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Geographic distances and ocean currents influence Caribbean *Acropora palmata* population connectivity in the Lesser Antilles

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Abstract :

The critically endangered coral species Acropora palmata used to dominate shallow Caribbean reefs but since the early 1980s, populations have dramatically declined. At the Caribbean scale, A. palmata is divided into two genetically divergent lineages and most of previous works investigating population connectivity among populations involved the western lineage (in Florida, the Bahamas, the Mesoamerican Reef System, and the Greater Antilles). Small scale genetic connectivity among A. palmata populations was globally found, possibly enhancing populations' recovery at the local scale. Yet, little is known regarding the genetic connectivity of populations of the eastern lineage, especially those of the Lesser Antilles, a fragmented archipelago located at the edge of the species distribution. Here, we filled this gap by investigating the genetic diversity, population structure and connectivity of A. palmata populations among 36 sampled sites from 11 islands of the Lesser Antilles using 14 hypervariable microsatellite loci. Globally, genetic diversity levels in A. palmata populations from the Lesser Antilles were lower compared to what was previously reported within the Wider Caribbean. The analysis of the genetic structure, crossed with spatial autocorrelation analysis, revealed an isolation-by-distance pattern at both reef and Lesser Antilles scales. A gene dispersal distance of less than a kilometer, and a northward gene flow direction, in agreement with ocean surface currents in the region were found. Altogether, our results suggest a restricted population connectivity and short distance dispersal of A. palmata larvae within the Lesser Antilles further limited by geographic distances among suitable habitat patches. Additionally, our results suggest that southernmost populations are potential sources of larvae for the most northerly islands and have a key role in reseeding A. palmata populations of the Lesser Antilles.

Keywords : Acropora, Lesser Antilles, Larval dispersal, connectivity, Genetic diversity, Isolation-by-distance

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Introduction

Branching corals of the Acroporidae family present an important role, in building and structuring world's coral reef ecosystems (Bruckner 2002). More than one hundred *Acropora* species have been identified in the Indo-Pacific region (Wallace 1999; Veron 2000), but only two species are described in the Caribbean region, the elkhorn coral *A. palmata* (Lamarck, 1816) and the staghorn coral *A. cervicornis* (Lamarck, 1816), with *A. prolifera* (Lamarck, 1816), being a first-generation hybrid of the two former species (van Oppen et al. 2000; Vollmer and Palumbi 2002), and not a hybrid species (Willis et al. 2006). In the past, *A. palmata* and *A. cervicornis* formed dense, monospecific and high-structural thickets in the Caribbean coral reefs, from shallow to intermediate depth (0.5-6 m and 7-15 m depth for *A. palmata* and *A. cervicornis* respectively; Goreau 1959; Bak 1975) . However, in the late 1970s and 1980s, their populations have declined dramatically, mostly due to the combined effects of "white band" disease, hurricanes, and other human-related factors (Precht et al. 2002; Williams and Miller 2005; Miller et al. 2009), to the point that Caribbean endemic *Acropora* species have been classified as 'critically endangered' since 2008 by the International Union for Conservation of Nature (IUCN), regulated by the US Endangered Species Act and listed on the Washington Convention (CITES, Appendix II; Aronson et al. 2008; Carpenter et al. 2008).

The decline of *A. palmata* and *A. cervicornis* populations has led the scientific community to follow their possible recovery by investigating the genetic structure and dynamics of these populations since the early 2000's. Indeed, molecular genetic approaches are one of the tools that can improve the conservation and management objectives in the marine realm (von der Heyden et al. 2014). In particular, the theoretical framework of population genetics offers the possibility to infer population connectivity in marine species and estimate the spatial extent of larval dispersal in marine organisms, above all for sessile organisms showing a dispersal phase through propagules. Identifying sources of propagules to be protected are critical needs for managers who are increasingly operating under the implicit assumption that climate change and other human-related disturbances are unlikely to improve in the short term.

Population connectivity is a force which maintains the genetic cohesion of a biological species over its distribution range (Mayr 1963). It represents the transfer of individuals among populations, which can if successful (*i.e.* the established individuals participate to the reproduction event) lead to a transfer of alleles among populations. In sessile marine organisms, this connectivity is insured by reproductive outputs, from the gametes up to competent larvae ready to settle. Genetic connectivity is the main process by which populations maintain their genetic diversity levels and homogenize their genetic variation. Indeed, classic island models of population genetics (Wright 1940) invoke gene flow (from migration) and genetic drift as the two main processes regulating genetic diversity (selection and mutation being comparatively negligible). For example, small habitat patches theoretically contain small populations so that alleles are expected to be lost due to the effect of genetic drift. Only immigration may counter this effect on a short time scale by introducing alleles (either already present or new ones). Maintaining high genetic diversity levels is particularly crucial for the subsistence of populations in highly variable environments or those subject to rapid anthropogenic changes (Miller and Ayre 2004; Reusch et al. 2005; Yeoh and Dai 2009). Indeed, genetic diversity can affect species productivity, population growth and stability, as well as inter-specific interactions within communities, and ecosystem-level processes (Hughes et al. 2008).

In addition to migration and genetic drift, the mode of reproduction (sexual or asexual) also affect the levels of population genetic diversity, above all in populations with known high clonal propagation. Indeed, asexual reproduction (or clonal reproduction) by fragmentation is an important propagation mode for branching corals with high growth rates (Highsmith 1982). Fragmentation allows the installation of a new structural coral colony on a reef by settlement of a coral fragment issued from a mother-colony already set up on the same reef. The new colony and the maternal colony are genetically identical, members of the same clone (or genet), despite being two distinct ramets. Mature coral colonies issued from clonal propagation and sharing the same genotype (i.e. forming a genet) therefore see their sexual reproductive output increased as compared to colonies represented by only one physical individual (Coffroth and Lasker 1998). Additionally, clonal reproduction counteracts high larval and juvenile mortality rates often

linked with sexual reproduction. However, because of the limited dispersal capacity of asexual reproduction and because species with dual reproduction tend to form multiclonal populations, the greatest genetic impact of clonality occurs at fine spatial scales within populations (Vallejo-Marín et al. 2010). Indeed, the greater the number of genetically identical ramets (*i.e.* clone mates), the smaller the effective population size relative to the apparent census population size. Consequently, genetic diversity and population viability can be significantly overestimated in census counts without knowledge of clonal extent (Rossetto et al. 2004). The consequences of a high clonal rate can therefore be dramatic, with a low genetic diversity within isolated populations and a possible increase of the associated dangers to stress events for potentially badly-adapted genets to new environmental conditions (Reusch et al. 2005). Long term effects of clonal reproduction depend on the balance between costs and benefits of this process (Lirman 2000). In this context, assessing the clonal propagation and genetic diversity levels in populations of endangered species is of primary importance.

The elkhorn coral *A. palmata*, as many other coral species, is known to reproduce both sexually and asexually, through fragmentation (Highsmith 1982). Because (1) sexual reproduction occurs only once a year, through the synchronized release of gametes in the water column (generally after the August full moon, Szmant 1986; Miller et al. 2016) and (2) pelagic larvae can settle from 5 days up to a maximum of 20 days after fertilization in conditions not propitious to earlier larval recruitment (Baums et al. 2005b), larval dispersal, in terms of distance and frequency, and genetic connectivity of this species are expected to be limited. Previous genetic studies on *A. palmata* Caribbean populations, both in terms of geographical variation of its clonal structure and spatial genetic structuring, have mainly been conducted along the reefs of the Gulf of Mexico (Florida, Baums et al. 2005a, b, 2006a), the Bahamas (Baums et al. 2005b, 2006a; Garcia Reyes and Schizas 2010; Mège et al. 2015) the Greater Antilles (Puerto Rico and US Virgin Islands, Baums et al. 2005b, 2006a; Garcia Reyes and Schizas 2010; Mège et al. 2015), the Mesoamerican Reef System (MRS, Baums et al. 2005b, 2006a; Porto-Hannes et al. 2015) and the islands off the Venezuelan coast (Los Roques National Park and the Netherlands islands of Curaçao and Bonaire, Baums et al. 2005b, 2006a; Zubillaga et al. 2008; Porto-Hannes et al. 2015; Mège et al.

2015). Over all, investigation on the population genetic structure of *A. palmata* in the Caribbean revealed a main phylogeographic split dividing *A*. *palmata* populations into two genetically divergent lineages, eastern and western, with the northern genetic break being located around the Eastern Puerto Rican region (Baums et al. 2005b, 2006a, b; Mège et al. 2015) and the southern being located somewhere between Panama and Curaçao (Baums et al. 2005b; Porto-Hannes et al. 2015). Within the western lineage, at a rather small scale (< ca. 500 km), genetic differentiation among sampling locations seemed to be weak and not related to geographic distances (Baums et al. 2005b; Porto-Hannes et al. 2015; Mège et al. 2015). Isolation-by-distance (IBD) patterns were observed 1) in the admixture region of Puerto Rico, partially explained by the mix of the two genetically divergent *A. palmata* eastern and western lineages (Mège et al. 2015) and 2) at large spatial scales involving inter-lineages comparisons (Porto-Hannes et al. 2015; Mège et al. 2015). So far, only two studies reported significant genetic structuring within the eastern lineage, though only two to three distant (shortest nautical distance < 600 km) sampling locations were involved in both cases (US Virgin Islands *vs*. Saint-Vincent and the Grenadines *vs*. Curaçao and Bonnaire in Baums et al. 2005b; Guadeloupe *vs*. Curaçao in Mège et al. 2015).

Across the Caribbean, *A. palmata* populations were found to be mostly self-recruiting, with sexual recruitment being more prevalent in the eastern lineage than in the western one (Baums et al. 2005, 2006). Nevertheless, the contribution of both reproductive modes to population structure was found to be unrelated to a purely geographic division between distinct genetic lineages (Baums et al. 2006a; Porto-Hannes et al. 2015; Mège et al. 2015). Also, it seems that asexual reproduction by fragmentation in *A. palmata* populations is more likely explained by differences among reefs in habitat characteristics and related environmental conditions (*e.g*. reef orientation and inclination, current dynamics, competition for space with other reef organisms…) than by differences between lineages (Baums et al. 2006a; Porto-Hannes et al. 2015; Mège et al. 2015).

As previously mentioned, most of these genetic works conducted on *A. palmata* populations involved the western lineage and only few populations from the eastern lineage were studied.

This eastern lineage is mainly characterized by populations from the Lesser Antilles, an arc of islands from 18°N to 11°N and 59°W to 70°W, part of the Eastern Caribbean ecoregion (Spalding et al. 2007), much less studied than the Western Caribbean ecoregion. While most conservation efforts in the Lesser Antilles have been conducted so far on the terrestrial fauna (birds, herpetofauna, insects, etc) and flora because of high rates of endemism in islands (e.g. Francisco-Ortega et al. 2007; Hedges and Díaz 2011; Latta 2012), conservation strategies regarding marine species are rising in response to increasing damages observed on coral reef ecosystems (see for example, Young et al. 2012).

In this context, estimating genetic diversity and connectivity of *A. palmata* populations in the Lesser Antilles archipelago is needed to provide information regarding the extent over which source reefs can eventually rescue damaged reefs through input of coral larvae, in order to improve management, protection and conservation of this endangered species. Thus, the main objectives of this study were (1) to estimate the levels of genetic diversity of *A. palmata* populations of the Lesser Antilles and compare them to those of already studied Caribbean populations, (2) to investigate *A. palmata* spatial scales of larval dispersal in the Lesser Antilles, and (3) to explore the possible contributing factors explaining the observed genetic differences among *A. palmata* populations in this region. To do so, *A. palmata* colonies were sampled in 36 study sites from 11 islands of the Lesser Antilles, in a hierarchical framework. Fourteen hypervariable microsatellite loci were used, first to determine the number of genotypes among the sampled colonies in order to estimate the genetic diversity and clonality, and secondly, to assess the population genetic structure and the connectivity level among *A. palmata* populations of the Lesser Antilles.

