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A comparison of populations of island and adjacent mainland species of Caribbean *Selenops* (Araneae: Selenopidae) spiders

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ABSTRACT

The role of the landscape in structuring populations has been the focus of numerous studies, in particular, the extent to which islands provide opportunities for isolation, and the consistency of such an effect across lineages. The current study examines this phenomenon using a series of relatively widespread taxa, all within a single genus of spiders, *Selenops*. We focus on the Caribbean Islands and adjacent Mesoamerican mainland to examine how the islands *per se* dictate structure across lineages. We use molecular genetic data from mitochondrial and nuclear genes to examine the population structure of seven species of *Selenops*. Comparisons are made between species found in the Greater Antilles, Lesser Antilles, and adjacent mainland. Results indicate that geography has little effect on the population structure of mainland species. In contrast, population structure appears to be partitioned by island in the insular Caribbean. Within islands, the amount of population structure for each species is variable and may be dictated more by ecological or demographic parameters, rather than geographic location. The overall conclusion is that the extent to which a given lineage is structured is highly variable across species, with this variability overwhelming any general signal of geographical isolation.

1. Introduction

The genetic structure of populations of organisms is largely dictated by isolation over space and time (Slatkin, 1985, 1987; Wright, 1943, 1951). However, the interplay between these parameters, and the consistency and replicability across lineages, is complex. Here we use multiple widespread species across a variably fragmented landscape to examine the extent to which isolation is dictated by distance and/or fragmentation. We focus on Central America and the Caribbean Basin, a region that provides an ideal situation for examining these interactions because it includes a large contiguous landmass (Central America), a set of old islands (Greater Antilles; ~55 My), and a set of geologically recent islands (Lesser Antilles; ~3–20 My). This system allows the examination of relative isolation in structuring populations across multiple lineages.

Mesoamerica is the landmass that acts as a bridge for the interchange between the flora and fauna of the Neotropical and Nearctic regions. This area is geologically complex, with both very ancient (~100 My) and recently derived landforms (<3 My). Despite the continuity of this landmass, studies of multiple taxa, including both plants and animals, have shown large genetic breaks that correspond to geographic barriers, as well as patterns of isolation by distance (Demastes et al., 1996; Sullivan et al., 1997; Parkinson et al., 2000; Flores-Villela and Goyenechea, 2001; Cavers et al., 2003; Novick et al., 2003; Devitt, 2006; Hasbún et al., 2005).

The Caribbean Basin, which is also geologically complex, comprises numerous islands that range in age from ~3–55 My. Higher-level biogeographic studies are typically the focus in the region, while population-level studies have been fewer, and thus far, primarily conducted in vertebrates and plants (e.g., Ogden and Thorpe, 2002; Stenson et al., 2002; Thorpe and Stenson, 2003; Carstens et al., 2004; Glor et al., 2004; Thorpe et al., 2005; Francisco-Ortega et al., 2008; Lavin and Beyra Matos, 2008) with a few additional studies on butterflies (Davies and Bermingham, 2002), fruitflies (Wilder and Hollocher, 2003), beetles (Velez and Feder, 2006), crickets (Oneal, 2009), and spiders (Huber and Astrin, 2009; Huber et al., in press). As might be expected, population structuring within and between islands has been demonstrated to be reduced in volant taxa, in particular in bats in which Carstens et al. (2004) demonstrated that although some bat species are monophyletic within islands, molecular variance is not partitioned

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among islands. In contrast, *Anolis* lizards have undergone extensive divergence within islands. In Dominica and Martinique, Malhotra and Thorpe (2000) and Thorpe and Stenson (2003), respectively, have demonstrated molecular and morphological divergence in populations of anoles. Similarly, Glor et al. (2004) have shown that allopatric divergence due to vicariance has played an important part in the diversification of Cuban anoles. In addition to geographical barriers, habitat differentiation and ecological speciation have likely played a role in the diversification of Lesser Antillean anoles (Ogden and Thorpe, 2002; Thorpe and Stenson, 2003; Thorpe et al., 2005). Among invertebrates, studies even on the volant taxa have demonstrated a surprising level of structure, with overall population genetic patterns similar to that of many non-volant vertebrate taxa (Davies and Bermingham, 2002; Wilder and Hollocher, 2003; Oneal, 2009).

