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A potential invasion route of *Cactoblastis cactorum* within the Caribbean region matches historical hurricane trajectories

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Abstract The cactus moth, *Cactoblastis cactorum* mainly distributed throughout central and northeastern Argentina was intentionally introduced in the Caribbean region in 1957 as a biological control agent of cacti species of the genus *Opuntia*. This moth invaded during the last 20–30 years the North American continent, threatening the major center of biodiversity of native *Opuntia* species. Although human induced and natural dispersal have been invoked to explain its expansion in the non-native distribution range, there is still no evidence to support natural dispersal. In particular, hurricanes are one of the major environmental factors affecting species dispersal in the region. In this study we used mitochondrial DNA to examine

whether the spatial distribution of haplotype variation of *C. cactorum* is at least partially explained by hurricane trajectories within the Caribbean region. DNA sequences for the mitochondrial gene cytochrome oxidase I were obtained for a sample of 110 individuals from the Antillean islands. This information was combined with existing sequences in the GenBank for the same gene for the Caribbean and Florida (N = 132 sequences). Genetic diversity descriptors, a haplotypic network, a spatial analyses of molecular variance and a landscape genetic analysis of migration conditioned by hurricane tracks were conducted to test our hypothesis. Our results revealed a significant spatial grouping of haplotypes consistent with the more frequent hurricane trajectories in the Caribbean region. Significant isolation by distance conditioned by hurricane tracks was detected. Populations of Florida were genetically closer to those of Cuba than to the rest of the population sampled. Within the region, Cuba appears as a reservoir of genetic diversity increasing the risk of invasion to

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Mexico and the US. Despite commercial transportation of *Opuntia* promoted dispersal to Florida, our results support the hypothesis that natural disturbances such as hurricanes played a role dispersing this invasive insect. Future conservation programs of North American *Opuntia* species requires taking into account hurricane mediated dispersal events and permanent whole regional monitoring and international control policies to prevent future range expansions of *C. cactorum*.

Keywords Cytochrome oxidase I · Biological invasions · Cactus moth · *Cactoblastis cactorum* · Dispersal · Phylogeography

Introduction

Biological invasions are currently one of the major threats to biodiversity worldwide (Vitousek et al. 1996; Alonso et al. 2001; Richardson 2011), and identifying the factors that explain dispersal patterns of invasive species within non-native regions becomes a central issue for conservation biology, emergence of novel diseases and eradication programs (Abdelkrim et al. 2007; Estoup and Guillemaud, 2010). Invasive species arrive to non-native habitats following human commercial routes, deliberated or unconscious human mediated introductions, or through the breakdown of historical barrier to dispersal due to climate changes (Cadotte et al. 2006; Nentwig 2007; Richardson 2011). After establishment, dispersal of invasive species within their non-native range depends on the interaction among anthropogenic, physical and biotic factors (Sakai et al. 2001; Levine et al. 2004) and understanding the role of contemporary ecological–environmental factors as dispersal agents or as barriers to migration within non-native habitats is one of the central challenges to control invasive species (Estoup and Guillemaud 2010; Lombaert et al. 2011; Boucher et al. 2013; Richardson 2011).

The cactus moth, *Cactoblastis cactorum*, inhabiting Uruguay, Paraguay, central and northeastern Argentina, and south of Brasil (Heinrich 1939), is an oligophagous herbivore of several cacti species within the subfamily Opuntioidea including most of the species of the genus *Opuntia* (Zimmermann et al. 2007). Out of its native range it can also consume

