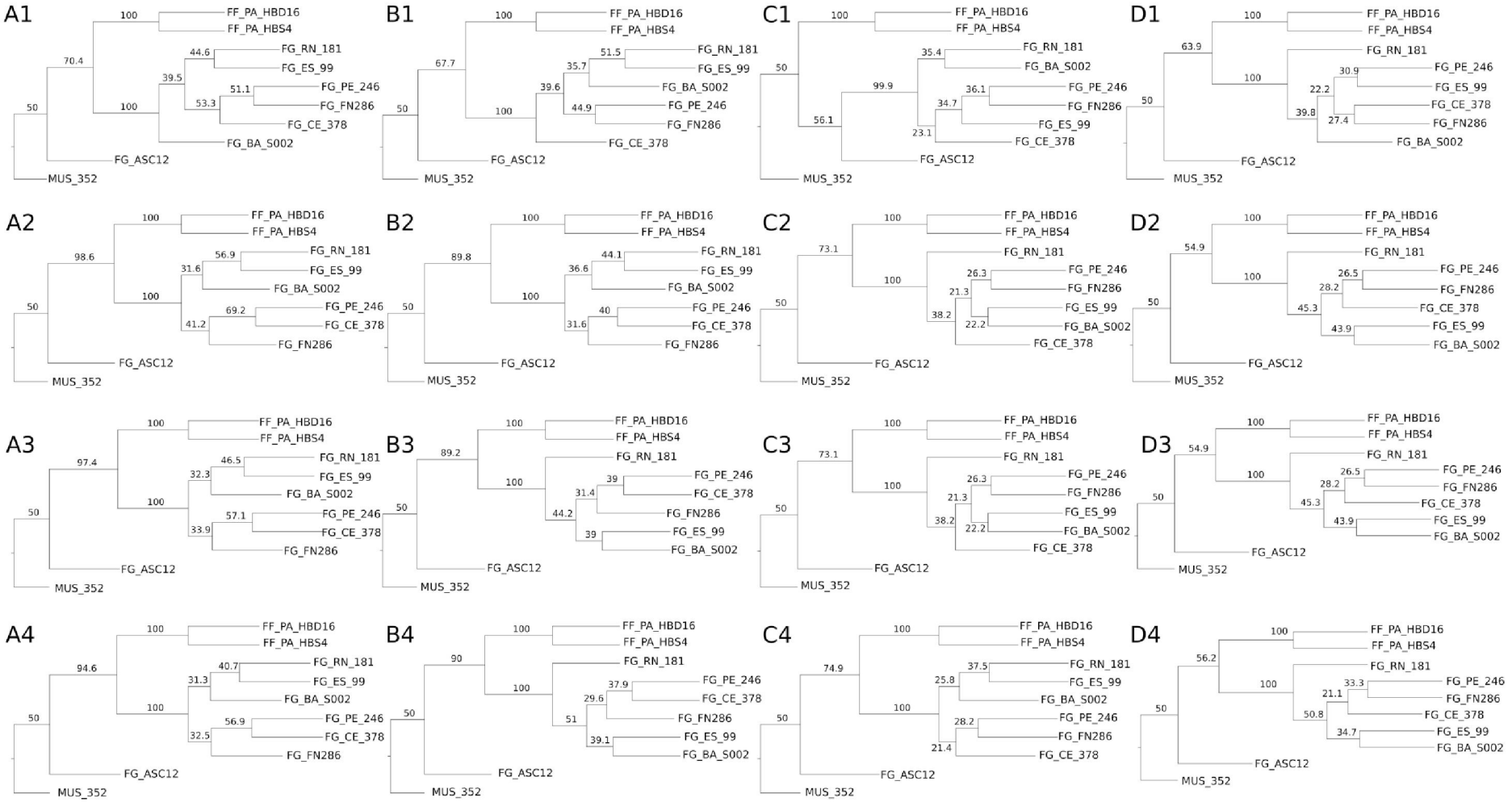

Figure S5 - Lineage tree of Atlantic *Favia* generated in SVDQuartetsE. Phylogeny based on datasets with minimum mean depth = 20. (A) *Holobiont* datasets with minor allele count = 2. (A1) 0% missing data; (A2) 10% missing data; (A3) 20% missing data; and (A4) 30% missing data. (B) *Holobiont* datasets with minor allele count = 3. (B1) 0% missing data; (B2) 10% missing data; (B3) 20% missing data; and (B4) 30% missing data. (C) *Coral* datasets with minor allele count = 2. (C1) 0% missing data; (C2) 10% missing data; (C3) 20% missing data; and (C4) 30% missing data. (D) *Coral* datasets with minor allele count = 3. (D1) 0% missing data; (D2) 10% missing data; (D3) 20% missing data; and (D4) 30% missing data. *Mussismilia hispida* was used as an outgroup.

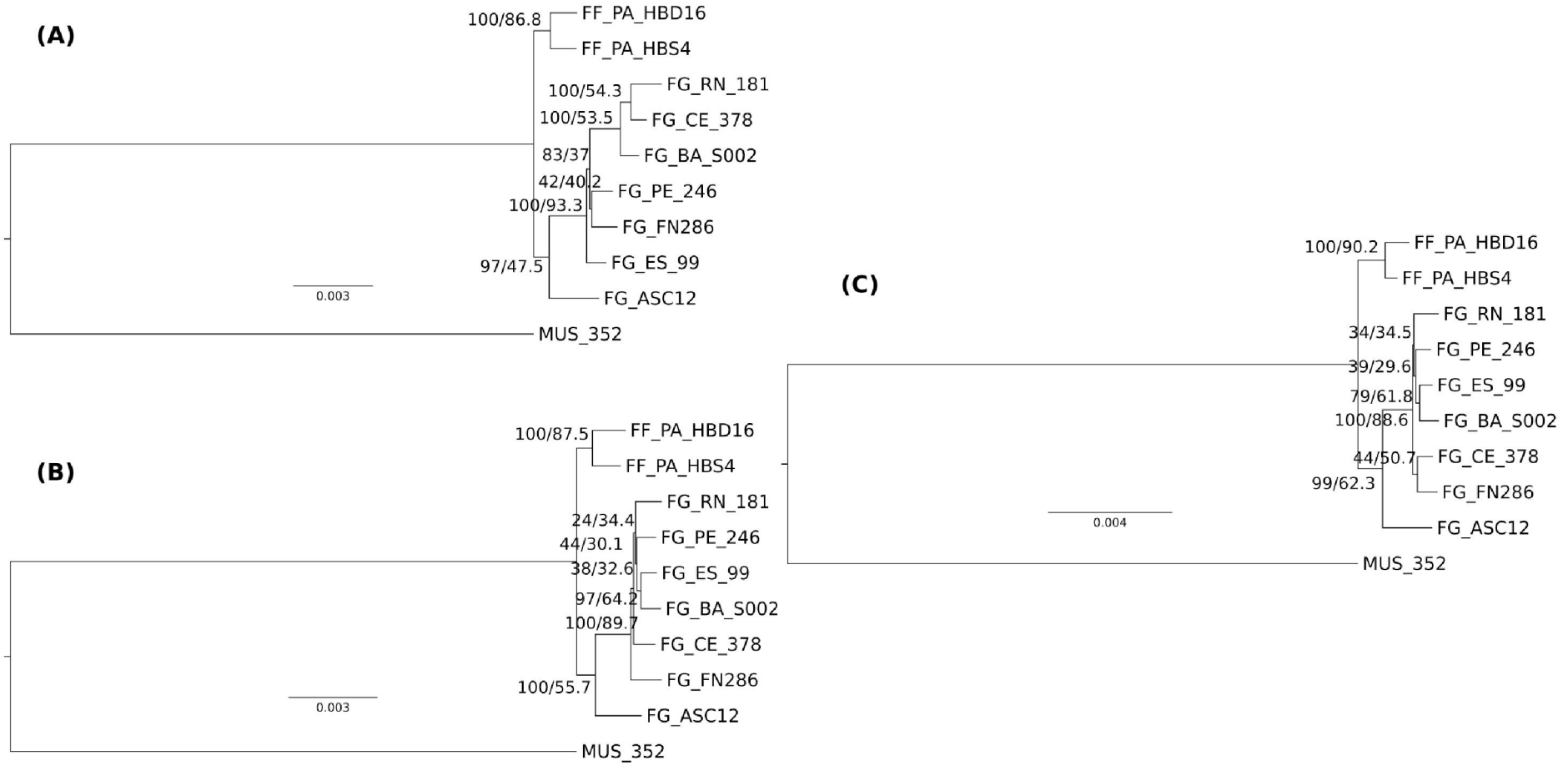

Figure S6 - Maximum likelihood (MI) trees of Atlantic *Favia* generated in IQTREE for UCE datasets. Phylogenies based on (A) 75% taxon occupancy; (B) 90% taxon occupancy; and (C) 100% taxon occupancy. Numbers on branches represent bootstrap support/site concordance factor. *Mussismilia hispida* was used as an outgroup.

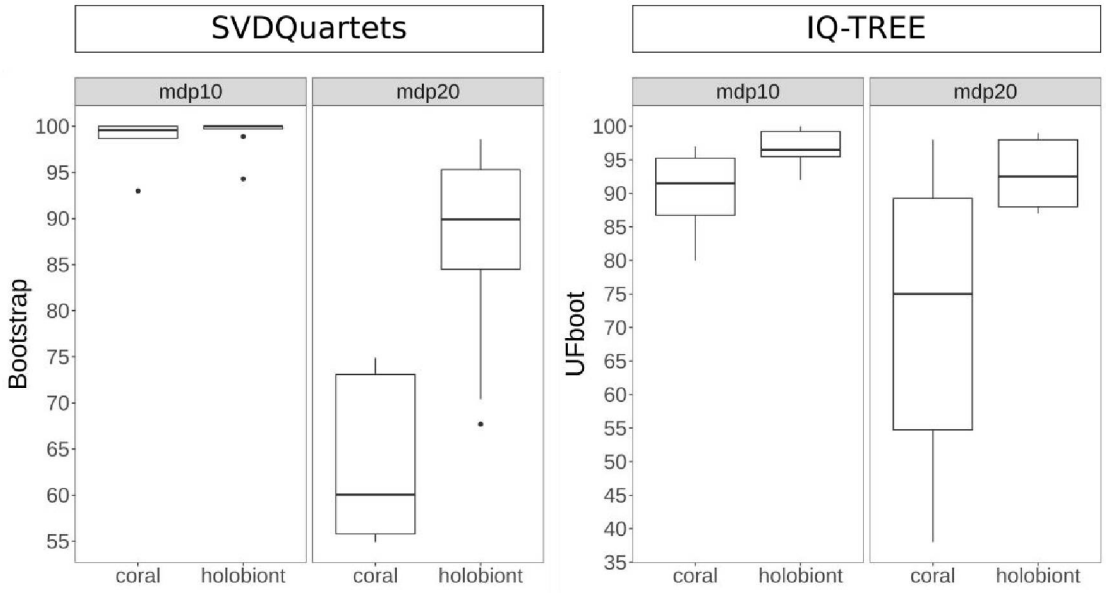

Figure S7 - Boxplot of branch support values for *coral* and *holobiont* datasets used in concatenation and coalescent-based analyses. mDP - minimum mean depth; UFboot - ultrafast bootstrap.

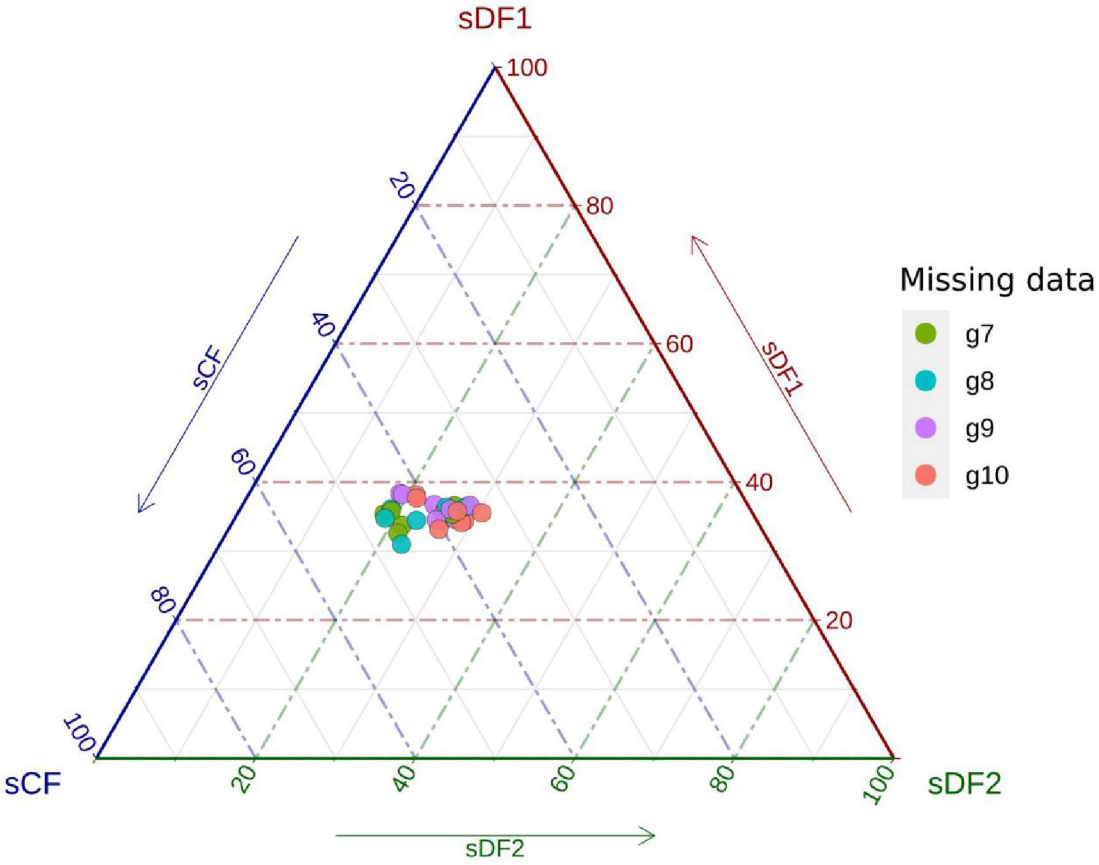

Figure S8 - Ternary plot showing the distribution of site concordance (sCF) and the two site discordance factors (sDF1 and sDF2) for the backbone topology obtained from different percentages of missing data in the analysis of SNP data performed in IQTREE. G10 - 0% missing data; G9 - 10% missing data - G8 - 20% missing data; and g7 - 30% missing data.

