Received: 28 September 2016 | Revised: 3 April 2018 | Accepted: 4 April 2018

DOI: 10.1111/mec.14702

ORIGINAL ARTICLE

WILEY MOLECULAR ECOLOGY

Host-targeted RAD-Seq reveals genetic changes in the coral *Oculina patagonica* associated with range expansion along the Spanish Mediterranean coast

Karine Posbic Leydet[1] | Carsten G. B. Grupstra[2,3] | Rafel Coma[4] | Marta Ribes[3] | Michael E. Hellberg[1]

[1]Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana

[2]Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands

[3]Institut de Ciències del mar, Barcelona, Spain

[4]Centre d'Estudis Avançats de Blanes, Blanes, Girona, Spain

Correspondence
Karine P. Leydet, Department of Biological Sciences, Louisiana State University, Baton Rouge, LA.
Email: keleydet@syr.edu

Present addresses
Karine Posbic Leydet, Department of Biology, Syracuse University, Syracuse, New York.
and
Carsten G. B. Grupstra, Rice University, Houston, Texas.

Funding information
Department of Biological Sciences, Louisiana State University; Spanish Government: Project CSI-Coral, Grant/Award Number: CGL2013-43106-R; Generalitat de Catalunya, Grant/Award Number: 2014SGR1029

Abstract

Many organisms are expanding their ranges in response to changing environmental conditions. Understanding the patterns of genetic diversity and adaptation along an expansion front is crucial to assessing a species' long-term success. While next-generation sequencing techniques can reveal these changes in fine detail, ascribing them to a particular species can be difficult for organisms that live in close association with symbionts. Using a novel modified restriction site-associated DNA sequencing (RAD-Seq) protocol to target coral DNA, we collected 595 coral-specific single nucleotide polymorphisms from 189 colonies of the invasive coral *Oculina patagonica* from the Spanish Mediterranean coast, including established core populations and two expansion fronts. Surprisingly, populations from the recent northern expansion are genetically distinct from the westward expansion and core populations and also harbour greater genetic diversity. We found that temperature may have driven adaptation along the northern expansion, as genome scans for selection found three candidate loci associated with temperature in the north but none in the west. We found no genomic signature of selection associated with artificial substrate, which has been proposed for explaining the rapid spread of *O. patagonica*. This suggests that this coral is simply an opportunistic colonizer of free space made available by coastal habitat modifications. Our results suggest that unique genetic variation, possibly due to limited dispersal across the Ibiza Channel, an influx of individuals from different depths and/or adaptation to cooler temperatures along the northern expansion front may have facilitated the northward range expansion of *O. patagonica* in the western Mediterranean.

KEYWORDS
coral, invasion, Mediterranean, *Oculina patagonica*, RAD-Sequencing, range expansion

1 | INTRODUCTION

Many species, both native and non-native, are expanding their ranges (e.g., Cavanaugh et al., 2014; McDevitt et al., 2014; White, Perkins, Heckel, & Searle, 2013). To do so, invasive species must first disperse to and then become established in a new region. Population bottlenecks associated with colonization may lead to reduced genetic diversity, potentially limiting the ability of newly founded populations to adapt and persist (Frankham & Ralls, 1998; Lee, 2002). This genetic paradox in invasive species (i.e., how bottlenecked

populations can still become successful) has intrigued researchers, who continue to explore possible mechanisms underlining this mystery (Frankham, 2005; Schrieber & Lachmuth, 2017).

The success of expansions has been attributed to many types of genetic changes, some of them contrary to expected bottlenecks. While uncommon, some invasive populations possess increased genetic diversity relative to the source populations. This has been attributed to admixture of distinct populations within the invaded range, due to either multiple introductions from different sources (Kolbe et al., 2004; Novak & Mack, 1993; Roman, 2006) or to hybridization with native populations (Ayres & Strong, 2001; Hohenlohe et al., 2013). Rapid adaptive evolution, as revealed by selective sweeps and outlier loci, has also been associated with successful invasions (Bernardi, Azzurro, Golani, & Miller, 2016; Puzey & Vallejo-Marín, 2014).

Understanding changes in genetic diversity associated with range expansions can help shed light on the evolutionary response to novel environments during the expansion process, as can identifying putative genes targeted by selection in the newly expanded populations. Linking particular genetic changes to environmental variables can also reveal the forces underpinning evolutionary change (Buckley, Butlin, & Bridle, 2012). While, to date, many studies have focused on single range expansion events (e.g., Colautti & Barrett, 2013; Lancaster et al., 2016), comparing dual expansion fronts from a single core can elucidate region-specific genetic mechanisms and environmental factors associated with evolutionary change during expansion (Dlugosch & Parker, 2008; Kennedy et al., 2017).

The development of high-throughput sequencing of reduced representation libraries, such as genotyping-by-sequencing and restriction site-associated DNA sequencing (RAD-Seq), has improved our understanding of range expansions by enabling the screening of large numbers of loci thus enhancing the power to identify genetic signatures of adaptation associated with expansion (White et al., 2013; Zenni & Hoban, 2015) and the environmental factors potentially driving local adaptation (Buckley et al., 2012). However, for organisms that harbour endosymbionts, including many corals, reduced representation libraries can be contaminated with unwanted symbiont DNA, thus allocating time, money and sequence data to the wrong organism and resulting in low coverage of host sequences (Leese et al., 2012; Toonen et al., 2013). Furthermore, symbiont variation or switching may provide a more rapid and versatile way to respond to environmental conditions than genetic mutation and selection of the host itself (Rosenberg, Koren, Reshef, Efrony, & Zilber-Rosenberg, 2007; Rosenberg & Zilber-Rosenberg, 2011). Therefore, if not accounted for during next-generation sequencing methods, symbiont loci will confound measures of host genetic diversity and selection. As such, new next-generation sequencing techniques are necessary to target host DNA and separate its evolutionary response from that of its symbionts. Here, we implement a novel RAD-Seq method to target DNA from a coral that has shown a recent range expansion.

The coral *Oculina patagonica* was thought to have been introduced into the Mediterranean in the mid-20th century (Fine, Zibrowius, & Loya, 2001; Zibrowius, 1974); however, recent genetic work suggests it may have a far longer history in the eastern Atlantic (Leydet & Hellberg, 2015). At odds with this long genetically inferred history, *O. patagonica* was first reported from the Mediterranean in 1973 (Zibrowius & Ramos, 1983) off the southeastern coast of Spain. Recently, it has been documented to be present and increasingly abundant along most of the Spanish Mediterranean coast.

The range expansion of *O. patagonica* is evident not only from idiosyncratic reports, but also from detailed ecological surveys of major benthic organisms. Colonies along the northern coast have been monitored annually for 19 years (Serrano, Coma, Ribes, et al., 2013). There, *O. patagonica* was found at just one location in 1992 (just south of the Ebro Delta, Figure 1), but by 2010 had spread northward and colonized 19% of 223 surveyed locations. These direct observations indicate a northern expansion. Relatively low census numbers west of the Almeria–Oran front (Serrano, Coma, & Marta, 2013; Terrón-Sigler, Casado-Amezúa, & Torre, 2015) point to a likely westward population expansion. In contrast to these sparse or changing distributions in the north and west, *O. patagonica* was reportedly present in 90%–95% surveyed locations along the southeastern coast (Serrano, Coma, Ribes, et al., 2013). These data, along with additional observational data and studies (Fine et al., 2001; Rubio-Portillo, Vázquez-Luis, Izquierdo Muñoz, & Ramos Esplá, 2014; Zibrowius & Ramos, 1983), suggest that populations along ~300 km of the southeastern coast of Spain are the core of the species distribution from where the westward and northward expansions originated. The combination of dynamic and stable ranges of *O. patagonica* in Spanish waters thus allows us to genetically examine and compare two expansions from a single core.

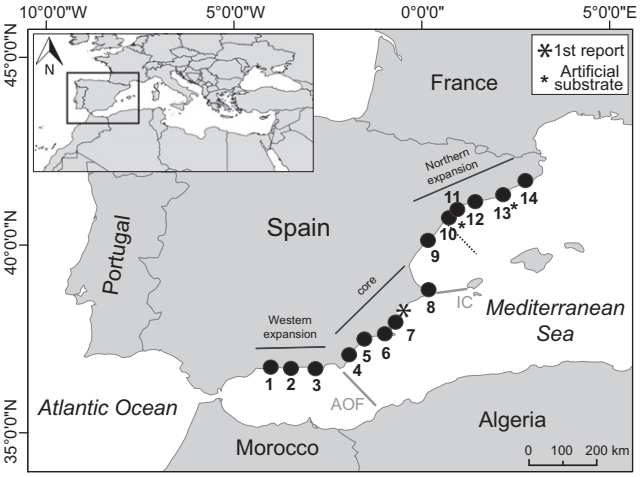

FIGURE 1 Map of the collection sites along the Mediterranean coast of Spain, by zone and site number (Table 1). On the basis of ecological surveys, colonies were collected from within the core zone (populations 4–8), westward expansion (populations 1–3) and the northern expansion (populations 10–14). The first reported site is the Alicante Harbor where *Oculina patagonica* was first reported in Spain in 1973 (colonies not collected). The dashed line represents the Ebro Delta. The asterisks associated with sites 10 and 13 indicate that individuals from these sites were sampled from artificial substrate. The Almeria–Oran front (AOF) and Ibiza Channel (IC) are indicated

These range expansions in *O. patagonica* have been attributed to increased sea surface temperatures as well as coastal habitat modifications (Rubio-Portillo et al., 2014; Serrano, Coma, & Marta, 2013; Terrón-Sigler et al., 2015). Whether these factors have led to genetic changes and local adaptation remains to be explored. Corals are known to adapt to varying temperatures (e.g., Bay & Palumbi, 2014; Smith-Keune & van Oppen, 2006), and this may have played a role in the expansion of *O. patagonica*. Furthermore, coastal infrastructure can alter water flow, light penetration and sedimentation rates in shallow coastal waters (Bulleri & Chapman, 2010), which can then affect coral growth (Fabricius, 2005). Leached chemicals from artificial surfaces could negatively affect settlement and growth of sessile organisms (Chase, Dijkstra, & Harris, 2016). Nonetheless, *O. patagonica*'s ability to grow under a wide range of environmental conditions and on many substrates (Armoza-Zvuloni et al., 2012; Fine et al., 2001) suggests that it can tolerate these ecological alterations caused by artificial habitats, potentially due to local adaptation.

Here, we investigate the dual range expansion of *O. patagonica* along the Spanish coast using a modified RAD-Seq protocol to enrich for coral DNA. After first testing for and confirming the presence of two range expansions, we ask (a) Are the expansions genetically similar to or distinct from core populations? (b) Does genetic diversity at the two range expansions differ relative to the core populations? (c) Which better explains changes in genetic diversity: geographic distance from core populations or environmental variables? and (d) Are there genomic signatures of local adaptation associated with environmental variables potentially facilitating the expansions?

