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Postglacial range expansion shaped the spatial genetic structure in a marine habitat-forming species: Implications for conservation plans in the Eastern Adriatic Sea

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Abstract

Aim: Understanding how historical and contemporary processes shaped and maintain spatial patterns of genetic diversity is a major goal for conservation biologists. Here, we characterized the pattern of neutral genetic diversity and we inferred underlying processes in the habitat-forming octocoral *Paramuricea clavata* in the Adriatic Sea, a peculiar phylogeographic region of the Mediterranean Sea.

Location: Eastern coast of the Adriatic Sea.

Methods: We genotyped seven microsatellites in 454 individuals of *P. clavata* from 13 populations recolonized after the Last Glacial Maximum (LGM). We estimated the levels of contemporary connectivity and genetic drift and we reconstructed the demographic history of these populations.

Results: The pattern of spatial genetic structure resulted from the combination of hierarchical genetic clusters and isolation by distance (IBD). A significant decrease in genetic diversity and an increase of the frequencies of individual alleles likely due to allele surfing from the south to the north of the area were observed as expected after a postglacial sequential recolonization. Based on maximum likelihood analyses, the foundation of these populations was not linked to dramatic change in population size.

Main conclusion: Oceanographic barriers to gene flow combined to the restricted dispersal of *P. clavata* likely maintain the hierarchical structure and the IBD pattern. We suggest that the latitudinal genetic gradient results from a northward “serial founder events” recolonization. By integrating patterns and processes, we bridge the gap between the evolutionary and the conservation biology of *P. clavata*, providing management guidelines, which will benefit the associated coralligenous biodiversity.

KEYWORDS

allele surfing, genetic drift, latitudinal genetic gradient, Mediterranean Sea, Octocoral, postglacial range expansion

1 | INTRODUCTION

Range expansion is a process occurring in the evolutionary history of most species (Hewitt, 2000). It may significantly imprint contemporary patterns of genetic diversity with direct implications for biodiversity conservation (Eckert, Samis, & Loughheed, 2008; Excoffier, Foll, & Petit, 2009). The colonization of vacant favorable habitats often relies on founder events, which produce differentiation between newly founded and source populations through genetic drift (Peter & Slatkin, 2013; Waters, Fraser, & Hewitt, 2013). Range expansion may follow different dynamics and thus leave distinct genetic imprints depending on the strength of founder events or the species life history traits, such as dispersal (Austerlitz, Jung-Muller, Godelle, & Gouyon, 1997; Austerlitz, Mariette, Machon, Gouyon, & Godelle, 2000; Hewitt, 2000). Focusing on postglacial recolonization after the Last Glacial Maximum (LGM 24,000–18,000 years ago; Lambeck & Purcell, 2005), range expansion is expected to involve step-by-step founder events along the recolonization axis (Hewitt, 2000). This “serial founder events” model (Austerlitz et al. 1997; Slatkin & Excoffier, 2012) is characterized by a chronological succession of smooth founder events, which causes a steady increase of genetic drift along the axis of expansion and leads to a negative gradient of genetic diversity from the source to the edge of the expansion range. Meanwhile, clines in allele frequencies may be observed with frequencies increasing as a function of the distance from the source population (Peter & Slatkin, 2013). In extreme cases, some alleles can reach high frequencies in populations located on the edge of the expansion by stochastically “surfing” the wave of expansion. Hence, the “serial founder events” model questioned the common interpretation of clines in allele frequencies as signatures of positive selection along environmental gradients (Slatkin & Excoffier, 2012). Considering the contrasted impacts of selection and drift on population evolutionary potential, understanding the processes underlying a cline in allele frequencies is central to develop relevant conservation policies (Eckert et al., 2008).

The Adriatic Sea is recognized as a peculiar phylogeographic region of the Mediterranean Sea due to the genetic differentiation of the Adriatic populations from the rest of the Mediterranean reported across multiple species (e.g. *Crangon crangon*, Luttikhuisen, Campos, van Bleijswijk, Peijnenburg, & van der Veer, 2008; *Ruditapes decussatus* Cordero, Peña, & Saavedra, 2014), including species with long-distance dispersal (e.g. *Paracentrotus lividus*, Maltagliati, Di Giuseppe, Barbieri, Castelli, & Dini, 2010 but see Paterno et al., 2017). This pattern was explained by the interaction between the complex geological history of the Mediterranean (glaciation periods) and the semi-enclosed nature of the Adriatic (Patarnello, Volckaert, & Castilho, 2007). Nevertheless, little is known about the processes shaping and maintaining patterns of genetic diversity in the Adriatic. Genetic homogeneity was observed over the whole Adriatic basin in some species (e.g. *Loligo vulgaris* and *Sepia officinalis*, Garoia et al., 2004; *Paracentrotus lividus*, Paterno et al., 2017; *Dicentrarchus labrax*, Šegvić-Bubić et al., 2016), while significant genetic differentiations were reported

between the north and the south of the Sea (e.g. *Scomber scombrus*, Papetti et al., 2013; *Aphanius fasciatus*, Buj et al., 2015) as well as between the eastern and western coast (e.g. *Scorpaena porcus*, Boissin et al., 2016; *Symphodus tinca*, Carreras et al., 2017). During the LGM, the Adriatic Sea level was between 135 and 115 meters lower than today, leaving the northern and central sectors dry (Velić & Malvić, 2011; Sikora, Mihanović, & Vilibić, 2014; Figure 1). Combined with its south to north orientation, this palaeogeographic context was used to hypothesize a northward postglacial recolonization of the Adriatic from southern refugia (Bianchi, Morri, Chiantore, & Montefalcone, 2012). While previous studies suggested an impact of LGM on the patterns of genetic diversity (e.g. Buj et al., 2015; Koblmüller, Steinwender, & WeiS, 2015), the dynamic of this postglacial recolonization and its imprint on genetic diversity are poorly known. Moreover, putative implications for the conservation of the Adriatic biodiversity are barely considered. This gap between evolutionary and conservation biology is particularly detrimental because a significant part of the eastern Adriatic coast, corresponding to the Croatian coast, was identified as a conservation priority area (Giakoumi et al., 2013). This prioritization was justified by the occurrence of coralligenous habitat, which was recognized as a priority habitat by the EU Habitat Directive (92/43/EEC) due to its high diversity (~1700 species) and vulnerability (Ballesteros, 2006). In this study, we thus integrate an evolutionary approach into a conservation perspective to improve our understanding of the evolution of Adriatic biodiversity and to refine existing management policies.