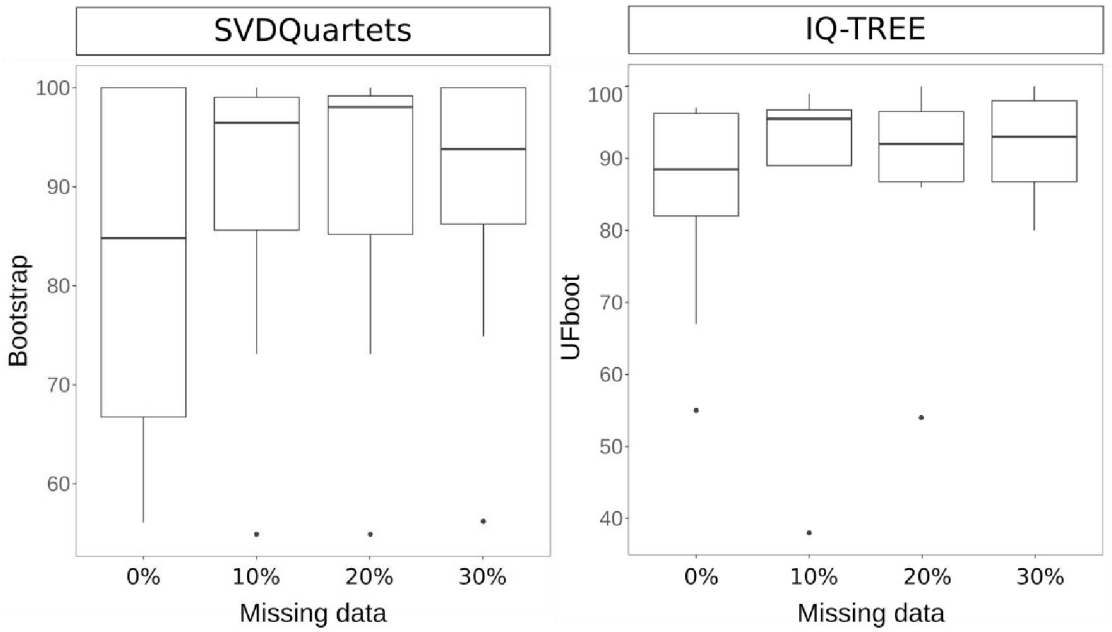

Figure S9 - Boxplot of bootstrap branch support values for each missing data threshold applied to datasets used in concatenation and coalescent-based analyses. UFboot - ultrafast bootstrap.

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Chapter II: Genetic structure and phylogeography of the Atlantic stony coral *Favia* (Scleractinia, Faviidae)

Abstract

Scleractinian corals are sensitive to environmental variation and are directly affected by changes in their habitat. Knowledge on metapopulation dynamics is essential to understand the drivers of population genetic diversity, adaptation and resilience. These metrics might also be used to design management plans aiming at mitigate the effects of environmental stressors such as local anthropization, overfishing, disease and global warming on coral reefs. We employed single nucleotide polymorphisms (SNPs) recovered via ezRAD, a subset of the reduced representation sequencing (RADseq) approaches, to assess population structuring within the Atlantic genus *Favia*. Regardless of varying levels of missing data, four main genetic clusters were recovered: *F. fragum* from the Caribbean, *F. gravida* from Ascension Island, and two Brazilian populations of *F. gravida*. AMOVA revealed genetic structuring among the Caribbean, Brazil, and Ascension, with significant differences among sampling sites within regions. Hierarchical structuring analysis of datasets with increasing missing data provided more resolution into geographically coherent subpopulations. We obtained significant isolation by distance across *Favia* spp. populations, but Brazilian populations seem to be structured by geographic barriers created by river discharge and not exclusively by distance. Within Brazil, allelic richness and gene diversity were higher in the east population of Aracruz (ES), followed by the Abrolhos Bank, which was hypothesized to have served as a refugium for modern scleractinians during periods of low sea level. Our results uncovered previously unknown structuring between East and Northeast populations of *F. gravida*, corroborate the hypothesis that Abrolhos acted as a refuge to the Brazilian coralline fauna in the past, and suggest that the Ascension Island population requires extra attention in conservation planning due to its genetic isolation.

Keywords: single nucleotide polymorphisms, ezRAD, isolation by distance, refugium, genetic isolation

Introduction

Population connectivity in the marine environment is highly influenced by factors such as oceanic currents, larval behavior (Cowen, Paris & Srinivasan, 2006), pelagic larval duration and geographic distance (Selkoe & Toonen, 2011). For many benthic animals, such as Scleractinian corals, the movement of individuals between different populations is largely, but not exclusively, restricted to the free-living larval stage, which can limit their dispersal capacity (Cowen & Sponaugle, 2009). In these cases, some populations are unable to recover

after local extinction events. This happens not because their habitat is unsuitable, but because insufficient recruits reach these populations due to their isolation (Taylor et al. 1993). Considering that the extent of genetic exchange between coral populations is a good proxy to coral resilience, knowledge on metapopulation connectivity patterns and gene diversity is fundamental to identify isolated reefs and estimate their relative importance to the overall genetic diversity (Hellberg et al. 2002; Van Oppen and Gates, 2006). Such measures are essential to fully understand how species respond to environmental stressors, such as overfishing, pollution, disease and local anthropization (Harvel et al. 2007; Zaneveld et al. 2016; Carlson, Foo, and Asner, 2019), and help predict how these species will react to global environmental shifts, especially considering the risk upon marine organisms facing climate change (Doney et al. 2012). Ultimately, these data may be incorporated into conservation and management plans that target at-risk populations in their mitigation strategies as a way of reducing the likelihood of extinction (Almany et al. 2009; DeWoody et al. 2021; Endo et al. 2019).

Brazilian reefs span more than 3,000 km along the coastal region, forming the only true coral reefs of the South Atlantic, harboring 23 species of symbiotic scleractinian corals, six of which are endemic to Brazil (reviewed in Leão et al. 2016). Unlike the framework of the Caribbean reefs, mainly formed by coralline algae and corals (Montaggioni 2005), it was recently discovered that the Abrolhos Bank, the largest reef structure of the South Atlantic, was built primarily by bryozoans, with a secondary contribution of corals and hydrocorals (Bastos et al. 2018). Unlike Caribbean and Indo-Pacific reefs, which are more diverse and dominated by corals with branching morphologies, species with massive morphology are the most abundant in Brazilian reefs (Leão, Kikuchi and Testa, 2003). The more prevalent scleractinians, such as the genus *Mussismilia*, present large corallites, a trait tightly linked to the resistance of massive colonies to high sedimentation and turbidity (Loiola, Oliveira and Kikuchi, 2013; Sanders and Baron-Szabo, 2005). The unique coral assemblages of the Southwestern Atlantic have evolved to inhabit an environment that could be considered challenging for other scleractinians (Leão, Kikuchi and Testa, 2003), such as the inshore shallow reefs of the eastern coast of Brazil, which are heavily affected by riverine sediment input, mostly terrigenous sand and mud (Bastos et al. 2015; Domingues 2009; Vieira et al. 2019). These river deltas may act as barriers to the dispersion of reef organisms. For instance, the São Francisco and Doce river deltas possibly restrict the geographic distribution of *Millepora* spp. (Souza et al. 2017) and the distribution of *Mussismillia hispida* endosymbionts (*Symbiodinium* spp. - Picciani et al. 2016).

One of these species is the brooding coral *Favia gravida* (Verril, 1868), frequently found in shallow intertidal pools, but occasionally in deeper reefs up to 15m (Leão et al. 2003; Teschima et al. 2019; Table 1), presenting high morphological plasticity both within and between populations (Laborel 1971; Amaral & Ramos, 2007). Information on the dispersal potential and the connectivity patterns among *F. gravida* populations is scarce. Although presenting multiple events of larval release per year, the larvae of *F. gravida* remain in the water column only for a short period of time (Calderon, Castro and Pires, 2000). Because the larvae are likely to settle in proximity to the "mother" colony, they are presumably unable to exchange recruits with distant populations, reducing gene flow (Jones et al. 2009). Indeed, Nunes, Norris and Knowlton (2011) and Teschima et al. (2021) recovered signifficant genetic diferentiation among *F. gravida* populations, but the first study lack spacial resolution and the later, which had a comprehensive geographic range and did not recovered genetic differentiation along the Brazilian coast, lacked marker resolution. Hence, the results may not be a good representation of the populational structuring within this species. Furthermore, evidence of incipient speciation between two morphotypes of *F. fragum* across a depth gradient and habitat partitioning (Carlon and Budd 2002; Carlon and Lippé, 2011) indicates that genetic structuring in the species occurs even in small geographic scales. Also, the occurrence of selfing within *F. fragum* populations (Carlon and Lippé, 2011), which might lead to reduced genetic diversity, might influence the estimation of other diversity and population differentiation metrics, and ultimately affect population adaptation (Hartfield, Bataillon, and Glémin, 2017; Awad and Roze, 2018; Jullien et al. 2019).

Here, we examine the patterns of population differentiation in the Atlantic *Favia* spp. based on robust single nucleotide polymorphism (SNP) data obtained through ezRAD, a reduced representation sequencing (RADseq) approach tailored for the study of non-model organisms (Toonen et al. 2013). We assessed the occurrence of gene flow between the Caribbean *F. fragum* and Southeastern Atlantic *F. gravida*, including a population from the isolated Ascension Island, at the mid-Atlantic Province, which is likely a divergent lineage within the Atlantic *Favia* (Teschima et al. 2021; Chapter I). Given the restricted dispersion capacity of *Favia* and its phylopatric settlement behavior, we expect to recover high genetic differentiation among these three provinces. Furthermore, given the large number of river deltas and the influence of ocean currents along the coast, we also expect to recover significant genetic structuring within the Brazilian *Favia*. Finally, given the evidence from single marker analyses, we expect to recover genetic structuring between the two *F. fragum* morphotypes.

Methods

Sampling

We selected individuals from each of eight populations of *Favia gravida*, seven from the Brazilian coast and one from Ascension Island, located at the mid-Atlantic ridge between Brazil and Africa, and two populations of the Caribbean *Favia fragum*, from Panama, corresponding to the two different morphotypes identified by Carlon and Budd (2002) (Figure 1, Table 1). These two morphotypes, designated Tall and Short, occur at extremes of a 5.0m depth gradient and are also partially isolated in seagrass and reef habitats, respectivelly (Carlon et al. 2011). Colony fragments were collected by snorkeling and/or SCUBA. Coral tissue samples were preserved in DMSO solution (Gaither et al., 2011) or 90% alcohol and stored at -20°C until extraction.

Table 1 - Geographic distribution and number of samples (N) of *Favia* sequenced for the study. Sampling site codings are used in figures and text.