2 | METHODS

2.1 | Sampling and sequencing

Oculina patagonica colonies were collected between 20 August and 31 August 2014 from 14 localities spanning their distribution along the Mediterranean coast of Spain (Figure 1, Table 1). We obtained tissue samples from 13 colonies from each site except for the northernmost (site 14 in Figure 1), from which 20 were collected. Colonies were sampled via SCUBA, breaking off a 2 cm^2 piece of live tissue and preserving it in 95% ethanol. We also obtained a "symbiont-free" *Oculina* sp. colony lacking algal endosymbionts (*Symbiodinium*) from a deep-water (80 m) population off the southeastern coast of North America (Eytan, Hayes, Arbour-Reily, Miller, & Hellberg, 2009). This colony was necessary to target coral-specific sequence reads (see below). Based on five nuclear genes, the level of sequence divergence between *Oculina* spp. from this deep population (*Oculina* Banks) and a Spanish population (Cabo de Palos) is about 0.02 nucleotide substitutions per site (Leydet & Hellberg, 2015), demonstrating its genetic similarity to our target populations.

We extracted genomic DNA from the samples using the QIAGEN DNeasy Kit following the manufacturer's protocols with the following modifications: we allowed tissues to lyse at 56°C overnight; immediately, following lysis samples were treated with RNase A (4 μl of 100 mg/ml) (QIAGEN) and then incubated for 2 min at room temperature; and DNA was eluted in 200 μl of AE buffer after incubation at room temperature for an hour to maximize DNA yield. Species identification was confirmed by sequencing the mitochondrial cytochrome oxidase I (*COI*) gene using previously designed primers (Folmer, Black, Hoeh, Lutz, & Vrijenhoek, 1994) and protocols (Leydet & Hellberg, 2015).

To prescreen for potential clonemates, we sequenced a variable nuclear marker (p14: fatty acid elongase; 206 bp; Leydet & Hellberg, 2015), because mitochondrial genes generally evolve slowly in corals (Hellberg, 2006). During the p14 screening, a colony collected from Barcelona (site 13, Figure 1) was identified as the Mediterranean coral *Cladocora caespitosa*. We used this individual, as well as four *C. caespitosa* colonies from Pantelleria Island, Italy, collected in May 2011, to test for possible hybridization between this species and *O. patagonica* (see below and Supporting Information Figure S6 for additional information). Sequencing was performed using BigDye chemistry version 3.1 on an ABI 3130XL at the Louisiana State University Genomics Facility.

The "symbiont-free" status of the deep *Oculina* sp. colony was verified by attempted PCR amplification of several alga-specific markers: ITS2 (LaJeunesse, 2002), *psbA* minicircle coding region (Barbrook, Visram, Douglas, & Howe, 2006), cp23S–rDNA domain V (Santos et al., 2002) and the flanking region of the microsatellite marker B7SYM15 (Pettay & Lajeunesse, 2007). Positive (*Oculina* containing *Symbiodinium*; Leydet & Hellberg, 2016) and negative (H_2O) controls were run simultaneously. The lack of amplicons confirmed that no *Symbiodinium* was present in the "symbiont-free" coral colony.

DNA quantification and concentration of all samples were determined using NanoDrop and Qubit 2.0 Fluorometer at the LSU Genomics Facility. Samples were submitted to SNPsaurus (Eugene, OR) and sequenced using a novel modified RAD-Seq protocol adapted from Boucher, Casazza, Szövényi, and Conti (2016). Because *Oculina* often harbours endosymbiotic algae with large genomes, traditional genotyping-by-sequencing methods can result in an overrepresentation of unwanted symbiont sequence fragments (Leese et al., 2012; Toonen et al., 2013). Therefore, to maximize coverage of the host coral genome and clarify interpretation of the resulting SNPs, we employed the following approach.

A RAD library was created from 100 ng genomic DNA from the "symbiont-free" *Oculina* sp. sample. This DNA was double-digested with PstI-HF and MfeI-HF (New England Biolabs) and ligated to complementary adapters that allowed the resulting amplified fragments to be converted to biotinylated RNA baits. Fragments with insert sizes 100–350 bp in size were isolated by gel extraction from a portion of the ligated product prior to amplification and the in vitro transcription reaction to create the RNA baits. This bait library template was also converted into one that could be sequenced along with the captured libraries described below. Nextera sequences and indices were added to the bait fragments using long primers matching the adapters in a short PCR to create the baits library. Shotgun sequencing libraries were prepared from 189 submitted samples, plus one "no-capture" control replicate, using 5 ng DNA of each sample in a 1/10th Nextera (Illumina, Inc.)

TABLE 1 Collection sites. Site numbers correspond to those in Figure 1. Environmental variables (sea surface temperature and sampling depth) for sites can be found in Supporting Information Table S1

	Site	n^a	n^b	Substrate	Latitude	Longitude
West	1. Torrox	13	13	Natural	36°43′34″N	3°57′16″W
	2. Sacratif	13	12	Natural	36°41′40″N	3°27′55″W
	3. Punta peña del Moro	13	11	Natural	36°41′53″N	2°51′30″W
Core	4. Carboneras	13	11	Natural	36°59′40″N	1°53′21″W
	5. Cabo Cope	13	9	Natural	37°25′39″N	1°30′03″W
	6. Muelle del Curra	13	11	Natural	37°35′16″N	0°58′33″W
	7. La Zenia	13	6	Natural	37°55′03″N	0°43′12″W
	8. Xàbia	13	10	Natural	38°45′51″N	0°13′26″E
North	9. Alcossebre	13	7	Natural	40°15′33″N	0°18′11″E
	10[c]. L'Ampolla	13	13	Artificial	40°48′29″N	0°42′39″E
	11. Roca de l'Illot	13	13	Natural	40°50′49″N	0°45′24″E
	12. Torredembarra	13	13	Natural	41°08′34″N	1°24′53″E
	13[c]. Barcelona	13	13	Artificial	41°17′43″N	2°09′09″E
	14[d]. Roca Muladera, Es Bullents, Fenals, Punta Santa Ana, Sa Palomera	20	19	Natural	41°41′39″N	2°50′42″E

[a]Number of individuals collected and sequenced.
[b]Number of individuals analysed (excludes 28 individuals with low number of sequence reads and >50% missing data; Supporting Information Figure S2).
[c]Sampled from artificial substrate.
[d]Also referred to as "northernmost population."

reaction with unique dual indices to distinguish the individuals. The samples were pooled and size-selected for insert sizes 170–370 bp. The pooled libraries were then used in two successive overnight hybridizations to the biotinylated bait library, followed by capture using Dynabeads® MyOne™ Streptavidin C1 magnetic beads (Thermo Fisher) and amplification. The final captured libraries were sequenced in two paired-end Illumina HiSeq 3000 runs (one 2 × 100 bp and one 2 × 150 bp) at the Center for Genome Research and Biocomputing, Oregon State University.

2.2 | Genotyping

SNPsaurus processed raw sequence reads using a custom pipeline and scripts based in part on the program BBMap (Bushnell B, sourceforge.net/projects/bbmap/). Reads that passed the default Illumina pipeline quality control were merged into long pseudo-reads with the "bbmerge" tool. The pseudo-reads and individual paired-end reads were then assembled into longer contigs with "tadpole." The bait reads were collapsed into unique reads and aligned to the contigs using "bbmap." The longest contigs that matched bait reads were selected to represent each bait locus. These representative loci were further collapsed to remove redundancy, ultimately creating a contig reference. Next, the paired-end reads were trimmed to remove Nextera adapter sequences using "bbduk." Then, 21 very abundant (present >0.2% of the total reads) sequences found in the samples were removed so that misalignment of these reads to the reference set of loci would not cause artefacts. The trimmed reads were aligned to the contig reference with "bbmap" using an 88% identity threshold given the sequence diversity seen in the reads.

After alignment, the sample contigs were converted to a variant call format (VCF) genotype table with SAMtools (Li et al., 2009) and then filtered for depth (>9 reads), minor allele frequency (≥0.05) and presence (≤25% missing data in a population) with VCFtools (Danecek et al., 2011). To minimize linkage of SNPs, only a single SNP from each contig was retained. The VCF was then filtered using a custom script to remove probable duplicated loci (loci that were heterozygous in nearly all samples, suggesting two fixed paralogous loci were aligned to the same reference). Individuals missing >50% data and loci missing >20% data were excluded from further genetic analyses. The final VCF file was converted into file formats necessary for subsequent analyses using PGDSPIDER 2.0.9.0 (Lischer & Excoffier, 2012). Searches for contigs representing the SNPs were performed in BLASTn and BLASTx (Altschul, Gish, Miller, Myers, & Lipman, 1990).

2.3 | Range expansion

We first tested for genetic signatures of the two range expansions suggested by direct observations and ecological data (see Introduction) using an approach outlined by Peter and Slatkin (2013) and Peter and Slatkin (2014). In brief, the method applies a founder effect algorithm to test for population expansion vs. equilibrium isolation-by-distance and to infer the most likely expansion origin.

2.4 | Population subdivision

To test for subdivision, we used a Bayesian clustering analysis implemented in STRUCTURE 2.3.4 (Pritchard, Stephens, & Donnelly, 2000), which detects significantly genetically differentiated clusters or

populations (*K*). We ran the program for 500,000 MCMC steps following a burn-in of 100,000 steps using the admixture model with correlated allele frequencies. We set sampling locations as a priori (LOCPRIOR model) because we expected structure signal to be weak (Hubisz, Falush, Stephens, & Pritchard, 2009) based on our previous survey of subdivision within *O. patagonica* in the Mediterranean (Leydet & Hellberg, 2015). We performed 10 iterations for each inferred number of genetic clusters, $K = 1$–6, and used the Evanno method (Evanno, Regnaut, & Goudet, 2005) implemented in STRUCTURE HARVESTER (Earl & vonHoldt, 2012) to determine the most likely number of genetic clusters. We reran STRUCTURE on any genetic clusters found in our initial STRUCTURE run to test for substructuring. In addition to the ecological data and test for range expansion, the results from this test allowed us to then group the populations into westward and northward expansion zones and a core zone (see Table 1) on which subsequent analyses were conducted.

To further examine population subdivision, we performed an analysis of molecular variance (AMOVA) implemented in GENODIVE 2.0b27 (Meirmans & Van Tienderen, 2004). We first performed an AMOVA comparing all populations and all zones. Then, we compared the two expansions (west vs. north). Finally, we compared each expansion zone to the core zone separately. We ran 10,000 permutations to estimate significance.