Materials and methods

Sampling

A total of 1,042 colonies of *Acropora palmata* were sampled in 36 localities from 11 islands from the Lesser Antilles, from the northern islands of St. Martin and St. Barthélemy to the southernmost islands of St. Vincent and the Grenadines (Table 1, Figure 1), covering a latitudinal

transect of ca. 600 km. Most of these islands are volcanic, mountainous and present fringing reefs subject to considerable terrigenous inputs from erosion (Bouchon et al. 2008). Most *A. palmata* colonies (n = 642) sampled from sites coded from PAC01 to PAC28 were collected in April and May 2015 during "PACOTILLES" campaign on board RV ANTEA (IRD). Other colonies from Guadeloupe (n = 353) and St. Barthélemy (n = 47) were collected between May 2011 and October 2014 during specific field trips. Fragments of colonies (tip of branch) were collected by snorkeling, between 1 and 5 m depth. For the site Caye à Dupont (Guadeloupe), 80 colonies were sampled exhaustively in a 30 m radius circle (see Japaud et al. 2015). For all the other sites, colonies were sampled along an imaginary transect following the coastline until ca. 50 colonies per site were reached (usually between 2 and 3 hours), though avoiding small but thick colonies nearby (<1m) large colonies (that may correspond to the breakage of branches of the large colonies and their subsequent re-attachment). Sampled colonies were photographed underwater for most of the sites (n = 15/21) of the PACOTILLES campaign and snipped fragments placed in individually labeled zip bag, numbered along each transect. After sampling, coral fragments were transferred into Falcon tubes containing 70% ethanol and stored at room temperature until processing.

Molecular analyses

Total genomic DNA was extracted from 5-10 polyps per fragment, using a DNA Purification Kit (formerly Gentra Puregene, Qiagen, Valencia, CA, USA) following the manufacturer's protocol. Fourteen *A. palmata* specific microsatellite loci (Baums et al. 2005a, 2009) were PCR amplified following the protocol described in (Japaud et al. 2015). Amplified fragments were sent to the GENTYANE platform (INRA, Clermont-Ferrand, France), where they were resolved on an ABI 3730XL sequencer with a GeneScan LIZ-500 internal size standard (Applied Biosystems). Alleles were sized using GENEMAPPER v. 4.0 (Applied Biosystems). We used GMCONVERT (Faircloth 2006) to convert the exported GENEMAPPER table of genotypes.

Data analyses

Our dataset was tested for scoring errors and null alleles using MICRO-CHECKER v. 2.2.3 (van Oosterhout et al. 2004). All distinct multilocus genotypes (MLGs) and clones were distinguished

among colonies using GENALEX v. 6.502 (Peakall and Smouse 2006, 2012). Associated probabilities of identity (*PI*) were further estimated in order to assess the probability that two different sampled colonies present an identical MLG just by chance given our set of 14 microsatellite markers.

Since *A. prolifera* colonies could be present within our sampling [i.e. hybrids between *A. palmata* and *A. cervicornis* may present an *A. palmata* morphology (Acropora Biological Review Team 2005)], we performed a discriminant analysis using STRUCTURE v. 2.3.4 (Pritchard et al. 2000). For this, we added to our *A. palmata* MLGs obtained from the analysis of 1,042 colonies some reference MLGs of *A. cervicornis* (n = 25) and *A. prolifera* (n = 7), which had been previously genotyped (with the exact same set of loci) (Japaud et al. 2014, 2015). By fixing K=2, we enforced colonies to belong either to an A. *palmata* cluster, or to an *A. cervicornis* cluster (in this case, known *A. prolifera* are expected to present intermediate percentages of membership to each cluster). Percentage of membership of each sampled colony to each cluster were obtained pooling the results of 10 independent runs with CLUMPP v. 1.1.2 (Jakobsson and Rosenberg 2007), after running STRUCTURE (5×10^4 iterations, burn-in = 5×10^3) under an admixture ancestry model, using species information as LOCPRIOR (*A. palmata*, *A. cervicornis*, or *A. prolifera* based on morphology) and assuming correlated allele frequencies. Additionally, a correspondence analysis was performed over all these genotypes with GENETIX v.4.05.2 (Belkhir et al. 2004), in order to illustrate and confirm the clustering analysis.

Genotypic richness, genotypic diversity and genotypic evenness were estimated to evaluate the part of clonality (asexual reproduction) for each site. Genotypic richness (N_g/N) was calculated as the number of unique identified MLGs (N_g) over the total number of sampled colonies (N). Genotypic richness ranges from nearly 0 to 1: the closer to 1, the higher the number of MLGs and, thus, the smaller the number of clones. Genotypic diversity (G_O/G_E) was estimated as the observed genotypic diversity (G_O; Stoddart and Taylor 1988) over the expected genotypic diversity (G_E) to access the relative importance of sexual reproduction in a population. Observed genotypic diversity was calculated as:

254 $$G_O = \frac{1}{\sum_i^k g_i^2}$$

255 where g_i is the relative frequency of the i^{th} of k MLGs. As expected for a full sexually reproducing
256 population, expected genotypic diversity (G_E) equals the total number of sampled and analyzed
257 colonies (N). Genotypic evenness (G_O/N_g; Coffroth and Lasker 1998) was estimated as the ratio
258 between the observed genotypic diversity (G_O) and the number of unique identified MLGs (N_g).
259 Genotypic evenness measures the distribution of genotype abundances: a population with
260 equally abundant genotypes yields a value equal to 1 while a population dominated by a single
261 genotype gives a value close to 0. For populations presenting only one genotype, genotypic
262 evenness has no meaning and is equal to 1. Based on the combination of genotypic diversity
263 (G_O/G_E) and genotypic evenness (G_O/N_g), sites were classified into four categories to facilitate
264 discussion (Baums et al. 2006a): asexual, mostly asexual, mostly sexual and sexual. Clustering
265 among groups was realized in R using the 'kmeans' function of the R 'Stats' package (R Core
266 Team 2016). All subsequent analyses were conducted keeping only one representative per MLG
267 and per sampling site.
268 Null allele frequencies (r) were estimated for each locus and within each sampling site using the
269 expectation maximization algorithm (Dempster et al. 1977) implemented in FREENA (Chapuis
270 and Estoup 2007). Genotypic linkage disequilibria, fixation index estimates (F_{IS}; Weir and
271 Cockerham 1984) and significant departures from Hardy–Weinberg equilibrium were estimated
272 and tested using the exact tests implemented in the online GENEPOP v. 4.2 (Raymond and
273 Rousset 1995) with default Markov Chain parameters. Observed heterozygosity (H_O) and
274 unbiased expected heterozygosity (H_E) were estimated with GENALEX v. 6.502 (Peakall and
275 Smouse 2006, 2012). Allelic richness (rarefied or extrapolated for N = 50 with 95% confidence
276 bounds) was estimated within each sampling site using the 'ARES' package in R (van Loon et al.
277 2007; R Core Team 2016) and for island estimates, allelic richness was averaged over sample
278 sites. Genetic differentiation among populations was estimated i) using Weir and Cockerham's
279 (1984) estimator θ in GENEPOP and ii) using Weir's (1996) unbiased F_{ST} estimated using the
280 ENA method in FREENA (Chapuis and Estoup 2007) with correction for null alleles and the

significance of the test (H_0: F_{ST} = 0) assessed using the 95% confidence interval obtained through bootstrap resampling over loci in FREENA. An analysis of molecular variance (AMOVA) (Excoffier et al. 1992) implemented in ARLEQUIN version 3.5.2 (Excoffier and Lischer 2010) was conducted based on Weir and Cockerham's (1984) F_{ST} estimates to examine the partition of the genetic variance among *A. palmata* samples in the Lesser Antilles. With this purpose the 34 samples were grouped according to their island of origin with two exceptions: Les Saintes sample was grouped together with Guadeloupe samples, and Union Island sample was grouped together with Bequia samples.

Genetic structuring was further investigated using a Bayesian clustering approach to estimate the most likely number of clusters (K) among all MLGs using STRUCTURE v. 2.3.4 (Pritchard et al. 2000). Log-likelihood values for each K (number of inferred populations: 1–37) were computed by running an admixture ancestry model with no location prior and assuming correlated allele frequencies (5 replicates, 5×10^5 iterations, burn-in = 2×10^3). Following the recommendations of Evanno et al. (2005), the ad hoc statistic ΔK was calculated using STRUCTURE Harvester (Earl and VonHoldt 2012).

Similarities or dissimilarities among island populations were further visualized through a principal coordinates analysis (PCoA) using the "covariance-standardized" PCoA method in GENALEX v. 6.502 (Peakall and Smouse 2006, 2012) and based on a pairwise genetic distance matrix using the "codom-genotypic" option. To specifically test for isolation-by-distance (IBD) pattern. (Mantel 1967) tests were performed in R with the function 'mantel.rtest' of the package 'ade4', with 10^4 permutations of the corrected pairwise (F_{ST} / (1 - F_{ST})) matrix estimated in FREENA among sites and islands, and the geographic distance matrix. For geographic distance estimates, we used the shortest distance among sites considering islands as barriers to larval dispersal estimated using the 'costDistance' function of the package 'gdistance' in R (van Etten 2015; R Core Team 2016). Geographic distances for each pair of islands were estimated using the center of each island as a landmark.

To visualize the fine-scale spatial genetic structure of *Acropora palmata* and estimate gene dispersal distance throughout the islands of the Lesser Antilles in the context of IBD, we

estimated the genetic similarity between every pair of individuals *i* and *j* with Loiselle's kinship coefficient (F_{ij}, Loiselle et al. 1995) and regressed the obtained values on the spatial distance between individuals and its natural logarithm in a spatial autocorrelogram, in SPAGEDI v. 1.5 (Hardy and Vekemans 1999, 2002). Loiselle's kinship coefficient was estimated among colonies organized in 10 automatically defined spatial distance intervals to reach an even number of pairwise comparisons within each interval. The significance of kinship among individuals within each distance interval was obtained using 10^4 permutations.

Wright's neighborhood size was further estimated as $Nb \approx -(1-F_N)/\ b_{Ld}$ where b_{Ld} is the regression slope of pairwise values on the logarithm of spatial distance, and F_N is the kinship coefficient estimated between adjacent individuals. Because this relationship holds best when the regression is computed within short geographic distances (Rousset 2000), assuming a two-dimensional population at drift-dispersal equilibrium, F_N et b_{Ld} were estimated using an iterative procedure described in SPAGEDI by regressing pairwise kinship coefficients on ln(distance) over a restricted distance range (set to 0-30km, based on significant kinship coefficient estimates within distance intervals and the average geographic distance between sites located on the same island). The mean-squared distance of gene dispersal, σ, was then inferred in SPAGEDI from the neighborhood size as Nb is related to σ as follows: $Nb \approx 4\pi De\sigma^2$, where De is the effective density (Rousset 2000; Vekemans and Hardy 2004) which can be approximated as $D\ .\ Ne/N$ where Ne/N is the ratio of the effective to the census population sizes. There are no estimates of this ratio in *A. palmata* available in the literature. Yet, the fertilization potential of *A. palmata* is likely limited by the fact that 1) this species is a simultaneous hermaphrodite that release gametes (viable only few hours) in the water column once a year, in late summer (Fogarty et al. 2012; Miller et al. 2016a), 2) *A. palmata* is genotypically depauperate in some areas of its range (see for example Baums et al. 2006; Japaud et al. 2015 among others) and 3) different genotypes do not participate synchronically to the reproduction event, nor systematically every year (Miller et al. 2016a). Therefore, we used 0.1 and 0.01 as arbitrary upper and lower estimates for Ne/N, and D, *A. palmata* density, based on observed estimates across various reefs available in the literature (see results).