Species	Region	Sampling site	N	Depth (m)	Code	Lat, Long
F. fragum	Caribbean	Hospital Bight, Panama (short morphotype)	10	3.0 - 5.0	PAS	9.30N, 82.14W
		Hospital Bight, Panama (tall morphotype)	8	1.0	PAT	9.30N, 82.14W
F.gravida	Brazil	Fortaleza, Ceará	8	3.0 - 4.0	FOR	3.71S, 38.82W
		Fernando de Noronha Archipelago, Pernambuco	10	3.0 - 5.0	FN	3.85S, 32.44W
		Maxaramguape, Rio Grande do Norte	8	0.5 - 2.0	MAX	5.39S, 35.25W
		Tamandaré, Pernambuco	10	0.5 - 2.0	TAM	8.73S, 35.08W
		Boipeba, Bahia	11	0.5 - 4.0	BOI	13.58S, 38.82W
		Abrolhos Archipelago, Bahia	9	8.0 - 15.0	ABR	18.20S, 38.78W
		Aracruz, Espirito Santo	2	0.5 - 1.5	ARA	20.01S, 40.15W
	Mid-Atlantic Ridge	Ascension Island	9	-	ASC	7.93S, 14.36W

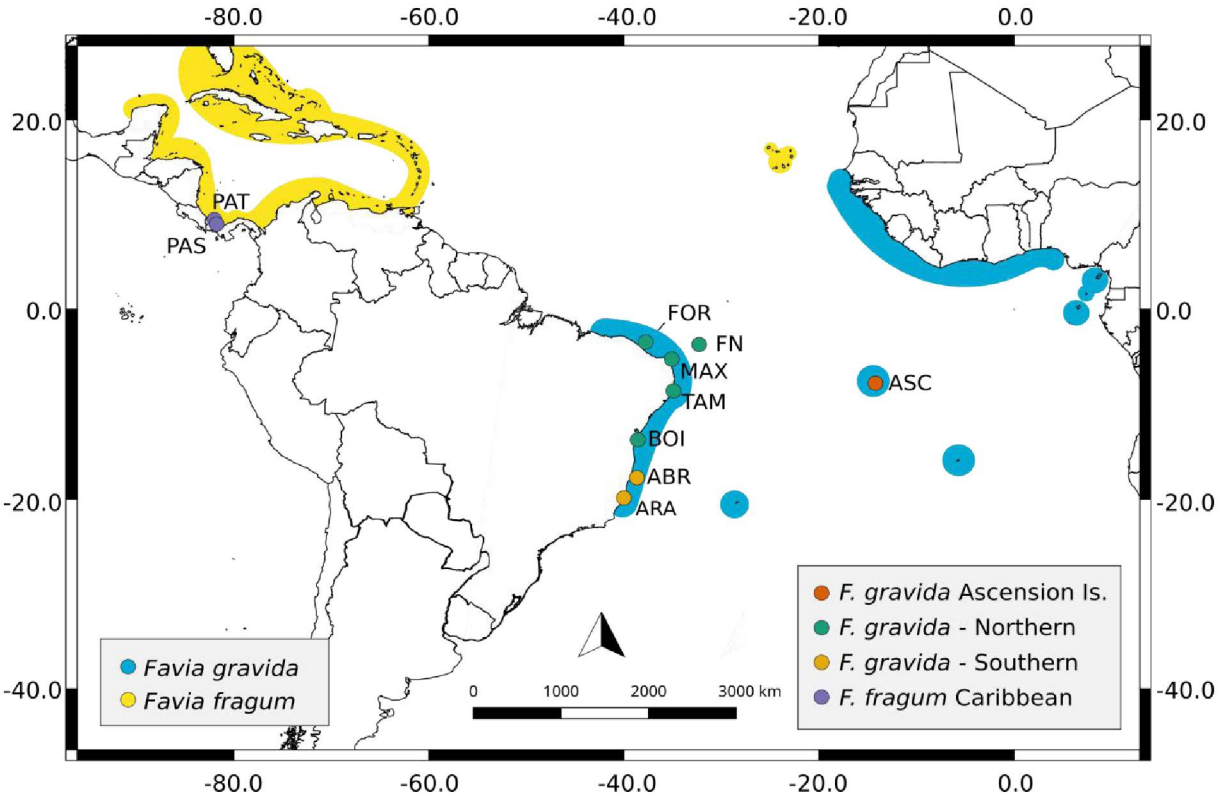

Figure 1 - Known geographic distribution of *Favia fragum* and *F. gravida* samples modified from Aronson et al. (2008). Circles corresponding to sampling sites are color coded according to clusters obtained in the DAPC and sNMF analyses. Sampling sites on the map are coded according to Table 1.

Molecular analysis

We extracted DNA from tissue samples of *F. fragum* using the Omega E.Z.N.A Tissue DNA kit and Invitrogen PureLink Genomic DNA kit in the case of *F. gravida*, following the manufacturers' instructions. Extractions were purified using 1.8X AmPureXP magnetic beads. DNA quality was assessed via electrophoresis in 1.5% agarose gel, ensuring that only high molecular weight DNA was carried over to the digestion step. Quantification was performed using dsDNA High Sensitivity Assay kit in the Qubit 2 Fluorometer.

Libraries were prepared following the ezRAD protocol (Toonen et al. 2013). Briefly, samples were digested using the enzyme DpnII (New England Biolabs), in 50µL reactions containing 5µL DpnII NEB 10X Buffer, 2 units of DpnII, and 200-1000ng of DNA. Digestions were incubated at 37°C for 3 hours, then heat-inactivated for 20 minutes at 65°C, purified using 1.8X AMPureXP beads, and considered successful if their electrophoretic pattern in UV transilluminated 1.5% agarose gels was smear-like. Further steps were performed using the KAPA HyperPrep Library kit (Roche Sequencing Store) following Knapp et al. (2016) with minor modifications. DNA samples were end-repaired and a-tailed, and then adapter ligation was performed using IDT xGen Stubby Adapters and Unique Dual

Index (UDI) primer pairs. Index-ligated products were size selected with Mag-Bind Magnetic Beads (Omega Bio-Tek) targeting fragments in a 350-700bp range in two steps, with DNA:bead ratios of 1:0.6 and 1:0.2, respectively. Samples were amplified using six to ten PCR cycles with KAPA HiFi Hotstart Ready-mix (Omega Bio-Tek) and purified using 1:1 DNA:AMPure XP beads. Libraries were validated using Qubit dsDNA HS kit, Agilent 2100 Bioanalyzer, and qPCR, and sequenced as paired-end (2x150bp) reads on the Illumina HiSeq 4000 sequencer at the Research Technology Support Facility (RTSF) Genomics Core, at Michigan State University.

Bioinformatics

We assessed raw read quality with FASTQC (Andrews, 2010) and subsequent processing was performed with the bioinformatic pipeline dDocent (Puritz et al. 2014). The dDocent software is faster, has a smaller memory footprint and result in loci with better taxon coverage than other widely used RADseq pipelines (Jungwirth, 2017). First, universal adapters and reads with Phred <30 were excluded from further analyses. We randomly chose three individuals from each population to create the *de novo* assembly reference onto which all samples would be mapped. We used dDocent scripts ReferenceOpt.sh and RefMapOpt.sh to select the optimal combination of parameters for the *de novo* assembly, aiming at maximizing the number of paired mapping reads while minimizing the number of mismatched reads. We set the minimum level of similarity among sequences in the same cluster, or clustering threshold (*c*), to 90%, minimum within individual coverage level (*k1*) to 3, and the minimum number of individuals sharing a read (*k2*) to 4. Within dDocent, sequences from all individuals were mapped against the reduced representation reference and SNPs were called using FreeBayes (Garrison and Marth, 2012). We performed a local BLAST against complete genomes of *Breviolum*, *Cladocopium*, *Fugacium*, and *Symbiodinium* species in order to detect and remove endosymbiont contamination. To create an exclusively coral dataset we also BLASTed the reference contigs against a local scleractinian database assembled from 29 nuclear and 12 complete mitochondrial coral genomes (listed in Table S2 - Chapter I).

The resulting raw variant call files (VCF) were filtered using VCFTools (Danecek et al. 2011). We applied a minimum quality filter of 30 and a minimum mean depth of 3, then removed individuals with more than 55% missing loci and kept only loci with no more than 10% missing data. Finally, we filtered out alleles with minor allele frequency of <0.01 and kept a single SNP per locus.

Population structure

Population structure was further assessed with two multivariate methods: non-negative matrix factorization (sNMF) and discriminant analysis of principal components (DAPC). The implementation of DAPC in *adegenet* (Jombart & Collins, 2011) subjects the SNP matrix to a PCA and performs DA on a optimum number of the first principal components, selected via cross-validation (leave out) procedure. We used two approaches to define the groupings for DAPC: *a priori* information of sampling sites and the optimal number of clusters estimated by *k*-means clustering analysis. The sNMF approach was carried out with the R package LEA (Frichot & François, 2015). The program estimates the proportion of the genome from each sample that originated from a certain number of gene pools, or putative ancestral populations (*k*). The ancestry coefficients were estimated for 1-10 ancestral populations, and the optimal value of *k* was selected based on the cross-entropy criterion (CEC) after 100 replicates for each *k* value. To detect fine-scale genetic substructure we performed the analysis hierarchically, starting with the full dataset and subsequently removing the more divergent populations/clusters in each round. To test for possible effects of missing data, the analyses were run on datasets with 0%, 10% and 20% missing data.

The existence of isolation by distance (IBD) was assessed with a Mantel test performed with the R package *vegan* (Dixon, 2003), comparing matrices of pairwise genetic and geographic distances based on 1,000 permutations. For the genetic distances, we calculated pairwise Fst/(1-Fst) values and geographic distances in kilometers were approximated as the shortest distances connecting sampling sites by sea using Google Earth (Gorelick et al. 2017). We tested four strata, considering different spatial scales: *F. fragum* and *F. gravida* from all sampling sites; only *F. gravida* samples, including Brazil and Ascension Island; only *F. gravida* from the Brazilian coast, and only the Northeast Brazilian population identified by the sNMF and DAPC.

Genetic diversity

We estimated the number of private alleles, rarefied allelic richness, Nei's gene diversity (expected heterozygosity - Nei, 1973), and pairwise Fst (Weir and Cockerham, 1984) with the R packages *hierfstat* (Goudet, 2005) and *poppr* (Kamvar, Tabima and Grünwald, 2014) for the sampling sites and also the clusters recovered in the populations structure analysis. To avoid bias due to variable sampling sizes, private alleles were estimated using subsamples based on the smaller sample size within the populations. To verify if there is association

between alleles we estimated the standardized index of association (r_d), which accounts for the number of loci sampled, and detect signatures of linkage disequilibrium (LD) among loci (Agapow and Burt, 2001). Significance was assessed from a one-sided permutation test. Fst-based analysis of molecular variance (AMOVA; Excoffier, Smouse and Quattro, 1992) was implemented with the R packages *ade4* (Dray and Dufour, 2007) and *poppr*, to test for the existence of genetic structuring both among regions (mid-Atlantic ridge, Brazilian coast, and the Caribbean) and among sampling sites within regions (Table 1). The significance was assessed using a Monte Carlo test employing 1,000 permutations.

Phylogeographic analysis

Phylogenetic trees were estimated with a concatenation-based analysis in IQ-TREE v.2.1.2 (Minh et al., 2020) under TVM (transversion model) and the FreeRate model of heterogeneity across sites (Soubrier et al. 2012), selected with the aid of ModelFinder (Kalyaanamoorthy et al., 2017). Branch support was assessed using the 1,000 ultrafast bootstrap (UFboot) replicates and we computed site concordance factors (sCF) as an additional measure of branch support (Mihn, Hahn, & Lanfear, 2020). Coalescent-based analysis was performed in SVDquartets (Chifman and Kubatko, 2014), implemented in PAUP* 4.0 (Swofford, 2001) employing exaustive quartet search and 100 bootstrap pseudoreplicates. Ascension Island samples were used as outgroup, in accordance with results from Chapter I.

Results

Bioinformatics

A total of 85 individuals were successfully sequenced. FASTQ files had an average of 3,6 million 151bp reads per library. After trimming and removal of low-quality reads, the dataset consisted of 1,654,067 raw SNPs with an average sequencing depth of 18X. A total of 157 contigs that blasted against the Symbiodiniaceae database were removed from further analyses, resulting in the holobiont dataset. The coral (host) dataset consisted of 862,411 SNPs contained in contigs that successfully blasted against our local Scleractinian database. Seventeen samples with >55% missing loci were removed from further analyses. After the remaining filtering steps, we created subsets of the data with different amounts of missing data (Table 2).

Table 2 - SNP count for each dataset containing different percentages of missing data.

Dataset	Missing data (%)	SNP count	
		Holobiont	Coral
G8	20	21,691	10,159
G9	10	8,617	3,612
G10	0	1,429	998

Since there are no available reference genomes for Atlantic Favia or for any other Atlantic Faviidae, and only 157 of our unique contigs BLASTed against endosymbiont genomes, the most common biological contaminant in coral samples, with significantly larger genome size (Table S1), we believe that most of the remaining contigs in the holobiont dataset belong to coral DNA that was not represented in our local database. Given that both holobiont and coral datasets recovered the same patterns of population structure (Figure S1), with the holobiont providing more resolution possibly due to the larger number of SNPs, we will present only the results from the holobiont datasets in the following sections.

Population structure

The sNMF analysis of the dataset with no missing data (*g10*) recovered four distinct ancestral gene pools (k = 4): *F. fragum* from Panamá, *F. gravida* from Ascension Island in addition to East (BR East) and Northeast (BR Northeast) Brazilian *F. gravida* populations (Figure 2A). All populations showed some level of admixture, especially between BR Northeast and BR East. The alignment with 10% missing data (*g9*) provided enhanced resolution within the Brazilian coast, recovering Fernando de Noronha Archipelago as a separate population (k = 5, Figure 2B). The least filtered alignment, with 20% missing data (*g8*), failed to produce an “elbow-like” cross-entropy plot, resulting in equally low CEC values when k ranged from 5 to 7. Regardless, the pattern was the same across datasets, with higher k values recovering geographically coherent subpopulations nested within the main clusters, except for three individuals from the Short morphotype of *F. fragum*, that were placed in a separate cluster (Figure 2C).

In order to investigate fine-scale genetic structure of *F. gravida* along the Brazilian coast, we performed separate analyses for those samples. The dataset with no missing data again

yielded the lowest resolution. The optimal number of ancestral populations was $k = 2$ according to the *g10* dataset, dividing the Brazilian coast into BR East and BR Northeast populations, with the exception of three individuals from Boipeba (BA) and one sample from Fortaleza (CE) that had a larger percentage of their ancestral gene pool assigned to BR East (Figure 2D). The *g9* dataset recovered four populations: three northeastern subpopulations, plus Fortaleza and the Fernando de Noronha Archipelago (PE) (Figure 2E). The *g8 dataset* further resolved Boipeba (BA) into a separate cluster (Figure 3F). Maxaranguape (RN) and Tamandaré (PE) samples were grouped in a fourth cluster, while Abrolhos Archipelago and Aracruz were recovered as a single subpopulation ($k = 5$, Figure 2F). Samples from Tamandaré (PE) showed the lowest levels of admixture across all datasets and k values.