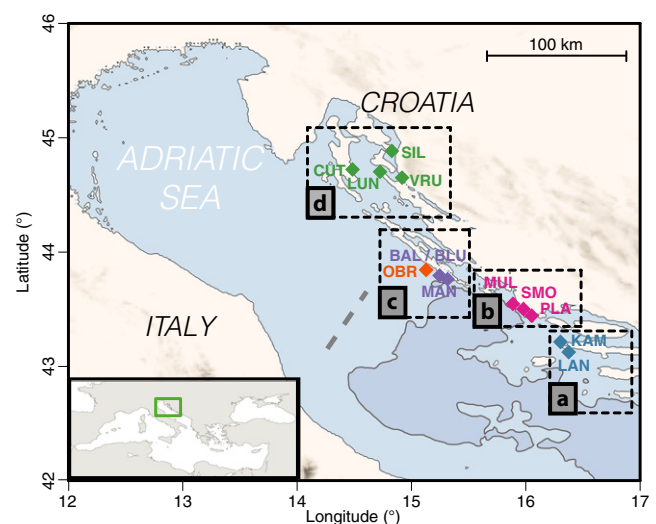


FIGURE 1 Hierarchical sampling of *Paramuricea clavata* in 13 locations from four areas along the Eastern Adriatic coast. Areas are delimited by black dotted lines (a: Vodnjak, b: Rogoznica, c: Kornati, d: Kvarner). The color of each diamond corresponds to the main assigned cluster with STRUCTURE for $K = 5$ (see Figure 2a). Northern and Central biogeographic sectors are delimited by the thick grey dotted line following Bianchi et al. (2012). The dark blue area delimited by the thin dark grey line, which represents the isobath 120 m, corresponds approximately to the paleo-sea during the LGM (Lambeck & Purcell, 2005; Sikora et al., 2014) [Colour figure can be viewed at wileyonlinelibrary.com]



The red gorgonian, *Paramuricea clavata*, is a habitat-forming octocoral with a key role in the structure and functioning of coralligenous habitat (Ballesteros, 2006), and thus it is of major interest for conservation purposes. Characterized by a patchy distribution in the Western Mediterranean and in the Adriatic (Boavida, Assis, Silva, & Serrão, 2016), this long-lived and gonochoric species reproduces annually and shows late sexual maturity (13 years of age) with a short larval phase (Coma, Zabala, & Gili, 1995). The larval phase was estimated between 8 and 25 days in aquarium (Linares, Coma, Garrabou, Díaz, & Zabala, 2008) but field observations reported high settlement rates near the mother colony (Coma et al., 1995). *P. clavata* is impacted by several local and global stressors (Linares & Doak, 2010) including mass mortality events (Arizmendi-Mejía, Ledoux, et al., 2015; Garrabou et al., 2009). The spatial genetic structure of shallow (0–60 m depth) red gorgonian populations has been characterized from local, regional to global scales. At the global scale, Mokhtar-Jamaï et al. (2011) used 39 populations sampled over the whole Mediterranean, including one Adriatic population, to characterize the spatial genetic pattern, which resulted from the interplay between isolation by distance (IBD) and regional genetic clusters. The significant genetic differentiation among populations separated by tens of meters supports a low effective dispersal capacity. Focusing on the Adriatic, the results, albeit based on a single population from the Croatian coast, were concordant with studies supporting a genetic differentiation from the rest of the Mediterranean. At regional scale, Arizmendi-Mejía, Linares, et al. (2015) demonstrated a strong heterogeneity in the contemporary genetic drift and connectivity. This work also suggested a lack of marked founder effect during the colonization of a vacant habitat. At local scale, Mokhtar-Jamaï et al. (2013) showed a high level of self-recruitment over a two square meters area, as expected from the species restricted dispersal capacity and the significant genetic differentiation among close by populations. In spite of these studies, the evolutionary history of *P. clavata* remains poorly understood. In addition, a recent characterization of the demographic structure of *P. clavata* in the Eastern Adriatic revealed well-structured and mature populations composed of both small and large-size colonies, highlighting their conservation value (Kipson et al., 2015).

Here, we aimed to improve the knowledge of the evolutionary processes shaping and maintaining the genetic diversity of *P. clavata* in the Eastern Adriatic with a particular focus on the interplay between the legacy of postglacial range expansion and contemporary processes. Based on a hierarchical sampling (13 populations from four areas and including populations surveyed by Kipson et al. (2015)) conducted along the Croatian coast, we: (a) characterized the spatial patterns of neutral genetic structure; (b) reconstructed the populations' demographic history; and (c) inferred the contemporary underlying processes with emphasis on connectivity. Integrating the obtained results, we discuss their implications for the conservation of this species and associated coralligenous biodiversity.

2 | MATERIALS AND METHODS

2.1 | Sampling design

Individuals of *P. clavata* from 13 populations belonging to four areas along the Croatian coast (Kvarner, Kornati, Rogoznica and Vodnjak; Figure 1; Table 1) were collected by SCUBA diving. Sampling was conducted at depths from 30 to 45 m in 2009 and 2011. Given that the sea-level was between 135 and 115 m lower than today during the LGM, these populations were recolonized during the last 18,000 years. One apical fragment (2–3 cm) was taken from 23 to 55 mature individuals (i.e. colonies higher than 20 cm) (Table 1). Two populations (BAL and BLU) belong to the same site but different depths (30 and 40 m depth, respectively). The resulting 456 apical fragments were conserved in 95% ethanol and stored at -20°C prior to DNA extraction.