species of the genus *Cylindropuntia* and *Consolea* (Zimmermann et al. 2007). Driven by biological control policies, this moth was introduced in Australia in 1926 to control the demographic expansion of alien *O. stricta* populations that had negative effects on crop and livestock production (Julien and Griffiths 1998). Given the success of this biological agent, it was subsequently introduced to South Africa (1933), New Caledonia (1933), and Hawaii (1950) (Zimmermann and Pérez-Sandi 2006; Zimmermann et al. 2007) to control *O. ficus-indica* and other invasive *Opuntia* species. Larvae from this moth intentionally arrived to the Caribbean in 1957 promoted by human efforts to control weedy native populations of *Opuntia* in the island of Nevis (Bennett and Habeck 1995). This occurred without taking into account the negative side effects of introducing invasive alien species to control native species (Louda et al. 2003). Dispersal within the Caribbean may have presumably occurred by explicit human induced introductions in other islands (US Virgin Islands, Antigua, Montserrat), incidental transportation with ornamental cacti (Pemberton 1995) and/or by natural factors like hurricanes and tropical storms (Drake and Farrow 1988; Torres 1992; Courtenay 1995; Stiling 2002; Pratt et al. 2006; Zimmermann et al. 2007). During the late 1980s, this invasive species arrived to Florida where it started an aggressive expansion favored by the presence of available host species throughout the southeastern United States (Habeck and Bennet 1990). To date, the cactus moth has expanded northward to Bull Islands (South Carolina) through the Atlantic coast of US and through the Gulf of Mexico coast reaching Terrebonne Parish (Louisiana; Rose et al. 2011). In 2007, the species was detected in Isla Mujeres (México), 6 km offshore from the Yucatán Peninsula (NAPPO 2006) but was rapidly eliminated by Mexican environmental authorities (Zimmermann et al. 2007). In contrast to other parts of the world invaded by *Opuntia*, there is a high risk of losing cacti biodiversity within the Americas (see Jezorek et al. 2012). Thus understanding the causal agents of dispersal behind the expansion of this invasive insect in the Caribbean region remains a central issue for conservation of cacti biodiversity (Johnson and Stiling 1998; Zimmermann et al. 2004).

Previous genetic studies suggest that at least three independent introductions of this moth in Florida (Simonsen et al. 2008; Marsico et al. 2011) are likely related to commercial transportation of ornamental

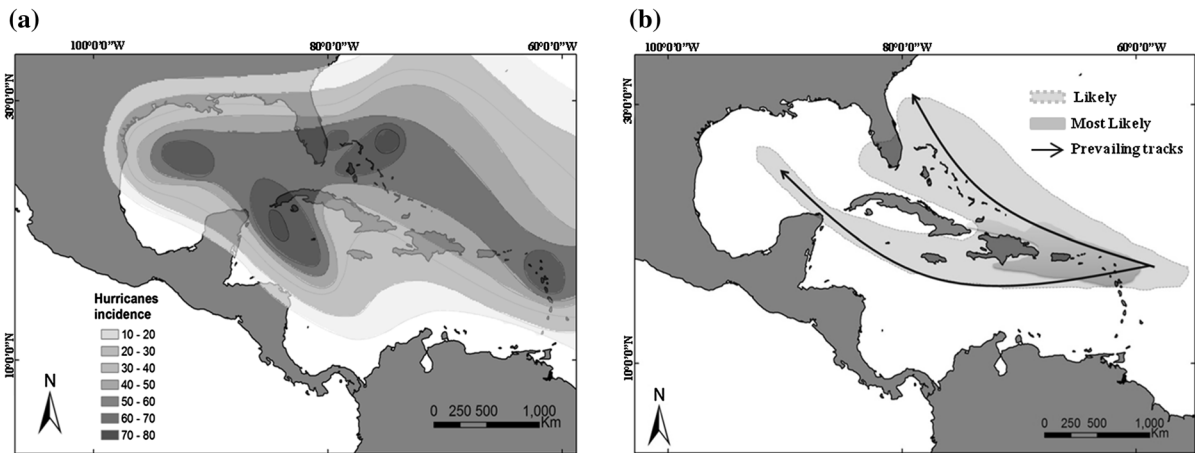


Fig. 1 Spatial distribution of hurricane frequency in the Caribbean region. **a** Values of isopleths represent the frequency of hurricanes that hit a given area between 1871 and 1986 (figure taken from Lugo et al. 2000). **b** Prevailing hurricane tracks for

July and August in Caribbean and Atlantic Ocean area following Landsea (1993), Landsea et al. (1996) and NOAA (<http://www.nhc.noaa.gov/climo/>)

cacti from Puerto Rico and Rep. Dominicana between 1981 and 1993, highlighting the role of human mediated dispersal (Pemberton 1995; Zimmermann et al. 2000a, b). However, because there has been no direct examination of the potential role of natural dispersal towards continental areas in North America, this hypothesis cannot be ruled out (Johnson and Stiling 1998).