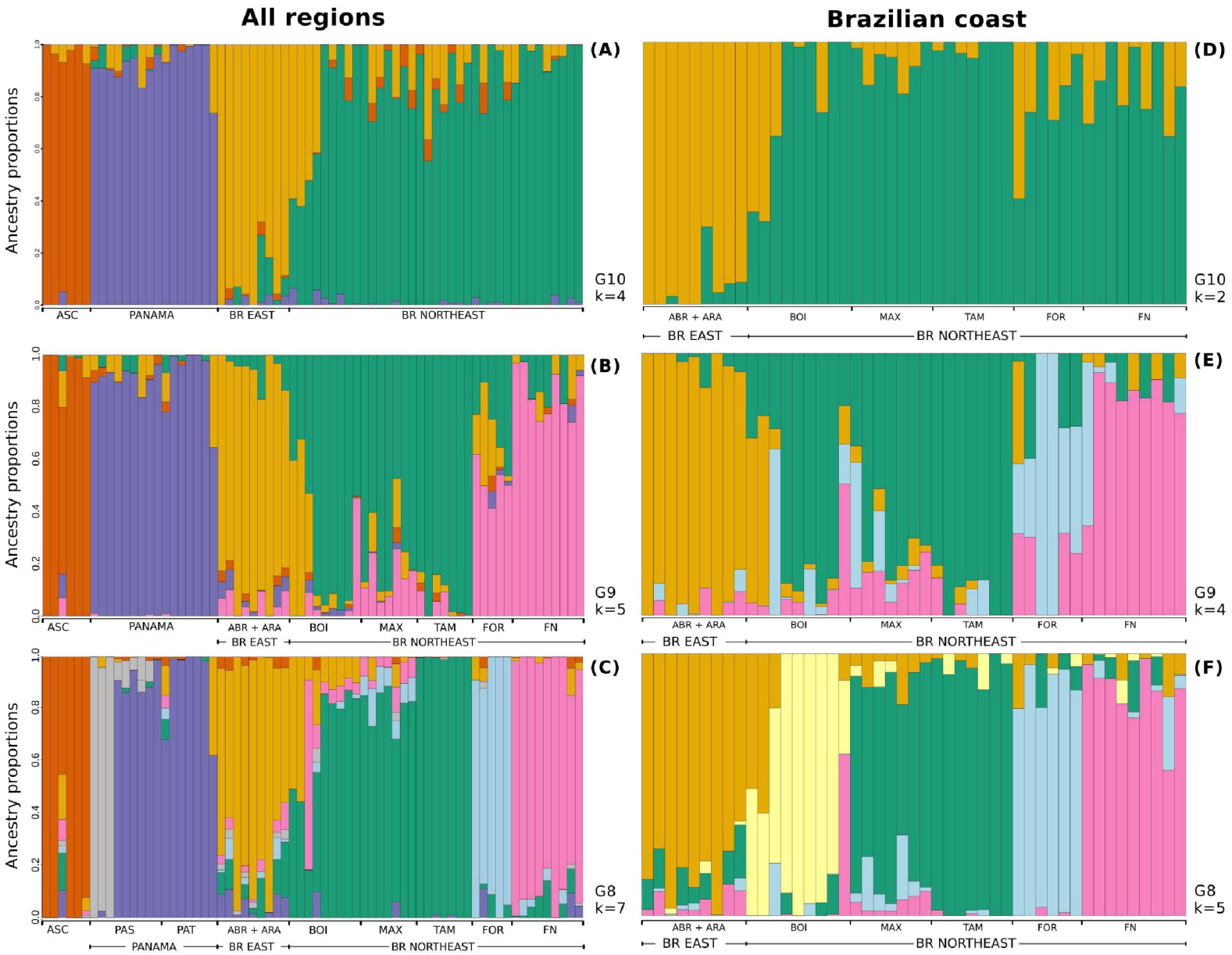
All regions
Brazilian coast
Ancestry proportions
(A)
G10
k=4
ASC
PANAMA
BR EAST
BR NORTHEAST
(D)
G10
k=2
ABR + ARA
BOI
MAX
TAM
FOR
FN
BR EAST
BR NORTHEAST
(B)
G9
k=5
ASC
PANAMA
ABR + ARA
BOI
MAX
TAM
FOR
FN
BR EAST
BR NORTHEAST
(E)
G9
k=4
ABR + ARA
BOI
MAX
TAM
FOR
FN
BR EAST
BR NORTHEAST
(C)
G8
k=7
ASC
PAS
PAT
ABR + ARA
BOI
MAX
TAM
FOR
FN
PANAMA
BR EAST
BR NORTHEAST
(F)
G8
k=5
ABR + ARA
BOI
MAX
TAM
FOR
FN
BR EAST
BR NORTHEAST

Figure 2 - sNMF barplots for (A-C) Atlantic *Favia* and (D-F) Brazilian *F. gravida*. (A) dataset with no missing data (G10) and k=4; (B) dataset with 10% missing data (G9) and k=5; and (C) dataset with 20% missing data (G8) and k=8. (D) dataset with no missing data (G10) and k=2; (E) dataset with 10% missing data (G9) and k=3; and (F) dataset with 20% missing data (G8) and k=4. K is the optimal value obtained from cross-entropy analysis. ABR - Abrolhos (BA); ARA - Aracruz (ES); ASC - Ascension Island; BOI - Boipeba (BA); FN - Fernando de Noronha (PE); FOR - Fortaleza (CE); MAR - Maxaranguape (RN); PAS - *F. fragum* short morphotype (Panama); PAT - *F. fragum* tall morphotype (Panama); TAM - Tamandaré (PE)

The same general pattern was observed in the DAPC analysis (Figure 3). When sampling sites were used as *a priori* information, the first axis clearly separated *F. gravida* from *F. fragum*, while the second axis mostly isolated the Ascension Island samples (Figure 3A). With no prior information, the k-means analysis recovered $k = 4$ as the optimal number of clusters (Figures 3B and 3C), corresponding to the four main ancestral gene pools observed in the sNMF analysis (Figure 2A). The samples from Boipeba and Fortaleza that had higher ancestral proportions corresponding to BR East in the sNMF analysis were also assigned to that cluster in the DAPC (Figure 3D).

To assess fine-scale spatial distribution within the Brazilian *F. gravida* we ran a second DAPC using only samples from the Brazilian coast (Figure 4). The first axis explained ~49% of the genetic variation, mainly separating samples from Tamandaré and Maxaranguape from the remaining populations. Tamandaré was the most isolated site, which agrees with the low levels of admixture revealed by sNMF. The second axis explained ~24% of the genetic variation, separating the two subpopulations from BR East. With no prior information on sampling sites, the k-means recovered $k = 2$ as the optimal number of clusters and samples were separated into BR East and BR Northeast (Figure 4B).

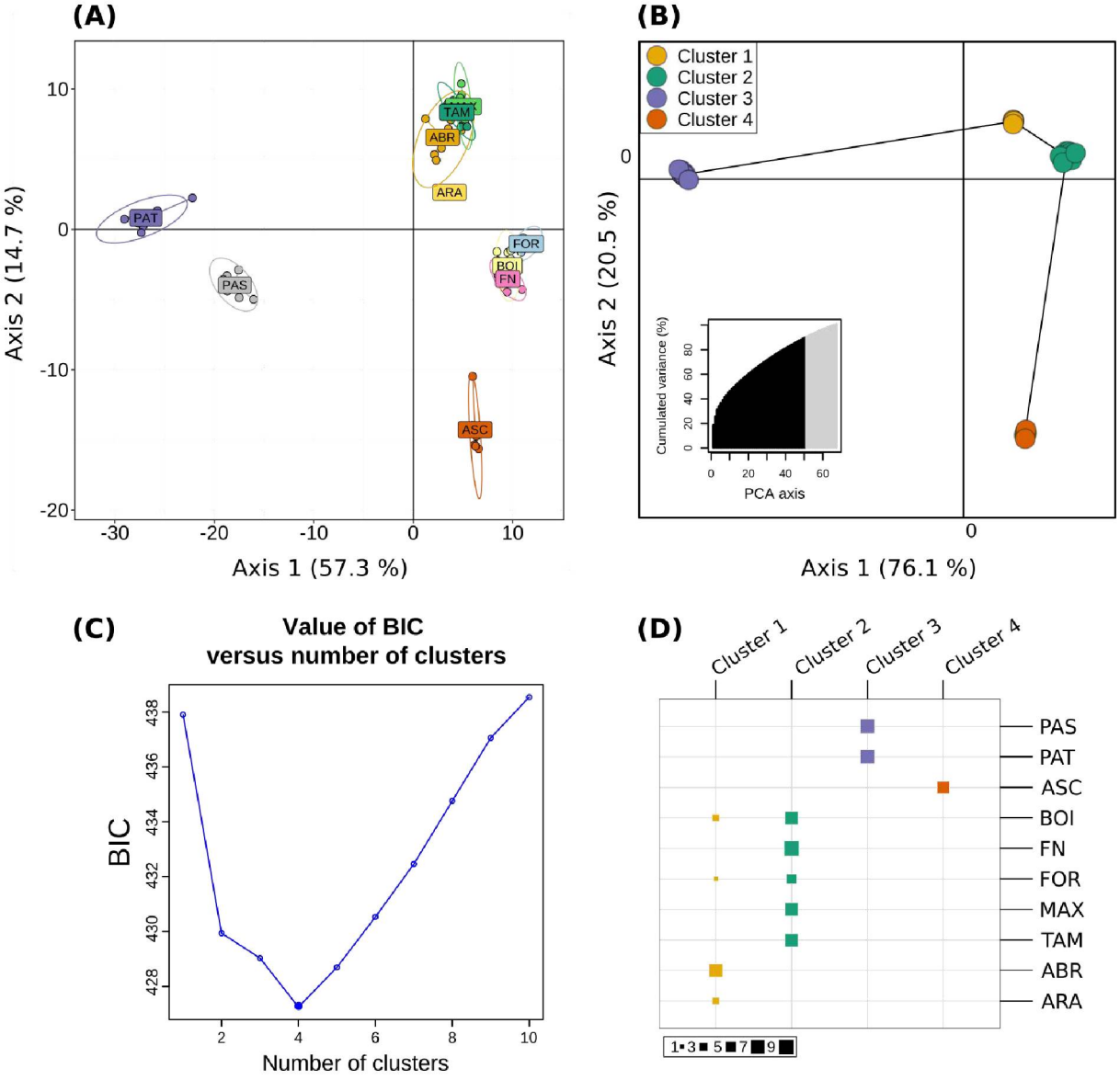

Figure 3 - A) Discriminant analysis of principal components (DAPC) plot of Atlantic *Favia* samples with the *g9* dataset using sampling sites as *a priori* grouping information. (B) DAPC plot with no prior information, where the colors represent distinct clusters (k=4). The number of PCs retained is indicated by the black bars in the inset bar graph. (C) Optimal numbers of clusters recovered by the Bayesian Information Criterion (BIC). (D) Distribution of the number of individuals from each sampling site that were assigned to each DAPC cluster in (B). Sampling sites are coded according to Table 1.

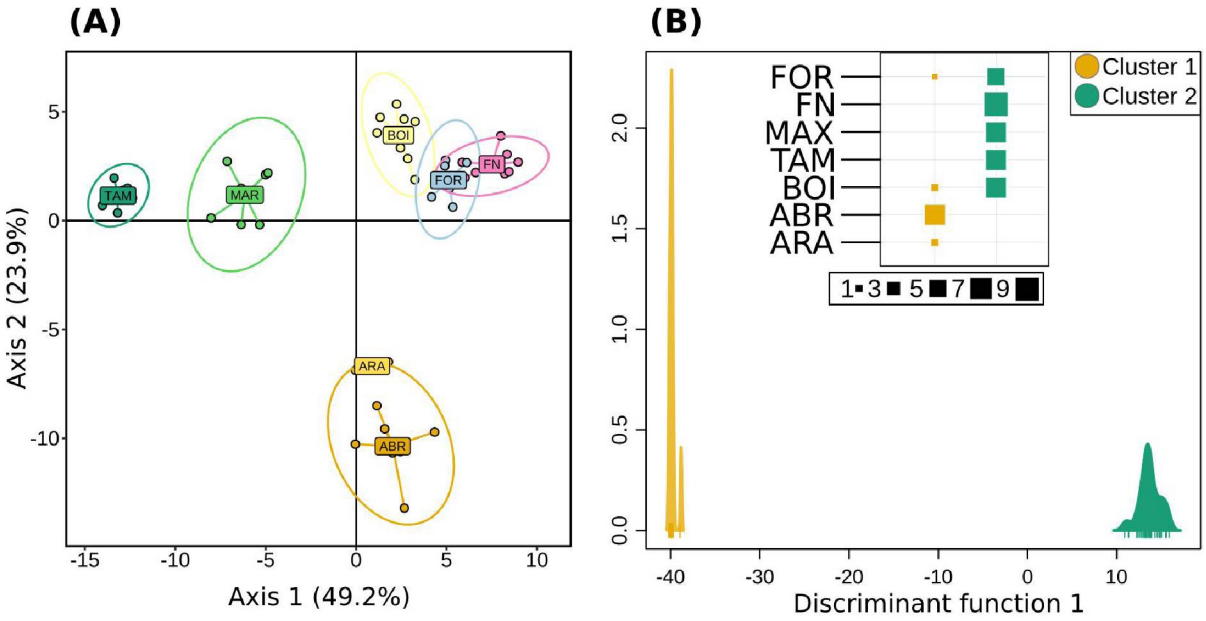

Figure 4 - A) Discriminant analysis of principal components (DAPC) plot of Brazilian *Favia gravida* samples with the *g9* dataset using sampling sites as *a priori* grouping information; and (B) DAPC showing the density plot where colors represent distinct clusters (k=2) recovered by the Bayesian Information Criterion (BIC). Sampling sites are coded according to Table 1.