2.2 | DNA extraction, microsatellite genotyping and genetic diversity analyses

The genomic DNA extraction, genotyping of seven microsatellite loci and preliminary analyses including quality control, estimations of genetic diversity and tests of Hardy-Weinberg equilibrium are detailed in Appendix S1 in supporting information.

The following analyses were conducted on 454 individuals.

2.3 | Characterizing the spatial genetic structure

A clustering analysis using STRUCTURE 2.2 (Pritchard, Stephens, & Donnelly, 2000) was conducted to evaluate the number of genetic clusters (K) from the individuals' genotypes without assumptions on population boundaries. We considered the admixture model with correlated allele frequencies with and without the recessive allele option to deal with null alleles (Falush, Stephens, & Pritchard, 2003, 2007). Ten independent runs were performed for each K (varying from 1 to 10) with a burn-in period of 150,000 followed by 500,000 iterations. The K value corresponding to "upper most hierarchical level of structure" was determined using the ΔK method (Evanno, Regnaut, & Goudet, 2005). This result was complemented based on the plot of the logarithm of the likelihood of observing the data ($\ln P(D)$) as a function of the number of genetic clusters (K) to determine complementary K values with biological relevance (Waples & Gaggiotti, 2006). CLUMPP 1.1 (Jakobsson & Rosenberg, 2007) and DISTRICT 1.1 (Rosenberg, 2003) were used for graphical output. We also conducted a discriminant analysis of principal components (DAPC, Jombart, Devillard, & Balloux, 2010) in ADEGENET (Jombart, 2008). Contrary to STRUCTURE, DAPC describes patterns of diversity without assumption about the underlying population genetic model (Jombart et al., 2010). Data were transformed into principal components and discriminant analyses were used to maximize variation among-groups while minimizing within group variations. We used population locations as group prior and the a -score to define the optimal number of principal components (PCs = 36) while retaining 12 discriminant functions.

TABLE 1 Characteristics of the surveyed populations of *Paramuricea clavata* in the Eastern Adriatic. For each population, the area of origin, the sample name, the coordinates, the number of sampled colonies, the depth and the conservation status are given

Area	Sample name	Latitude	Longitude	Number of individuals	Depth (m)	Status
Vodnjak	LAN	43 10'44" N	16 18'38" E	33	40	Natura 2000
	KAM	43 10'05" N	16 18'34" E	55	40	Natura 2000
Rogoznica	SMO	43 30'38" N	15 56'32" E	35	35	Unprotected
	PLA	43 29'36" N	15 58'09" E	35	35	Unprotected
	MUL	43 30'48" N	15 55'07" E	35	35	Unprotected
Kornati	MAN	43 48'01" N	15 15'59" E	29	40	MPA; Natura 2000
	BAL	43 48'14" N	15 15'18" E	31	30	MPA; Natura 2000
	BLU	43 48'14" N	15 15'18" E	39	40	MPA; Natura 2000
	OBR	43 50'11" N	15 13'12" E	31	40	MPA; Natura 2000
Kvarner	VRU	44 39'11" N	14 55'36" E	46	45	Unprotected
	LUN	44 42'15" N	14 44'02" E	23	35	Natura 2000
	CUT	44 43'29" N	14 29'36" E	32	35	Natura 2000
	SIL	44 53'12" N	14 50'13" E	30	35	MPA; Natura 2000

Note: BAL and BLU corresponded to the same location but were sampled at different depths (30 and 40 m depth, respectively).

Global and pairwise F_{ST} were computed using Weir & Cockerham's estimator of F_{ST} (Weir & Cockerham, 1984) in GENEPOP 4.1.4 (Rousset, 2008). Genotypic differentiation between populations was tested using an exact G test (Raymond & Rousset, 1995) with default parameters. Isolation by distance (IBD) pattern was analyzed through the correlation of genetic and geographic distances between populations (Rousset, 1997). Geographic distances were measured among populations using MARMAP 0.9.3 (Pante & Simon-Bouhet, 2013). The significance of the correlation between the genetic distances ($F_{ST}/(1 - F_{ST})$) and the logarithms of geographic distances ($\ln(d)$) was tested by the Mantel test in GENEPOP with 10,000 permutations. In two-dimension models, the inverse of the slope of the linear regression between $F_{ST}/(1 - F_{ST})$ and $\ln(d)$ is an estimate of the "neighborhood size" ($N_b = 4\pi D\sigma^2$, with D the effective density and σ^2 the mean square parent-offspring distance, Rousset, 1997).

In addition, we conducted two sets of Spearman non-parametric correlation tests. First, we tested the occurrence of a gradient in genetic diversity and drift by testing for the correlation between the latitude of each population with H_e , $A_{r(44)}$ (see Appendix S1) and population-specific F_{ST} (see below). Then, we tested the occurrence of clines in allele frequencies by testing for the correlation between the frequency of each allele computed with GENEPOP 4.1.4 (Rousset, 2008) for each population and the latitude. Among the 125 different alleles from our dataset, we focused on 80 alleles present in at least four populations (1/3 of the populations).

2.4 | Inferring underlying evolutionary processes: contemporary connectivity and genetic drift

Contemporary connectivity between populations was estimate with BAYESASS 3.0 (Wilson & Rannala, 2003). BAYESASS was run three

times with different seed values, 25×10^6 iterations, a burn-in period of 25×10^5 and a sampling frequency of 2000. The mixing parameters were adjusted to achieve acceptance rates of 20%–40%, following Rannala (2007). Convergence was achieved for the three runs and only one run was retained.