In other regions, invasive insects are known to be favored by warm winds promoting dispersal (Grapputo et al. 2005; Dudaniec et al. 2008). In Isla Mujeres (7 km from the Yucatán Peninsula in Mexico), the arrival of the moth was associated with the occurrence of hurricane Stan in 2005 (Zimmermann and Pérez-Sandi 2006). Parallel to their devastating environmental consequences (Lugo et al. 2000; Chazdon 2003), hurricanes in the Caribbean are known to reduce population size in several species exposing them to genetic bottlenecks (Hurtado et al. 2012; Szczys et al. 2012; but see Vega et al. 2007), and to promote dispersal among isolated islands (Fleming and Murray 2009). Within the Caribbean region, the historical records of winds and hurricanes indicate a consistent spatio-temporal pattern (Landsea 1993; Landsea et al. 1996; Lugo et al. 2000; Muscarella et al. 2011) characterized by two major east–west trajectories (Fig. 1). One that enters the Gulf of Mexico and a second trajectory that passes through the Bahama’s archipelago reaching the Atlantic coast of Florida (Landsea 1993; Landsea et al. 1996; Lugo et al. 2000).

If these two major patterns of winds and hurricane promoted *C. cactorum* dispersal to the continent, at least two sources of invasion matching the geographic patterns of this environmental agent should be observed. In turn, such a pattern could also explain the presence in Florida of two genetically different groups of haplotypes recorded in previous studies, one on the Gulf coast of Florida and the other on the Atlantic coast (Simonsen et al. 2008; Marsico et al. 2011). On the other hand, if commercial transportation were the main source of dispersal to Florida, continental individuals should be genetically closer to those belonging to Rep. Dominicana and Puerto Rico than to those of the rest of the islands in the Caribbean (Simonsen et al. 2008).

In this study we used a mitochondrial gene (cytochrome oxidase I) to identify: (a) whether potential dispersal routes of the invasive cactus moth (*C. cactorum*) within the Caribbean and Florida matches or not major wind and hurricane trajectories and (b) if Rep. Dominicana and Puerto Rico still appears as important sources of commercial dispersal towards Florida.

Materials and methods

Insect collection and DNA sampling

We sampled several Antillean islands between 2011 and 2012, searching for the presence of *Cactoblastis*

Table 1 Geographic locations and host species of sampled populations of *C. cactorum* in the Caribbean islands

Country	Population	Geographic coordinates		Host species
1. St. Kitt—Nevis	Nevis	17°6'51.2"N	62°32'53.2"W	<i>O. dilleni</i>
2. Antigua	Antigua	16°59'52.8"N	61°45'16.5"W	<i>O. dilleni</i>
3. Puerto Rico	Guanica	17°56'52.7"N	66°52'42.2"W	<i>O. ficus-indica</i>
4. Rep. Dominicana	La Romana	18°29'45.4"N	68°59'23.3"W	<i>O. ficus-indica</i>
5. Jamaica	Palisadores	17°56'52.7"N	66°52'42.2"W	<i>O. tuna</i>
6. Cuba	Santiago de Cuba	19°57'42.3"N	75°41'23.6"W	<i>O. dilleni</i>
7. Cuba	Trinidad	21°45'43.2"N	80°0'33.9"W	<i>O. dilleni</i>
8. Cuba	Pinar del Río	22°8'23.2"N	83°58'13"W	<i>O. stricta</i> var. <i>dilleni</i>

cactorum (Lepidoptera: Pyralidae) on all possible host cacti species following Zimmermann and Pérez-Sandi (2006). In all infested plant populations we sampled one larvae per plant for a total of 110 larvae (7–17 larvae collected at each population) throughout the region. Our sample included eight populations across six countries (Table 1): one population in the island of Nevis where the insect was intentionally introduced in 1957 (Simmonds and Bennett 1966), one population in the island of Antigua where the insect was also introduced in 1960, one population in Rep. Dominicana (La Romana), and Puerto Rico (Guanica), and one population in Jamaica (Palisadores) where the insect was detected in 2005 (Zimmermann and Pérez-Sandi 2006). Finally three populations were sampled in Cuba (Pinar del Río, Trinidad and Santiago de Cuba). The insect was first detected in Cuba in 1980 close to Guantánamo (near Santiago de Cuba) (Blanco and Vázquez 2001) but there is no record of the colonization events in other parts of the island (Table 1). Most sampled populations were found on *Opuntia dilleni* plants, and occasionally on *O. stricta* var. *dilleni*, *O. ficus-indica*, and *O. tuna* (Table 1).