Finally, an eventual directional gene flow in *A. palmata* along the Lesser Antilles was tested. Since islands of the Lesser Antilles are approximately distributed along a North-South axis, it was tested whether gene flow was oriented southward or northward. To do so, the relative directional migration coefficient among islands based on the Jost's D index (D_M) was estimated using the online application DIVMIGRATE (5×10^3 bootstraps, $\alpha = 0.05$; Jost 2008; Sundqvist et al. 2016). Two D_M were estimated between each pair of island populations, representing both directions: from island A to island B and *vice versa*.

Results

Species identification

Among the 1,042 A. *palmata* colonies analysed, a total of 726 distinct MLGs were identified. From these, 96 (13%) were represented by at least two colonies while the rest (87%) by only one colony. The estimated probability that two genetically different colonies have identical MLG by chance using the 14 microsatellite loci (*PI*) was 9.9×10^{-15}. Therefore, colonies harboring the same MLG were interpreted as biological clones.

The clustering analysis conducted over all the 758 MLGs (726 *A. palmata*, 25 *A. cervicornis* and seven *A. prolifera*) with STRUCTURE revealed that all seven known *A. prolifera* individuals had a maximum likelihood of membership of 70.9% to *A. palmata* cluster (Online Resource 1). We therefore applied a minimum threshold of 70.9% of membership to *A. palmata* cluster. Out of the 726 *A. palmata* MLGs, five were identified as belonging to possible hybrids (with likely membership to *A. palmata* cluster varying between 14.5 and 66.5%; Online Resource 1; Figure 2) and were therefore excluded from the dataset. For more safety, three additional colonies were also excluded because of their close proximity to *A. prolifera* MLGs on the correspondence analysis (Figure 2), even though their membership to *A. palmata* cluster varied between 99 and 100%. Therefore, a total of eight MLGs corresponding to eight colonies *a posteriori* identified as possible hybrids were excluded from the *A. palmata* dataset. Noteworthy, these colonies for which we had underwater pictures taken during sampling all had an *A. palmata* morph.

Genotypic diversity and clonality

Genotypic richness (N_g/N) and genotypic diversity (G_O/G_E) ranged from nearly 0 for FjL (Guadeloupe) and PAC09 (Saint-Vincent) (i.e., for each site, only one MLG was found over all the colonies sampled) to 1 in PAC23 (Saint-Martin), PAC27 (Saba), AL and AM (Guadeloupe), PAC04 and PAC06 (Martinique) and PAC11 in Bequia (i.e., each sampled colony presented a distinct MLG) (Table 1). Mean genotypic richness per site (± standard error) was 0.75 ± 0.04 (n = 35) and mean genotypic diversity per site was 0.64 ± 0.05 (n = 35). The smallest genotypic evenness (G_O/N_g) was found in PAC15 (Saint Lucia) (0.21) where 17 MLGs were found but one of them represented 50% of the 42 sampled colonies. The highest genotypic evenness was maximal (G_O/N_g = 1) for the seven sites where all sampled colonies presented distinct MLGs (PAC23, PAC27, AL, AM, PAC04, PAC06 and PAC11), as well as for the two sites where a single MLG was found (FjL and PAC09), though not informative. Mean genotypic evenness per site calculated without these two latter sites was 0.79 ± 0.04 (n = 33).

Based on the combination of genotypic diversity (G_O/G_E) and genotypic evenness (G_O/N_g), *A. palmata* stands (corresponding to each sampling site) were classified into four categories (Table 1, Figure 3): asexual, mostly asexual, mostly sexual and sexual (Baums et al. 2006b). The 'asexual' category gathered the two sites with a single MLG per site, FjL and PAC09. The 'mostly asexual' category included four sites characterized by very low values of genotypic diversity and genotypic evenness (ranged from 0.04 to 0.28 and from 0.21 to 0.49 respectively): SB1, PAC03, PAC10 and PAC15. The 'mostly sexual' category was composed by 14 sites with moderate values of genotypic diversity and genotypic evenness (from 0.33 to 0.72 and from 0.57 to 0.89 respectively): SB3, SB4, PAC21, PAC22, PAC28, LM, PC, PT, TA, PAC01, PAC02, PAC17, PAC12 and PAC13. The 'sexual' category consisted of 15 sites with the highest values of genotypic diversity and genotypic evenness (> 0.78 and >0.90 respectively): PAC23, PAC24, PAC25, PAC27, PAC20, AL, AM, FjPE, IG, IP, Lz, PAC04, PAC06, PAC08, PAC11 (Figure 3).

When looking at estimated indices per island, the number of distinct MLGs found ranged from 30 (in Saint Lucia, N=60) to 256 (in Guadeloupe, N=395). Mean genotypic richness (N_g/N) per island ranged from 0.41 ± 0.25 (n = 3, Saint Vincent) to 1 for Saba with a single sampling site and

all the colonies presenting a unique MLG. Mean genotypic diversity (G_O/G_E) per island ranged from 0.34 for Saint Lucia (0.34 ± 0.25; n = 2) and Saint Vincent (0.34 ± 0.25; n = 3) to 1 for Saba. Mean genotypic evenness (G_O/N_g) per island ranged from 0.52 ± 0.31 (n = 2, Saint Lucia) to 0.96 ± 0.03 (n = 3, Saint-Martin). Genotypic evenness for Saba was maximal (G_O/N_g = 1) because all the colonies of the single sampling site of the island presented unique MLGs. High observed standard errors illustrate the unevenness of genotypic indices estimated among sites of a same island (Table 1).

Genetic diversity

Keeping only one representative per MLG (N_g= 718), observed heterozygosity (H_O) across loci ranged between 0.493 for PAC10 in Saint Vincent and 0.714 for PAC11 in Bequia (mean ± s.e. = 0.624 ± 0.008; Table 1). Across all loci, expected heterozygosity (H_E) per site ranged between 0.571 for PAC09 in Saint Vincent and 0.742 for IP in Guadeloupe (mean = 0.684 ± 0.006; Table 1). Estimated F_{IS} per site across all loci ranged between -0.001 and 0.215, respectively for LM in Guadeloupe and for PAC10 in Saint Vincent and significant departures from Hardy–Weinberg equilibrium were found in 17 out of 36 sampling sites, and 12 remained significant after Bonferroni correction (all heterozygote deficits, Table 1). Among the 3,278 pairwise tests of linkage disequilibrium comparing all loci at each of the 36 sampling sites, only 5 were significant after Bonferroni correction (0.15%, $P < 0.05$). Overall loci, estimated allelic richness (AR) per site ranged from 87.5 for PAC20 in Antigua to 191.6 for PT in Guadeloupe (Table 1). Observed and expected heterozygosity estimates per locus within study sites, as well as per locus F_{IS} are provided in Online Resource 2.

When grouping sites per island (i.e. considering that each island represents a population), mean observed heterozygosity across all loci ranged between 0.553 ± 0.031 for Saint Vincent and 0.663 ± 0.051 for Bequia (Table 1), mean expected heterozygosity ranged between 0.618 ± 0.027 for Saint Vincent and 0.704 ± 0.023 for Bequia, and mean allelic richness ranged from 102.1 ± 8.6 for Antigua to 137.0 ± 7.4 for Guadeloupe (mean overall islands = 125.6 ± 4.1), where a higher number of diverse sites were sampled. The smallest allelic richness estimates were

found in Antigua, St Vincent (mean over 3 sites: 106.9 ± 5.7), Bequia (105.2 in one site, the other one being composed of clones) and Union (106.1 in one site).

Because the proportion of null alleles for marker #1490 exceeded 20% in most of the populations of the sampling sites (Online Resource 2; n = 25/36), this marker, initially kept for MLG identification, was further excluded for the following genetic connectivity analyses (Chapuis and Estoup 2007).

Population structure

As a single MLG was found for FjL in Guadeloupe and for PAC09 in Saint Vincent, each MLG from these monoclonal sites was pooled with the genotypes of the closest site, respectively FjPE (2.1 km of distance) and PAC10 (1 km of distance), in order to keep the maximum of genetic information for further analyses.

Matrices of pairwise-F_{ST} estimated using GENEPOP and FREENA were highly related ($R^2 = 0.94$, $P < 0.0001$). Because of the presence of null alleles in nearly all loci (Online Resource 2), we decided to present only the estimates from FREENA, which were estimated taking into account the occurrence of null alleles (though estimated based on HW equilibrium, an assumption unlikely met).

Within Guadeloupe, a weak genetic structure was observed among the 13 sampled sites, with only two pairs of sites significantly differentiated from each other: Anse Laborde (AL) and Tête à l'Anglais (TA) (F_{ST} = 0.020*), which are located on distinct geographic part of Guadeloupe (Grande Terre and Basse Terre, respectively), and Caye à Dupont (CD) and Anse à la Barque (PAC28) (F_{ST} = 0.011*, Online Resource 3), located on the opposite sides of Basse Terre (Figure 1). Accordingly, no apparent clusters were identified by STRUCTURE among the sampling sites of Guadeloupe. Based on the PCoA results, this observed genetic structure was further not in agreement with the geographic distribution of the sampling sites of Guadeloupe (Online Resource 4).

This weak genetic differentiation observed among sites within a single island was confirmed in all other islands of the Lesser Antilles under study, showing in general low and non-significant

449 pairwise F_{ST} estimates within islands (Online Resource 3). Indeed, the variance attributed to the
450 genetic variation estimated among sites within islands was weak and not significant (AMOVA: vb
451 = 0.0129; percentage of variation = 0.29%, p-value = 0.175). Also, there was globally no
452 significant differentiation observed among sites belonging to the closest islands: no significant
453 differentiations were reported among sampling sites of the northern islands St. Martin, St.
454 Barthélemy, Saba and Antigua (with the exception of a single significant pairwise F_{ST} estimate
455 between one site in Antigua (PAC20) and one site in St. Barthélemy (SB3), F_{ST} = 0.019*, Online
456 Resource 3). Similarly, no significant genetic differentiations were reported among sites of St.
457 Lucia and St. Vincent, nor among sites of the southern islands of St. Vincent, Bequia and Union
458 (with the exception of a single weak but significant pairwise F_{ST} estimate between one site in
459 Bequia (PAC12) and the single site of Union (PAC13), F_{ST} = 0.009*, Online Resource 3).
460 In general, at the Lesser Antilles scale, no apparent differentiated clusters were identified when
461 performing Bayesian assignment tests (STRUCTURE; data not shown). However, a weak but
462 significant variance was attributed to the genetic variation estimated among islands (va =
463 0.0685; percentage of variation = 1.52%, p-value < 0.0001), and the genetic differentiation
464 between islands was generally higher than within island (Online Resource 3). Accordingly,
465 geographic distances among sites significantly explained 35% of the genetic variation
466 (F_{ST} / (1 - F_{ST})) across all sampling sites (P < 0.0001, Figure 4A). Furthermore, when sampling
467 sites with less than 10 distinct genotypes were removed, geographic distances explained 46% of
468 the genetic variation (P < 0.0001, Figure 4B), and up to 78% when sites with less than 20
469 genotypes were removed (P < 0.001, Figure 4C). Therefore, because of a restricted number of
470 genotypes at some sites together with the general weak and non-significant genetic
471 differentiation observed among sites within the same islands, the sites of each single island were
472 pooled to run subsequent data analyses, resulting in 11 populations of *A. palmata*,
473 corresponding to the 11 islands sampled across the Lesser Antilles.
474 A principal coordinates analysis (PCoA) conducted on these 11 island populations revealed that
475 principal components 1 and 2 represented 86.29% (cumulated inertia of both axes) of the
476 genetic heterogeneity among populations of *A. palmata* (Figure 5). Most importantly, Axis 1 with