We calculated the population-specific F_{ST} in GESTE (Foll & Gaggiotti, 2006). This method measures the genetic differentiation proper to each population and estimates the relative impact of genetic drift on the differentiation of the considered population (Gaggiotti & Foll, 2010).

2.5 | Demographic history

Based on the northward genetic gradient (see Results), we hypothesized that the postglacial recolonization of the Adriatic by *P. clavata* was done following a northward "serial founder events" range expansion model. We thus expected smooth and sequential founder events. We used the model of a single population with past variations in population size (Leblois et al., 2014) implemented in MIGRAINE (<http://kimura.univ-montp2.fr/~rousset/Migraine.htm>) to characterize the demographic history of the 12 genetically differentiated populations (BAL and BLU were pooled due to a lack of significant genetic differentiation; see Results). The detection of past change in population size is based on the ratio of current population size vs. ancestral population size ($N_{ratio} = N/N_{anc}$). A $N_{ratio} > 1$ corresponds to a population expansion and a $N_{ratio} < 1$ to a bottleneck/population contraction. Parameters used in this analysis are detailed in Appendix S2.

For multiple tests, significance levels were corrected using a false discovery rate (FDR) correction (Benjamini & Hochberg, 1995).



3 | RESULTS

3.1 | Microsatellite characteristics, Hardy-Weinberg equilibrium and genetic diversity

The results of genetic diversity analyses are shown in Table 2 and described in Appendix S1.

3.2 | Clustering analyses

STRUCTURE analyses were consistent considering null alleles as recessive alleles or missing data (not shown). The Evanno's method identified two different genetic clusters (Figure 2a; Appendix S3). The first cluster (hereafter the northern cluster) encompasses all the individuals from the Kvarner area (mean membership coefficient = 0.95). The remaining individuals were grouped in a second cluster (hereafter the southern cluster) with a high mean membership coefficient (0.91). When considering the likelihood of observing the data ($\ln P(D)$), an increase was observed from $K = 1$ to $K = 8$. Considering the increase of standard deviation beyond $K = 5$ (Appendix S3), we only described results for $K = 3$ to $K = 5$, which refined the sub-structure within the southern cluster. The third sub-cluster included the populations from the Kornati area (mean membership coefficient = 0.89) minus OBR, which showed an admixed profile between cluster 1 (mean membership coefficient = 0.54) and sub-cluster 3 (mean membership coefficient = 0.41). Individuals from Rogoznica belonged to a fourth sub-cluster (mean membership coefficient = 0.77). Individuals from OBR were grouped in a fifth sub-cluster (mean membership coefficient = 0.82). At $K = 5$, the mean assignment values were moderate to high (Figure 2a).

Figure 2b shows the results of the DAPC when considering the first two PCs, which represent 52.3% of the total variation in the data. The northern populations are separated from the rest of the populations along the first axis. The remaining populations showed a clinal distribution concordant to their geographic origin along the second axis.

3.3 | Isolation by distance and diversity gradient

The global F_{ST} was 0.09. The pairwise F_{ST} s ranged from 6×10^{-4} for BAL vs. BLU and 0.18 for BAL vs. SIL and BAL vs. LUN. The exact tests for genotypic differentiation were significant at the global level and between all population pairs (all p -values < 0.01) with the exception of BAL vs. BLU after FDR correction (Appendix S4).

The genetic distance ($F_{ST}/(1 - F_{ST})$) and the geographic distance ($\ln(d)$) were significantly correlated demonstrating a pattern of IBD ($p < 0.001$; Figure 2c). The slope of the regression was 0.017 resulting in a low neighbourhood size N_b equal to 58.8 individuals.

Regarding the correlation tests, $A_{r(44)}$ and H_e showed a significant decrease while the population-specific F_{ST} s showed a significant increase with the latitude (all p -values < 0.001; Figure 3). Over the 80 alleles analyzed, three showed a significant decrease (allele 169 in *Pcla-a*, allele 105 in *Pcla-9*, allele 220 in *Pcla-10*) and two showed a significant increase towards higher latitude (allele 105 in *Pcla-12*, allele 187 in *Pcla-14*) after FDR correction (Appendix S5).

3.4 | Contemporary connectivity, genetic drift and mutation vs. drift/gene flow:

BAYESASS inferred a high rate of self-seeding for nine of the 12 populations (>0.8). The self-recruitment of the three remaining populations (LAN, SIL and LUN) was still high (>0.67) and most of the

TABLE 2 Genetic diversity of each population of *Paramuricea clavata*.

	r	H_o	H_e	f	$A_{r(44)}$	$A_{p(44)}$	Population-specific F_{ST} (95% CI)
LAN	0.1	0.71	0.78	0.1**	8.7	0.1	0.085 (0.058–0.116)
KAM	0.08	0.78	0.8	0.01	9.28	0.18	0.062 (0.043–0.082)
SMO	0.05	0.73	0.74	0.01	7.43	0.3	0.099 (0.065–0.135)
PLA	0.08	0.69	0.71	0.02	7.09	0.47	0.116 (0.078–0.159)
MUL	0.12	0.71	0.76	0.06	7.04	0.25	0.126 (0.085–0.168)
MAN	0.06	0.73	0.73	−0.01	7.95	0.22	0.108 (0.071–0.143)
BAL	0.05	0.68	0.69	0.01	7.91	0.21	0.088 (0.057–0.121)
BLU	0.04	0.69	0.73	0.06	7.6	0.06	0.092 (0.060–0.124)
OBR	0.06	0.73	0.74	0.02	7.62	0.03	0.098 (0.065–0.135)
VRU	0.1	0.62	0.69	0.11**	6.73	0.29	0.135 (0.095–0.18)
LUN	0.05	0.64	0.64	−0.01	5.26	0.09	0.209 (0.140–0.283)
CUT	0.07	0.62	0.65	0.03	6.16	0.12	0.167 (0.115–0.223)
SIL	0.08	0.64	0.62	−0.04	6.29	0.25	0.165 (0.111–0.221)
Mean (SD)	0.07 (0.02)	0.69 (0.05)	0.71 (0.05)	0.01 (0.03)	7.31 (1.07)	0.19 (0.12)	

Note. r : frequency of null alleles estimated in FREENA; H_o : observed heterozygosity; H_e : gene diversity (Nei 1973); f : Weir and Cockerham (1984) estimator of F_{IS} (** significant at 0.01); $A_{r(44)}$: rarefied allelic richness considering a minimum of 44 genes at a locus in a population; $A_{p(44)}$: rarefied private allelic richness considering a minimum of 44 genes at a locus in a population; population-specific F_{ST} and 95% CI.