2.5 | Genetic diversity

To test for genetic clones (in addition to our initial p14 marker screen), we calculated the allele dissimilarity between all pairs of individuals within all populations using the R package *poppr* (Kamvar, Brooks, & Grünwald, 2015; Kamvar, Tabima, & Grünwald, 2014). Although establishing a cut-off is somewhat arbitrary, dissimilarities equal to or close to zero would indicate that those pairs of individuals are likely clones. We also used *poppr* to calculate the number of private alleles found in each population and in each zone.

To compare genetic diversity between core and expansion populations, we calculated allelic richness using FSTAT 2.9.4 (Goudet, 1995), which corrects for variation in population sample size. We also calculated average allelic richness for each zone and performed pairwise comparisons using two-sided tests in FSTAT. To estimate significance, we ran 1,000 permutations for all pairwise comparisons.

2.6 | Environmental data

Annual mean, maximum, minimum and range of sea surface temperatures (SST) for all collection sites were obtained from two different sources: (a) Bio-ORACLE 2002–2009 (http://www.bio-oracle.org/) and (b) Ocean Color 2003–2015 (https://oceancolor.gsfc.nasa.gov/). We included both sources because their temporal ranges were different (Supporting Information Table S1). Although these data represent surface temperatures and the depth at which colonies were collected varied between sites (see below), previous work suggests the accuracy of remotely sensed SST data is reliable from 0 to 10 m during the warm season in this region (Bernardello, Serrano, Coma, Ribes, & Bahamon, 2016). Although *O. patagonica* is found on both natural and artificial substrate throughout the Spanish coast (Rubio-Portillo et al., 2014; Serrano, Coma, & Marta, 2013; Terrón-Sigler et al., 2015), in this study, colonies from all but two sites (10 and 13 in Figure 1) within the northern expansion zone came from natural substrate. Finally, depth of each colony was averaged and analysed from each site (Supporting Information Table S1). We considered depth as an environmental variable because it is a common factor driving patterns of coral diversity and adaptation (e.g., Prada & Hellberg, 2013).

We performed principal component analysis (PCA) on all environmental variables to test whether zones differ in their habitat. We also used one-way ANOVA and subsequent Tukey's multiple comparison test to compare measures of depth and Ocean Color measure of temperature between locations. We were unable to statistically compare Bio-ORACLE measure of temperature among locations because of the lack of repeated measures.

2.7 | Environmental factors associated with genetic diversity

We performed PCA using the EIGENSOFT package (Patterson, Price, & Reich, 2006), which utilizes multilocus genotypes as input. We plotted the two components explaining the most variance of each PCA and visually distinguished geographic groupings and environmental variables of each population to examine genetic differentiation associated with populations, zones, measures of SST, depth and sampling substrate (Supporting Information Table S1). Because the populations sampled from artificial substrate were not geographically distributed across all zones but instead were restricted to the northernmost zone, we performed a PCA associated with this environmental variable for populations just within the northern expansion to remove any potential geographic effects on genetic variation. Although using PCAs to relate genetic data with environmental variables is only exploratory and thus limited, we were unable to implement more robust methods such as a hierarchical Bayesian method (Foll & Gaggiotti, 2006) due to our complex set of environmental variables (Supporting Information Figure S1), which prevented convergence of the aforementioned Bayesian method (results not shown).

2.8 | Loci under selection

To identify loci potentially under environmental selection, we used the F_{ST}-based genome scan method implemented in BayeScEnv 1.1 (de Villemereuil & Gaggiotti, 2015). BayeScEnv incorporates environmental differentiation and locus-specific effects to discriminate between signals of local adaptation relating to a particular environmental factor and spurious signals left by other processes, such as allele surfing, differences in mutation rate among loci and background selection, thus improving its ability to control for false positives. We first examined geographic location as the environmental factor for each expansion front separately. For the westward expansion, we used longitude to represent the spread to the west. For the

northern expansion, we used latitude to represent a poleward spread. We standardized latitude and longitude by dividing each by their standard deviation. We also investigated genomic signatures of local adaptation to temperature and depth for each expansion. We standardized all environmental variables by first computing the mathematical distance from the mean and then dividing by the standard deviation. Finally, we tested for genomic signatures of adaptation to substrate (natural vs. artificial) in the northern expansion zone. To minimize any confounding effects due to geographic distance and/or varying temperature, we analysed populations 10–13, which are in relatively close proximity (<400 km) and share similar environmental conditions except substrate use.

We conducted 20 pilot runs of 5,000 iterations each to adjust acceptance rates of the MCMC chain to the recommended range of 0.2–0.4. An additional burn-in of 10^6 iterations was run followed by a sample size of 10^6 iterations with a thinning interval of 20. The prior parameters were $\pi = 0.1$ and $p = 0.25$. We used the R package *coda* (Plummer, Best, Cowles, & Vines, 2006) to ensure chain convergence and acceptable autocorrelation (i.e., effective sample sizes of at least 1,000) (Supporting Information Table S2). BayeScEnv calculates two kinds of false discovery rate (FDR)-related statistics: posterior error probability (PEP) and *q*-value. We used an FDR cut-off of 5% for PEP (the more conservative statistic) to determine which loci were putatively under selection (Funk et al., 2016). We used our BLASTn and BLASTx searches of the contigs representing the SNPs (see above) to identify possible genes and functions associated with loci putatively under selection.

3 | RESULTS

3.1 | Sequencing and genotyping

RAD-sequencing of the baits resulted in 611,000 reads. After these reads were sorted and collapsed, reads with 2–39 counts were retained, yielding 14,000 bait sequences. A subset of nonbait samples consisting of 18,866,444 raw reads was used to construct the reference, which after trimming, removing high-repeat reads and merging, resulted in 821,531 sequences. These merged reads were assembled with the unmerged reads, producing 637,646 contigs, which were aligned to the bait reads. The alignment to the longest contig was used to select a representative contig locus for that bait locus, ultimately resulting in 595 SNPs (one per contig). Contig length ranged from 180 to 1,272 bp (mean = 317 bp). BLASTn (Altschul et al., 1990) searches resulted in only eight contigs matching to nucleotide sequences. However, BLASTx (Altschul et al., 1990) searches returned 341 contigs that matched to proteins inferred from sequences from other corals (189 contigs had an *E*-value $\leq 1 \times 10^{-5}$). No contigs aligned to *Symbiodinium*, whose full genome has been sequenced (Lin et al., 2015; Shoguchi et al., 2013), indicating that the protocol was successful in removing algal symbiont sequences.

Twenty-eight of the 189 samples did not pass quality cut-offs (low number of sequence reads and >50% missing data, Supporting Information Figure S2) and were therefore excluded from further analysis. Of the remaining 161 individuals, missing data ranged from 0% to 48.1%, with most (88%) of individuals containing <20% missing data (Supporting Information Figure S3). The per cent missing data per locus for these 161 individuals was no more than 14.3% (Supporting Information Figure S4). All loci were therefore retained for analysis.

Missing data were skewed among populations. Populations 1–9 had a higher proportion of individuals with >10% missing data compared to populations 10–14 (Supporting Information Figure S3). To determine whether inclusion of these individuals (with >10% missing data) would alter our results, we ran preliminary genetic analyses for a subset of 127 individuals that did not exceed 10% missing data. These alternative data sets produced similar results (data not shown), suggesting that missing data did not significantly alter our results. The final data set thus consisted of 161 individuals and 595 SNPs.

3.2 | Range expansion

The expansion model was strongly supported ($p = 0.0004$) over equilibrium isolation-by-distance and indicated the southeastern region as the likely origin (Figure 2). This is consistent with the ecological surveys supporting that southeastern populations are the core populations that have expanded both westward and northward.

3.3 | Population subdivision

The Evanno method ΔK (Evanno et al., 2005) and LnP(*K*) agreed that the most likely number of genetic clusters inferred by STRUCTURE was two with a genetic break occurring between populations 8 and 9 (Figure 3). In addition to the ecological data and test for range expansion, the results from this test (i.e., the genetic break between

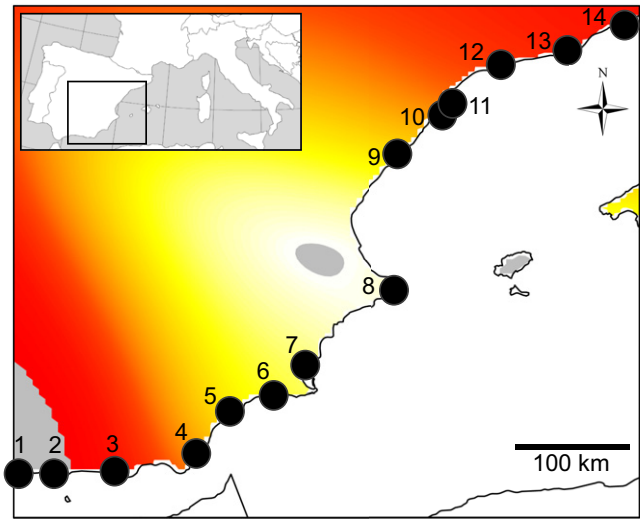

FIGURE 2 Range expansion map showing the most likely origin of the expansion (yellow) and least likely origin of expansion (red and grey). Numbers represent population IDs from Table 1 and Figure 1 [Colour figure can be viewed at wileyonlinelibrary.com]

populations 8 and 9) allowed us to group the populations into westward (populations 1–3) and northward expansion zones (populations 9–14) and a core zone (populations 4–8) (Table 1) on which subsequent analyses were conducted. Thus, according to our STRUCTURE results, all individuals from the western expansion and core were entirely assigned to one cluster and those from the northern expansion entirely to another cluster. We found no further substructuring.

AMOVA supported significant subdivision among populations and zones (Table 2a). The western and northern expansion zones significantly differed (Table 2b), and populations along the northern expansion were subdivided (Table 2d), but not those along the westward expansion front (Table 2c).

3.4 | Genetic diversity

Sequencing of the variable nuclear marker p14 (Leydet & Hellberg, 2015) indicated ≥4 genotypes in each of the sampled populations, suggesting that the populations were not overwhelming comprised of clonemates. The average pairwise allele dissimilarity between individuals from RAD-Seq SNP data across all populations was 18.7% (Supporting Information Figure S5). The lowest dissimilarity between any two individuals was 7.3%, meaning that those two were 92.7% similar in their multilocus genotype. Only eight pairs of individuals out of all possible pairwise comparisons had dissimilarities <10%. Although establishing a cut-off is somewhat arbitrary, given that we observed no dissimilarities <5%, we are confident that clonality was not a significant factor in our data set and subsequent genetic analyses.

We found that the northward expansion populations had higher allelic richness compared to both the westward expansion and core zones (1.532 vs. 1.507 and 1.499, respectively; pairwise $p = 0.046$, 0.002; Figure 4). The westward expansion and core zones did not differ from one another (1.507 vs. 1.499; $p = 0.509$). No zones harboured any private alleles.

3.5 | Hybridization in northern populations?