72.88% of inertia segregated the 11 populations along a north/south gradient (Figure 5). In addition, populations of closed islands were generally not significantly differentiated (Table 2). Accordingly, geographic distances among islands significantly explained 72% ($P < 0.0001$) of the genetic variation (F_{ST} / (1 - F_{ST})) among islands (Figure 4D), revealing a clear Isolation-by-Distance (IBD) pattern among *A. palmata* populations in the Lesser Antilles. This IBD pattern was further evidenced at the reef scale. Indeed, colonies sampled within a single site (or reef) (<10 km) were significantly more genetically similar than colonies belonging to distinct sampling sites, with decreasing similarity among colonies as the geographic distance among sampling sites increased (though still significant within distances up to 192 km, Figure 6). Based on Loiselle's kinship coefficient and its regression on the natural logarithm of geographic distance using the iterative procedure, we were able to estimate a neighborhood size of *A. palmata* in the Lesser Antilles ranging between 82 and 130 individuals (with a mean over iterations cycling of 106 individuals). Reported densities of *A. palmata* range from 1,000 to 27,000 genets/km^2 across various Caribbean reefs (Baums et al. 2006a), and 2,000 to 25,000 genets/km^2 across the Lesser Antilles (Japaud et al. 2015, and estimates from the present study). Giving these estimated bounds for *D* and assuming *De* = 2000 as the upper limit and *De* = 10 genets/km2 as the lower limit of estimates of effective population densities, we estimated a gene dispersal σ to be between 0.072 and 1.037 km, with a gene dispersal longer at lower densities. Lastly, while the genetic variation among *A. palmata* populations seemed organized along a north-south axis (see Figure 5), we did not evidence a significant directional gene flow among islands. Indeed, a single relative directional migration coefficient (D_M) appeared significant, from Union northward to Guadeloupe ($\alpha = 0.05$; Table 3). Nevertheless, when subtracting D_M coefficients of each island pair estimated from a southward direction to D_M coefficients of the same pair, but estimated from the northward direction, positive values (obtained when D_M coefficients estimated from a northward direction were higher than those estimated from the southward one), were obtained in 36 out of 55 pairwise comparisons (65%), suggesting a general northward gene flow (though not significant), among *A. palmata* populations along the arc of the Lesser Antilles.

Discussion

The molecular analysis of 1,042 *A. palmata* sampled colonies using a set of 14 microsatellite loci revealed that 8 individuals identified in the field as *A. palmata* on the basis of their morphological characteristics showed MLGs genetically close to *A. prolifera* MLGs. These samples were therefore removed from the *A. palmata* dataset. Using this same set of microsatellite loci, it was found that clonality proportion greatly varied among sampling sites. Hence, some *A. palmata* stands presented large patch of clones with a single MLG while others were only composed of colonies with distinct MLGs, even if the sampling sites were located on a same island (as in Guadeloupe for example). Nevertheless, mean genotypic index estimates across all sampling sites of the Lesser Antilles globally illustrated high genotypic richness and evenness (Ng/N = 0.75 ± 0.04; G_O/Ng = 0.79 ± 0.04). Regarding the genetic structuring of *A. palmata* populations of the Lesser Antilles, no apparent distinct clusters were identified. Nevertheless, pairwise genetic distances were correlated to geographic distances among populations, revealing an isolation-by-distance pattern with a maximum estimated gene dispersal for *A. palmata* of one kilometer.

Gene introgression from *Acropora cervicornis* to *Acropora palmata*

Several colonies were genetically identified as *A. prolifera* hybrids after being morphologically identified as *A. palmata* (see for example Online Resource 5). The 'palmate-morph' defined by (Vollmer and Palumbi 2002) for some *A. prolifera* F1 hybrids is not sufficient to explain a complete confusion in colony morphological identification. Rare backcrossing of *A. palmata* with the first generation hybrid *A. prolifera* may induce later generation hybrids and a consequent introgression of *A. cervicornis* genes into *A. palmata* genome, which may explain that some colonies genetically identified as *A. prolifera* could present a confusing *A. palmata* morphology (Miller and van Oppen 2003; Fogarty 2012). This observation suggests that the hybridization complex of Caribbean *Acropora* species may be more complicated that a unidirectional introgression of genes flowing from *A. palmata* towards *A. cervicornis* as previously described

(van Oppen et al. 2000; Vollmer and Palumbi 2002, 2007; Fogarty et al. 2012). Further investigations are needed 1) to evaluate how observed decreasing densities of both *A. palmata* and *A. cervicornis* may explain increasing observations of large thickets of this hybrid across the Caribbean (Japaud et al. 2014; Aguilar-Perera and Hernández-Landa 2017) and a decreased mortality of these hybrids in recent decades (Fogarty 2012), and 2) to evaluate how the increasing success of this hybrid may affect both *A. palmata* and *A. cervicornis* populations.

Possible influence of site-specific environmental conditions on clonality

In this study, estimates of genotypic indices varied considerably among sampling sites, even among closed sites or sites located within a same island. Mean genotypic richness per site was 0.75, smaller than estimates available for *A. palmata* western lineage and previously reported (*Ng/*N = 0.96 in Guadeloupe, Mège et al. 2015); *Ng/*N = 0.86 and 0.94 in Los Roques National Park, Venezuela, in Porto-Hannes et al. (2015). However, in these two cited studies, as well as in the present work, genotypic richness estimates varied greatly among sites (from 0.38 to 1.00 in Mège et al. (2015); from 0.65 to 0.98 in Porto-Hannes et al. (2015) and from 0.03 to 1.00 in here). Similarly to Mège et al. (2015) and Porto-Hannes et al. (2015), an opportunistic sampling strategy (i.e. sampling haphazardly) was adopted to assess genetic structure of the *A. palmata* populations of the Lesser Antilles (and to avoid an overrepresentation of clones) since specifically characterizing genotypic diversity and clonality of these populations was not our primary goal. For this reason, population dynamics implications based on the genotypic indices estimates should be interpreted carefully. Indeed, our estimates were higher than found in Baums et al. (2006a) who specifically investigated levels of clonality in this species using either a randomized sampling strategy (i.e. sampling colonies *a priori* selected following a procedure generating random coordinates, see Baums et al. 2005a) or an opportunistic sampling strategy (mean ± SD N_g/N per site = 0.52±0.26 and 0.51±0.31, respectively), even when compared to sampling sites from the western lineage only (mean ± SD N_g/N per site = 0.64±0.18 and 0.71±0.01, respectively).

Nevertheless, the difference in estimates of genotypic richness may result from differences in site-specific environmental conditions rather than other factors like a difference in sampling strategy (Mège et al. 2015). For example, in our study, estimates of genotypic indices were low and consistent across sampling sites presenting somehow similar environmental characteristics than of Caye à Dupont. a site where *A. palmata* clonality was specifically investigated using an exhaustive sampling within a 30 m radius circle (Japaud et al. 2015) and for which it was found a N_g/N = 0.125. This reef, as well as Duvernette Island reef (N_g/N = 0.14), Blue Lagoon reef (N_g/N = 0.17) in St Vincent, and Ilet Fajou reef in Guadeloupe (N_g/N = 0.03) were all characterized by high hydrodynamism, a shallow flat bottom and a high coral colony density, constituting a set of general characteristics that seems to advantage the asexual expansion of the branching *Acropora* corals (Japaud et al. 2015). Indeed, the proportion of asexual reproduction by fragmentation in a population is known to be related to site-specific geoclimatic conditions such as intensity and frequency of swell, waves, hurricanes and topography (Coffroth and Lasker 1998; Baums et al. 2006b). In contrast, reefs where *A. palmata* stands presented few or no clones could be related to areas with less suitable habitat and low population densities (Mège et al. 2015). Alternatively, *A. palmata* populations presenting scarce colonies with few or no clones could be relicts of old and dense populations which faced past important stressor events (such as "white band" disease, coral bleaching, hurricanes, algal over-growth or predation…), resulting in losses of colonies without any subsequent efficient recovery (Bruckner 2002; Acropora Biological Review Team 2005). Future studies investigating the recent demographic history of these populations sequencing large fractions of genomes analysed with Approximate Bayesian Computation (Beaumont et al. 2002) may specifically allow to test for this hypothesis (Hoffman et al. 2011).

Low genetic diversity estimates for *Acropora palmata* in the Lesser Antilles

Resilience of populations depends on genetic diversity that is necessary to the species adaptation success facing changes in environmental conditions (Miller and Ayre 2004; Yeoh and Dai 2009). In *A. palmata*, the genetic diversity estimated in the present study was globally lower (mean H_E per site = 0.684 ± 0.038) than any estimates of genetic diversity found in similar

588 studies conducted by Baums et al. (2005b), Mège et al. (2015) and Porto-Hannes et al. (2015) with
589 H_E per site = 0.75, 0.761 and 0.869, respectively. These differences in genetic diversity can partly
590 be explained by the fact that different microsatellite loci were used in the present study: 14 loci
591 were used here, including the five loci exclusively used in the previous studies of Baums et al.
592 (2005b) and Mège et al. (2015) and the four loci exclusively used in Porto-Hannes et al. (2015).
593 Therefore, to compare our estimates of genetic diversity to those found in the previous
594 published studies, the five common loci were kept to re-estimate previous indices (Online
595 Resource 6). This new computation indeed increased the estimated genetic diversity per site of
596 the present study (mean H_E = 0.71), though it remained globally lower than those published in
597 similar *A. palmata* studies. When comparing our genetic diversity estimates with those available
598 for the western lineage only, we found that estimates in Guadeloupe (mean H_E = 0.73 overall
599 sites) were similar to those previously reported for this same island [H_E = 0.74 in Mège et al.
600 (2015)], but for St. Vincent and the Grenadines (SVG), the genetic diversity (H_E = 0.65) was
601 slightly lower than those reported by Baums et al. (2005b) (H_E = 0.69). This difference may
602 partially be explained by the monoclonal site PAC09 on Duvernette Island, south St. Vincent
603 (H_E = 0.40 for PAC09 with the five common loci). Lower levels observed in the Lesser Antilles
604 when compared to other Caribbean reefs, and even reefs off the Venezuelan coast (Baums et al.
605 2005b; Mège et al. 2015, Porto-Hannes et al. 2015) may be of particular concern for the
606 resilience capacity of particular *A. palmata* populations in case of eventual disturbances, given
607 their location at the eastern boundary of the Caribbean Sea and their genetic isolation from the
608 west lineage. Nevertheless, the genetic diversity is not the only factor to take into account to
609 predict population resilience ability. Indeed, reproduction modes and recruitment are also
610 critical (Ayre and Hughes 2000; Knowlton 2001).
611 *Acropora palmata* is a broadcast-spawning coral species. During massive reproductive events,
612 the probability of gametes meeting in open-ocean is enhanced by high densities of gametes
613 synchronically released by a high number of colonies. Since *A. palmata* is an obligate outcrosser,
614 the production of larvae issued from sexual reproduction is only possible after fertilization
615 between gametes produced by genetically distinct colonies (Fukami et al. 2003; Baums et al.

2005a). Therefore, since efficient recruitment of larvae issued from sexual reproduction enhances population genetic diversity, lower diversity levels may be related to a deficit in sexually produced recruits linked with unfavourable conditions. Indeed, it has been shown that recovery of *A. palmata* populations from larval recruitment issued from sexual reproduction may be limited following environmental perturbations (Quinn and Kojis 2005; Bouchon et al. 2008; Williams et al. 2008).