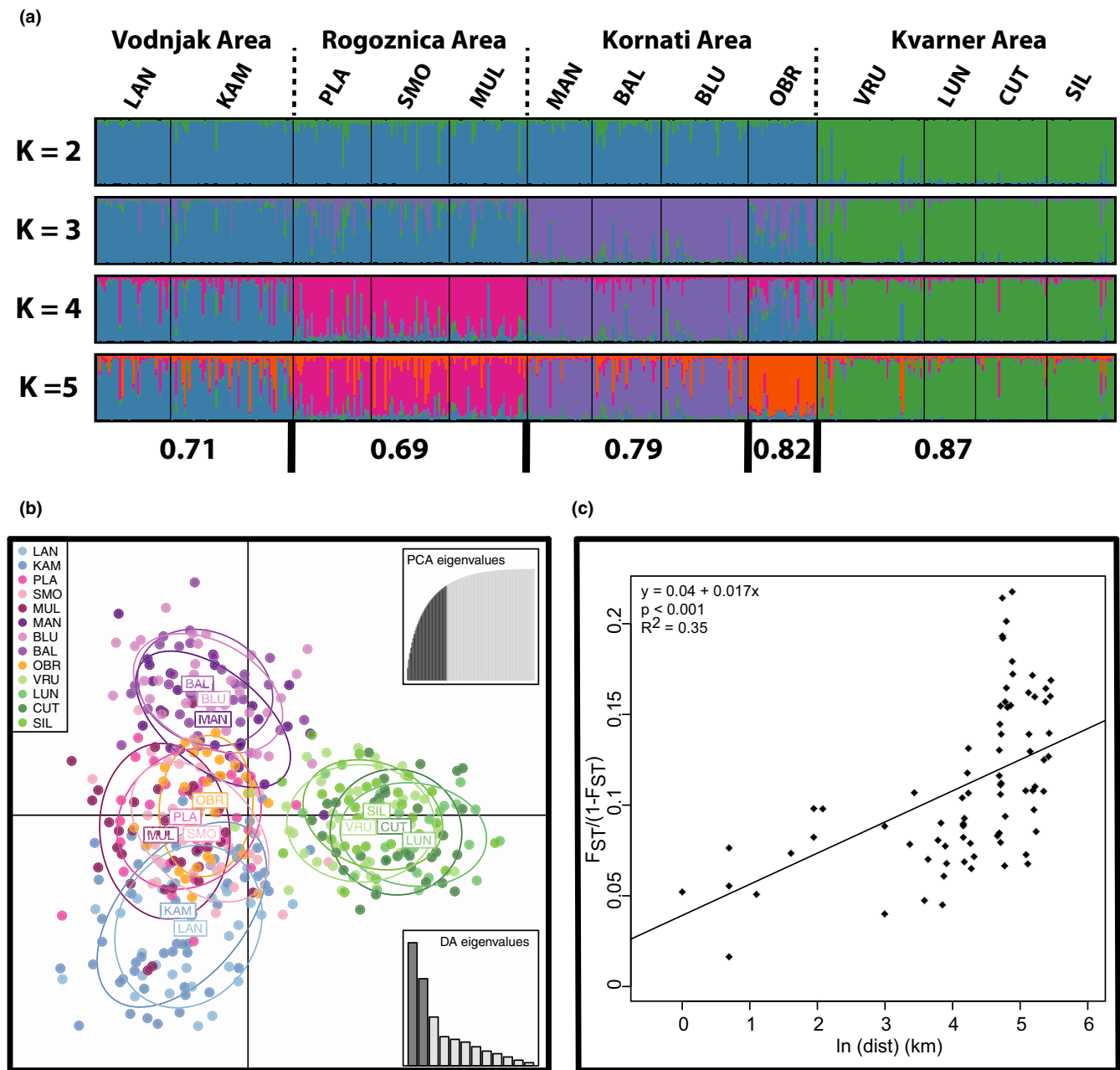


FIGURE 2 (a) Result of the clustering analysis of *Paramuricea clavata* from the Eastern Adriatic conducted with STRUCTURE considering 2–5 clusters (K). Each individual is represented by a vertical line partitioned in K -colored segments, which represent the individual membership fraction in K clusters. Black vertical lines delineate the different populations. Samples names and geographic areas are shown above the assignment plots, while the mean membership coefficient for each cluster considering $K = 5$ are shown below the assignment plots. (b) Scatter plot of the discriminant analysis of principal components (DAPC) based on a a -score of 36. Each dot corresponds to one individual ($n = 454$) from each of the 13 populations, which are represented by different colors. Inertia ellipses center on the mean for each population and include 67% of the sampling points. The two axes of the scatter plot explained 30.6% and 21.7% of the total genetic variation in the dataset. (c) Isolation by distance: correlation between genetic ($F_{ST}/(1-F_{ST})$) and geographic distances ($\ln(d)$) for each pair of populations ($p < 0.001$) [Colour figure can be viewed at wileyonlinelibrary.com]

migrants detected in these populations came from neighboring population: KAM, CUT and VRU, respectively (Table 3).