During sampling in the field, larvae were placed in 1.5 ml vials filled with ethanol at a 95 % concentration. Our survey was complemented with previous data gathered from GenBank including information from other populations within the region [two from Florida (hereafter Gulf and Atlantic coast), and one from Mexico (Isla Mujeres), and Rep. Dominicana (Las Tablas)] (Simonsen et al. 2008; Marsico et al. 2011) to have a complete geographic representation of the Caribbean distribution of *C. cactorum* (Fig. 3).

We performed the DNA extraction with DNEasy® blood and tissue Kit (QIAGEN, MD, USA, cat. 60504) following the manufacturer protocol for purifying total DNA from animal tissues based on a spin-column. We

used only larvae legs to extract DNA. We sequenced 836 bp of the gene cytochrome oxidase I (*COI*) for all collected individuals using the primer pair Jerry-Pat II (Simon et al. 1994; Caterino and Sperling 1999; Jerry: 5'-CAACATTTATTTTGATTTTTTGG-3'; PatII: 5'-TCCATTACATATAATCTGCCATATTAG-3'). We performed PCR amplification in a PXC 0.2 thermal cycler (Thermo Electron Corporation, US), using a reaction of 20 µl containing: buffer 1× (Tris-HCl 20 mM, pH 8.4, KCL 50 mM), 1.5 mM of MgCl₂, dNTPs 0.1 mM each, Taq 1 µl, 0.5 µM of each primer, 30 ng of DNA and enough milliQ water to attain the final volume of 20 µl. The PCR protocol initiated with one cycle of 95 °C during 1 min, followed by 35 cycles of 94 °C for 15 s, 57 °C for 15 s, 72 °C for 1 min, and a final elongation step of 72 °C for 7 min. We generated sequences for all individuals in the forward and reverse direction and aligned them using Mega 5 (Tamura et al. 2011).

Data analyses

For the sample of populations acquired in our field survey, we obtained the following genetic diversity estimates: number of segregation sites (*S*), number of haplotypes, and nucleotide diversity (π) using DNAsp (Rozas et al. 2003). Subsequent analyses were performed combining our sample of 110 sequences (individuals) with genetic data gathered from GenBank and published studies for other 132 individuals (Simonsen et al. 2008; Marsico et al. 2011). Based on previous surveys in Southeastern US, all GenBank data for the US Gulf of Mexico and Atlantic coast of Florida (Simonsen et al. 2008; Marsico et al. 2011) were considered as single populations (hereafter Gulf and Atlantic coast population respectively). These two areas included genetic data collected approximately

along 500 km in each coast (Simonsen et al. 2008; Marsico et al. 2011). Final analyses included genetic information for 12 populations and 242 individuals.

We constructed a network of haplotypes using TCS 1.21 (Clement et al. 2000) combining our data with that obtained from GenBank for the same gene and species (Simonsen et al. 2008; Marsico et al. 2011). For this analysis we used only 725 bp fragments following existing sequences length in the GenBank for the studied species. The network was constructed with a link probability of 95 % between pairs of haplotypes and assembled following the parsimony criteria minimizing the number of mutations required to account for differences between haplotypes.

To explore the existence of genetically differentiated groups of populations in the region, we performed an Spatial Analysis of Molecular Variance (SAMOVA; Dupanloup et al. 2002) in ARLEQUIN 3.5 (Excoffier et al. 2005). In these analyses F_{CT} correspond to the among groups component of genetic variation, F_{ST} correspond to the among populations within groups component of genetic variation, and F_{SC} to the within populations component of genetic variation. SAMOVA simulates different partitions of n populations into K groups retaining the partition with the highest F_{CT} value. Subsequent Analysis of Molecular Variance (AMOVA) in ARLEQUIN 3.5 (Excoffier et al. 2005) was performed to estimate fixation indices (F_{SC} , F_{ST} , F_{CT}) for the optimum K .