In a recent study, Miller et al. (2016) reported that different genotypes of a single *A. palmata* population did not participate synchronically to the reproduction event, or even systematically every year. Therefore, because small colonies were not targeted during our sampling in order to avoid oversampling clones, low levels of genetic diversity may result from a bias linked to our sampling strategy. Indeed, the genetic diversity estimates from our sampled coral colonies may rather reflect genetic diversity levels from past recruitment events, e.g. the last years or decades, than current levels from integrated generations. Without stress events, a coral colony may live for decades or centuries, but because of branch breakage and regrowth, estimating the age of a coral colony (i.e. physical individual) from its size remains hazardous. Therefore, it is difficult to evaluate at which point the observed results obtained from potential relict colonies truly reflect the current situation. In conclusion, estimating genetic diversity could not be sufficient to predict resilience of *A. palmata* populations of the Lesser Antilles without taking into account sexual reproduction and larval recruitment. An examination of the genetic diversity within recruits is therefore warranted.

Isolation-by-distance and limited larval dispersal

Previous studies using five microsatellite loci showed that the Caribbean *A. palmata* population was genetically divided into two distinct lineages, with the northern break found around the Puerto Rican region (Baums et al. 2005b, 2006b, a; Mège et al. 2015). Therefore, considering the location of the Lesser Antilles, we hypothesized that the populations of the 11 sampled islands in the present study belong to the eastern phylogeographic lineage. This was confirmed here since we did not identify distinct genetic clusters among the *A. palmata* populations analysed.

644 Nevertheless, a significant genetic structure was found among *A. palmata* sampled populations,
645 revealing, for the first time, a pattern in agreement with the geographical seascape. Indeed, it
646 was found that *A. palmata* gene flow in the Lesser Antilles was oriented along a north-south axis,
647 with increasing genetic divergence related to increasing geographic distance among islands. This
648 IBD pattern was identified both at the reef scale (since individuals within short distance classes
649 up to 192 km were significantly more related than between distance classes), and at the Antilles
650 Arc scale, among geographically isolated populations. Though such IBD has already been found
651 in *A. palmata*, it was restricted to the Puerto Rican sea shore and attributed to a genetic
652 admixture zone between western and eastern lineages (Mège et al. 2014). Within each lineage,
653 no IBD pattern were reported among *A. palmata* populations in previous studies for which the
654 sampling scheme allowed to test for an IBD at a local scale. Indeed, within the western lineage,
655 the weak genetic differentiation observed along the Mesoamerican Barrier Reef System was not
656 related to geographic distances among sampling sites (Porto-Hannes et al. 2015), and within the
657 eastern lineage, the three sampled populations of Culebra (north Puerto Rico), Guadeloupe and
658 Curaçao were not found to be significantly differentiated (Mège et al. 2014).
659 The specific geographic context of the Lesser Antilles archipelago, with small islands more or
660 less regularly spaced from each other by few kilometers and further aligned along a north-south
661 axis likely explains the observed IBD among *A. palmata* populations. An IBD pattern usually
662 characterizes populations with limited connectivity across different suitable habitat patches,
663 reflecting gene flow occurring in a stepping-stone model. That is already known in several corals
664 and other marine species, with limited larvae dispersal, studied among fragmented habitat
665 patches (Palumbi 2003; Cowen et al. 2006; Galindo et al. 2006; Hellberg 2007; Andras et al.
666 2013; Postaire et al. 2017). Indeed, for marine sessile species like corals, gene flow among
667 populations depends on the first living stages of these organisms, mostly insured by
668 reproductive outputs (gametes), fertilized eggs and pelagic larvae. In *A. palmata*, the larval
669 pelagic phase is recognized as relatively short since *Acropora* larvae are competent to settle 3 to
670 5 days after fertilization (Fogarty 2010, 2012). With a larval phase of 4-5 days, the potential of
671 dispersal for Caribbean *Acropora* pelagic larvae has been estimated to several tens of kilometres

(Baums et al. 2005; Hemond and Vollmer 2010; Drury et al. 2018), with possible local retention up to 47.5% on specific reefs (Drury et al. 2018). Nevertheless, it has been shown that, depending on the environmental constraining conditions, the pelagic phase for *A. palmata* larvae may last up to 20 days (Harrison and Wallace 1990; Hayashibara et al. 1993; Baums et al. 2005b; Hemond and Vollmer 2010; Ritson-Williams et al. 2010), suggesting a higher dispersal potential. Although our estimates of σ, half the mean square parent-offspring distance, vary giving the value of the effective population density (*De*) used for the computations (between 70 m to *ca*. 1 km), our results suggest that gene dispersal is highly restricted by geographic distances, which confirm that the capacity of dispersal among *A. palmata* populations of the Lesser Antilles islands is likely very limited. Yet, this dispersal kernel is likely facilitated by oceanic sea surface currents (Heck and McCoy 1978; Veron 1995), which show a dominant north-west direction during *A. palmata* spawning period (Online Resource 7). Indeed, even if a significant northward gene flow along the Lesser Antilles could not be significantly demonstrated over the Lesser Antilles, 65% of the observed D_M estimates suggest a same direction for *A. palmata* gene flow and main oceanic sea surface currents. This finding still need further investigations, with additional samples originating from the southern Caribbean reefs. If confirmed, it would imply that southern reefs act as source of gametes and larvae to the Lesser Antilles, an hypothesis also suggested by (Baums et al. 2005b).

Consequences for resilience and conservation of endangered *Acropora palmata* populations in the Lesser Antilles

Globally, the present results reveal that the genetic diversity of *A. palmata* populations of the Lesser Antilles is lower than previously estimated for *A. palmata* populations of the Caribbean region. This is of great concern since lower genetic diversity may reduce the resilience ability against environmental perturbations (Reush et al. 2005). Additionally, observed northward gene flow through the Lesser Antilles archipelago, together with the southern known boundary of the eastern *A. palmata* lineage (Baums et al. 2005b; Mège et al. 2014) suggest that populations from the southernmost islands of the Lesser Antilles (likely including Grenada, Trinidad and Tobago

and the Leeward Antilles), and those of the north coast of South America (at least Venezuela), have a potential key role in broadcasting larvae to the more northern islands of the Lesser Antilles. If confirmed, preserving these southernmost *A. palmata* populations should be a priority, especially since the southern populations analyzed in our study (St Vincent, Union and Bequia) showed the smallest allelic richness estimates, together with Antigua. Yet, because of the heterogeneous societal and institutional situation of the Lesser Antilles, conservation aspects to protect *A. palmata* at a regional scale may be difficult to implement.

Promoting genetic diversity through a high genotypic diversity seems to be the basis for viable and sustainable restoration projects of coral populations. In the Lesser Antilles, as well as in other parts of the Caribbean Sea, a great number of restoration projects for *A. palmata* populations have been undertaken in the last decades, mainly through the transplantation of colonies issued from fragments (Young et al. 2012; Lirman et al. 2014). As discussed above, it is crucial to insure genotypic diversity within these restored fragments. In this context, other restoration projects were carried out by transplanting colonies issued from sexual reproduction after gametes collection in natural populations (Chamberland et al. 2015). Nevertheless, this strategy requires a preliminary evaluation of potential source populations of gametes.

As genotypic richness is negatively correlated with colony density (Baums et al. 2006a), denser *A. palmata* populations, likely composed of numerous clones, may not represent the best sources of gametes. On the opposite, scattered populations may exhibit higher genotypic richness, although producing less gametes. Knowing this trade-off, a high density of colonies in a population may not therefore be a sufficient criterion to select source populations of *A. palmata* gametes and fragments for transplantation.

Additionally, we showed that the genetic structure of *A. palmata* populations of the Lesser Antilles exhibit an isolation-by-distance pattern, both at the reef scale among individuals and at the Antilles Arc scale (sampling extending over c.a. 1,000 km) among geographically isolated populations. Thus, the hypothesis of genetic adaptation of *A. palmata* colonies to local and specific environmental conditions, even at limited spatial scale, may not be ruled out (Devlin-Durante and Baums 2017). In this context, enhancing genetic diversity of reefs through the

transplantation of fragments issued from distant genetically differentiated populations may not be suitable if source populations are not fully adapted to the local environmental conditions of the transplantation sites (Baums 2008; Devlin-Durante and Baums 2017). Therefore, special attention must be paid to the selection of the source populations for collecting fragments or gametes for coral reef restoration projects, not only regarding the density of coral colonies and their genotypic richness but also regarding the genetic divergence between the source population and that of the transplantation site.

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977

978 **Figure captions**

979 **Figure 1** Studied area and location of the 36 studied *Acropora palmata* stands (black dots). A:
980 location of the Lesser Antilles within the Caribbean Sea, B: sampling locations in the Lesser
981 Antilles, C: sampling locations in Guadeloupe Island

982 **Figure 2** Correspondence analysis representing individual *Acropora* colonies based on their
983 genotypes obtained from the analysis of 14 microsatellite loci. Grey circles represent colonies
984 morphologically identified as *A. prolifera* (Japaud et al. 2014), grey squares show colonies with
985 percentage of membership to *A. palmata* cluster of less than 73% and grey triangles show three
986 additional colonies removed based on their close vicinity to *A. prolifera* MLGs on the
987 correspondence analysis. Black circles represent *A. cervicornis* and white circles *A. palmata*
988 colonies kept for all analyses.

989 **Figure 3** Sexual dynamics of 36 sampled *Acropora palmata* stands in the Lesser Antilles,
990 analysed using 14 microsatellite loci and derived from their clonal structure, based on the
991 combination of genotypic evenness (G_O/Ng) and genotypic diversity (G_O/G_E). Stands are divided
992 as in Baums et al. (2006a) into four categories ranging from asexual to sexual to facilitate further
993 discussion

994 **Figure 4** Relationship between genetic ($F_{ST}/1\text{-}F_{ST}$) and geographic (in km) distances estimated
995 among *Acropora palmata* sampling sites in the Lesser Antilles. A: all sampling sites (34 sites), B:
996 only sampling sites with N > 10 (27 sites), C: only sampled sites with N > 20 (11 sites), D: among
997 islands (i.e. pooling sampled sites per island).