KAM showed the lowest population-specific F_{ST} (0.06; 95% CI: 0.04–0.08) whereas the highest value was observed for LUN (0.21; 95% CI: 0.14–0.28). Based on 95% CI, various populations showed significantly different values (Table 2).

3.5 | Demographic history

According to MIGRAINE, no past demographic changes were detected except in SIL and LUN. These two northern populations showed contractions (SIL: $N_{ratio} = 1.2 \times 10^{-4}$ [$2.57 \times 10^{-5} - 1.4 \times 10^{-2}$]; LUN: $N_{ratio} = 1.1 \times 10^{-1}$ [$1.73 \times 10^{-6} - 3.14 \times 10^{-1}$]).



In spite of the flat shapes of the two-dimensional likelihood ratio surfaces, which is likely due to a lack of information in the dataset (Leblois et al., 2014), the two contractions likely occurred in the recent past (tens to hundreds of generations). Regarding stable populations, estimations of θ based on the 2D profile likelihood ratios ranged between 1.1 and 11 (Appendix S2). When considering $\mu = 5 \times 10^{-4}$ (Sun et al., 2012), the corresponding N values were between 550 and 5,250 individuals.

4 | DISCUSSION

4.1 | Pattern of spatial genetic structure of *P. clavata* in the Eastern Adriatic

Along the eastern Adriatic coast, the genetic structure of *P. clavata* follows a hierarchical structure composed of two levels. At the first level, populations from the north (Kvarner area) are segregated from the other populations and the resulting northern and southern clusters are characterized by high membership coefficients (0.95 and 0.91, respectively). Interestingly, these clusters coincide, respectively, with the northern and central Adriatic biogeographic sectors (Bianchi et al., 2012). Genetic isolation between the north and the central Adriatic biogeographic sectors was previously reported along the western coast in the shore crab *Carcinus aestuarii* and was explained by an impermeable barrier to gene flow due to seasonal cyclonic gyres (Schiavina, Marino, Zane, & Melià, 2014). Our results suggest that this biogeographic division and the related barrier may be

extended to the eastern coast (see also Buj et al., 2015; Koblmüller et al., 2015). The second level of structure corresponds to the four sub-clusters identified within the southern cluster. These sub-clusters, concordant with the geographic origin of the individuals, suggest the existence of three barriers to gene flow. Considering the mean membership coefficient (0.75), these putative barriers seem more permeable than the biogeographic barrier previously described. Nevertheless, OBR is, for instance, isolated from the neighboring cluster despite its relative spatial proximity (<10 km). Complementary studies including samples from intermediate positions between Kornati and Kvarner areas and using coupled-physical-biological models (e.g. Schiavina et al., 2014) are needed to formally test the relative influence of barriers to gene flow vs. restricted dispersal (see below) in the maintenance of these clusters.

When focusing on the population level, we demonstrated a pattern of isolation by distance (IBD) characterized by a low neighborhood size ($N_b = 58.8$ individuals). The low rates of contemporary connectivity among populations support the significant pairwise genetic differentiations and the IBD pattern. Indeed, auto-recruitment rates are high in all the populations and most of the connectivity occurred between neighboring populations in accordance with the restricted dispersal of *P. clavata* (Mokhtar-Jamāi et al., 2013). While IBD was expected considering previous findings in the same species (e.g. Arizmendi-Mejía, Linares, et al., 2015) and the northward currents along the Eastern coast (Orlic, Gacic, & LaViolette, 1992), our study is one of the few examples of IBD in the Adriatic (see also Souche et al., 2015).

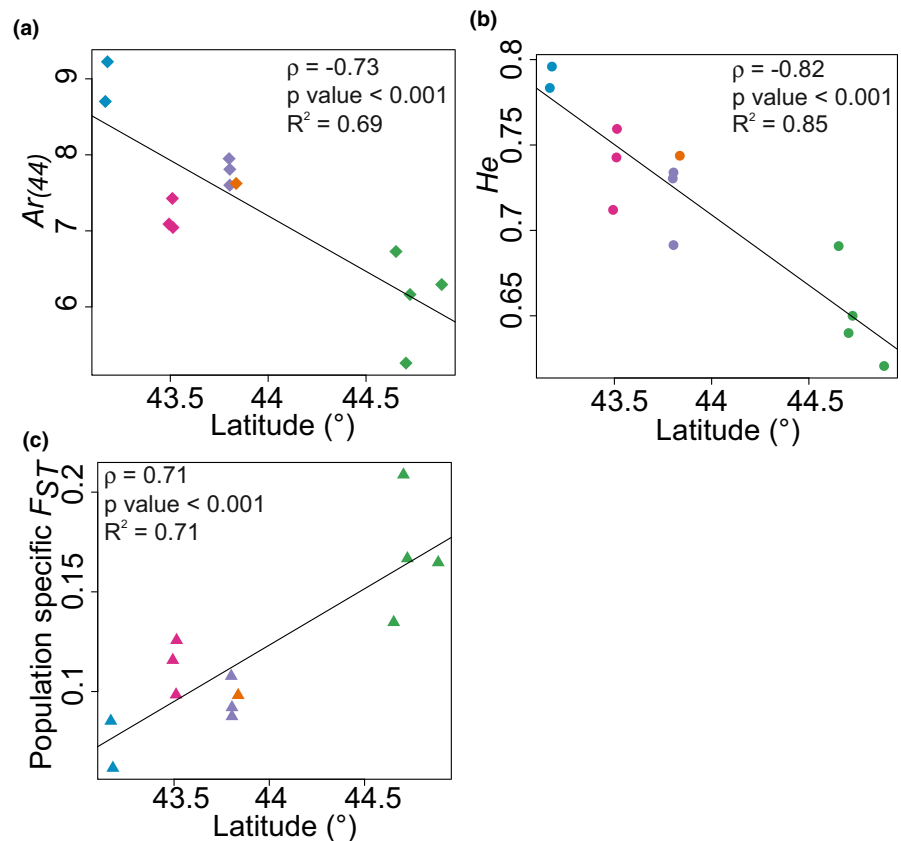


FIGURE 3 Non-parametric Spearman correlation tests between populations of *Paramureicea clavata* latitude and: (a) $Ar_{(44)}$; (b) H_e ; and (c) population-specific F_{ST} . In each plot, colors correspond to the main assigned cluster with STRUCTURE for $K = 5$ (see Figure 2a) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Contemporary migration rates and 95% confidence intervals computed with BAYESASS between the 12 genetically differentiated populations. Rows and columns correspond to receiving and source populations, respectively. Migration rates significantly different from 0 based on the 95% CI are highlighted and italic in grey. The rates of autorecruitment are in bold