To further evaluate if population genetic differentiation follow a pattern of isolation by distance the correlation between genetic and Euclidean geographic distance matrices was estimated using a Mantel test. The hypothesis that major tracks of hurricanes and tropical storms played a significant role on the distribution of genetic variation was examined using CIRCUITSCAPE (McRae and Shah 2009). Using historical records of major hurricane and tropical storm tracks and incidence in the region (Landsea 1993; Landsea et al. 1996; Lugo et al. 2000) we built a matrix indicating resistance between pairs of populations (resistance matrix). Following circuit theory this program calculated a matrix of connectivity among all pairs of populations (analogue of electrical resistance) using the resistance matrix (analogue of electrical current) (McRae et al. 2008). The advantage of this method is that it calculated the total resistance based on multiple potential paths of least resistance between populations. A partial Mantel test was then performed

to evaluate if the initial correlation between genetic and Euclidean geographic distance matrices is improved when the information of the connectivity matrix was explicitly considered (isolation by resistance hypothesis). In this analysis, a significant increment in the correlation between genetic and Euclidean geographic distances indicate that our hypothesis of environmental barriers to gene dispersal mediated by hurricanes and tropical storms at least partially contributed to the spatial distribution of genetic variation (McRae and Shah 2009).

Results

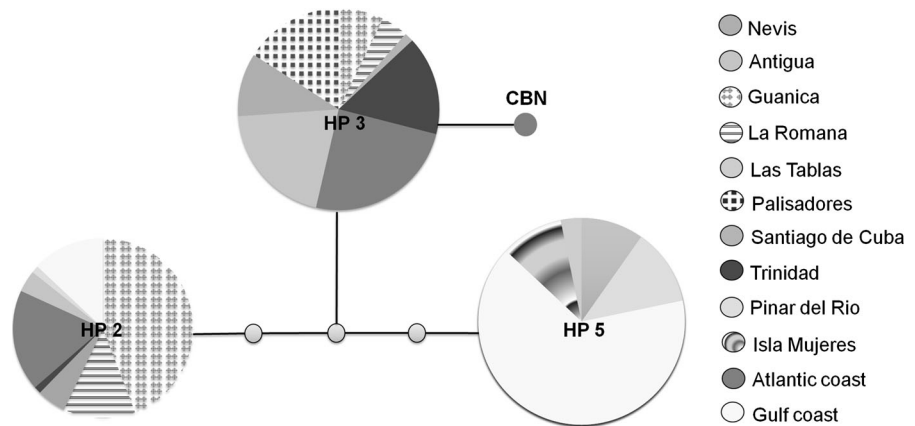
Our results confirmed the number of haplotypes detected in previous studies in the region (Table 2). Following the notation used by Simonsen et al. 2008, we found haplotypes 2, 3 and 5, and haplotype CBN detected by Marsico et al. (2011). We also detected equivalent values in the number of nucleotide differences among haplotypes (Table 2). Mean nucleotide diversity was 0.00177, (range 0–0.00277; Table 2), and we found the highest nucleotide diversity in Santiago de Cuba, whereas the lowest was found in Nevis, Isla Mujeres (Mexico) and Palisadores (Jamaica). Haplotypes 2 and 5 were the most genetically distant with three base pair differences (Fig. 2). Two mutations differentiated Haplotypes 3 and 5,

Table 2 Descriptive summary of genetic diversity using *COI* data (725 bp fragment length) for *Cactoblastis cactorum* in its invasive range in the Caribbean islands

Population	N	Number of haplotypes	S	π
Nevis	7	1	0	0
Antigua	17	2	3	0.00127
Guanica	39	2	3	0.00094
La Romana	13	2	3	0.00159
Palisadores	11	1	0	0
Santiago de Cuba	14	3	5	0.00277
Trinidad	15	3	5	0.00189
Pinar del Río	12	2	4	0.00092
Mean	16	2	2.87	0.0094

N , sample size (number of collected larvae) in each location; Number of haplotypes; S , nucleotide differences among haplotypes; π , nucleotide diversity

Fig. 2 Network of haplotypes for the mitochondrial gene cytochrome oxidase I for invasive populations of the cactus moth *Cactoblastis cactorum* in the Caribbean. HP 2, 3 and 5 correspond to haplotypes describe by Simonsen et al. (2008) while CBN correspond to a haplotype described by Marsico et al. (2011)



while only one base pair difference was detected between Haplotype 3 and CBN (Fig. 2).