We investigated whether the genetic distinctness and relatively high genetic diversity of northernmost populations could be the result of hybridization with a co-occurring and morphologically similar coral, *C. caespitosa*. The haplotype network for the variable nuclear marker p14 (Supporting Information Figure S6) showed that all sequences from *Oculina* spp. (including *O. patagonica* from this study) share similar alleles across a large geographic scale and are distinct from *C. caespitosa* (at least 20 mutation steps between *Oculina* and *Cladocora* alleles), suggesting that these species are not hybridizing.

TABLE 2 Analysis of molecular variance performed (a) for all populations, (b) between expansions (west vs. north), (c) between western expansion and core and (d) between northern expansion and core. Significant *F*-statistic values are in bold

Source of variation	% variation	FSTAT
(a) For all populations		
Within populations	0.983	0.017
Among populations	0.004	**0.004**
Among zones	0.013	**0.013**
(b) Between expansions (west vs. north)		
Within populations	0.981	0.019
Among populations	0.001	0.001
Among zones	0.018	**0.018**
(c) Between western expansion and core		
Within populations	0.994	0.006
Among populations	0.005	**0.005**
Among zones	0.001	0.001
(d) Between northern expansion and core		
Within populations	0.980	0.020
Among populations	0.003	**0.004**
Among zones	0.017	**0.017**

3.6 | Environmental data

The PCA constructed using environmental data revealed that the four zones are significantly differentiated (Figure 5). PC1 explained 54.6% of the variation, and PC2 explained another 39.2% (cumulative = 93.8%).

According to one-way ANOVAs, all measures of SST (Ocean Color) differed among zones ($p < 0.001$). An ANOVA revealed that the average sampling depths differed significantly among zones ($F = 34.68$, $p < 0.0001$), and post hoc Tukey's multiple comparisons tests indicated that the average sampling depth for the northern

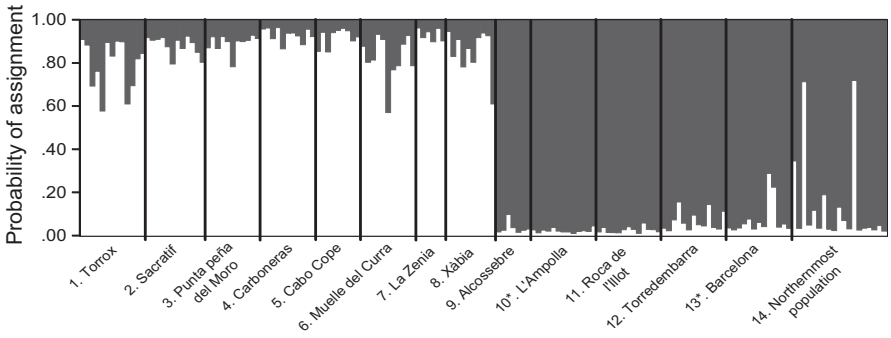

FIGURE 3 STRUCTURE bar plot for $K = 2$. Individuals (bars) are grouped by population along the *x*-axis, with the probability of assignment to a particular genetic cluster (represented by different shades) along the *y*-axis

expansion zone (4.1 m) was significantly greater than the west (2.1 m) and the core zones (1.6 m) ($p < 0.0001$).

3.7 | Environmental factors associated with genetic diversity

Principal component analysis showed genetic differentiation associated with zones (Figure 6), SST (Figure 7 and Supporting Information Figure S7) and depth (Supporting Information Figure S8). Differentiation was most evident for minimum temperature and temperature range. These effects were significant, but subtle, with the first and second eigenvectors explaining 3.24% ($p < 0.01$) and 2.42% ($p = 0.01$) of the variation, respectively. We found no association with population (Supporting Information Figure S9), indicating that genetic differentiation does not exist at this small scale, nor did we find an association with substrate (Supporting Information Figure S10).

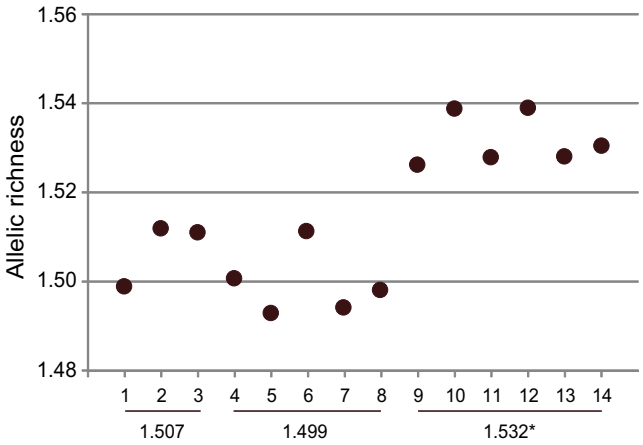

FIGURE 4 Allelic richness calculated for each population. Averages are shown below the graph. The asterisk indicates that the northern expansion had significantly greater allelic richness compared to the westward expansion and core populations. *p*-Values of pairwise comparisons are as follows: 1–3 vs. 4–8 ($p = 0.509$), 1–3 vs. 9–14 ($p = 0.046$) and 4–8 vs. 9–14 ($p = 0.002$)

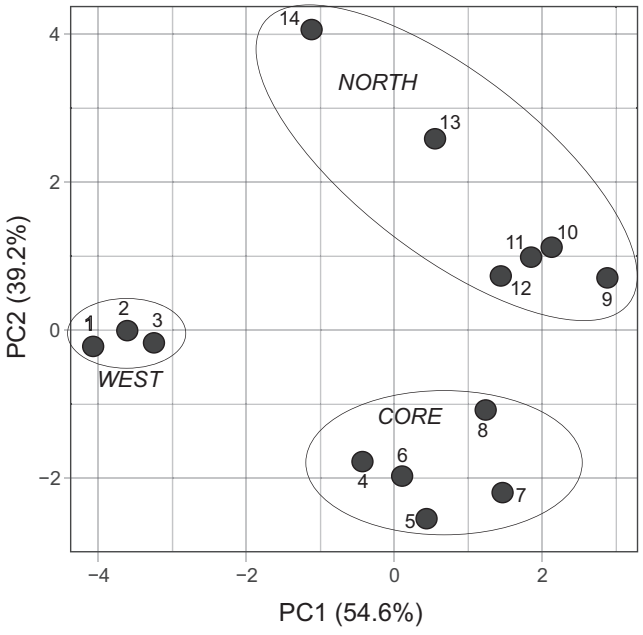

FIGURE 5 Principal component analysis constructed using all environmental data for each location including depth and all temperature measures (mean, min, max and range) (Supporting Information Table S1). Numbers represent population IDs from Table 1 and Figure 1. Core and expansion population groupings are indicated by the ellipses

3.8 | Loci under selection

We found no genomic signal for selection associated with geographic location, substrate or depth in either expansion, nor with temperature along the westward expansion front. However, we found three candidate loci putatively under selection and associated with temperature along the northern expansion.

The first candidate locus under selection was strongly associated with Bio-ORACLE minimum temperature (FDR value < 0.05). This same locus was also associated with Ocean Color minimum temperature (FDR value = 0.068). A BLASTX search of the contig found no matches. The second candidate locus was significantly associated with Bio-ORACLE's minimum temperature (FDR value < 0.05) and Ocean Color temperature range (FDR value < 0.05), but again a BLASTX search found no matches. The third candidate locus was marginally associated with Ocean Color mean temperature (FDR = 0.057). A BLASTX search of the contig matched (*E*-value = 6×10^{-6}) a 52 kDa repressor of the inhibitor of the protein kinase-like (accession number XP_015748588). We know of no data that tie this potential match to a role in adaptation to temperature and recognize that experimental manipulations would be needed to definitively test this or the other two candidate loci for thermal adaptation.

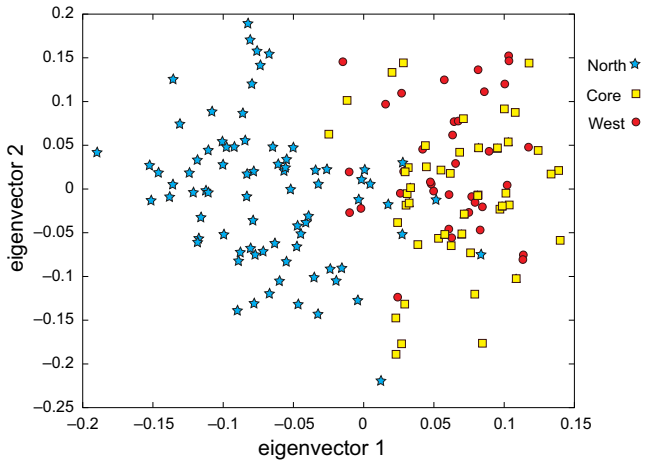

FIGURE 6 Principal component analysis plot of individuals constructed using genetic data and grouped by zone. The first eigenvector explains 3.24% of the variation ($p < 0.01$). The second eigenvector explains 2.42% of the variation ($p = 0.01$) [Colour figure can be viewed at wileyonlinelibrary.com]