In this study we use seven species from the broadly distributed spider genus *Selenops* to compare population-level structure across multiple lineages and between areas that differ in terms of isolation over both space and time. These spiders are non-web-building and range throughout the tropical and sub-tropical regions of the world. They are relatively common on both the mainland and the islands of the Caribbean (Muma, 1953; Crews, 2005; Crews et al., 2008), and appear to have been present in the region for a long time (at least 16 My — Iturralde-Vinent, 2001), being known from Dominican amber (Penney, 2008). The spiders are extremely dorsoventrally flattened, nocturnal, and very fast (achieving running speeds of 63 body lengths/second — Crews et al., 2008). These aspects may be responsible for the dearth of knowledge on their systematics and several other facets of their biology. However, from what is known about *Selenops* natural history (Crews et al., 2008), they appear to be poor dispersers and therefore might be expected to show a strong relationship between geographic and genetic structure.

Within species, multiple comparisons can be made between different regions, such as the mainland (ML), the Greater Antilles (GA), the northern Lesser Antilles (NLA), central Lesser Antilles (CLA) and the southern Lesser Antilles (SLA) as well as between species of different ages that occupy the same regions. A phylogenetic hypothesis has been put forth for the group (Crews, 2008), allowing assumptions regarding the relative ages of lineages. First, we examine consistency of geographic signatures across species, in particular whether genetic breaks and geographic breaks coincide on both the mainland and on islands, as well as within and between islands. Second, we examine within-island monophyly for the Caribbean species distributed across multiple islands. Third, we compare within-island structure between each species. Finally, we examine the extent to which the results obtained match those of other lineages of plants and animals, in the context of between the mainland and islands and between different island groups.

2. Methods

2.1. Taxon selection

Collections were made of seven species with populations that cover all four geographic regions mentioned above (Fig. 1). There are several species of *Selenops* that occur on the mainland, but most of them have very restricted distributions. However, two ML species, *S. bifurcatus* and *S. mexicanus*, are widespread and were collected throughout their ranges in México and Central America. *Selenops bifurcatus* ranges from Northern Guatemala to Costa Rica and *S. mexicanus* is found from Northern México to Northern South America (Fig. 2A) (Crews, unpublished data). A phylogenetic hypothesis indicates these two species are not sister taxa, but belong in a clade consisting of only Mesoamerican and southwestern North American species, and that *S. mexicanus* diverged before *S. bifurcatus* (Crews, 2008). The GA species are *S. insularis* and *S. lindborgi*, the former found in Cuba, Jamaica, Mona, Puerto Rico, Vieques and Hispaniola, with the latter found in eastern Hispaniola, Great Inagua, Puerto Rico, Vieques, Culebra, all of the British and US Virgin Islands and St. Kitts and Nevis (Fig. 2B and C). In many sites in Puerto Rico, the two species were collected from the same localities. A fifth species, *S. 'n. sp. 1'*, occurs in the northernmost part of the Lesser Antillean arc (NLA) on the islands of St. Maarten, Saba, and Anguilla (Crews, unpublished data) (Fig. 2C). The phylogeny indicates that this species is nested within the Caribbean clade and is sister to *S. 'n. sp. 2'* (Crews, 2008). The CLA species, *S. 'n. sp. 2'*, is found in Antigua, Montserrat, Guadeloupe and Isles Les Saintes (Fig. 2D). The SLA species *S. micropalpus*, is found in St. Vincent and several of the Grenadines, Martinique and Dominica (Fig. 2D). Phylogenetic data indicate that this species is more closely related to South American species and is not nested in the Caribbean clade (Crews, 2008). In a broader molecular phylogenetic study (Crews, 2008), all species used in this study were found to be monophyletic. *Selenops 'n. sp. 1'* and *'n. sp. 2'* are being formally described elsewhere, but are only tentatively named in this publication as the forthcoming publication is not yet complete. Each specimen in this study was given a unique number in the form of 'sel_001' — 'sel_XXXX', and this number was placed in the vial of each specimen. This unique number and precise locality data that correspond to the numbers located inside the symbols in Fig. 2 are given in Appendix 1. Voucher specimens are deposited in the Essig Museum of Entomology at UC Berkeley and the California Academy of Sciences.