We also created a subset of the data including only *F. fragum* samples and applied the same filtering that was used for the full dataset (Table 3). sNMF analysis using *g10* and *g9* equivalents revealed $k = 2$ as the lowest CEC values, with three individuals of the Short morphotype (PAS) assigned to a distinct subpopulation (Figure 5A). The lowest CEC value for *g8* was k = 3 and the remaining PAS samples were recovered in a separate cluster, while all the samples corresponding to the Tall morphotype (PAT) had high proportions of a distinct ancestral gene pool (Figure 5B). We performed a DAPC on the *g8* alignment with no prior information and $k = 3$ was returned as the optimal number of clusters (Figure 5C). All PAT individuals clustered together while the same 3 aforementioned PAS samples were placed in a separate cluster.

Table 3 - SNP count for each *Favia fragum* dataset containing different percentages of missing data.

Dataset	Missing data (%)	SNP count
G8	20	54,957
G9	10	30,998
G10	0	13,241

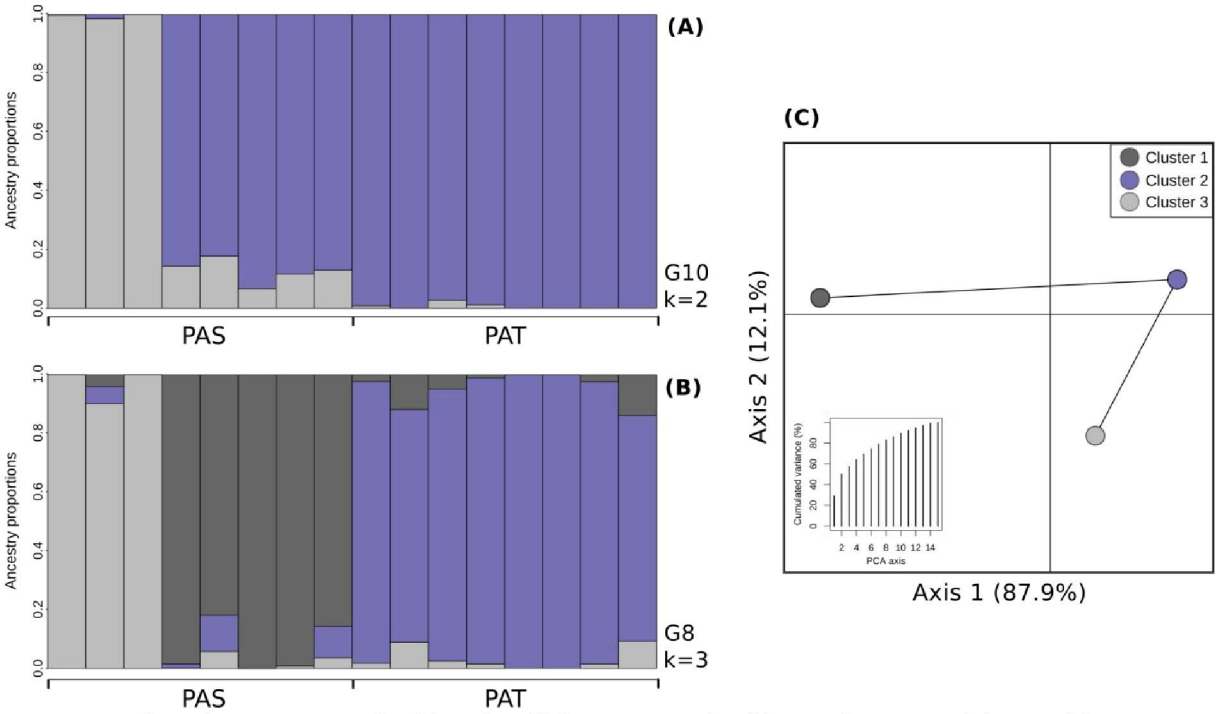

Figure 5 - Short (PAS - 3-4 m depth) and Tall (PAT - 1 m depth) morphotypes of the Caribbean *Favia fragum*. Assignment plots represent sNMF analysis of datasets with (A) no missing data (*g10*) and (B) 20% missing data (*g8*). (C) Discriminant Analysis of Principal Components (DAPC) plot based on the dataset with 20% missing data. Points representing different populations are color-coded according to Figure 6B.

The pairwise F_{st} values, computed according to Weir and Cockerham (1984), were consistent with the clustering recovered from DAPC and sNMF analyses (Figure 6). F_{st} values ranged from 0.025 (between Abrolhos and Aracruz, i.e. the two sampling sites that make up the BR East population) to 0.194 (between Aracruz and Ascension, in the mid-Atlantic Ridge).

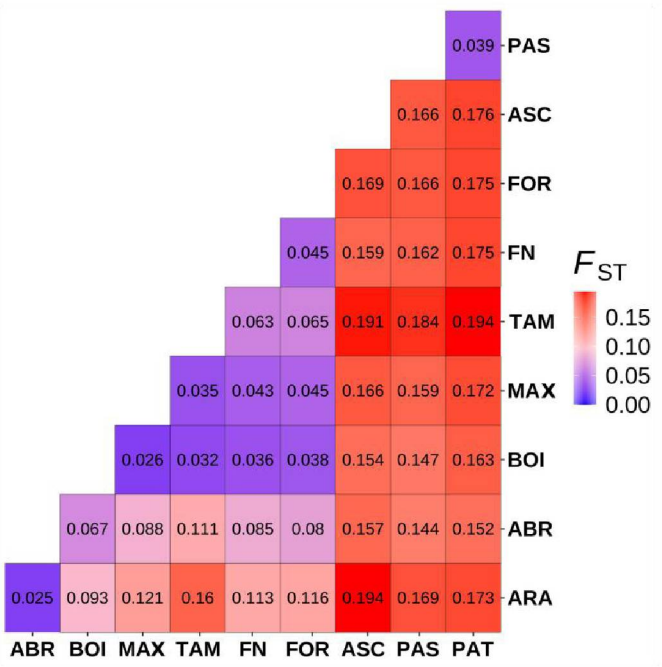

Figure 6 - Heatmap of pairwise Fst values (according to Wier and Cockerham, 1984) among Atlantic *Favia* sampling sites.

Hierarchical AMOVA revealed significant genetic variation among geographic regions (Brazil, Caribbean and the mid-Atlantic province), explaining 26.3% of the total variance. Differences among sampling sites within regions accounted for 11.3% of the molecular divergence, and most of the differentiation (62.2%) was due to genetic divergence within sampling sites (Table 4). When Brazilian samples were analyzed separately, 17.92% of the variation was attributed to differences between the East and Northeast populations, 8.89% among sampling sites within each population, and >73% of the variation was due to genetic differences within the sampling sites (Table 4).

Table 4 - Results of hierarchical locus-by-locus analysis of molecular variance (AMOVA) indicating percentage of variance, average Φ-statistic over all loci, and p-values corresponding to the significance of each component of variance based on 1,000 permutations

Source of variation	Df	% of variation	Φ-statistic	p-value
All samples (*F. fragum* + *F. gravida*)				
Among regions	2	26.38	0.2638	0.001*
Among sampling sites within regions	7	11.36	0.1543	0.001*
Among samples within sampling sites	58	62.25	0.3774	0.001*
Brazilian *F. gravida*				
Among populations	1	17.92	0.1792	0.001*
Among sampling sites within populations	5	8.89	0.1083	0.001*
Among samples within sampling sites	40	73.17	0.2682	0.001*

Note: Significant values are marked with asterisk (*).

The isolation by distance test (IBD) was also performed hierarchically (Figure 7). Results revealed significant correlation that was moderate when considering all sampling sites (r = 0.42, p = 0.001, Figure 7A), strong when only *F. gravida* was analyzed (r = 0.70, p = 0.001, Figure 8B), and weaker when only samples from the Brazilian coast were considered (r = 0.37, p = 0.003; Figure 7C). Smoothed local regression indicates that the significant correlations are quasi-linear. A negative, but non-significant (r = -0.274, p = 0.986) correlation was recovered when only the sampling sites from the Northeast population were analyzed.

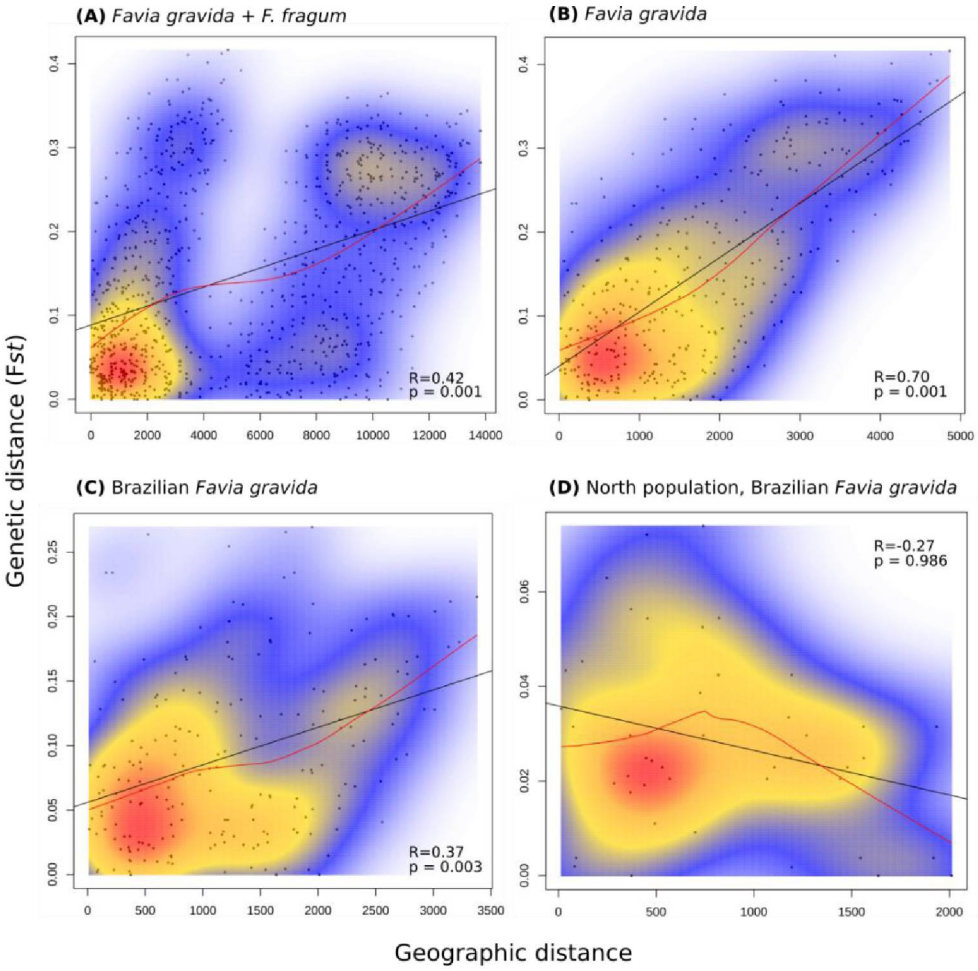

Figure 7 - Scatter plots of Mantel tests showing the relationship between genetic (Fst/(1-Fst)) and geographic distances considering (A) all Atlantic *Favia* samples; (B) *Favia gravida*; (C) *F. gravida* from the coast of Brazil; and (D) samples from the the Northeast population of Brazilian *F. gravida*. Red line indicates smoothed local regression.

Genetic diversity

Nei's unbiased gene diversity (expected heterozygosity) within sampling sites ranged from 0.056 in Tamandaré to 0.104 in the Abrolhos Bank. Mean allelic richness ranged from 1.238 (Ascension Island) to 1.312 (Aracruz, the southernmost sampling site from Brazil). After standardizing for the smaller sample size across sampling sites, Ascension Island had the highest count of private alleles. Inbreeding coefficient values were negative across all sampling sites. The standardized index of association (r_d) values indicate linkage disequilibrium for both Caribbean sampling sites and for Boipeba, Fortaleza and Tamandare, from the Brazilian coast (Table 5). Analyzing the groups recovered in the population structure analyses, values for Nei's unbiased gene diversity and mean allelic richness were lower in Ascension Island (0.064 and 1.239, respectively) and higher in the *BR East* population (0.111 and 1.290, respectively). Inbreeding coeffcient values were also negative across populations. Linkage disequilibrium was detected in the Caribbean and the BR Northeast population (Table 6).

Allelic richness and gene diversity estimates for subsamples of the data corresponding to the smaller sample sizes being analyzed recovered the same patterns of diversity (Table S1 and S2). The exception is the allelic richness values for the sampling sites, which were higher in Abrolhos instead of Aracruz.

Table 5 - Number of private alleles, mean allelic richness, Nei's unbiased gene diversity values, inbreeding coeficient (Fis) and standardized index of association (r_d) for Atlantic *Favia* spp. sampling sites. Sampling sites are coded according to Table 1. Private alleles were estimated based on a random subsample corresponding to the smaller sample size across sampling sites. CI - confidence interval; LL - lower limit; UL - upper limit.