In the island of Nevis, where *C. cactorum* was first introduced to the Caribbean in 1957, we only detected one haplotype (Fig. 3), while on the northwestern part of the actual distribution we found a greater concentration of genetic diversity (Fig. 3). Within Florida we found the higher diversity of haplotypes followed by Cuba. Populations in Trinidad and Santiago de Cuba presented all the haplotypes detected in the region except for the haplotype CBN only found in the Atlantic coast of Florida (Fig. 3). Whereas haplotype 5 is more prevalent within populations located in the Gulf of Mexico and the southern part of the Caribbean, haplotypes 2, 3 and CBN are more prevalent in the Atlantic coast of Florida and the north and east part of the Caribbean (Figs. 2, 3). Results from SAMOVA revealed the existence of a phylogeographic structure consistent with the haplotypic network (data shown in Table 3 for $K = 4$, Fig. 3). Although significant components of variation was detected for all possible number of clusters ($1 < K < 10$), the best one corresponded to $K = 4$ given that this presented the higher difference in F_{CT} value with that obtained for $K = 3$ and $K = 5$ ($K = 3$, $F_{ST} = 0.658$, $F_{CT} = 0.553$, $F_{SC} = 0.234$; $K = 4$, $F_{ST} = 0.653$, $F_{CT} = 0.628$, $F_{SC} = 0.068$; $K = 5$, $F_{ST} = 0.638$, $F_{CT} = 0.635$, $F_{SC} = 0.029$).

Analyses revealed the presence of insulation among four genetic groups given that a higher amount of genetic variation was detected at this level (62.8), followed by the variation within populations (34.67), and the variation among populations within groups (2.53) (Table 3). One group of populations correspond

to those present in the coast of the Gulf of Mexico, Isla Mujeres (Mexico), Las Tablas (Rep. Dominicana), and two Cuban populations (Pinar del Rio and Santiago de Cuba) with a higher frequency of haplotype 5 (Fig. 3). The other three groups have higher frequency of haplotypes 2 and 3 (Fig. 3). The group formed by populations of Antigua, Atlantic coast (Florida) and Trinidad (Cuba) present a fairly equal frequency of haplotypes 2 and 3. Populations of Palisadores (Jamaica) and Nevis have a clear dominance of haplotype 3 representing the third group while populations of La Romana (Rep. Dominicana) and Guanica (Puerto Rico) present a clear dominance of haplotype 2 representing the fourth group (Fig. 3).

Isolation by distance analysis revealed that geographic distances marginally accounted for genetic distances among populations (Mantel test $r = 0.214$, $P = 0.062$). However, considering our hypothesis of isolation by resistance mediated by hurricanes and tropical storms improved the correlation between geographic and genetic distant matrices (Partial Mantel test $r = 0.246$, $P = 0.036$) (Fig. 3). The absence of a correlation between the genetic and resistance matrices (Mantel test $r = -0.017$, $P = 0.553$) indicated that hurricanes and tropical storms do not account alone for the pattern of dispersal in the Caribbean.

Discussion

Our analyses revealed that the geographic distribution of genetic variation of the invasive moth, *C. cactorum*,