2.2. Molecular methods

DNA was extracted from a portion of a leg using a Qiagen DNeasy Tissue Kit following the manufacturer's protocol. Genomic DNA is stored at −80 °C in the Gillespie and Roderick Laboratories, UC Berkeley. DNA sequences are available from GenBank (GU109549–GU110746). Three primer pairs were used to amplify 4 gene fragments, including the mitochondrial genes, Cytochrome Oxidase I (CO1), 16S ribosomal DNA (16S) and N-alcohol dehydrogenase I (ND1), and the nuclear gene Histone 3a (H3) (Crews, 2008). These markers evolve at different rates and have become standards in spider molecular phylogenetics, with several primers available for each (Maddison and Hedin, 2003; Arnedo et al., 2004). We attempted to obtain sequence data for all gene fragments for all specimens, although this was not always possible. In the case of *S. insularis*, there was evidence for multiple copies of H3a in some specimens, thus these sequences were excluded from analyses for these specimens.

2.3. Population genetic analyses

Alignments of the protein-coding loci CO1, ND1 and H3 were performed manually using Mesquite v.2.5 (Maddison and Maddison, 2008), with the amino-acid translations used as a guide. The 16S data were aligned using secondary structure based on the model from Masta (2000). Although there were some sequence length differences within species, particularly within *S. micropalpus*, alignment was for the most part straightforward.

Partitioned Bayesian analyses were used to build gene trees for all seven species using MrBayes v. 3.1.2. Data were partitioned by codon position for protein coding genes, by stems and loops for ribosomal DNA, and by gene for both the maximum likelihood and Bayesian analyses to improve the fit of the substitution model to the data (Nylander, 2004; Brandley et al., 2005). The doublet model of nucleotide substitution was used for the stem-regions of 16S and the tRNA (Schöniger and von Haeseler, 1994; Kjer, 2004). The larger analyses with more than 100 individuals (*S. insularis* and *S. lindborgi*) were run in parallel on the CIPRES cluster