Sampling sites	N	Private alleles (N=2)	Allelic richness, 95% CI [LL; UL]		Gene diversity	Fis	r_d
PAS	8	619	1.272	[1.267; 1.278]	0.083	-0.386	0.016*
PAT	8	574	1.266	[1.260; 1.272]	0.081	-0.390	0.031*
ASC	6	867	1.238	[1.232; 1.243]	0.064	-0.440	0.005
FOR	5	227	1.265	[1.259; 1.270]	0.067	-0.450	0.025*
FN	9	254	1.258	[1.252; 1.263]	0.074	-0.412	0.007
MAX	7	146	1.261	[1.256; 1.267]	0.070	-0.439	0.002
TAM	7	96	1.246	[1.240; 1.252]	0.056	-0.501	0.007*
BOI	9	147	1.268	[1.262; 1.273]	0.083	-0.377	0.030*
ABR	7	508	1.290	[1.284; 1.296]	0.104	-0.272	0.013
ARA	2	421	1.312	[1.304; 1.321]	0.087	-0.307	-

Note: Significant values are marked with asterisk (*).

Table 6 - Number of private alleles, mean allelic richness, Nei's unbiased gene diversity values, inbreeding values (Fis) and standardized index of association (r_d) for Atlantic *Favia* spp. populations. Private alleles were estimated based on a random subsample corresponding to the smaller sample size across populations. CI - confidence interval; LL - lower limit; UL - upper limit. Asterisks (*) represent p-value < 0.01.

Population	N	Private alleles (N=6)	Allelic richness, 95% CI [LL; UL]		Gene diversity	Fis	r_d
Caribbean	16	4,107	1.272	[1.267; 1.277]	0.093	-0.333	0.015*
Asc	6	2,489	1.239	[1.234; 1.244]	0.064	-0.440	0.005
BR Northeast	37	1,287	1.262	[1.257; 1.267]	0.090	-0.325	0.011*
BR East	9	2,493	1.290	[1.285; 1.295]	0.111	-0.246	0.009

Note: Significant values are marked with asterisk (*).

Phylogeography

Topologies were congruent in both concatenation and coalescent-based trees (Figures 8 and 9), with *F. fragum* and Brazilian *F. gravida* recovered as reciprocally monophyletic with maximum bootstrap support. The *BR East* and *BR Northeast F. gravida* populations formed highly supported sister clades, but the structure observed within *BR Northeast* differed between concatenation and coalescent-based topologies. Standard ML analysis recovered Boipeba (BA) as sister to all other *BR Northeast* subpopulations, while in the coalescent-based approach Fortaleza (CE) is sister to all other *BR Northeast* clade subpopulations, and Boipeba is sister to a clade consisting of Maxaranguape (RN) and Tamandaré (PE). In both reconstructions one sample from Boipeba (BA) was recovered within the Fernando de Noronha Archipelago (PE) clade, which agrees with the sNMF results (Figure 2C and 2F), that recovered the same sample from Boipeba with most of its ancestral coefficient belonging to the Fernando de Noronha population. Within *F. fragum*, three highly supported clades were consistent with the clusters recovered in the sNMF and DAPC analyses (Figure 5).

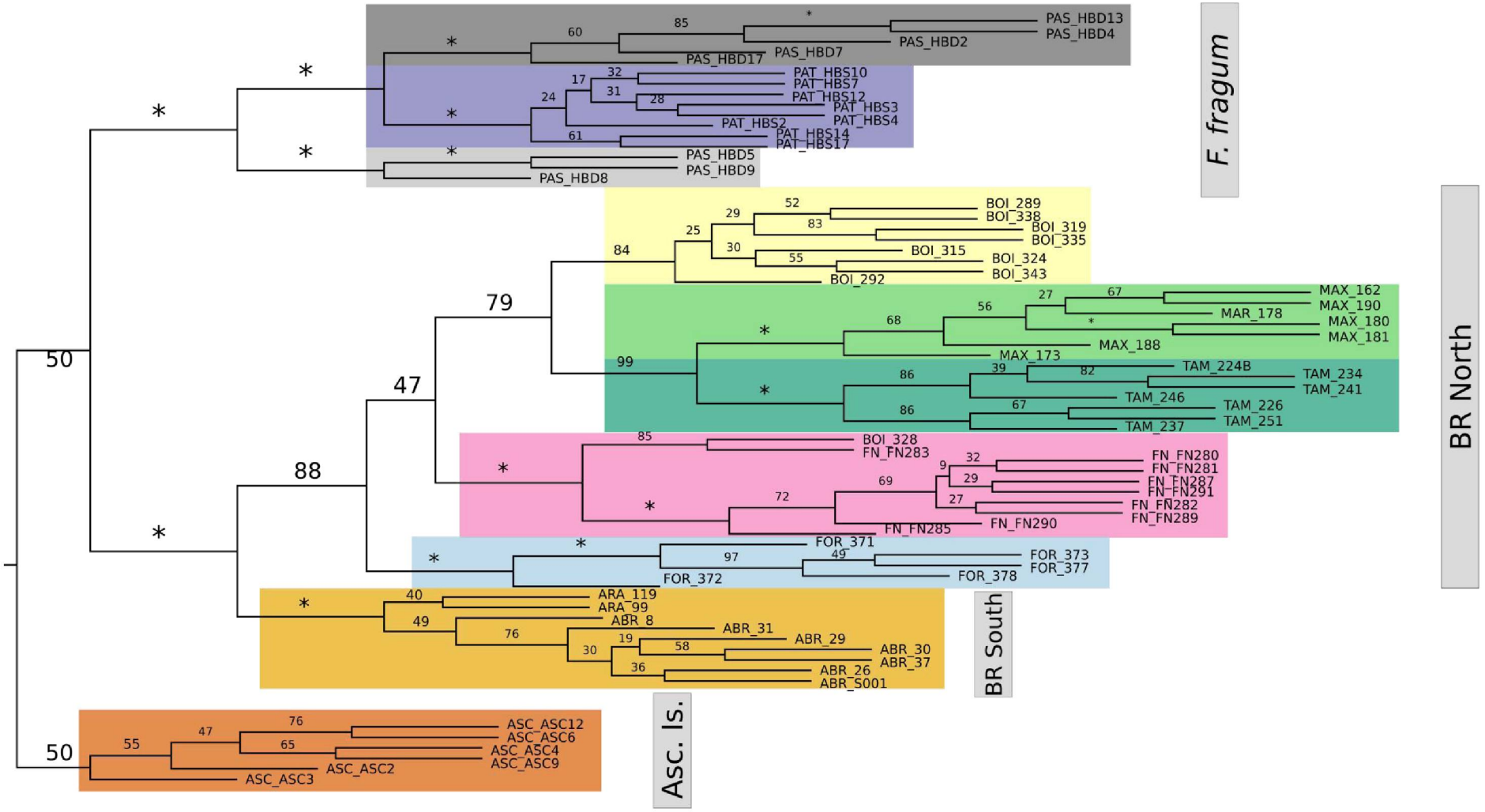

Figure 8 - Phylogeny of Atlantic *Favia* based on coalescent-based analysis performed in SVDQuartets. Values on branches are bootstrap support (BS). Colors correspond to sNMF barplots in Figure 2 and sampling sites are coded according to Table 1. Asterisks (*) correspond to BS = 100.

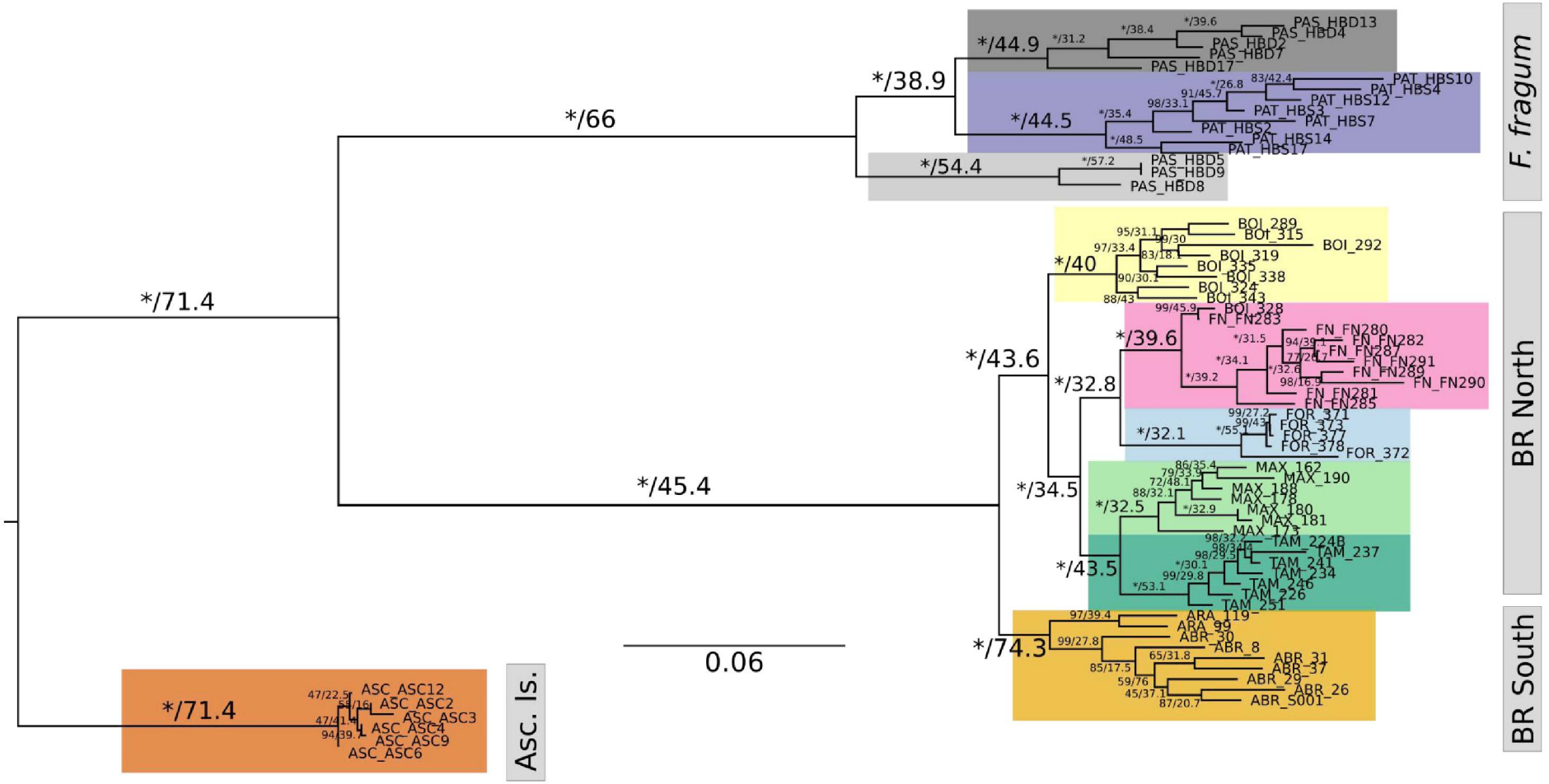

Figure 9 - Phylogeny of Atlantic *Favia* based on maximum likelihood analysis of concatenated SNP data performed in IQ-TREE. Values on branches are ultrafast bootstrap support (UFboot) / site concordance factors (sCF). Scale bar represents substitutions per site. Colors correspond to sNMF barplots in Figure 2 and sampling sites are coded according to Table 1. Asterisks (*) correspond to UFboot = 100.

Discussion

Our results showed significant genetic variation within the Atlantic *Favia* among surveyed regions, as well as among sampling sites within regions. Using up to 21,691 SNP loci we recovered four distinct genetic clusters within the Atlantic *Favia* under two different approaches: *F. fragum* from Panamá, *F. gravida* from Ascension Island, and two geographically distinct *F. gravida* populations in Brazil. The four main genetic clusters were further divided into geographically coherent subpopulations when more missing data and hence a larger number of SNP loci were maintained in the analyses. We also found evidence of substructuring within the two *F. fragum* morphotypes, suggesting cryptic genetic divergence that is not associated with a depth gradient.

Genetic diversity

Linkage disequilibirum (LD) and negative Fis values are an indication of partially asexual and clonal populations (Balloux, Lehmann and Meeûs, 2003; Stoeckel et al. 2006; Adjeroud et al. 2014; Bentley and Mauricio, 2016). In *F. fragum*, evidence of self-fertilization based on microssatelite data explain the significant LD values (Carlon and Lippé, 2012), but contradicts the negative values of F_{is}, since inbreeding leads to positive F_{is}. Although we found no evidence of identical multilocus genotypes (MLG) in our data, even occasional occurrences of clonal reproduction may lead to deviation in Fis values within populations, increasing the probability of showing an excess of negative Fis and skewing the distribution towards highly negative values (Stoeckel and Masson, 2014; Reynes et al. 2020). One of the main advantages of non-outcrossing events is the upkeep of local populations when sexual reproduction is hindered (Miller and Ayre, 2004; Baums, Miller and Hellberg, 2006). Even without signs of clonal individuals within our populations, our results suggest some degree of asexual reproduction in *Favia* spp., which might allow the mainteinance of isolated populations.