LAN	KAM	SMO	PLA	MUL	MAN	BAL-BLU	OBR	VRU	LUN	CUT	SIL
LAN	0.67 (0.66–0.69)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)
KAM	0.88 (0.83–0.93)	0.03 (0–0.07)	0.02 (0–0.04)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.03)	0.01 (0–0.04)	0.01 (0–0.03)	0.01 (0–0.03)	0.01 (0–0.01)
SMO	0.87 (0.81–0.94)	0.87 (0.81–0.94)	0.03 (0–0.07)	0.01 (0–0.04)	0.01 (0–0.03)	0.01 (0–0.03)	0.01 (0–0.03)	0.01 (0–0.04)	0.01 (0–0.03)	0.01 (0–0.04)	0.01 (0–0.02)
PLA	0.01 (0–0.02)	0.01 (0–0.03)	0.9 (0.85–0.94)	0.01 (0–0.03)	0.01 (0–0.03)	0.02 (0–0.04)	0.01 (0–0.03)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)
MUL	0.01 (0–0.02)	0.02 (0–0.05)	0.01 (0–0.03)	0.88 (0.83–0.94)	0.01 (0–0.02)	0.02 (0–0.05)	0.01 (0–0.03)	0.01 (0–0.03)	0.01 (0–0.03)	0.01 (0–0.03)	0.01 (0–0.02)
MAN	0.01 (0–0.02)	0.01 (0–0.03)	0.01 (0–0.03)	0.01 (0–0.03)	0.88 (0.83–0.94)	0.02 (0–0.05)	0.01 (0–0.03)	0.01 (0–0.03)	0.01 (0–0.03)	0.01 (0–0.04)	0.01 (0–0.02)
BAL-BLU	0 (0–0.01)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.03)	0.93 (0.9–0.97)	0.01 (0–0.02)	0.01 (0–0.02)	0 (0–0.01)	0 (0–0.01)	0 (0–0.01)
OBR	0.01 (0–0.02)	0.02 (0–0.06)	0.02 (0–0.05)	0.01 (0–0.03)	0.01 (0–0.04)	0.03 (0–0.08)	0.84 (0.77–0.91)	0.01 (0–0.04)	0.01 (0–0.02)	0.01 (0–0.04)	0.01 (0–0.02)
VRU	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.03)	0.92 (0.88–0.96)	0.01 (0–0.02)	0.01 (0–0.03)	0.01 (0–0.02)
LUN	0.01 (0–0.03)	0.01 (0–0.03)	0.01 (0–0.03)	0.01 (0–0.03)	0.01 (0–0.03)	0.01 (0–0.03)	0.01 (0–0.03)	0.23 (0.18–0.28)	0.68 (0.66–0.69)	0.02 (0–0.04)	0.01 (0–0.03)
CUT	0.01 (0–0.02)	0.01 (0–0.03)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.03 (0–0.06)	0.01 (0–0.02)	0.9 (0.85–0.95)	0.01 (0–0.02)
SIL	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.01 (0–0.02)	0.02 (0–0.05)	0.01 (0–0.02)	0.23 (0.18–0.28)	0.67 (0.66–0.69)



Overall, the spatial genetic structure of *P. clavata* results from the combination of regional genetic clusters with IBD. This complex pattern contrasts with most of the studies conducted to date in the Adriatic, which demonstrated genetic homogeneity over the whole basin (e.g. Garoia et al., 2004; Maltagliati et al., 2010) or regional genetic clusters without internal structure (e.g. Carreras et al., 2017; Schiavina et al., 2014). The pattern characterized here is likely maintained by the joined effects of oceanographic barriers and restricted dispersal abilities (Aurelle & Ledoux, 2013), as reported in other Mediterranean habitat-forming species (e.g. Ledoux, Garrabou, et al., 2010). Besides, we also revealed a significant latitudinal decrease in genetic diversity combined with clines in allele frequencies, which raise the question of a persistent imprint of a northward “serial founder events” postglacial range expansion on the genetic diversity of *P. clavata*.

4.2 | Postglacial range expansion in *P. clavata* along the Croatian coast

The “serial founder events” model is characterized by a recurrent drift effect induced by the successive founder events, which lead to a decrease in genetic diversity along the recolonization axis with some alleles reaching high frequencies at the expansion edge through allele surfing (Austerlitz et al. 1997; Peter & Slatkin, 2013). The significant correlation between population-specific F_{ST} s and latitude is concordant with a northward increase in genetic drift. Focusing on allele frequencies, the frequency of some alleles increases toward the north of the area, with, for instance, allele 105 in *Pcla*-12 reaching frequency up to 0.35 in the northern samples. These clines may result from the surfing of the considered alleles along the wave of expansion. Latitudinal clines in allele frequencies have been reported in various marine species (e.g. Nanninga, Saenz-Agudelo, Manica, & Berumen, 2014; Schmidt et al., 2008). They were mainly explained by variation in natural selection along an environmental gradient (but see Maes & Volckaert, 2002). Rejecting the hypothesis of positive selection requires complementary analyses such as genome scan (e.g. Riquet, Daguin-Thiébaud, Ballenghien, Bierre, & Viard, 2013). Nevertheless, we contend that the combination of the genetic gradients and clines in allele frequency strongly supports recurrent drift effect induced by successive founder events rather than an effect of selection along an environmental gradient.