998 **Figure 5** Principal Coordinates Analysis (PCoA) based on genetic similarities among sampled
999 island populations of *Acropora palmata*, estimated through the analysis of 13 microsatellite loci

1000 **Figure 6** Spatial autocorrelogram based on Loiselle's kinship coefficient estimated over all
1001 microsatellite loci but Apal1490, among all sampled *Acropora palmata* colonies. Solid line =
1002 observed values, Dotted lines = upper and lower limits of the 95% confidence interval of

1003 Loiselle's kinship coefficient, obtained through 10 000 permutations of the genotypes among

1004 distance classes

1005

Figure1

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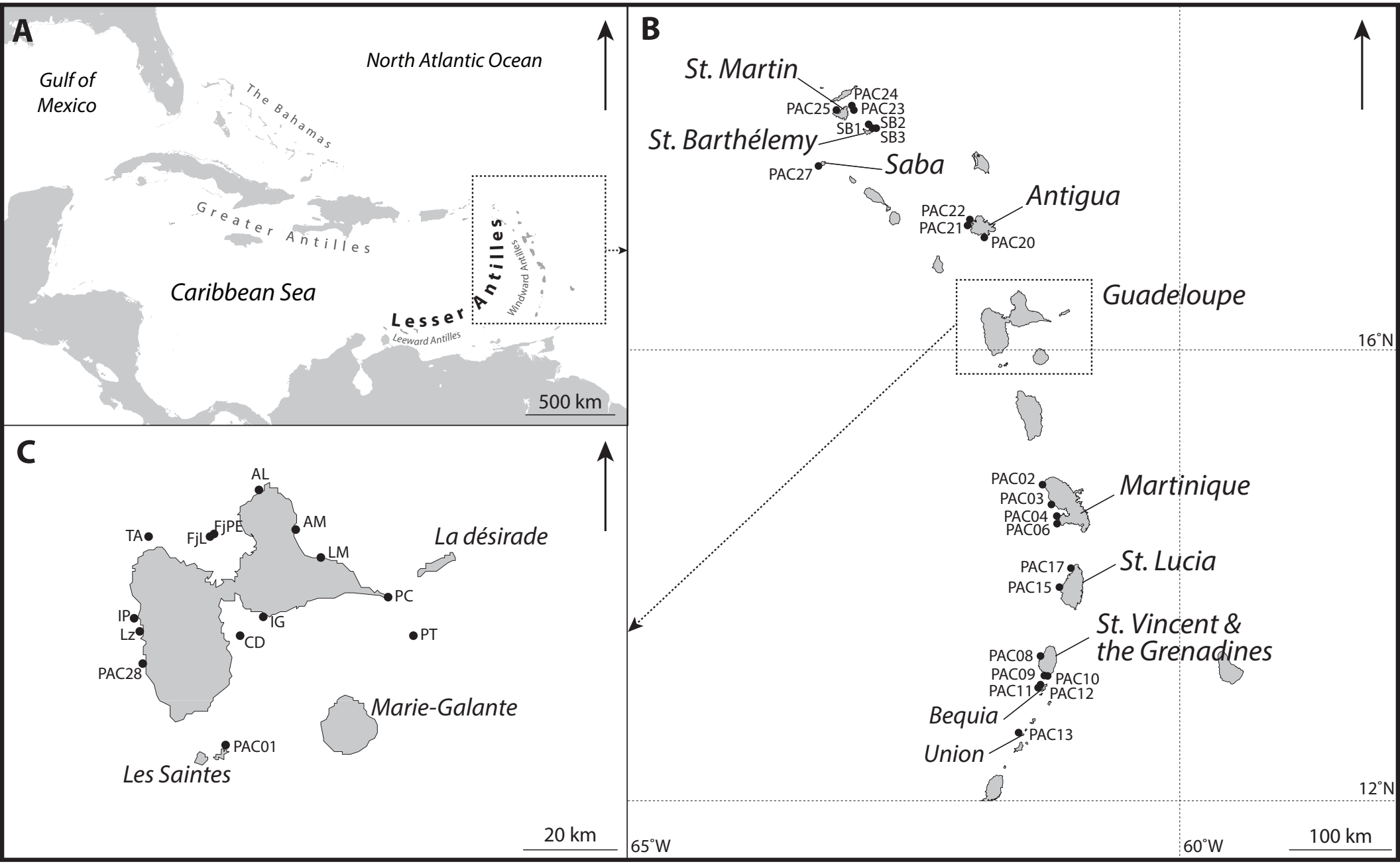
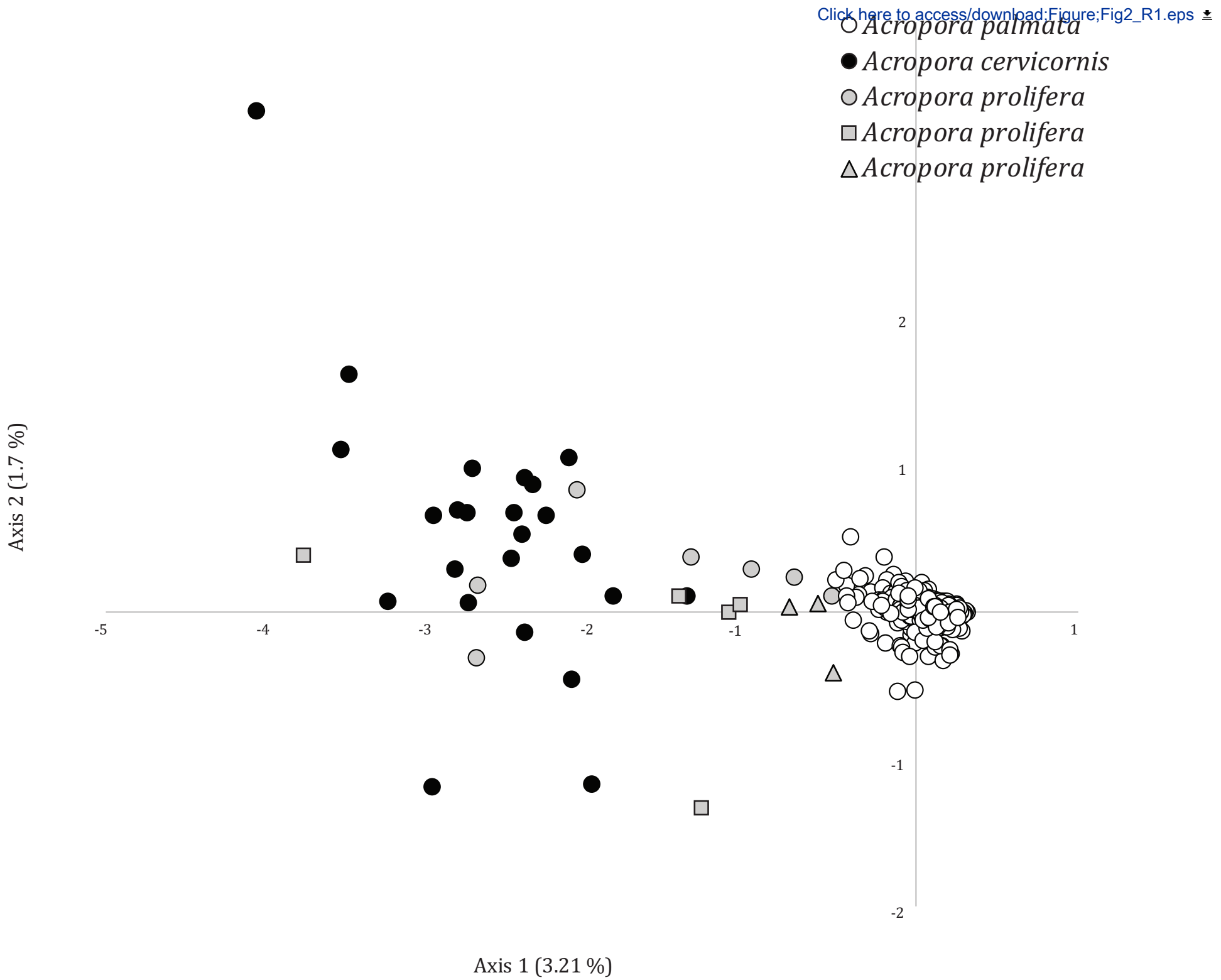