Since we did not identify any identical MLG across samples, genetic diversity measures were estimated considering all individuals in our dataset. The highest levels of allelic richness and gene diversity at the Brazilian coast were observed in what we called the BR East population, represented by colonies from Aracruz and the Abrolhos Bank, a large reef structure located off the coast of Bahia where 19 of the 23 species of symbiotic corals described in Brazil are found (Leão et al., 2016). During a period of decreased coral coverage caused by low sea-level and high sedimentation that initiated ~5 ky ago, bryozoan dominated

reef structures sheltered corals and hydrocorals in their flats, possibly acting as a refugium for Scleractinians (Bastos et al. 2018; Laborel, 1970; Leão, Kikuchi and Testa, 2003; Leão and Kikuchi, 2005; Dechnik et al. 2019). Paleoclimatic modeling suggests that reef-building corals were not necessarily restricted to the Abrolhos Bank in periods of low sea level, and that some species, such as *M. braziliensis*, had a limited near shore distribution along the northern coast of Bahia, where the species still currently occurs (Menezes et al. 2020). At the time of the regression phase, the coastline suffered progradation and the reefs grew closer to the coast (Kikuchi and Leão, 1998; Leão and Kikuchi, 2001). These inshore reefs are subjected to high sediment deposition and constant subaerial exposure, favoring species that are able to withstand more turbid waters and variations in temperature and salinity, such as *Favia* (Loiola et al. 2019; Pereira et al. 2020a, Pereira et al. 2020b). Based on subsurface core data it was estimated that during the Holocene, *F. gravida* was the Scleractinian with the fourth highest relative abundance at the Abrolhos reef bank and was also reported in near-shore reefs in the north of Bahia (Vasconcelos, Leão and Kikuchi, 2018). Although not responsible for much of the current coral cover, recruits of *F. gravida* are abundant in Abrolhos, especially in the inshore reefs (Loiola et al. 2019). Furthermore, the high level of allelic richness for *F. gravida* at the Aracruz sampling site, located south of the Abrolhos Bank, also indicates that regions other than this coral-rich bank might have acted as refugium during this period of sea-level change, maintaining past genetic diversity for some coral species. Although presenting high levels of allelic richness and gene diversity even when we standardized sampling sizes, Aracruz is unfortunately represented by only two individuals in our dataset, and a larger sampling size might give further information regarding the genetic diversity of this region. Aracruz is located ~50 km south of the Doce River delta, a region that recently suffered from an environmental disaster that resulted in the discharge of millions of cubic meters of mining waste after the collapse of a water dam. The waste reached coastal marine ecosystems within days, significantly increasing sedimentation, turbidity, and heavy metals concentration (Gomes et al. 2017; Rudorff et al. 2018). A study conducted prior to the disaster discovered a reef complex in the northern region of the Espirito Santo coast, only 70km north of the Doce River mouth, harboring eleven species of scleractinian corals (Mazzei et al. 2016). This study serves as a baseline for future surveys assessing the impact of the disaster in coral reefs of the region. But unfortunately, there is a lack o research focused on the patch reefs located in the central and southern regions of Espirito Santo, which includes Aracruz (Castro et al. 2001; Leão et al. 2016). This highlights the urgency of conducting studies in the area in order to fully understand and protect what is left of its diversity.

The oceanic dynamics between glacial and interglacial periods led to population reductions and/or expansions in coastal marine environments due to sea level fluctuations. During glacial periods, the drop in sea level reduced shallow coastal habitats around the world, traping some shallow water marine species in isolated refugia (Ludt and Rocha, 2015; Maggs et al. 2008). It is expected that populations that suffered significant reductions would have lower levels of allelic diversity, whereas this measure would be higher in populations that served as refugia, especially due to the maintenance of rare alleles (Comps et al. 2001; Leberg 1992; Provan and Bennet, 2008), which also explains the elevated number of private alleles in the BR East compared to the BR Northeast population. Thus, our data corroborate the hypothesis that during these periods of oceanic regressions, the Abrolhos Bank and other southern coral assemblages maintained their diversity and served later as source of propagules to other populations along the coast. Furthermore, simulation studies suggest that allelic richness is a good measure of long-term response to selection, acting as a good proxy for species adaptation to environmental changes, both in unstructured and subdivided populations (Caballero and García-Dorado, 2013; Greenbaum et al. 2014). Given that global climate change poses a threat to reef ecosystems (Doney et al. 2012; Gibson et al. 2011), it is important to identify and preserve populations that foster high genetic diversity, which are more likely to persist through environmental disturbances (Marchelli et al. 2017; Theodoridis et al. 2018).

Population structure

We found a clear differentiation among populations of Caribbean *F. fragum* and Brazilian and Ascension Island *F. gravida*; hierarchical analyses revealed further subdivision within these major regions. Strong genetic differentiation between Brazilian and Caribbean species is vastly recorded for marine organisms based on different genetic markers, for instance, sea anemone's allozymes (Vianna, Schama and Russo, 2003), intertidal fiddler crabs' (Laurenzano, Mantellato and Schubart, 2013), wrasses' (Rocha et al. 2005) and bridled goby's mtDNA (Volk et al. 2020, which also analyzed SNPs), and reef sharks' microsatellites (Bernard et al. 2017). This was also found in reef-building corals (Nunes, Norris and Knowlton, 2009), including *Favia* spp. (Nunes, Norris and Knowlton, 2011; Teshima, Zilberberg and Nunes, 2021). The main putative barrier to gene flow between these two regions is the Amazon River delta, the world's largest drainage system, that may have acted as a geographic barrier to the dispersion of marine organisms since the Early Pliocene (~5

Mya), when it reached its current geographic configuration (Latrubesse et al. 2010). Considering the age of the Amazon barrier and of the coral reefs of the Brazilian coast (~7,000 years, Leão et al. 2003), the strong genetic variation between the Caribbean and the Southern Atlantic recovered in this study is yet another evidence that these are indeed separate lineages with little to no admixture.

Structure analysis within nominal *F. gravida* divided the species into three main populations according to DAPC and sNMF analysis: Ascension Island, East and Northeast Brazilian populations. Although presenting some level of admixture with the Brazilian populations, Ascension Island was recovered as belonging to a different ancestral gene pool in all sNMF analyses (Figure 2A) and as a distinct cluster in the DAPC, with no overlap with other populations (Figure 2A-B). Furthermore, the F*st* values between Ascension Island and other *F. gravida* populations were comparable to, and in some cases higher than those between *F. gravida* and *F. fragum* populations (Fst = 0.205 between Ascension and Aracruz - Figure 6). Significant genetic differentiation based on nuclear and mitochondrial markers was already documented between Brazilian, mid-Atlantic and West-African samples of reef-building corals and hydrocorals (Nunes, Norris and Knowlton, 2009; Nunes, Norris and Knowlton, 2011; Souza et al. 2017). *F. gravida* populations from Ascension Island and Brazil did not share haplotypes from two nuclear markers (ITS and *masc1)* and were at least six mutational steps away from the remaining *Favia* spp. sampled by Teshima, Zilberberg and Nunes (2021). Ascension Island has a volcanic origin and it is located at the mid-Atlantic Ridge, approximately 3,000 km from the Brazilian coast. At this site, *F. gravida* was recorded as encrusting colonies down to depths of 5 m and also as free-living colonies in shallow-water tidal pools (Hoeksema, 2012; Zibrowius et al. 2014). Remote islands tend to have low diversity and high rates of endemic marine organisms (Dawson, 2016; Robertson, 2001), and the genetic isolation of island populations is not an uncommon trait. Low gene diversity and allelic richness and high genetic differentiation have been described for island populations of different fish species (Hemmer-Hansen et al. 2007; Pinheiro et al., 2017) and reef-building corals (Ayre and Hughes, 2004) when compared to their coastal counterparts. The low levels of admixture between Ascension and the remaining *F. gravida* populations, the low values of allelic richness (1.236) and gene diversity (0.064), and the high number of private alleles in this population compared to coastal sampling localities indicates that this is indeed an isolated and vulnerable site.

Population structure within the Brazilian coast

Population genetic studies of *F. gravida* show contrasting structure patterns along the Brazilian coast. Nunes et al. (2011) recovered significant differentiation between two sampling sites belonging to the recently discovered Northeast and East populations (Abrolhos and João Pessoa, divided by ~1,300km) based on the intron and exon of *B-tubulin* and the *Pax-C* intron. With a more comprehensive sampling scheme Teshima, Zilberberg and Nunes (2021*)* recovered a single haplotype from both ITS and *masc1* along the Brazilian coast, with private haplotypes being observed only in Rocas Atoll and the Fernando de Noronha Archipelago, but the authors appropriately acknowledge the possible limitations linked to the marker resolution. Ours is the first study to investigate the genetic structure of Brazilian *F. gravida* on such a broad scale using high-resolution markers, revealing two main populations that divide the coast into sampling sites from the Northeast and the East limit of the distribution. A similar structure pattern was observed in other works focusing on the endemic scleractinian coral *Mussismilia hispida*, the fire coral *Millepora nitida*, and the reef goby *Coryphopterus glaucofraenum*, which reported differentiation between Northern and Central/Southern populations and higher levels of admixture between neighboring sites (Peluso et al. 2018; Souza et al. 2017; Volk et al. 2020). Different from our results, individuals from Abrolhos and Northern Bahia were recovered in the same genetic cluster, with moderate to high levels of admixture. This result agrees with the influence of the South Equatorial Current (SEC), which divides itself into North Coastal Brazilian Current (NCBC) and the Brazil Current (BC) at around 10°S, north of the Boipeba sampling site (Peterson and Stramma, 1991). This incongruence can be explained by many factors. Unlike the species surveyed in the aforementioned studies, *Favia* brooded larvae display philopatric behavior, with evidence of inbreeding and presumably low dispersal capacity (Carlon & Olson, 1993; Calderon, Castro, & Pires, 2000) and most likely reduced genetic exchange among populations. Furthermore, BC, which is the southward branch of SEC, has a weaker transport capacity when compared to other Equatorial currents (Stramma, Ikeda and Peterson, 1990), and there is evidence that, during the months of June and July, the split of NCBC and BC shifts to around 15°S, south of Boipeba (DNH, 1993). Also, cyclonic circulations located close to the coast between 12° and 16°S and the northward reflection of the SEC when approaching the Vitoria-Trindade Ridge could hamper the transport of larvae moving southward (Stramma, Ikeda and Peterson, 1990). Finally, the stretch of ~500 km of coast separating Boipeba from the Abrolhos Bank harbors numerous river mouths, such as the Jequitinhonha River, that has a significant sediment load (Dominguez, Martin and Bittencourt,

2004), acting as an additional barrier to dispersal. Together, these features might be responsible for the observed structure between the major genetic clusters identified in our results.

More resolution was obtained with the addition of SNPs in alignments with increasing percentages of missing data. SNP count increased almost tenfold (from 2,466 to 24,133) between *g10* and *g8* datasets, further subdividing *BR Northeast*. sNMF clusters consistently recovered our sampling localities, which was also observed in our phylogeographic reconstructions. These results corroborate the aforementioned restricted gene flow among sites, most likely due to *F. gravida* restricted dispersion ability. Furthermore, the increased resolution indicates that the additional information provided by loci with moderate amounts of missing data adds resolution to phylogenetic and population genetics studies, a trend that was already reported using empirical and simulated data (Hodel et al. 2017; Huang and Knowles, 2016). Other than phylogenetic information content, an additional cause of spurious relationships is long-branch attraction (LBA), more prevalent in concatenation-based reconstructions, which may result from sparse sampling, fast evolving lineages and/or the choice of a distant outgroup (Bergsten, 2005; Liu, Xi and Davis, 2015). This factor contributed to the putative spurious recovery of *F. fragum* and Ascension Island *F. gravida* as sister clades in the IQ-TREE analysis performed in Chapter I (Chapter I - Figure 2), although the average sCF support was only 42.5%. In the present chapter, our phylogeographic reconstructions had a larger sample size, did not include the distant outgroup and are thus presumably not affected by LBA. Indeed, 71.5% of the PIS agree with the *F. fragum* + Brazilian *F. gravida* clade in the IQ-TREE analysis (Figure 9). Although LBA is seemingly no longer a concern in our data concatenation and coalescent-based analyses presented topological differences within the *BR Northeast* population. Relationships within *BR Northeast* based on the coalescent analysis are in accordance with sNMF results for Brazilian samples. Boipeba, Maxaranguape and Tamandaré, which were recovered in a clade with moderate support (Figure 8), were also clustered in a single ancestral gene pool based on the *g9* datasets (Figure 2E), while Fortaleza and Fernando de Noronha, the most basal branches in the coalescent tree, were recovered in a separate ancestral allele cluster. With the additional loci in the *g8* dataset, the cluster comprised of Fortaleza and Fernando de Noronha was split in two, and the Boipeba sampling site was also recovered in a separate ancestral population (Figure 2F), sister to Tamandaré and Maxaranguape in the coalescent tree. Coalescent-based reconstructions are more robust and tend to provide more reliable trees when samples are affected by incomplete lineage sorting (ILS - Pollard et al. 2006; Kubatko and Degnan, 2007),

a phenomenon that is likely present in our data based on results from ABBA-BABA statistics performed in Chapter I. Also, IQ-TREE treats heterozygosity, represented by IUPAC ambiguity codes, as uncertain base callings, splitting the tip likelihoods among the possible residues (Mihn et al. 2021), while SVDQuartets properly parses this information out as heterozygosity.