The population-specific demographic history analyses suggest that the recolonization occurred without dramatic change in population size. While a low analysis power linked to the restricted number of markers used cannot be totally ruled out, the absence of generalized founder effects is concordant with simulations testing the impact of life cycle characteristics on postglacial recolonization dynamics (Austerlitz et al., 2000). The late sexual maturity of *P. clavata* (Coma et al., 1995) induces that the first several years of growth of a recently founded population are mainly due to new migrants and not to the reproduction of local colonies. The initial number of founders thus increases before the first reproduction event, counterbalancing the effect of genetic drift and buffering the

founder effect (Austerlitz et al., 2000). Interestingly, a lack of founder effect and the diverse origins of recruits were demonstrated in a recently colonized population of *P. clavata* (Arizmendi-Mejía, Linares, et al., 2015).

Our current knowledge regarding the palaeogeography of the Adriatic combined with the genetic diversity pattern are consistent with a northward sequential recolonization of the Eastern Adriatic following the LGM. An alternative scenario suggesting a recolonization of the Northern and Central Adriatic from different small isolated patches of residual sea water was suggested for *Aphanius fasciatus* (Buj et al., 2015). Nevertheless, to our knowledge, fine spatial scale palaeogeographic data corroborating the occurrence of isolated patches of sea water in the Northern Adriatic are still lacking. Approximate Bayesian computation (ABC) based on spatially explicit simulations (e.g. Alvarado-Serrano & Hickerson, 2016; Wegmann, Leuenberger, Neuenchwander, & Excoffier, 2010) should be used to formally test the northward sequential recolonization scenario. Nevertheless, these methods imply the estimation of a high number of parameters and summary statistics, which is quite unrealistic considering our dataset (i.e. number of loci). Other spatially explicit methods (e.g. Bradburd, Ralph, & Coop, 2016; He, Prado, & Knowles, 2017; Peter & Slatkin, 2013) were developed to reveal the direction and the origin of expansion range of natural populations but they are based on Single Nucleotide Polymorphism (SNP) preventing their use in the present case.

Accordingly, a northward “serial founder events” range expansion following the LGM seems to be the most relevant process to explain the observed IBD, clines in allele frequencies and gradients of genetic diversity in the context of the palaeogeographic history of the Adriatic. While this remains to be formally tested, density dependant processes such as the “founders take all” principle (i.e. high-density blocking by founding lineage; Waters et al., 2013) combined with the restricted dispersal of *P. clavata* likely explain the retention of the genetic gradient. Complementary studies including populations of *P. clavata* from the south of the Adriatic and the neighbouring Ionian Sea and genotyped with a large number of SNPs should be conducted to identify putative glacial refugia and to refine this evolutionary scenario.

4.3 | Integrating patterns and processes for the conservation of *P. clavata* and associated coralligenous diversity

The conservation value of the 13 populations studied here has been previously demonstrated based on their demographic characteristics (e.g. high recruitment rates) and on the low impact of human-induced disturbances (i.e. high proportion of healthy colonies) (Kipson et al., 2015). Nevertheless, only nine are located within Natura 2000 sites with five belonging to Marine Protected Areas (Table 1). Considering these disparities in management policies and the detrimental effects of global change observed in the region (Kružić & Popijač, 2014), we propose evolutionary-based conservation guidelines.

The two main genetic clusters, which are concordant with two biogeographic sectors of the Adriatic, are characterized by distinct evolutionary histories and low levels of gene flow. We thus propose

these clusters as two distinct and mainly independent units of conservation. In comparison, the four sub-clusters within the southern cluster show shallower divergence times and higher gene flow and thus should be considered as different but interacting sub-units of conservation. Therefore, we suggest an extension of Natura 2000 sites to include currently unprotected *P. clavata* populations from Rogoznica area. Added to the existing MPA in the Kornati area and Natura 2000 site in Vodnjak area, this should create an effective network of protected areas (Table 1). This network will enhance the preservation of the long-term interactions between the sub-clusters while most of the contemporary connectivity, occurring mainly within sub-cluster, will be retained in the MPAs.

The importance of genetic drift in conservation of marine species was recently emphasized due to its impact on population viability (Hare et al., 2011). In the populations studied here, genetic drift and genetic diversity parameters are heterogeneous. Interestingly, the northern populations, which are more impacted by genetic drift and are genetically depleted, are also characterized by a high proportion of juveniles relative to adult colonies (Kipson et al., 2015), suggesting a lower reproductive potential in comparison to southern populations. Combining these genetic and demographic characteristics, the evolutionary potential of *P. clavata* is expected to vary among populations. This is particularly alarming considering the report of mortality events in this region (Kružić & Popijač, 2014). Accordingly, within the existing Natura 2000 sites, all direct anthropogenic pressures affecting the size structure and density of the northern populations (e.g. recreational diving, fishing) should be effectively regulated. This should preserve the reproductive potential and reduce the impact of genetic drift in considered populations. Due to the central ecological role of *P. clavata* as a habitat-forming species, these guidelines will benefit associated biodiversity rich coralligenous habitats.

From a general perspective, the restricted dispersal abilities and late sexual maturity of *P. clavata* are widespread life history traits within habitat forming species from coralligenous habitat (e.g. Ledoux, Mokhtar-Jamaï, et al., 2010). While complementary studies are needed, these life history traits likely underlie the genetic imprint of postglacial range expansion suggested by our results. We thus stress the need to broaden the usual perspective focused on contemporary processes in marine conservation and to consider processes acting on different temporal scales when designing management plans for these species.

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DATA ACCESSIBILITY

Microsatellite genotypes are available on Dryad.

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BIOSKETCH

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SUPPORTING INFORMATION

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

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