Figure2



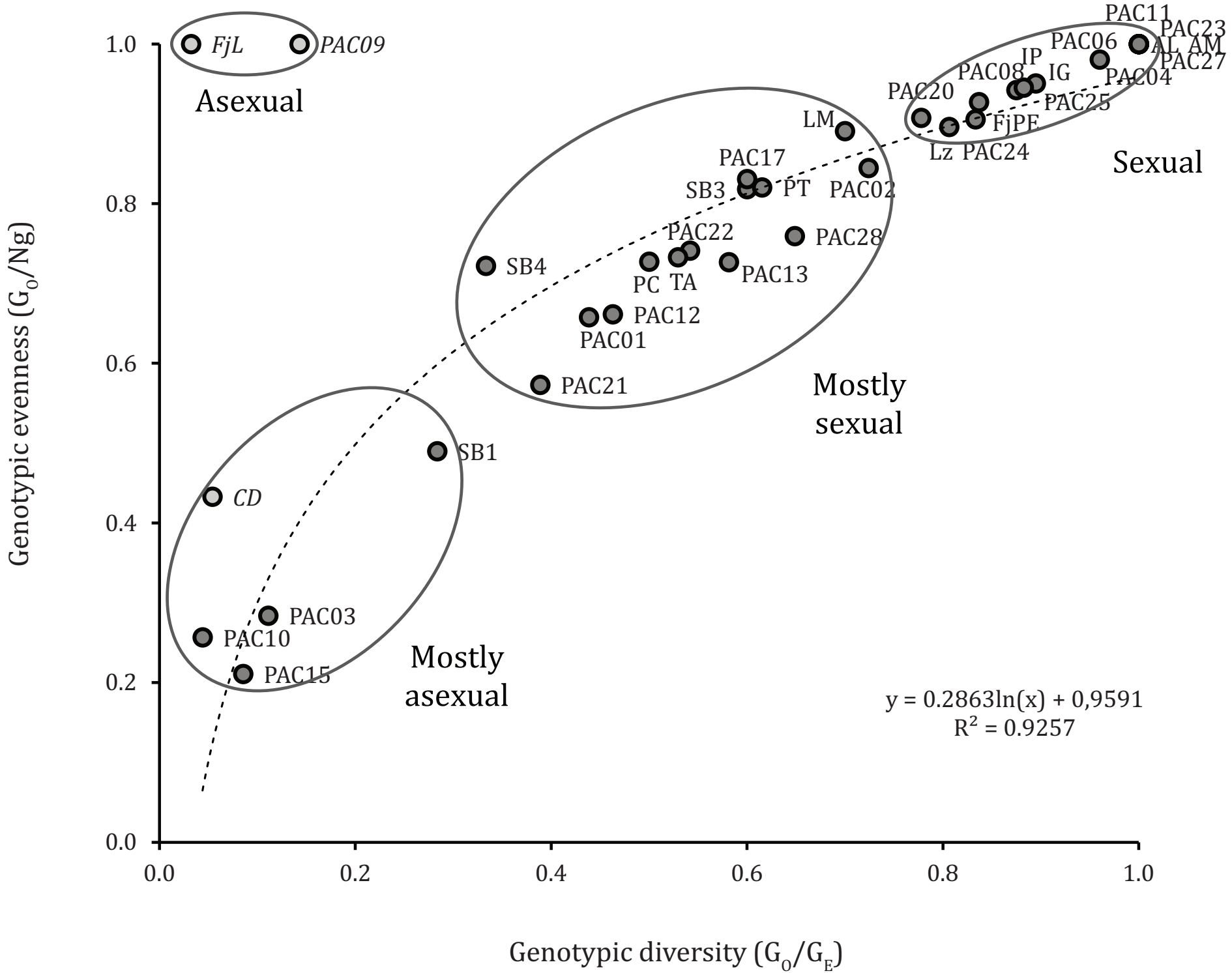


Figure4

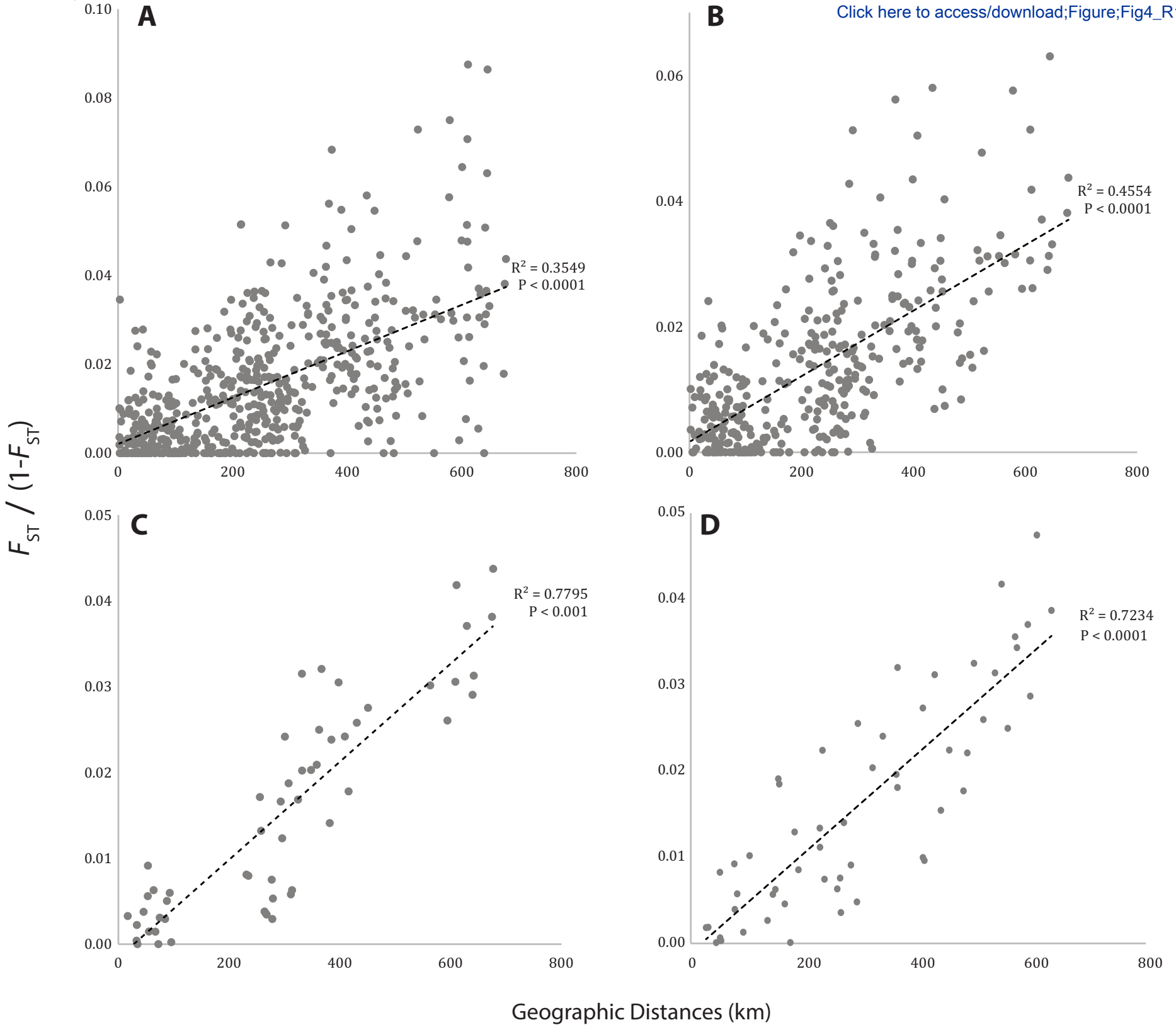


Figure5

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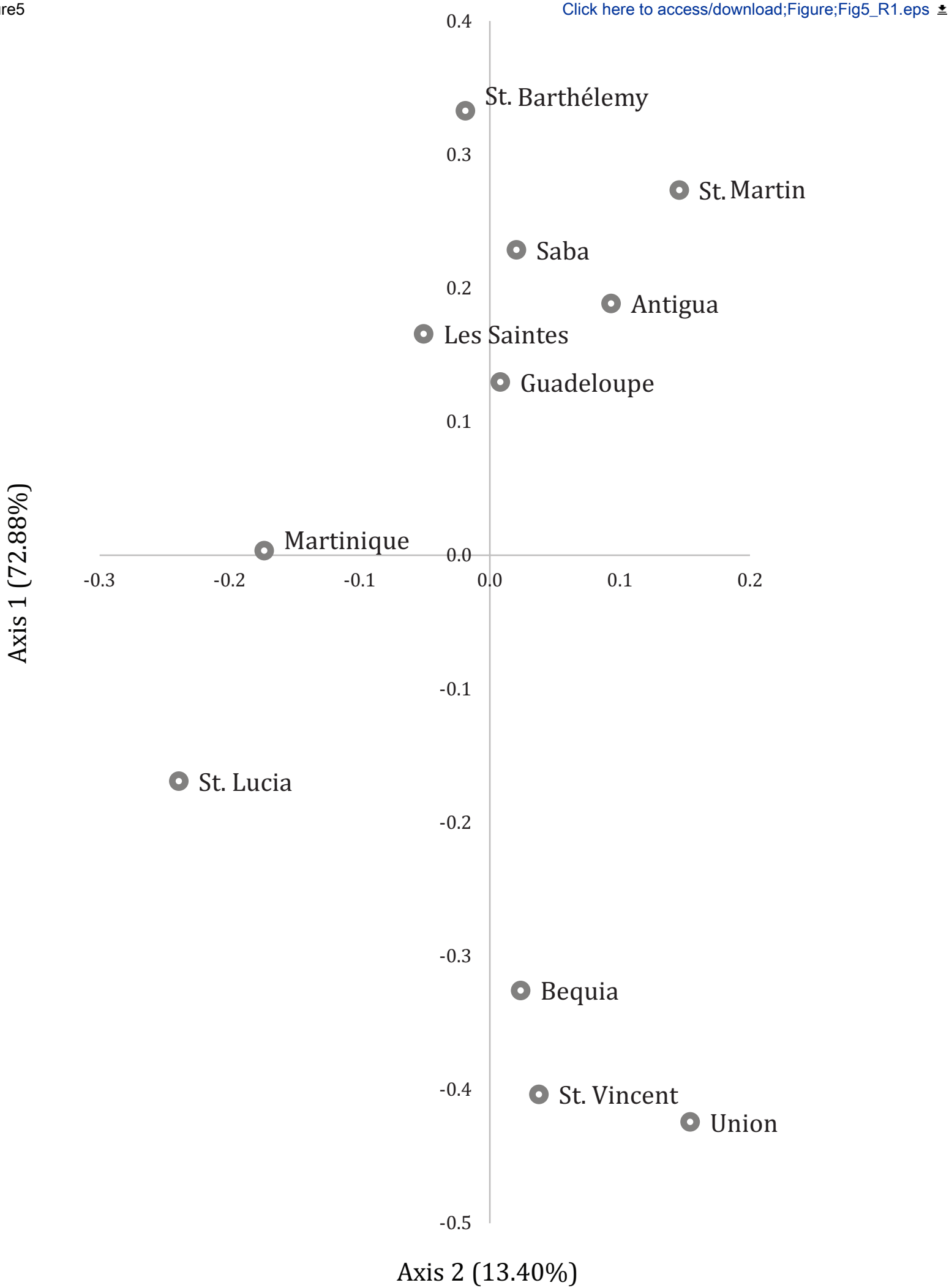

Figure6

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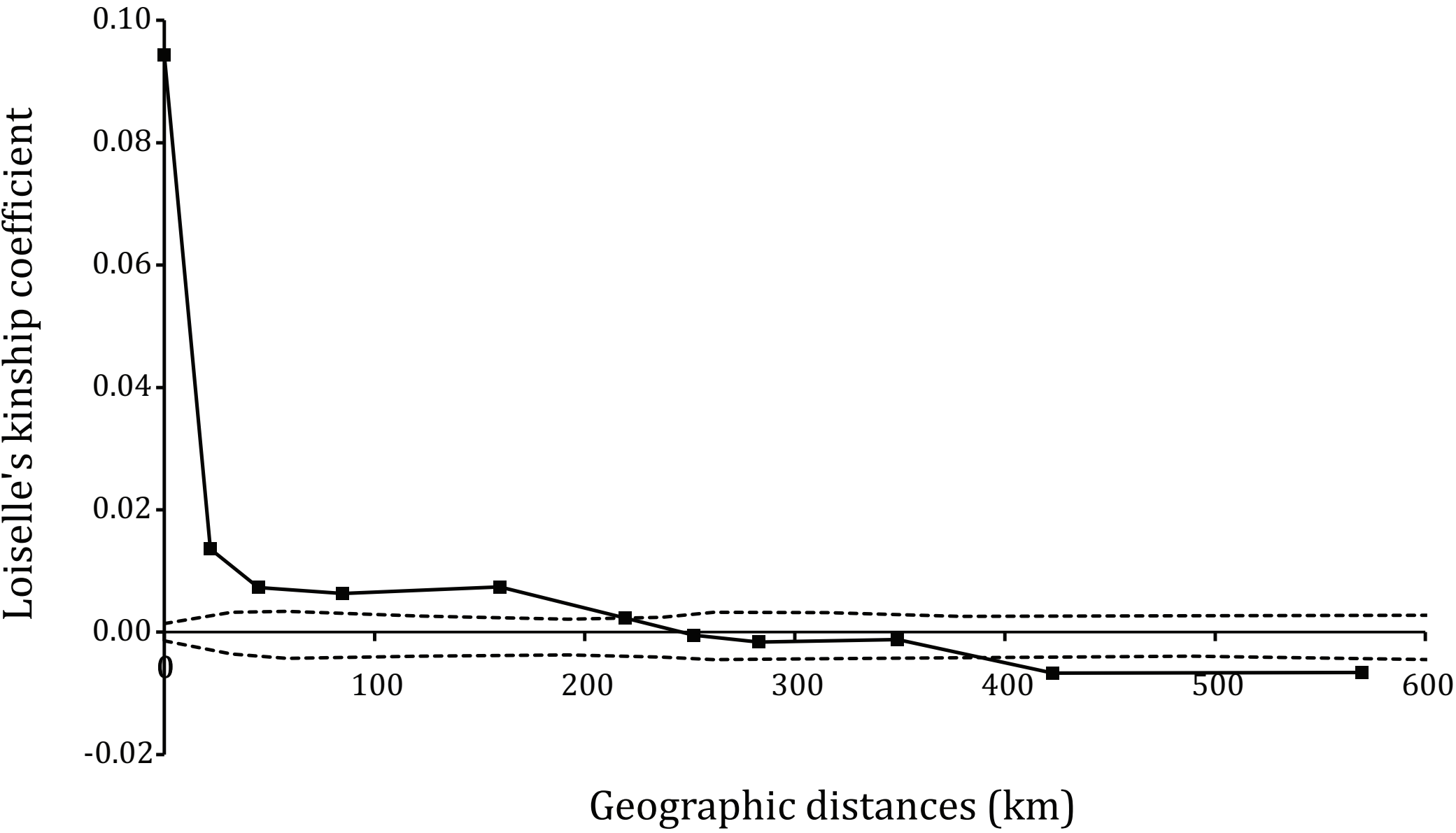

Table 1 Genetic diversity estimates in *Acropora palmata* stands sampled in the Lesser Antilles. *N*, Number of sampled colonies; *Ng*, Number of distinct multilocus genotypes (MLG); *Ng*/*N*, Genotypic richness; G_O, Observed genotypic diversity; G_O/G_E, Genotypic diversity with G_E, the expected genotypic diversity; G_O/Ng, Genotypic evenness; Cat, category in which each reef was classified based on the combination of Ng/N and G_O/G_E values: asexual (1), mostly asexual (2), mostly sexual (3), and sexual (4) (from Baums et al. 2006a) ; H_O, observed heterozygosity, H_E, unbiased expected heterozygosity; F_{IS}, inbreeding coefficient; AR: Allelic Richness.