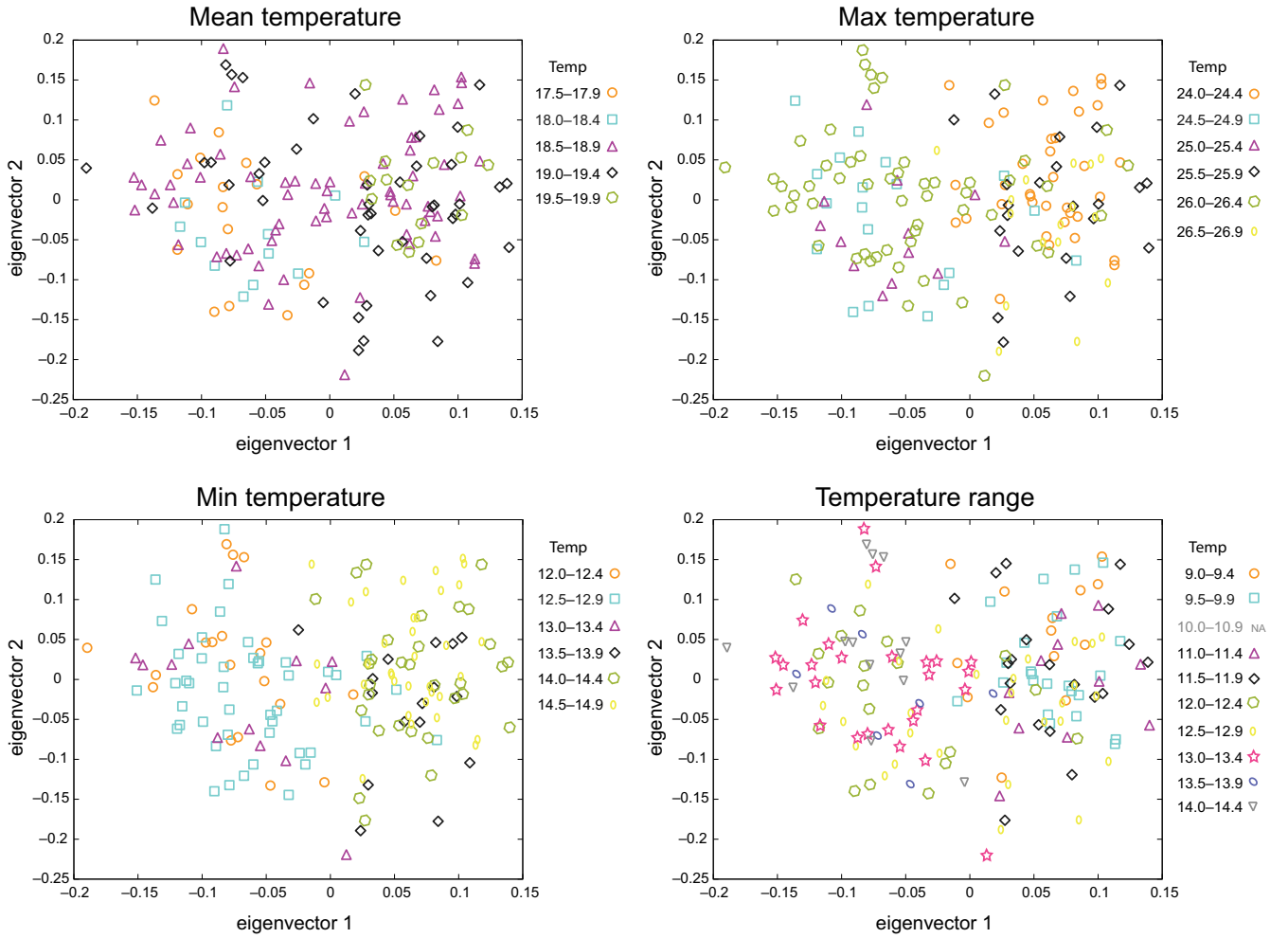

FIGURE 7 Principal component analysis plots of individuals constructed using genetic data and grouped by sea surface temperature measures (°C) obtained from Bio-ORACLE (2002–2009) (Supporting Information Table S1). The first eigenvector explains 3.24% of the variation ($p < 0.01$). The second eigenvector explains 2.42% of the variation ($p = 0.01$). See Supporting Information Figure S7 for PCA plots constructed with Ocean Color temperature data [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

In this study, we investigated coral-specific genetic change along an environmental gradient that encompasses established core populations and two expansion fronts using a RAD-Seq protocol that targeted coral DNA. The coral *O. patagonica* (Serrano, Coma, & Marta, 2013) was expected to harbour lower genetic diversity within its recently expanded range due to a bottleneck and the asexual reproduction capacity of this species (Kramarsky-Winter, Fine, & Loya, 1997). Instead, we found that the recently expanded northern populations harbour greater, and distinct, genetic diversity compared to the other populations and, unlike the other populations, may have adapted to local temperatures.

4.1 | RAD-Seq targeted to host DNA

Although the advent of next-generation sequencing of reduced representation libraries has vastly improved our ability to study nonmodel organism at a genomic scale, this can still be a daunting task for organisms that harbour endosymbionts. Unwanted symbiont DNA can contaminate these libraries, especially in corals, which harbour vast numbers of intracellular algal symbionts (as much as 6×10^6 *Symbiodinium* cells per cm^2 of coral tissue) (Stimson, Sakai, & Sembali, 2002) with large genomes (ca. 1,200–1,500 Mbp) (Lin et al., 2015; Shoguchi et al., 2013). By comparison, the genome of the coral *Acropora digitifera* is 420 Mbp (Shinzato et al., 2011), about one-third the size. Combined with the high densities of *Symbiodinium* within coral cells, the signal from coral genes could be swamped by its symbionts' DNA. Dissociating changes to host and symbiont genomes is crucial, given that spatiotemporal symbiont variation ("switching") may provide a quick way to respond to environmental change (Jones, Berkelmans, van Oppen, Mieog, & Sinclair, 2008). Thus, the response of the symbiont community may confound any coral-specific responses if their genomes are not carefully disentangled.

To focus sequencing efforts on the coral host, we implemented a new RAD-Seq method to capture and sequence coral sequence

fragments. Unlike other coral studies that take *Symbiodinium* contamination into account by mapping and sorting loci postsequencing (e.g., Forsman et al., 2017; Johnston et al., 2017), our method relies on presequencing techniques to eliminate symbiont DNA and therefore prevents the unnecessary sequencing of unwanted loci. Furthermore, it takes advantage of already well-established sequence capture technology in contrast to other presequencing separation and isolation of *Symbiodinium* cells (Bongaerts et al., 2017). As such, the method we used requires a "*Symbiodinium*-free" coral individual of the same or closely related species, which can easily be acquired via laboratory bleaching in the absence of naturally occurring "symbiont-free" colonies, as was available for this study. Although we were unable to take advantage of the reference genomes available for coral and symbiont (due to phylogenetic divergence and partial genome assembly, respectively), most contigs matched to coral proteins in BLASTX searches. Furthermore, we only retained contigs that aligned to our "symbiont-free" sample as an extra precaution. We are therefore confident that our loci are indeed coral-specific.

4.2 | The two Spanish expansions are genetically distinct

We found that the separate westward and northern expansions of *O. patagonica* are genetically distinct (Figure 3). While the westward expansion is similar to long-established core populations, the northern expansion (Serrano, Coma, & Marta, 2013) is genetically distinct from the core and westward expansion. The break between the two genetic clusters occurs between populations 8 and 9 (Figure 3), which coincides geographically with a shift in the environment (Figure 5), namely cooler temperatures, wider temperature ranges and deeper sampling depths.

Aside from an environmental shift, the observed genetic break could also stem from a barrier to dispersal at the Ibiza Channel (IC; Figure 1). The IC coincides with genetic breaks in other marine organisms (García-Merchán et al., 2012; Mokhar-Jamai et al., 2011), including the coral *C. caespitosa* (Casado-Amezúa, Kersting, Templado, & Machordom, 2014). Circulation across the IC is often blocked by the Northern Current, which carries waters south to the IC and then diverts north-eastward (Pinot, López-Jurado, & Riera, 2002; Ruiz et al., 2009). In the summer, the northeastern deflection of the Northern Current, caused by the formation of a gyre, is more intense (Pinot et al., 2002). Given that *O. patagonica* spawns at the end of the summer (Fine et al., 2001), these currents may restrict gene flow between populations on either side of the IC, thus explaining the observed genetic break between populations 8 and 9.

Elsewhere within our sampled range, the Almeria–Oran front (AOF between the westward expansion and core zones in Figure 1) coincides with a genetic break in some marine species (Patarnello, Volckaert, & Castilho, 2007), but not others (García-Merchán et al., 2012). Although this region also marks a shift in the environment (Figure 5), in *O. patagonica*, this front does not appear to be a genetic break, as populations on either side of the Almeria–Oran front are genetically similar (Figure 3).

4.3 | Increased genetic diversity in the northern expansion

Genetic diversity within the recent northern expansion was higher than in longer-established populations (Figure 4), unlike in many invasions (Cahill & Levinton, 2016; Herborg, Weetman, van Oosterhout, & Hanfling, 2007; Tsutsui, Suarez, Holway, & Case, 2000). In contrast, diversity within the westward expansion was the same as in the core populations. Although genetic diversity does not necessarily predict invasion success (Roman & Darling, 2007), genetic variation is the raw material for adaptation. Therefore, having more genetic variation may provide the northern populations with more material on which selection can act.

Could the observed increased diversity be attributed to *O. patagonica* hybridizing within the northern expanded range? The closest relative to *O. patagonica* in the Mediterranean is *C. caespitosa* (Fukami et al., 2004; Kitahara, Cairns, Stolarski, Blair, & Miller, 2010), even though classical taxonomy had long placed them in separate families. In some areas, the two can be easily confused in the field (C. Grupstra, personal observation). Their *COI* haplotypes differ by only a single SNP over 606 bp (*C. caespitosa COI* accession number KR297263), although nucleotide substitution rates tend to be very slow in coral mtDNA (Hellberg, 2006). *Cladocora caespitosa* occurs along the entire Spanish Mediterranean coast (Casado-Amezúa et al., 2014) and spawns at the end of summer (August–October) in the western Mediterranean (Kersting, Casado, López-Legentil, & Linares, 2013), as does *O. patagonica* (Fine et al., 2001). However, *C. caespitosa* is more abundant at deeper depths (>10 m) than *O. patagonica* (Casado-Amezúa et al., 2014; Kersting & Linares, 2012). In addition, our sequencing of variable nuclear marker p14 (Supporting Information Figure S6) found a high degree of divergence between *C. caespitosa* and *O. patagonica* individuals, including *O. patagonica* along the northern Spanish expansion. Whereas the average number of nucleotide differences for p14 within *Oculina* spp. is 1.4 bp, the average number of nucleotide difference between *Oculina* spp. and *Cladocora* is 20.5 bp. These differences suggest that interspecific hybridization does not explain the relatively high genetic diversity in the northern expansion.

Could the increased genetic variation in the northern expanded range be the result of multiple introductions? Close by our sampled range, *O. patagonica* occurs along the Mediterranean coasts of France and Italy. Gene flow from genetically differentiated Italian populations into northern Spain could explain the increased genetic diversity and genetic distinctness we found in northern Spain. Our recent work (Leydet & Hellberg, 2015), however, indicates that populations across the Mediterranean (3,200 km), including Spain and Italy, are not genetically differentiated from each other, although this finding was based on a five-locus data set. The significant differentiation we found here at a much smaller geographic scale (900 km) using 595 SNP loci suggests that we cannot rule out possible gene flow from genetically differentiated Italian populations, whose genetic distinctness was too subtle to detect with our previous five-locus data set.

In addition to admixture, an influx of differentiated individuals from different habitats could boost northern genetic diversity. Depth is increasingly being implicated in driving genetic structuring within coral populations (Pérez-Portela et al., 2016; Prada & Hellberg, 2013; Serrano et al., 2014) and their associated algal symbionts (Prada et al., 2014). Along the coast of Spain, *O. patagonica* is most commonly reported from depths less than 10 m (Coma et al., 2011; Serrano, Coma, & Marta, 2013; Terrón-Sigler et al., 2015); however, colonies have been found along the Catalan coast as deep as 28 m (Serrano, Coma, & Marta, 2013). Indeed, colonies collected from the two most northern sites (13 and 14) were from greater depths compared to the other sites (Supporting Information Table S1) and may harbour allelic variation from genetically differentiated deep populations. Such mixing could contribute variation for selection to act upon, although genes coming from deeper water might be expected to fare poorly in warmer surface waters. Indeed, while we found an association between genetic structure and depth (Supporting Information Figure S8), we did not find evidence of genomic signature of selection linked to depth. Additional sampling along a depth cline is needed to evaluate the role of deep *O. patagonica* populations on increased genetic variation along the coast of Catalonia.