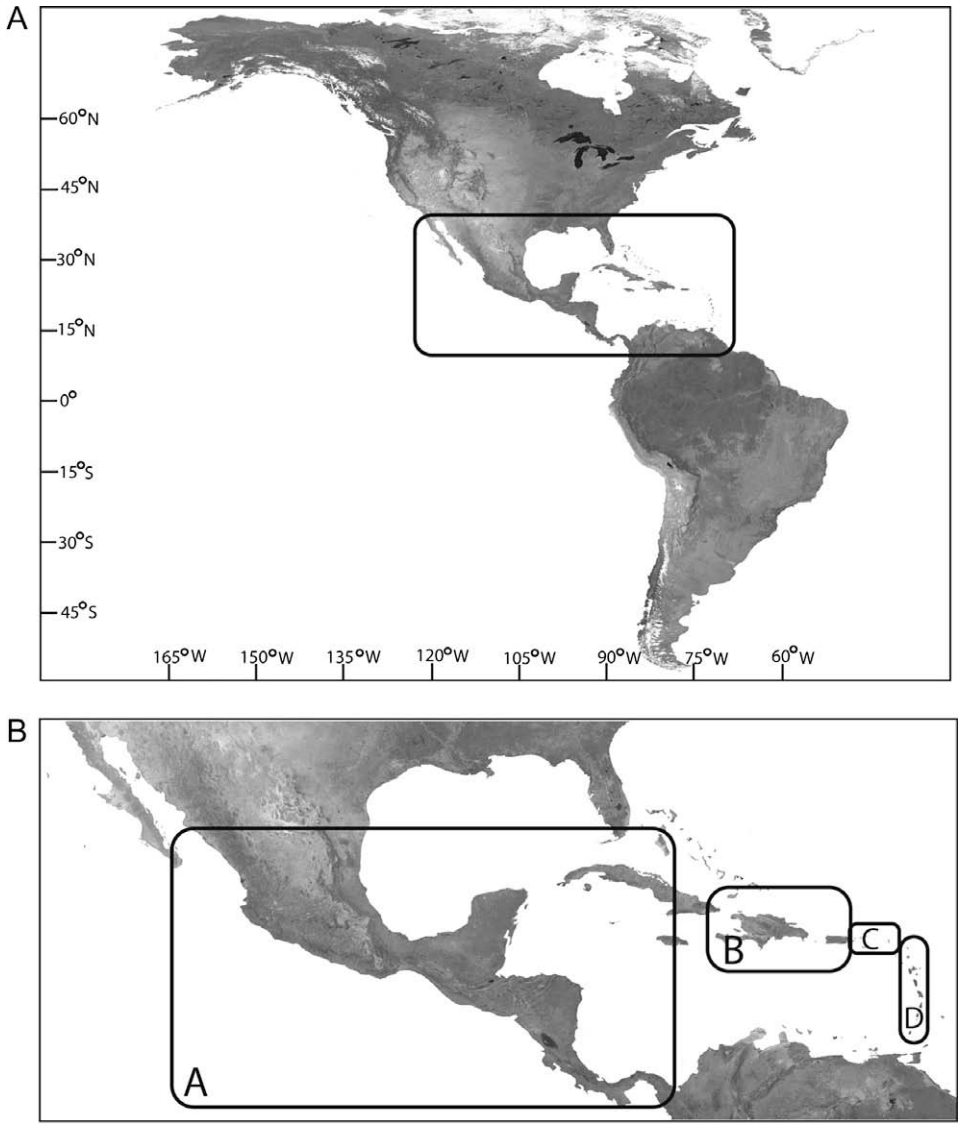

Fig. 1. Map of the study area. (A) This map depicts the Americas, the boxed region showing the primary study area, expanded in (B). (B) This is the boxed area in (A) expanded and separated into the regions depicted in Fig. 2A–D. Box (A) encloses the mainland (ML), (B) encloses the Greater Antilles (GA), box (C) surrounds the Virgin Islands, Culebra, Vieques and the northernmost islands of the inner and outer arcs of the Lesser Antilles and box (D) contains the remainder of Lesser Antilles (LA).

at the San Diego Supercomputing Center. Convergence of each analysis was estimated using cumulative and slide plots in AWTY (Nylander et al., 2008), and if a dataset was found not to have converged it was run for more generations. Models for each of the data partitions were determined using MrModeltest v. 2.3 (Nylander, 2004). Models were chosen using the Akaike Information Criterion (AIC; Akaike, 1973; see Posada and Buckley, 2004) and are listed in Appendix 2. Analyses were run for varying numbers of generations, depending on the size of the dataset (Table 1). The mitochondrial and nuclear DNA datasets were analyzed separately and combined for each species. Trees were rooted based on previous analyses of all species (Crews, 2008). Statistical parsimony was also used to construct haplotype networks using TCS v. 2.1 (Clement et al., 2000) from the mtDNA datasets for each species.

Standard diversity indices including gene diversity, nucleotide diversity and pairwise differences were computed using Arlequin v.3.11 (Excoffier et al., 2005). This program was also used to compute the analyses of molecular variance (AMOVA) to test whether molecular variance is partitioned by island. Samples were grouped by island to examine covariance among islands (F_{CT}), among populations within islands (F_{SC}) and among individuals within populations (F_{ST}). In a dataset if there was more than one occurrence of one population with only a single individual, this sample was combined with a group on the most geographically proximate island. All calculations were made for each species allowing up to 5% missing data, and specimens with more than this were eliminated from the analyses.

The program IBDWS v. 3.15 (Isolation by Distance Web Service) (Jensen et al., 2005; Ngan, 2006) was used to investigate the existence of any correlation between genetic distance and geographic distance using partial Mantel tests. Genetic distances (standard F_{ST}) were calculated by the program from the DNA data matrices using the K2P model of nucleotide substitution. These analyses were conducted with raw data as well as with log(geographic distance) as the ranges of some of the geographic distances were large. The maximum number (30,000) of randomizations the program allows was used in all analyses.

3. Results

There were no supported differences between the mitochondrial and nuclear DNA gene trees in the separate Bayesian analyses,