Isolation by distance

We found a significant positive correlation between genetic and geographic distances, suggesting the occurrence of isolation by distance (IBD) in the Atlantic *Favia*, which is one of the main factors leading to genetic differentiation among populations (Sexton, Hangartner and Hoffmann, 2013). However, simulation studies show that heavily structured populations, as it is the case of our species sometimes show spurious significant IBD patterns (Cushman and Landguth, 2010; Meirmans, 2012). In our analysis, the positive correlation was maintained when Caribbean *F. fragum* and the population from Ascension Island were removed but became negative and non-significant when we analyzed only the subset of sites from the Northeast population. Boipeba (BA) and Fortaleza (CE), the two most distant sampling sites within *BR Northeast* (~1,500 km apart) have a pairwise Fst = 0.041, while Boipeba and Abrolhos (from *BR East*) are ~470 km apart and have a pairwise Fst = 0.068. This indicates that the positive IBD pattern is recovered at the larger geographic scales, but it does not seem to be a key component of genetic variation in *F. gravida* along the Brazilian coast. This pattern was reported for numerous taxa, such as plant populations in Central Brazil (Telles and Diniz-Filho, 2005), multiple reef organisms from the Hawaiian Archipelago (Selkoe et al. 2014), a Mediterranean sponge (Riesgo et al. 2019) and the green abalone at the Baja California Peninsula (Mejía-Ruíz et al. 2020). In all cases, the genetic-spatial correlation went from strongly positive and significant to weakly positive or negative and non-significant when analyses were conducted within regions. Many other factors might lead to genetic structure in marine populations, such as fresh water discharge from rivers, habitat partitioning, oceanographic processes, and selection, which can all result in different structure patterns depending on the species biology and/or demographic history (Ciannelli et al. 2010; Hedgecock 1994; Jørgensen et al. 2005; Kyle and Boulding, 2000; Pelc, Warner and Gaines, 2009; White et al. 2010). Hence, the structure observed between *BR Northeast* and *BR East* is probably the product of the aforementioned barriers separating the two major populations rather than the sheer geographic distance among them.

Favia fragum morphotypes

The two *F. fragum* morphotypes used in our analyses are found over a depth gradient. The Tall morphotype (PAT) preferentially occurs in the seagrass and the Short morphotype (PAS) in coral reefs, with large quantitative phenotypic variation between them (Carlon and Budd, 2002; Carlon et al. 2011). The significant morphological variation and the evidence of genetic differentiation based on allozyme loci led the authors to suggest the presence of incipient speciation in *F. fragum* associated with a depth gradient. However, evidence of hybridization between PAS and PAT based on microsatellite markers was reported at the seagrass habitat, where the two morphotypes co-occur in some sites (Carlon and Lippé, 2011). Samples of PAS and PAT used in our study had no habitat overlap, with PAS occurring strictly in deeper reefs. Our results recovered low levels of genetic variation between PAS and PAT (Fst = 0.029). However, hierarchical sNMF showed signs of finer structuring, assigning three individuals of PAS to a distinct ancestral gene pool regardless of missing data percentage. Allowing more missing data increased resolution and recovered the remaining PAS individuals in a third population with distinct ancestral coefficients, which was corroborated by the PCA and also the phylogenetic reconstructions, that recovered these three populations in highly supported clades. This suggests that the Short morphotype of *F. fragum* may actually encompass more than one population, as previously uncovered by microsatellite data (Carlon and Lippé, 2011). Our PAT samples, on the other hand, have no structuring, with some individuals showing signs of admixture with both PAS subpopulations. This clear subdivision within the short morphotype indicates the existence of cryptic genetic variation in *F. fragum* within microhabitats.

Conclusion

Compared to previous molecular surveys of Atlantic *Favia*, the present study was performed across a much broader geographic range, encompassing the entire distribution of the species along the Brazilian coast. We employed thousands of high-resolution genetic markers, revealing unprecedented fine-scale population structure patterns for the species. Our results are an important step towards building a comprehensive body of knowledge of the population dynamics of reef-building organisms, especially along the Brazilian coast, that presents a high percentage of Scleractnia endemism and harbor the only real coral reefs of the South Atlantic. We also found evidence of cryptic genetic variation within one of the morphotypes of the Caribbean *F. fragum*. Furthermore, we provide evidence of extreme

isolation and low genetic diversity of a *F. gravida* population from the remote Ascension Island, which deserves special attention in conservation efforts.

Acknowledgment

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nivel Superior - Brasil (CAPES). Samples of *Favia gravida* were collected with support from Fundação O Boticário de Proteção à Natureza's grant awarded to MSB (FBPN 1040-20151). Samples of *Favia fragum* were collected with support from National Science Foundation (DEB-05-43661) awarded to DBC. Lab work and sequencing was funded with support from National Science Foundation (NSF 1416889 & 1924604) awarded to RJT. We thank Carla Zilberberg and Mariana Teshima for providing Ascension Islands samples, and Ana Paula Winter and Julian Olaya Restrepo for field assistance.

Supplemental Data

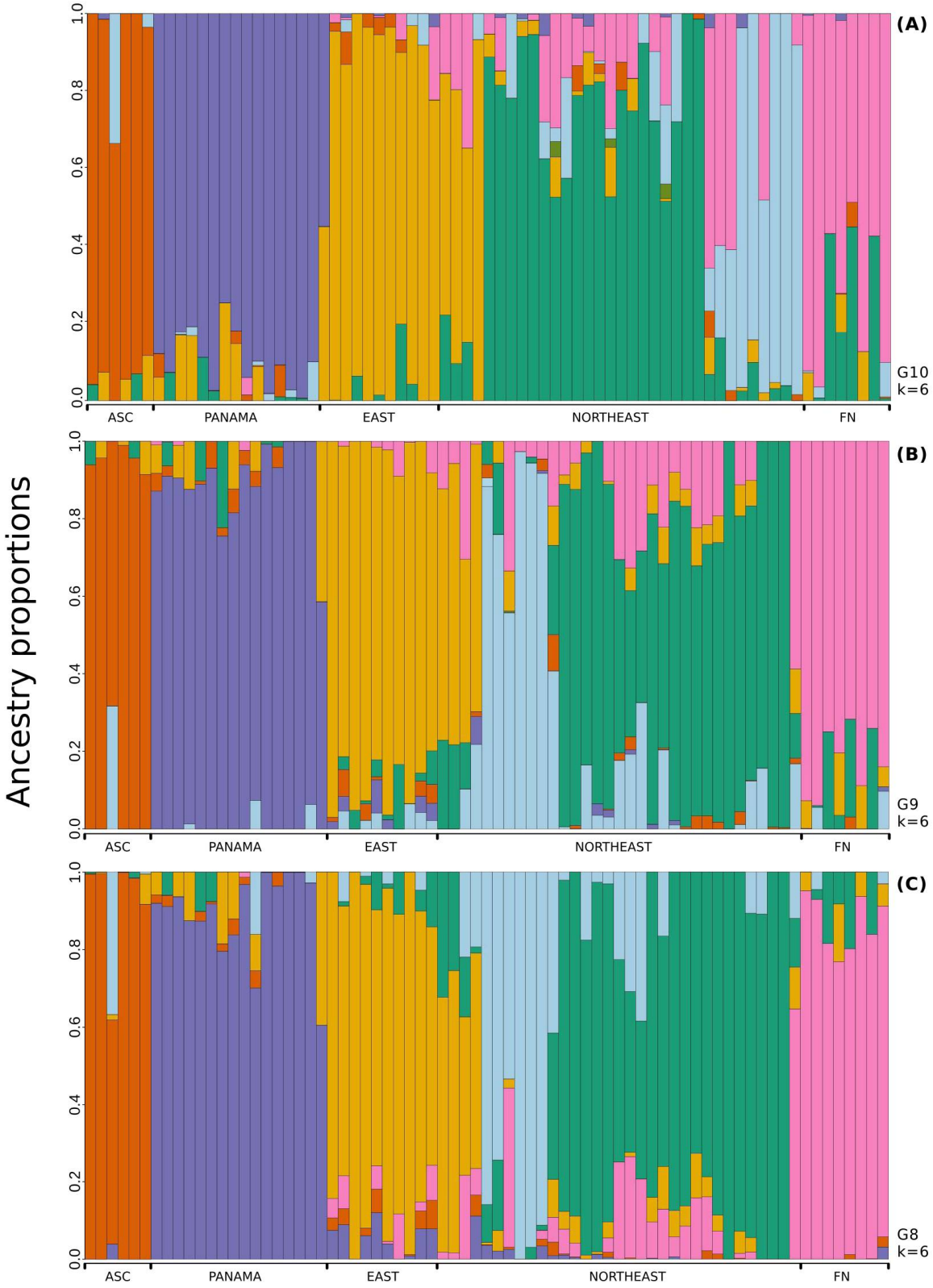

Figure S1 - sNMF barplots for the *coral* datasets of Atlantic *Favia*. (A) dataset with no missing data (G10) and k=6; (B) dataset with 10% missing data (G9) and k=6; and (C) dataset with 20% missing data (G8) and k=8. K is the optimal value obtained from cross-entropy analysis. ASC - Ascension Island; FN - Fernando de Noronha.

Table S1 - Mean allelic richness and Nei's unbiased gene diversity values for Atlantic *Favia* spp. sampling sites estimated with a subsample corresponding to the smaller sample size across sampling sites.. Sampling sites are coded according to Table 1. CI - confidence interval; LL - lower limit; UL - upper limit.

Sampling sites	N	Allelic richness, 95% CI [LL; UL]		Nei's gene diversity
PAS	2	1.314	[1.306; 1.321]	0.083
PAT	2	1.298	[1.291; 1.305]	0.081
ASC	2	1.252	[1.245; 1.260]	0.040
FOR	2	1.301	[1.293; 1.308]	0.088
FN	2	1.295	[1.288; 1.303]	0.087
MAX	2	1.291	[1.284; 1.299]	0.041
TAM	2	1.270	[1.263; 1.278]	0.055
BOI	2	1.282	[1.275; 1.290]	0.059
ABR	2	1.334	[1.327; 1.342]	0.049
ARA	2	1.312	[1.303; 1.321]	0.037

Table S2 - Mean allelic richness and Nei's unbiased gene diversity values for Atlantic *Favia* spp. sampling sites estimated with a subsample corresponding to the smaller sample size across sampling sites.. Sampling sites are coded according to Table 1. CI - confidence interval; LL - lower limit; UL - upper limit.

Sampling sites	N	Allelic richness, 95% CI [LL; UL]		Nei's gene diversity
Caribbean	6	1.274	[1.269; 1.280]	0.075
Ascension	6	1.239	[1.234; 1.244]	0.064
BR Northeast	6	1.260	[1.254; 1.265]	0.063
BR East	6	1.297	[1.292; 1.303]	0.107

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Conclusão geral

Nossos resultados corroboram estudos moleculares que recuperam *Favia fragum* e *F. gravida* como espécies distintas cuja distribuição não apresenta simpatria. Observamos instabilidade nas topologias recuperadas a partir de análises concatenadas, que foram influenciadas pelo número de posições informativas nos conjuntos de dados obtidos com diferentes parâmetros de filtragem, além de possivelmente terem sido afetadas pela ocorrência de segregação incompleta de linhagens e a utilização de um grupo externo distante. Por tanto, acreditamos que a instabilidade nas topologias advindas de análises concatenadas seja resultado de inconsistência estatística dada a inabilidade da análise concatenada em incorporar as diferentes histórias evolutivas dos marcadores utilizados. Porém, nossas análises coalescentes foram consistentes e robustas, recuperando uma única topologia bem suportada para todos os conjuntos de dados analisados, separando *Favia* do Atlântico em três linhagens distintas: a Ilha de Ascenção como clado mais basal, e o clado Brasileiro de *F. gravida* como grupo irmão de *F. fragum* do Caribe.

Os resultados das análises de estruturação populacional corroboram a diferenciação entre as três províncias e o alto grau de isolamento da linhagem de Ascenção, além de dividir a costa brasileira em ao menos duas populações distintas. A medida que um número maior de SNPs foi incorporado às análises em conjuntos de dados mais permissivos, a estruturação observada na costa brasileira se tornou ainda mais acentuada, e quase todos os sítios de coleta foram recuperados como populações distintas. Esta forte estruturação populacional reflete o comportamento de assentamento filopátrico da espécie e sua baixa capacidade de dispersão. Ademais, também recuperamos diferenciação dentro dos morfotipos de *F. fragum* no Panamá, revelando estruturação em um mesmo local de coleta. A evidência de diversidade críptica dentro das duas espécies sugere a possibilidade de que existam mais espécies ainda não reconhecidas ao longo da distribuição de *Favia* no Atlântico. Considerando o conceito unificado de espécies, as três linhagens correspondentes às províncias Caribenha, Brasileira e meio-Atlântica podem ser consideradas metapopulações evoluindo de maneira independente. Em trabalhos futuros de taxonomia integrativas, a incorporação de múltiplas linhas de evidência, como a utilização de micromorfologia e de microestruturas, poderão potencialmente corroborar os resultados obtidos pelas análises coalescentes.

Estimativas de diversidade recuperaram maior diversidade genética na população Sul da costa brasileira, que incluí o Banco de Abrolhos. Este resultado corrobora a hipótese de que esta região pode ter servido como refúgio para corais escleractíneos durante períodos de

variação no nível do mar após o último máximo glacial. Os menores valores de diversidade genética foram observados na linhagem da Ilha de Ascenção, o que sugere que esta potencial nova espécie seja também extremamente vulnerável dado seu isolamento.

Apesar de atualmente existir um consenso sobre a validade de *F. gravida*, a espécie ainda não foi incluída na Lista Vermelha da IUCN. *Favia fragum* é a única espécie de *Favia* listada, com uma distribuição que engloba o Mar do Caribe, a costa Brasileira, as ilhas meio-Atlânticas, o Golfo da Guiné e Cabo Verde, e cujo grau de ameaça é considerado "Pouco Preocupante". Caso as três linhagens obtidas em nossa reconstrução filogenética passem a ser consideradas nas estimativas de ameaça, esperamos que a linhagem de Ascenção passe a ser listada como "Quase Ameaçada" ou "Vulnerável", dada sua população reduzida, alto grau de isolamento e os baixos valores de diversidade genética. Independente das implicações taxonômicas, os resultados obtidos nesta tese demonstram claramente a existência de ao menos três clados distintos de *Favia* no Atlântico, apresentando pouca ou nenhuma conectividade genética entre eles, o que requer planos de conservação independentes.

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