4.4 | Environmental factors facilitating northern range expansion

Like many other invasions (Cavanaugh et al., 2014; Pateman, Hill, Roy, Fox, & Thomas, 2012; Yamano, Sugihara, & Nomura, 2011), temperature has been linked to the geographic and demographic spread of *O. patagonica*, mainly by extending its seasonal growth period (Serrano, Coma, & Marta, 2013). We found that populations along the Spanish Mediterranean coast appear to be genetically differentiated along a temperature gradient. Furthermore, we found three candidate loci putatively under selection associated with temperature, which suggests thermal adaption may play a role along the northern expansion, although other environmental factors that covary with temperature may be the actual driver of adaptation. Experimental manipulations coupled with gene expression studies comparing core and expanded populations are needed to more effectively test for adaptation to cooler temperatures within the northern expansion front (Lancaster et al., 2016).

Modification of coastal habitats has also been linked to the Mediterranean expansion of *O. patagonica* (Coma et al., 2011; Salomidi, Katsanevakis, Issaris, Tsiamis, & Katsiaras, 2013; Serrano, Coma, & Marta, 2013; Terrón-Sigler et al., 2015). We did not find genetic differentiation associated with substrate, nor did we find evidence of genomic signatures of local adaptation to substrate. Although additional paired sampling from both substrate types along the entire Spanish coast as well as experimental tests is needed to provide a more powerful test for local adaption to artificial substrate, our results suggest that *O. patagonica* may not be locally adapted to artificial substrate. Instead, it seems more likely that it is an opportunistic colonizer, taking advantage of the increased space availabilities provided by artificial habitats (Serrano, Coma, & Marta, 2013).

5 | CONCLUSION

Examination of the host genetics of the coral *O. patagonica* over the environmental gradient along which this species spans in the western Mediterranean has allowed us to show that the northern expanded populations are genetically distinct and more diverse than the southern long-established populations as well as westward expanded populations. Limited dispersal across the IC, an influx of individuals from different depths and/or adaptation to cooler temperatures along the northern expansion front may explain this unique genetic variation.

Our study provides evidence that rapid northward expansion of *O. patagonica* may have been facilitated by high genetic variation and thermal adaptation within the host. Because symbionts can also contribute to local adaptation to new thermal regimes (Baird, Bhagooli, Ralph, & Takahashi, 2009; Baird, Cumbo, Leggat, & Rodriguez-Lanetty, 2007), studies of *Oculina*-associated zooxanthellae and other microbes are also needed to assess the role they may play in the coral's range expansion.

ACKNOWLEDGEMENTS

We thank Jérôme Goudet for compiling a new version of FSTAT suitable for large SNP data sets, Paul Etter and Eric Johnson for next-generation data support, Pierre de Villemereuil for BayeScEnv support and Scott Herke for help and advice on sample preparation for next-generation sequencing. We also thank Eduard Serrano for helping to sample site 14 and Erik Caroselli for *Cladocora* samples from Italy. Finally, we thank the LSU Brown Lab Discussion Group, Robb Brumfield and Brant Faircloth for helpful feedback on earlier drafts of this manuscript and three anonymous reviewers for their comments that helped improve this manuscript. Financial support was provided by the Department of Biological Sciences at Louisiana State University to MEH and by the Spanish Government under the project CSI-Coral (CGL2013-43106-R) to MR and RC who are part of the Marine Biogeochemistry and Global Change Research group of the "Generalitat de Catalunya" (2014SGR1029).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA ACCESSIBILITY

Raw RAD-Seq genetic data generated in this study have been deposited in the NCBI Sequence Read Archive (SRA) (2 × 100 bp run: accession no. SAMN05786114–SAMN05786230, SAMN05821346–SAMN05821417, BioProject PRJNA343301; 2 × 150 bp run: accession no. SAMN05821418–SAMN05821606, BioProject PRJNA344385; baits sequences: accession no. SAMN05821614, BioProject PRJNA344386). The VCF file containing the final SNP data as well as other helpful files has been uploaded onto Dryad Digital Repository (https://doi.org/10.5061/dryad.kh049).

AUTHOR CONTRIBUTIONS

The study was designed and conceived by all authors. Collections were carried out by C.G., R.C. and M.R. The genetic data were obtained, the genetic analyses were performed and the manuscript was drafted by K.P.L. The final manuscript was read, edited and approved by all authors.

ORCID

Karine Posbic Leydet http://orcid.org/0000-0002-7019-7078

REFERENCES

Altschul, S. F., Gish, W., Miller, W., Myers, E. W., & Lipman, D. J. (1990). Basic local alignment search tool. *Journal of Molecular Biology*, *215*(3), 403–410. https://doi.org/10.1016/S0022-2836(05)80360-2

Armoza-Zvuloni, R., Kramarsky-Winter, E., Rosenfeld, H., Shore, L. S., Segal, R., Sharon, D., & Loya, Y. (2012). Reproductive characteristics and steroid levels in the scleractinian coral *Oculina patagonica* inhabiting contaminated sites along the Israeli Mediterranean coast. *Marine Pollution Bulletin*, *64*(8), 1556–1563. https://doi.org/10.1016/j.marpolbul.2012.05.020

Ayres, D. R., & Strong, D. R. (2001). Origin and genetic diversity of *Spartina anglica* (Poaceae) using nuclear DNA markers. *American Journal of Botany*, *88*(10), 1863–1867.

Baird, A. H., Bhagooli, R., Ralph, P. J., & Takahashi, S. (2009). Coral bleaching: The role of the host. *Trends in Ecology & Evolution*, *24*(1), 16–20. https://doi.org/10.1016/j.tree.2008.09.005

Baird, A. H., Cumbo, V. R., Leggat, W., & Rodriguez-Lanetty, M. (2007). Fidelity and flexibility in coral symbioses. *Marine Ecology Progress Series*, *347*, 307–309. https://doi.org/10.3354/meps07220

Barbrook, A. C., Visram, S., Douglas, A. E., & Howe, C. J. (2006). Molecular diversity of dinoflagellate symbionts of Cnidaria: The *psbA* minicircle of *Symbiodinium*. *Protist*, *157*(2), 159–171. https://doi.org/10.1016/j.protis.2005.12.002

Bay, R. A., & Palumbi, S. R. (2014). Multilocus adaptation associated with heat resistance in reef-building corals. *Current Biology*, *24*(24), 2952–2956. https://doi.org/10.1016/j.cub.2014.10.044

Bernardello, R., Serrano, E., Coma, R., Ribes, M., & Bahamon, N. (2016). A comparison of remote-sensing SST and in situ seawater temperature in near-shore habitats in the western Mediterranean Sea. *Marine Ecology Progress Series*, *559*, 21–34. https://doi.org/10.3354/meps11896

Bernardi, G., Azzurro, E., Golani, D., & Miller, M. R. (2016). Genomic signatures of rapid adaptive evolution in the bluespotted cornetfish, a Mediterranean Lessepsian invader. *Molecular Ecology*, *25*(14), 3384–3396. https://doi.org/10.1111/mec.13682

Bongaerts, P., Riginos, C., Brunner, R., Englebert, N., Smith, S. R., & Hoegh-Guldberg, O. (2017). Deep reefs are not universal refuges: Reseeding potential varies among coral species. *Science Advances*, *3*(2), e1602373. https://doi.org/10.1126/sciadv.1602373

Boucher, F. C., Casazza, G., Szövényi, P., & Conti, E. (2016). Sequence capture using RAD probes clarifies phylogenetic relationships and species boundaries in *Primula* sect. Auricula. *Molecular Phylogenetics and Evolution*, *104*, 60–72. https://doi.org/10.1016/j.ympev.2016.08.003

Buckley, J., Butlin, R. K., & Bridle, J. R. (2012). Evidence for evolutionary change associated with the recent range expansion of the British butterfly, *Aricia agestis*, in response to climate change. *Molecular Ecology*, *21*(2), 267–280. https://doi.org/10.1111/j.1365-294X.2011.05388.x

Bulleri, F., & Chapman, M. G. (2010). The introduction of coastal infrastructure as a driver of change in marine environments. *Journal of Applied Ecology*, *47*(1), 26–35. https://doi.org/10.1111/j.1365-2664.2009.01751.x

Cahill, A. E., & Levinton, J. S. (2016). Genetic differentiation and reduced genetic diversity at the northern range edge of two species with different dispersal modes. *Molecular Ecology*, *25*(2), 515–526. https://doi.org/10.1111/mec.13497

Casado-Amezúa, P., Kersting, D. K., Templado, J., & Machordom, A. (2014). Regional genetic differentiation among populations of *Cladocora caespitosa* in the Western Mediterranean. *Coral Reefs*, *33*(4), 1031–1040. https://doi.org/10.1007/s00338-014-1195-5

Cavanaugh, K. C., Kellner, J. R., Forde, A. J., Gruner, D. S., Parker, J. D., Rodriguez, W., & Feller, I. C. (2014). Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(2), 723–727. https://doi.org/10.1073/pnas.1315800111

Chase, A. L., Dijkstra, J. A., & Harris, L. G. (2016). The influence of substrate material on ascidian larval settlement. *Marine Pollution Bulletin*, *106*(1), 35–42. https://doi.org/10.1016/j.marpolbul.2016.03.049

Colautti, R. I., & Barrett, S. C. H. (2013). Rapid adaptation to climate facilitates range expansion of an invasive plant. *Science*, *342*(6156), 364–366. https://doi.org/10.1126/science.1242121

Coma, R., Serrano, E., Linares, C., Ribes, M., Díaz, D., & Ballesteros, E. (2011). Sea urchins predation facilitates coral invasion in a marine reserve. *PLoS ONE*, *6*(7), e22017. https://doi.org/10.1371/journal.pone.0022017

Danecek, P., Auton, A., Abecasis, G., Albers, C. A., Banks, E., DePristo, M. A., … Sherry, S. T. (2011). The variant call format and VCFtools. *Bioinformatics*, *27*(15), 2156–2158. https://doi.org/10.1093/bioinformatics/btr330

de Villemereuil, P., & Gaggiotti, O. E. (2015). A new FST-based method to uncover local adaptation using environmental variables. *Methods in Ecology and Evolution*, *6*(11), 1248–1258. https://doi.org/10.1111/2041-210X.12418

Dlugosch, K., & Parker, I. (2008). Founding events in species invasions: Genetic variation, adaptive evolution, and the role of multiple introductions. *Molecular Ecology*, *17*(1), 431–449. https://doi.org/10.1111/j.1365-294X.2007.03538.x

Earl, D. A., & vonHoldt, B. M. (2012). STRUCTURE HARVESTER: A website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources*, *4*(2), 359–361. https://doi.org/10.1007/s12686-011-9548-7

Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. *Molecular Ecology*, *14*(8), 2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x

Eytan, R. I., Hayes, M., Arbour-Reily, P., Miller, M., & Hellberg, M. E. (2009). Nuclear sequences reveal mid-range isolation of an imperilled deep-water coral population. *Molecular Ecology*, *18*(11), 2375–2389. https://doi.org/10.1111/j.1365-294X.2009.04202.x

Fabricius, K. E. (2005). Effects of terrestrial runoff on the ecology of corals and coral reefs: Review and synthesis. *Marine Pollution Bulletin*, *50*(2), 125–146. https://doi.org/10.1016/j.marpolbul.2004.11.028

Fine, M., Zibrowius, H., & Loya, Y. (2001). *Oculina patagonica*: A non-lessepsian scleractinian coral invading the Mediterranean Sea. *Marine Biology*, *138*(6), 1195–1203. https://doi.org/10.1007/s002270100539

Foll, M., & Gaggiotti, O. (2006). Identifying the environmental factors that determine the genetic structure of populations. *Genetics*, *174*(2), 875–891. https://doi.org/10.1534/genetics.106.059451

Folmer, O., Black, M., Hoeh, W., Lutz, R., & Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, *3*(5), 294–299.