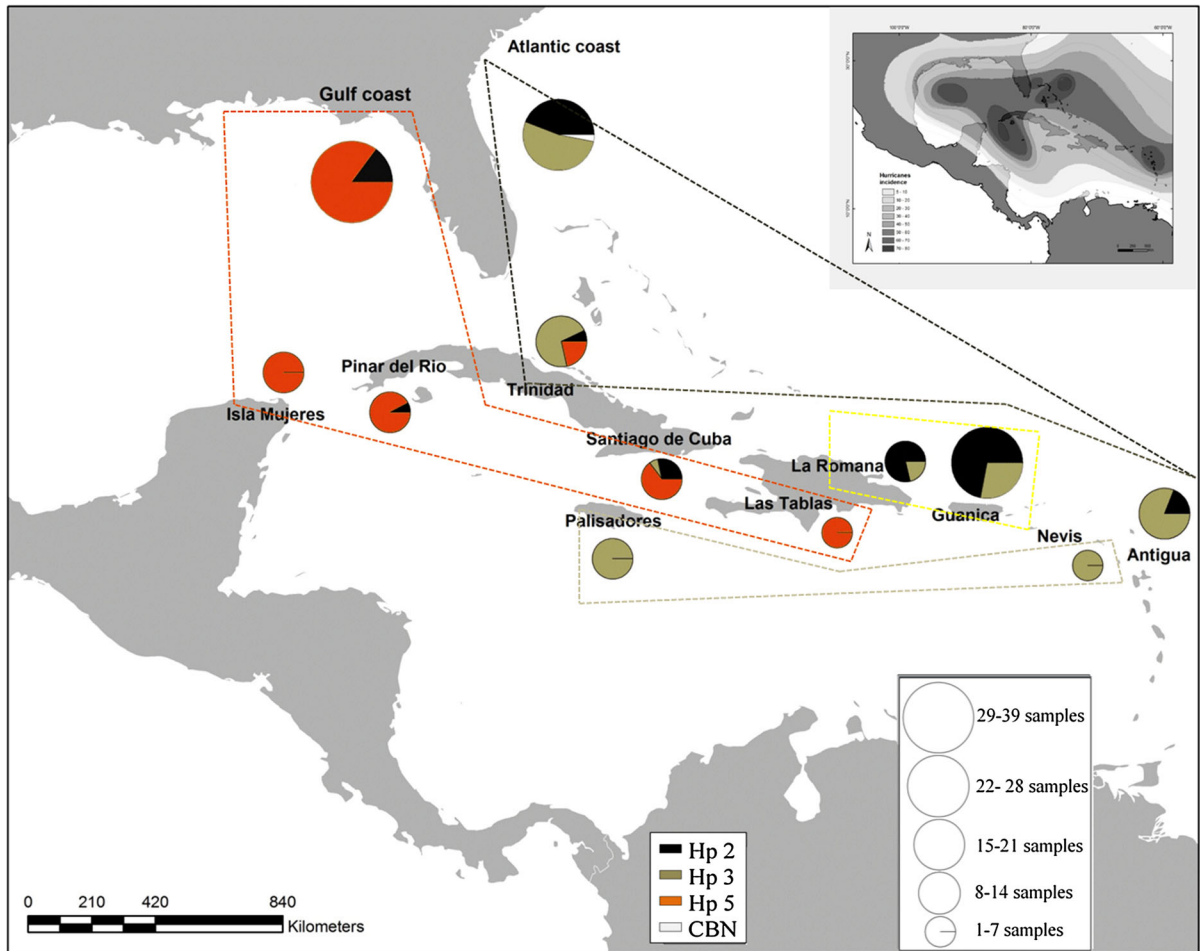


Fig. 3 Geographic distribution of *Cactoblastis cactorum* haplotypes found in 12 non native locations within the invasive range in the Caribbean region and Florida (US). Pie sizes correspond to sample size for each population included in the analyses. Different colors correspond to different haplotypes.

(using the mitochondrial gene COI) was likely conditioned by spatial patterns of hurricanes and tropical storms in the Caribbean. The marginally significant correlation between genetic and geographic distance among populations was statistically improved when the effect of hurricanes and tropical storms were included in the model supporting our isolation by resistance hypothesis mediated by these environmental agents. The geographic distribution of haplotypic variation suggest that despite genetic differentiation between the Gulf and Atlantic coasts of Florida has been related to independent events of colonization promoted by commercial transportation of cacti from

Haplotypes are labeled following Simonsen et al. (2008) and Marsico et al. (2011). Dotted lines outline the four groups obtained in the SAMOVA analysis. The upper right map of the region indicate the frequency of incidence of hurricanes following Lugo et al. (2000), see Fig. 1 for more details

Rep. Dominicana and Puerto Rico (Simonsen et al. 2008; Marsico et al. 2011), hurricanes and tropical storms also played a role on the occurrence of independent events of migration to the United States (Johnson and Stiling 1998). Despite one of the populations of Rep. Dominicana (Las Tablas) formed a group with the Florida population in the Gulf coast and the other Rep. Dominicana population (La Romana) presented high frequency of the haplotype that dominates in the Florida population of the Atlantic coast, Cuban populations were genetically related with both Florida populations. Given the absence of commercial and turistic interchange between United