Island and Site	Code	Latitude (N)	Longitude (W)	*N*	*Ng*	*Ng/N*	G_O	G_O/G_E	G_O/Ng	Cat	H_O	H_E	F_{IS}	AR
St. Martin	SM			**102**	**97**	**0.97 ± 0.02**	**30.58 ± 13.35**	**0.93 ± 0.05**	**0.96 ± 0.03**		**0.599 ± 0.005**	**0.675 ± 0.012**	**0.119 ± 0.031**	**115.9 ± 6.6**
Île Tintamarre I	PAC23	18°06'34''	62°58'51''	4	4	1.00	4.00	1.00	1.00	4	0.589	0.694	0.172	
Île Tintamarre II	PAC24	18°07'33''	62°58'21''	50	46	0.92	41.67	0.83	0.91	4	0.608	0.652	*0.067*	
Trou David	PAC25	18°04'24''	63°07'09''	48	47	0.98	46.08	0.96	0.98	4	0.601	0.680	*0.119*	
St. Barthélemy	SB			**47**	**28**	**0.59 ± 0.08**	**6.24 ± 1.41**	**0.41 ± 0.1**	**0.68 ± 0.1**		**0.606 ± 0.008**	**0.693 ± 0.004**	**0.115 ± 0.011**	**126.2 ± 18.4**
Anse de Grand Cul-de-Sac	SB1	17°54'46''	62°47'59''	19	11	0.58	5.39	0.28	0.49	2	0.615	0.696	0.107	
Îlet Frégate	SB3	17°56'22''	62°49'55''	15	11	0.73	9.00	0.60	0.82	3	0.590	0.698	0.137	
Pointe Milou	SB4	17°54'50''	62°49'04''	13	6	0.46	4.33	0.33	0.72	3	0.613	0.684	0.101	
Saba	Sa													**129.5**
Southeast coast	PAC27	17°37'04''	63°13'35''	39	39	1.00	39.00	1.00	1.00	4	0.621	0.720	*0.131*	
Antigua	An			**61**	**44**	**0.76 ± 0.05**	**10.14 ± 2.52**	**0.57 ± 0.12**	**0.74 ± 0.1**		**0.601 ± 0.026**	**0.667 ± 0.014**	**0.102 ± 0.026**	**102.1 ± 8.6**
Nanton Point	PAC20	16°59'52''	61°45'37''	7	6	0.86	5.44	0.78	0.91	4	0.552	0.640	0.148	
Five Islands	PAC21	17°04'53''	61°54'50''	28	19	0.68	10.89	0.39	0.57	3	0.610	0.680	0.099	
Shipstern Point	PAC22	17°07'46''	61°53'31''	26	19	0.73	14.08	0.54	0.74	3	0.642	0.682	0.058	
Guadeloupe	Gu			**395**	**256**	**0.79 ± 0.08**	**17.86 ± 3.5**	**0.71 ± 0.08**	**0.89 ± 0.03**		**0.655 ± 0.010**	**0.692 ± 0.012**	**0.053 ± 0.01**	**137 ± 7.4**
Anse à la Barque	PAC28	16°05'16''	61°46'14''	48	41	0.85	31.14	0.65	0.76	3	0.672	0.710	*0.123*	
Anse Laborde	AL	16°29'11''	61°29'50''	12	12	1.00	12.00	1.00	1.00	4	0.687	0.714	0.044	
Anse Maurice	AM	16°23'38''	61°24'13''	18	18	1.00	18.00	1.00	1.00	4	0.663	0.689	0.029	
Îlet Fajou I	FjL	16°21'16''	61°34'21''	31	1	0.03	1.00	0.03	1.00	1	0.571	0.571	NA	
Îlet Fajou II	FjPE	16°21'35''	61°35'32''	42	39	0.93	36.75	0.88	0.94	4	0.683	0.718	*0.037*	
Îlet Gosier	IG	16°11'60''	61°29'20''	17	16	0.94	15.21	0.89	0.95	4	0.672	0.707	*0.092*	

Îlets de Pigeon	IP	16°10'00''	61°47'24''	15	14	0.93	13.24	0.88	0.95	4	0.693	0.742	0.041	
Le Moule	LM	16°20'05''	61°20'30''	14	11	0.79	9.80	0.70	0.89	3	0.655	0.690	-0.001	
Pointe à Lézard	Lz	16°08'29''	61°46'47''	50	45	0.90	40.32	0.81	0.90	4	0.603	0.680	0.052	
Pointe des Châteaux	PC	16°15'00''	61°10'50''	16	11	0.69	8.00	0.50	0.73	3	0.658	0.718	0.084	
Îles de la Petite Terre	PT	16°10'36''	61°06'17''	16	12	0.75	9.85	0.62	0.82	3	0.635	0.647	0.018	
Tête à l'Anglais	TA	16°22'54''	61°45'50''	36	26	0.72	19.06	0.53	0.73	3	0.647	0.693	0.069	
*Caye à Dupont**	*CD*	*16°09'26''*	*61°32'33''*	*80*	*10*	*0.13*	*4.33*	*0.05*	*0.43*	*2*	*0.679*	*0.718*	*0.064*	
Les Saintes	LS													**124**
Pointe Zozio	PAC01	15°52'60''	61°34'15''	75	50	0.67	32.89	0.44	0.66	3	0.577	0.673	*0.123*	
Martinique	Ma			**70**	**53**	**0.81 ± 0.15**	**10.94 ± 3.76**	**0.71 ± 0.21**	**0.71 ± 0.17**		**0.626 ± 0.015**	**0.705 ± 0.005**	**0.103 ± 0.02**	**133.7 ± 16.8**
Caye de la Perle	PAC02	14°50'27''	61°13'31''	21	18	0.86	15.21	0.72	0.84	3	0.584	0.708	*0.161*	
Les Roches Rouges	PAC03	14°38'15''	61°08'21''	23	9	0.39	2.56	0.11	0.28	2	0.657	0.717	0.072	
Îlet Ramier	PAC04	14°32'40''	61°04'50''	7	7	1.00	7.00	1.00	1.00	4	0.626	0.700	0.096	
Pointe Burgos	PAC06	14°29'28''	61°05'20''	19	19	1.00	19.00	1.00	1.00	4	0.638	0.695	*0.084*	
St. Lucia	SL			**60**	**30**	**0.56 ± 0.16**	**7.19 ± 3.61**	**0.34 ± 0.25**	**0.52 ± 0.31**		**0.599 ± 0.007**	**0.693 ± 0.006**	**0.123 ± 0.011**	**126.8 ± 4.6**
Jambette Point	PAC15	13°51'39''	61°04'28''	42	17	0.40	3.59	0.09	0.21	2	0.593	0.699	*0.133*	
Pigeon Island	PAC17	14°05'31''	60°58'05''	18	13	0.72	10.80	0.60	0.83	3	0.606	0.687	*0.112*	
St Vincent	SV			**83**	**44**	**0.41 ± 0.25**	**12.28 ± 11.02**	**0.34 ± 0.25**	**0.73 ± 0.24**		**0.553 ± 0.031**	**0.618 ± 0.027**	**0.156 ± 0.048**	**106.9 ± 5.7**
Châteaubelair Island	PAC08	13°17'58''	61°14'54''	41	37	0.90	34.31	0.84	0.93	4	0.596	0.666	*0.096*	
Duvernette Island	PAC09	13°07'36''	61°12'29''	7	1	0.14	1.00	0.14	1.00	1	0.571	0.571	NA	
Blue Lagoon	PAC10	13°07'33''	61°11'40''	35	6	0.17	1.54	0.04	0.26	2	0.493	0.616	0.215	
Bequia	Be			**52**	**37**	**0.85 ± 0.15**	**12.57 ± 10.57**	**0.73 ± 0.27**	**0.83 ± 0.17**		**0.663 ± 0.051**	**0.704 ± 0.023**	**0.061 ± 0.037**	**105.2**
Ships Stern	PAC11	12°59'43''	61°16'29''	2	2	1.00	2.00	1.00	1.00	4	0.714	0.726	0.024	
Wash Rock	PAC12	13°00'44''	61°14'59''	50	35	0.70	23.15	0.46	0.66	3	0.611	0.681	*0.098*	
Union	Un													
Rapid Point	PAC13	12°36'43''	61°27'08''	50	40	0.80	29.07	0.58	0.73	3	0.625	0.657	*0.041*	**106.1**
Total				**1034**	**718**	**0.75 ± 0.04**	**16.47 ± 2.29**	**0.64 ± 0.05**	**0.79 ± 0.04**		**0.624 ± 0.008**	**0.684 ± 0.006**	**0.09 ± 0.008**	**125.6 ± 4.1**

Table 2 Pairwise genetic (lower as pairwise-F_{ST}) and geographic distance (upper, in km) matrices among islands. Pairwise-F_{ST} were estimated using the ENA method provided in FREENA software. Significant pairwise-F_{ST} are indicated in bold (the H_0 hypothesis F_{ST} =0 was rejected if the 95% confidence interval obtained through bootstrap resampling over loci did not include zero)

		SM	**SB**	**Sa**	**An**	**Gu**	**LS**	**Ma**	**SL**	**SV**	**Be**	**Un**
St. Martin	**SM**	0	31	53	175	257	292	440	514	573	597	634
St. Barthélemy	**SB**	0.002	0	52	144	227	263	411	486	546	570	608
Saba	**Sa**	0.000	0.001	0	165	235	264	408	479	535	557	592
Antigua	**An**	0.000	0.006	0.005	0	92	135	281	361	429	454	498
Guadeloupe	**Gu**	**0.006**	**0.011**	**0.007**	0.001	0	45	189	269	337	363	408
Les Saintes	**LS**	0.005	0.008	0.004	0.003	0.000	0	149	227	294	319	364
Martinique	**Ma**	**0.015**	**0.010**	**0.010**	**0.009**	**0.008**	0.006	0	82	156	182	231
St. Lucia	**SL**	**0.025**	**0.022**	**0.017**	**0.019**	**0.014**	**0.013**	0.006	0	77	103	154
St. Vincent	**SV**	**0.033**	**0.040**	**0.030**	**0.030**	**0.024**	**0.025**	**0.018**	0.009	0	27	77
Bequia	**Be**	**0.028**	**0.034**	**0.024**	**0.022**	**0.018**	**0.020**	**0.013**	**0.010**	0.002	0	51
Union	**Un**	**0.037**	**0.045**	**0.036**	**0.032**	**0.027**	**0.031**	**0.022**	**0.019**	0.004	**0.008**	0

Table 3 Estimated direction of gene flow in *A. palmata* along the Lesser Antilles. Lower matrix: relative directional migration coefficients among islands, based on the Jost's D index (D_M) (significant relative coefficient indicated in bold). Upper matrix: schematic representation of the relative directional migration coefficients: positive values indicate northward gene flow and are represented as ▲ (n = 36), negative values indicate southward gene flow and are represented as ▼ (n = 19)

		SM	SB	Sa	An	Gu	LS	Ma	SL	SV	Be	Un
St. Martin	**SM**		▼	▼	▲	▼	▲	▼	▼	▲	▲	▲
St. Barthélemy	**SB**	-0.019		▼	▲	▼	▲	▼	▼	▲	▲	▲
Saba	**Sa**	-0.163	-0.063		▲	▲	▲	▼	▼	▲	▲	▲
Antigua	**An**	0.024	0.039	0.222		▼	▲	▼	▼	▲	▲	▲
Guadeloupe	**Gu**	-0.194	-0.035	0.011	-0.465		▲	▲	▼	▲	▲	▲
Les Saintes	**LS**	0.209	0.006	0.138	0.102	0.402		▼	▼	▲	▲	▲
Martinique	**Ma**	-0.086	-0.065	-0.058	-0.102	0.052	-0.114		▲	▲	▲	▲
St. Lucia	**SL**	-0.055	-0.035	-0.076	-0.041	-0.048	-0.085	0.074		▲	▲	▲
St. Vincent	**SV**	0.028	0.009	0.122	0.073	0.238	0.208	0.219	0.207		▼	▲
Bequia	**Be**	0.008	0.006	0.051	0.060	0.147	0.085	0.139	0.047	-0.009		▼
Union	**Un**	0.081	0.036	0.135	0.100	**0.165**	0.111	0.134	0.065	0.084	-0.001	