Forsman, Z. H., Knapp, I. S. S., Tisthammer, K., Eaton, D. A. R., Belcaid, M., & Toonen, R. J. (2017). Coral hybridization or phenotypic variation? Genomic data reveal gene flow between *Porites lobata* and *P. Compressa*. *Molecular Phylogenetics and Evolution*, *111*, 132–148. https://doi.org/10.1016/j.ympev.2017.03.023

Frankham, R. (2005). Resolving the genetic paradox in invasive species. *Heredity*, *94*(4), 385–385. https://doi.org/10.1038/sj.hdy.6800634

Frankham, R., & Ralls, K. (1998). Conservation biology: Inbreeding leads to extinction. *Nature*, *392*(6675), 441–442. https://doi.org/10.1038/33022

Fukami, H., Budd, A. F., Paulay, G., Solé-Cava, A., Chen, C. A., Iwao, K., & Knowlton, N. (2004). Conventional taxonomy obscures deep divergence between Pacific and Atlantic corals. *Nature*, *427*(6977), 832–835. https://doi.org/10.1038/nature02339

Funk, W. C., Lovich, R. E., Hohenlohe, P. A., Hofman, C. A., Morrison, S. A., Sillett, T. S., … Day, M. D. (2016). Adaptive divergence despite strong genetic drift: Genomic analysis of the evolutionary mechanisms causing genetic differentiation in the island fox (*Urocyon littoralis*). *Molecular Ecology*, *25*, 2176–2194. https://doi.org/10.1111/mec.13605

García-Merchán, V. H., Robainas-Barcia, A., Abelló, P., Macpherson, E., Palero, F., García-Rodríguez, M., … Pascual, M. (2012). Phylogeographic patterns of decapod crustaceans at the Atlantic-Mediterranean transition. *Molecular Phylogenetics and Evolution*, *62*(2), 664–672. https://doi.org/10.1016/j.ympev.2011.11.009

Goudet, J. (1995). FSTAT (version 1.2): A computer program to calculate *F*-statistics. *Journal of Heredity*, *86*(6), 485–486.

Hellberg, M. E. (2006). No variation and low synonymous substitution rates in coral mtDNA despite high nuclear variation. *BMC Evolutionary Biology*, *6*(1), 24. https://doi.org/10.1186/1471-2148-6-24

Herborg, L. M., Weetman, D., van Oosterhout, C., & Hanfling, B. (2007). Genetic population structure and contemporary dispersal patterns of a recent European invader, the Chinese mitten crab, *Eriocheir sinensis*. *Molecular Ecology*, *16*(2), 231–242. https://doi.org/10.1111/j.1365-294X.2006.03133.x

Hohenlohe, P. A., Day, M. D., Amish, S. J., Miller, M. R., Kamps-Hughes, N., Boyer, M. C., … Luikart, G. (2013). Genomic patterns of introgression in rainbow and westslope cutthroat trout illuminated by overlapping paired-end RAD sequencing. *Molecular Ecology*, *22*(11), 3002–3013. https://doi.org/10.1111/mec.12239

Hubisz, M. J., Falush, D., Stephens, M., & Pritchard, J. K. (2009). Inferring weak population structure with the assistance of sample group information. *Molecular Ecology Resources*, *9*(5), 1322–1332. https://doi.org/10.1111/j.1755-0998.2009.02591.x

Johnston, E. C., Forsman, Z. H., Flot, J.-F., Schmidt-Roach, S., Pinzón, J. H., Knapp, I. S. S., & Toonen, R. J. (2017). A genomic glance through the fog of plasticity and diversification in *Pocillopora*. *Scientific Reports*, *7*(1), 5991. https://doi.org/10.1038/s41598-017-06085-3

Jones, A. M., Berkelmans, R., van Oppen, M. J., Mieog, J. C., & Sinclair, W. (2008). A community change in the algal endosymbionts of a scleractinian coral following a natural bleaching event: Field evidence of acclimatization. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1641), 1359–1365. https://doi.org/10.1098/rspb.2008.0069

Kamvar, Z. N., Brooks, J. C., & Grünwald, N. J. (2015). Novel R tools for analysis of genome-wide population genetic data with emphasis on clonality. *Frontiers in Genetics*, *6*, https://doi.org/10.3389/fgene.2015.00208

Kamvar, Z. N., Tabima, J. F., & Grünwald, N. J. (2014). Poppr: An R package for genetic analysis of populations with clonal, partially clonal, and/or sexual reproduction. *PeerJ*, *2*, e281. https://doi.org/10.7717/peerj.281

Kennedy, J. P., Garavelli, L., Truelove, N. K., Devlin, D. J., Box, S. J., Chérubin, L. M., & Feller, I. C. (2017). Contrasting genetic effects of red mangrove (*Rhizophora mangle* L.) range expansion along West and East Florida. *Journal of Biogeography*, *44*(2), 335–347. https://doi.org/10.1111/jbi.12813

Kersting, D. K., Casado, C., López-Legentil, S., & Linares, C. (2013). Unexpected patterns in the sexual reproduction of the Mediterranean scleractinian coral *Cladocora caespitosa*. *Marine Ecology Progress Series*, *486*, 165–171. https://doi.org/10.3354/meps10356

Kersting, D. K., & Linares, C. (2012). *Cladocora caespitosa* bioconstructions in the Columbretes Islands Marine Reserve (Spain, NW Mediterranean): Distribution, size structure and growth. *Marine Ecology*, *33*(4), 427–436. https://doi.org/10.1111/j.1439-0485.2011.00508.x

Kitahara, M. V., Cairns, S. D., Stolarski, J., Blair, D., & Miller, D. J. (2010). A comprehensive phylogenetic analysis of the Scleractinia (Cnidaria, Anthozoa) based on mitochondrial CO1 sequence data. *PLoS ONE*, *5*(7), e11490. https://doi.org/10.1371/journal.pone.0011490

Kolbe, J. J., Glor, R. E., Schettino, L. R., Lara, A. C., Larson, A., & Losos, J. B. (2004). Genetic variation increases during biological invasion by a Cuban lizard. *Nature*, *431*(7005), 177–181. https://doi.org/10.1038/nature02807

Kramarsky-Winter, E., Fine, M., & Loya, Y. (1997). Coral polyp expulsion. *Nature*, *387*, 137.

LaJeunesse, T. (2002). Diversity and community structure of symbiotic dinoflagellates from Caribbean coral reefs. *Marine Biology*, *141*(2), 387–400. https://doi.org/10.1007/s00227-002-0829-2

Lancaster, L. T., Dudaniec, R. Y., Chauhan, P., Wellenreuther, M., Svensson, E. I., & Hansson, B. (2016). Gene expression under thermal stress varies across a geographic range expansion front. *Molecular Ecology*, *25*, 1141–1156. https://doi.org/10.1111/mec.13548

Lee, C. E. (2002). Evolutionary genetics of invasive species. *Trends in Ecology & Evolution*, *17*(8), 386–391. https://doi.org/10.1016/S0169-5347(02)02554-5

Leese, F., Brand, P., Rozenberg, A., Mayer, C., Agrawal, S., Dambach, J., … Sands, C. J. (2012). Exploring Pandora's box: Potential and pitfalls of low coverage genome surveys for evolutionary biology. *PLoS ONE*, *7*(11), e49202. https://doi.org/10.1371/journal.pone.0049202

Leydet, K. P., & Hellberg, M. E. (2015). The invasive coral *Oculina patagonica* has not been recently introduced to the Mediterranean from the western Atlantic. *BMC Evolutionary Biology*, *15*, 79. https://doi.org/10.1186/s12862-015-0356-7

Leydet, K. P., & Hellberg, M. E., (2016). Discordant coral–symbiont structuring: Factors shaping geographical variation of Symbiodinium communities in a facultative zooxanthellate coral genus, Oculina. *Coral Reefs*, *35*, 583. https://doi.org/10.1007/s00338-016-1409-0

Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., … Durbin, R. (2009). The sequence alignment/map format and SAMtools. *Bioinformatics*, *25*(16), 2078–2079. https://doi.org/10.1093/bioinformatics/btp352

Lin, S., Cheng, S., Song, B., Zhong, X., Lin, X., Li, W., … Ji, Z. (2015). The *Symbiodinium kawagutii* genome illuminates dinoflagellate gene expression and coral symbiosis. *Science*, *350*(6261), 691–694. https://doi.org/10.1126/science.aad0408

Lischer, H. E. L., & Excoffier, L. (2012). PGDSpider: An automated data conversion tool for connecting population genetics and genomics programs. *Bioinformatics*, *28*(2), 298–299. https://doi.org/10.1093/bioinformatics/btr642

McDevitt, A. D., Montgomery, W. I., Tosh, D. G., Lusby, J., Reid, N., White, T. A., … Yearsley, J. M. (2014). Invading and expanding: Range dynamics and ecological consequences of the greater white-toothed shrew (*Crocidura russula*) invasion in Ireland. *PLoS ONE*, *9*(6), e100403. https://doi.org/10.1371/journal.pone.0100403

Meirmans, P. G., & Van Tienderen, P. H. (2004). GENOTYPE and GENODIVE: Two programs for the analysis of genetic diversity of asexual organisms. *Molecular Ecology Notes*, *4*(4), 792–794. https://doi.org/10.1111/j.1471-8286.2004.00770.x

Mokhar-Jamai, K., Pascual, M., Ledoux, J.-B., Coma, R., Feral, J. P., Garrabou, J., & Aurelle, D. (2011). From global to local genetic structuring in the red gorgonian *Paramuricea clavata*: The interplay between oceanographic conditions and limited larval dispersal. *Molecular Ecology*, *20*(16), 3291–3305. https://doi.org/10.1111/j.1365-294X.2011.05176.x