Table 3 Analysis of molecular variance (AMOVA) using COI data for the four groups of populations of *Cactoblastis cactorum* in the Antillean islands and Florida detected by SAMOVA (see “Results”)

Source of variation	df	Sum of squares	Percentage of variation	Fixation indices
Among groups (F_{CT})	3	150.083	62.80	0.627
Among populations within groups (F_{ST})	8	8.449	2.53	0.653
Within populations (F_{SC})	230	112.629	34.67	0.068
Total	241	271.261		

Fixation indices corresponded to the SAMOVA model for $K = 4$. All variance components were significantly different from zero ($P < 0.0001$) after 1,023 permutations

States and Cuba, our results support the hypothesis that natural dispersal represent an important factor during the invasion of the cactus moth in the Caribbean. Thus, it is likely that a combination of human mediated and natural dispersal explain the pattern of haplotypic differentiation between the Gulf and the Atlantic coast of Florida. Still other sources of dispersion like turistic and commercial transportation as well as other not explored environmental conditions should be explicitly examined in future studies.

Although previous studies recorded the effects of hurricanes on biodiversity, ecosystem functioning and population dynamics for the Caribbean (Chazdon 2003), we are still far from understanding its consequences on the genetic structure of species in the region (but see Fleming and Murray 2009; Apodaca et al. 2013). Genetic data obtained before and after the occurrence of hurricanes reveal that in some cases they exert a strong effect reducing genetic variation while in others, they increase genetic diversity promoting gene flow and dispersal. Because island species usually have lower population size and reduced genetic diversity compared with mainland populations, hurricanes are likely to reinforce the consequences of genetic drift, inbreeding and founder effects (Hedrick 2011). To date the role that hurricanes play upon the genetic structure and dispersal of invasive species is almost unknown. Our results revealed that hurricanes likely contributed to the geographic genetic structure of *C. cactorum* during the last 60 years since the invasion in the Caribbean

started. In turn, our results suggest that native species vulnerable to hurricane effects would also express a similar phylogeographic structure following an east-west pattern and the presence of at least two insulation groups according to major hurricane spatial patterns (Hedges 1996). To our knowledge this is one of the first attempts to show an association between hurricane tracks and dispersal patterns in an invasive species.

In general, higher genetic diversity is usually found within areas were invasive species first established after migration (Avisé 2000). In contrast, our results indicated an east-west pattern of reduction in genetic diversity. This pattern parallel the history of dispersion within the region and the observed reduction in the population size of the host cacti in the islands were *C. cactorum* first arrived (Nevis) (Pemberton and Liu 2007; Zimmermann et al. 2007), suggesting that, as the moth reduces the population size of its local hosts, it becomes exposed to increasing levels of genetic drift. However, the pattern of isolation by distance indicated a mutation–migration–drift balance, suggesting that reduced haplotypic diversity in older colonized sites would not exert a significant effect on the spatial distribution of genetic variation. Given that the molecular marker expressed low levels of genetic variation, this may have increased the signal of genetic drift in the analyses. Further analyses are now being conducted to demonstrate the existence of a pattern of reduced genetic drift following the east-west increase in genetic diversity using more variable molecular markers. In addition, since this east-west pattern of reduction in genetic diversity of populations is consistent with directionality of hurricanes and tropical storms within the region these natural disturbances may affect other native species as well.

Finally, since Cuba constitute a reservoir of genetic variation within the region and a natural corridor toward the continent, the occurrence of future invasions to the nearest continental areas of Florida and the Yucatan Peninsula (Mexico) impacted by hurricanes should be permanently monitored. In particular, locations near the coast inhabited by cacti species. If hurricanes affect genetic variation and dispersal of invasive species in the Caribbean, these effects should be considered in future risk assessments of biological invasions within this tropical region. In addition, as hurricanes could strongly affect dispersal patterns, future authorizations of new introductions for

biological control in the Caribbean requires a coordinated international policy at a regional scale to avoid side negative effects as those recorded for *C. cactorum* (Zimmermann and Pérez-Sandi 2006).

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Conflict of interest The authors declare no conflict of interest.

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