Novak, S. J., & Mack, R. N. (1993). Genetic variation in *Bromus tectorum* (Poaceae): Comparison between native and introduced populations. *Heredity*, *71*, 167–176. https://doi.org/10.1038/hdy.1993.121

Patarnello, T., Volckaert, F. A., & Castilho, R. (2007). Pillars of Hercules: Is the Atlantic-Mediterranean transition a phylogeographical break? *Molecular Ecology*, *16*(21), 4426–4444. https://doi.org/10.1111/j.1365-294X.2007.03477.x

Pateman, R. M., Hill, J. K., Roy, D. B., Fox, R., & Thomas, C. D. (2012). Temperature-dependent alterations in host use drive rapid range expansion in a butterfly. *Science*, *336*(6084), 1028–1030. https://doi.org/10.1126/science.1216980

Patterson, N., Price, A. L., & Reich, D. (2006). Population structure and eigenanalysis. *PLoS Genetics*, *2*(12), e190. https://doi.org/10.1371/journal.pgen.0020190

Pérez-Portela, R., Cerro-Gálvez, E., Taboada, S., Tidu, C., Campillo-Campbell, C., Mora, J., & Riesgo, A. (2016). Lonely populations in the deep: Genetic structure of red gorgonians at the heads of submarine canyons in the north-western Mediterranean Sea. *Coral Reefs*, *1–14*, https://doi.org/10.1007/s00338-016-1431-2

Peter, B. M., & Slatkin, M. (2013). Detecting range expansions from genetic data. *Evolution*, *67*(11), 3274–3289. https://doi.org/10.1111/evo.12202

Peter, B. M., & Slatkin, M. (2014). The effective founder effect in a spatially expanding population. *Evolution*, *69*(3), 721–734. https://doi.org/10.1111/evo.12609

Pettay, D. T., & Lajeunesse, T. C. (2007). Microsatellites from clade B *Symbiodinium* spp. specialized for Caribbean corals in the genus *Madracis*. *Molecular Ecology Notes*, *7*(6), 1271–1274. https://doi.org/10.1111/j.1471-8286.2007.01852.x

Pinot, J.-M., López-Jurado, J., & Riera, M. (2002). The CANALES experiment (1996–1998). Interannual, seasonal, and mesoscale variability of the circulation in the Balearic Channels. *Progress in Oceanography*, *55*(3), 335–370. https://doi.org/10.1016/S0079-6611(02)00139-8

Plummer, M., Best, N., Cowles, K., & Vines, K. (2006). CODA: Convergence diagnosis and output analysis for MCMC. *R News*, *6*(1), 7–11.

Prada, C., & Hellberg, M. E. (2013). Long prereproductive selection and divergence by depth in a Caribbean candelabrum coral. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(10), 3961–3966. https://doi.org/10.1073/pnas.1208931110

Prada, C., McIlroy, S. E., Beltrán, D. M., Valint, D. J., Ford, S. A., Hellberg, M. E., & Coffroth, M. A. (2014). Cryptic diversity hides host and habitat specialization in a gorgonian-algal symbiosis. *Molecular Ecology*, *23*(13), 3330–3340. https://doi.org/10.1111/mec.12808

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155*(2), 945–959.

Puzey, J., & Vallejo-Marín, M. (2014). Genomics of invasion: Diversity and selection in introduced populations of monkey flowers (*Mimulus guttatus*). *Molecular Ecology*, *23*(18), 4472–4485. https://doi.org/10.1111/mec.12875

Roman, J. (2006). Diluting the founder effect: Cryptic invasions expand a marine invader's range. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1600), 2453–2459. https://doi.org/10.1098/rspb.2006.3597

Roman, J., & Darling, J. A. (2007). Paradox lost: Genetic diversity and the success of aquatic invasions. *Trends in Ecology & Evolution*, *22*(9), 454–464. https://doi.org/10.1016/j.tree.2007.07.002

Rosenberg, E., Koren, O., Reshef, L., Efrony, R., & Zilber-Rosenberg, I. (2007). The role of microorganisms in coral health, disease and evolution. *Nature Reviews Microbiology*, *5*(5), 355–362. https://doi.org/10.1038/nrmicro1635

Rosenberg, E., & Zilber-Rosenberg, I. (2011). The hologenome concept. In E. Rosenberg & U. Gophna (Eds.), *Beneficial microorganisms in multicellular life forms* (pp. 323–340). Berlin, Heidelberg, Germany: Springer Berlin Heidelberg.

Rubio-Portillo, E., Vázquez-Luis, M., Izquierdo Muñoz, A., & Ramos Esplá, A. A. (2014). Distribution patterns of alien coral *Oculina patagonica* De Angelis D'Ossat, 1908 in western Mediterranean Sea. *Journal of Sea Research*, *85*, 372–378. https://doi.org/10.1016/j.seares.2013.07.007

Ruiz, S., Pascual, A., Garau, B., Faugère, Y., Alvarez, A., & Tintoré, J. (2009). Mesoscale dynamics of the Balearic Front, integrating glider, ship and satellite data. *Journal of Marine Systems*, *78*, S3–S16. https://doi.org/10.1016/j.jmarsys.2009.01.007

Salomidi, M., Katsanevakis, S., Issaris, Y., Tsiamis, K., & Katsiaras, N. (2013). Anthropogenic disturbance of coastal habitats promotes the spread of the introduced scleractinian coral *Oculina patagonica* in the Mediterranean Sea. *Biological Invasions*, *15*(9), 1961–1971. https://doi.org/10.1007/s10530-013-0424-0

Santos, S. R., Taylor, D. J., Kinzie Iii, R. A., Hidaka, M., Sakai, K., & Coffroth, M. A. (2002). Molecular phylogeny of symbiotic dinoflagellates inferred from partial chloroplast large subunit (23S)-rDNA sequences. *Molecular Phylogenetics and Evolution*, *23*(2), 97–111. https://doi.org/10.1016/S1055-7903(02)00010-6

Schrieber, K., & Lachmuth, S. (2017). The Genetic Paradox of Invasions revisited: The potential role of inbreeding × environment interactions in invasion success. *Biological Reviews*, *92*(2), 939–952. https://doi.org/10.1111/brv.12263

Serrano, X., Baums, I., O'Reilly, K., Smith, T., Jones, R., Shearer, T., … Baker, A. (2014). Geographic differences in vertical connectivity in the Caribbean coral *Montastraea cavernosa* despite high levels of horizontal connectivity at shallow depths. *Molecular Ecology*, *23*(17), 4226–4240. https://doi.org/10.1111/mec.12861

Serrano, E., Coma, R., & Marta, R. (2013). Pattern of *Oculina patagonica* occurrence along the Iberian Peninsula Coastline: A first step to understand the factors affecting its invasion dynamics. *Rapports Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée [CIESM]*, *40*, 603.

Serrano, E., Coma, R., Ribes, M., Weitzmann, B., Garcia, M., & Ballesteros, E. (2013). Rapid northward spread of a zooxanthellate coral enhanced by artificial structures and sea warming in the western Mediterranean. *PLoS ONE*, *8*(1), e52739. https://doi.org/10.1371/journal.pone.0052739

Shinzato, C., Shoguchi, E., Kawashima, T., Hamada, M., Hisata, K., Tanaka, M., … Ikuta, T. (2011). Using the *Acropora digitifera* genome to understand coral responses to environmental change. *Nature*, *476*(7360), 320–323. https://doi.org/10.1038/nature10249

Shoguchi, E., Shinzato, C., Kawashima, T., Gyoja, F., Mungpakdee, S., Koyanagi, R., … Fujiwara, M. (2013). Draft assembly of the *Symbiodinium minutum* nuclear genome reveals dinoflagellate gene structure. *Current Biology*, *23*(15), 1399–1408. https://doi.org/10.1016/j.cub.2013.05.062

Smith-Keune, C., & van Oppen, M. (2006). Genetic structure of a reef-building coral from thermally distinct environments on the Great Barrier Reef. *Coral Reefs*, *25*(3), 493–502. https://doi.org/10.1007/s00338-006-0129-2

Stimson, J., Sakai, K., & Sembali, H. (2002). Interspecific comparison of the symbiotic relationship in corals with high and low rates of bleaching-induced mortality. *Coral Reefs*, *21*(4), 409–421. https://doi.org/10.1007/s00338-002-0264-3

Terrón-Sigler, A., Casado-Amezúa, P., & Torre, F. E. (2015). Abundance and distribution of the rapid expansive coral *Oculina patagonica* in the Northern Alborán Sea (Western Mediterranean). *Marine Biodiversity Records*, *8*, e45. https://doi.org/10.1017/S1755267215000238

Toonen, R. J., Puritz, J. B., Forsman, Z. H., Whitney, J. L., Fernandez-Silva, I., Andrews, K. R., & Bird, C. E. (2013). ezRAD: A simplified method for genomic genotyping in non-model organisms. *PeerJ*, *1*, e203. https://doi.org/10.7717/peerj.203

Tsutsui, N. D., Suarez, A. V., Holway, D. A., & Case, T. J. (2000). Reduced genetic variation and the success of an invasive species. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(11), 5948–5953. https://doi.org/10.1073/pnas.100110397

White, T. A., Perkins, S. E., Heckel, G., & Searle, J. B. (2013). Adaptive evolution during an ongoing range expansion: The invasive bank vole (*Myodes glareolus*) in Ireland. *Molecular Ecology*, *22*(11), 2971–2985. https://doi.org/10.1111/mec.12343

Yamano, H., Sugihara, K., & Nomura, K. (2011). Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures. *Geophysical Research Letters*, *38*(4), https://doi.org/10.1029/2010GL046474

Zenni, R. D., & Hoban, S. M. (2015). Loci under selection during multiple range expansions of an invasive plant are mostly population specific, but patterns are associated with climate. *Molecular Ecology*, *24*(13), 3360–3371. https://doi.org/10.1111/mec.13234

Zibrowius, H. (1974). *Oculina patagonica*, scléractiniaire hermatypique introduit en Méditerranée. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, *26*(2), 153–173. https://doi.org/10.1007/BF01611381

Zibrowius, H., & Ramos, A. (1983). *Oculina patagonica*, scléractiniaire exotique en Méditerranée- nouvelles observations dans le Sud--Est de l'Espagne. *Rapports Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée [CIESM]*, *28*, 297–301.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Leydet KP, Grupstra CGB, Coma R, Ribes M, Hellberg ME. Host-targeted RAD-Seq reveals genetic changes in the coral *Oculina patagonica* associated with range expansion along the Spanish Mediterranean coast. *Mol Ecol*. 2018;27:2529–2543. https://doi.org/10.1111/mec.14702