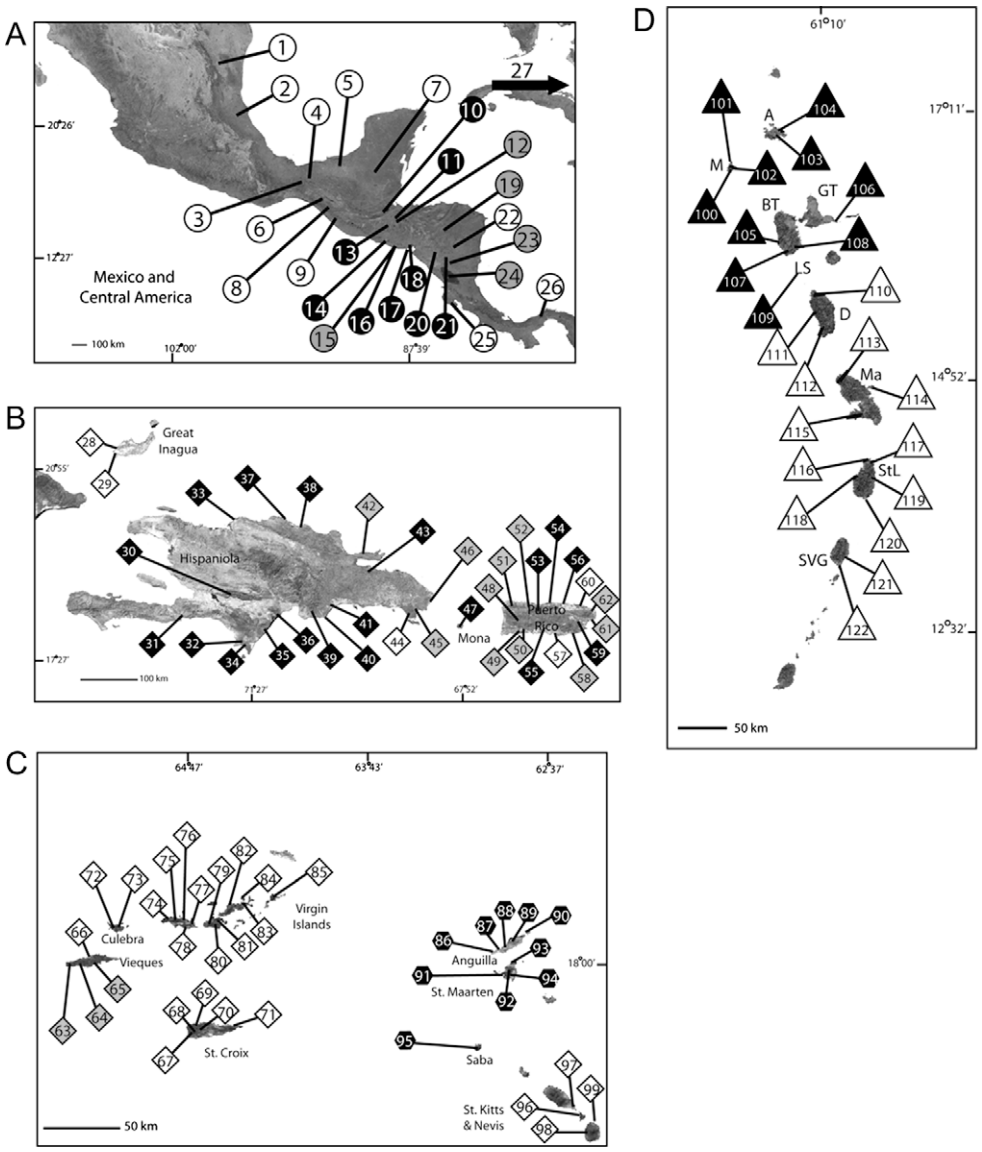

Fig. 2. Collection localities of species used in this study. Each letter shown here corresponds to the boxed areas of Fig. 1B. The numbers inside the shapes correspond to Appendix 1, which provides detailed locality information and unique specimen numbers. (A) This map shows the collecting localities of the mainland species *Selenops bifurcatus* and *S. mexicanus*. White circles are those of *S. mexicanus*, black circles are those of *S. bifurcatus*, and gray circles indicate a locality from which both species were collected. Number 27 in the arrow refers to two specimens of *S. mexicanus* collected in St. Maarten and is discussed in the text. (B) This map shows the Greater Antillean region that was sampled for this study and includes the partial distributions of *S. insularis* and *S. lindborgi*. Collecting localities of *S. insularis* are depicted by black diamonds, and collecting localities of *S. lindborgi* are depicted by white diamonds. Gray diamonds indicate localities where both species were collected. (C) This map shows Culebra, Vieques, the Virgin Islands, Anguilla, St. Maarten, Saba and St. Kitts and Nevis. Gray diamonds indicate collection localities of *S. insularis* and *S. lindborgi*, white diamonds indicate collection localities of *S. lindborgi* and black hexagons indicate collection localties of *S. 'n. sp. 1'*. (D) This map shows the remainder of the Lesser Antilles. Black triangles indicate the collection localities of *S. 'n. sp. 2'* and white triangles indicate the collection localities of *S. micropalpus*. A = Antigua, M = Montserrat, BT = Basse-Terre, GT = Grande Terre, LS = Les Saintes, D = Dominica, Ma = Martinique, StL = St. Lucia, SVG = St. Vincent and the Grenadines.

Table 1
Dataset size and number of generations and trees eliminated as burn-in from the Bayesian analyses of the concatenated data for each species. Each dataset consisted of 2086 bps, two runs were completed for each analysis, though both runs were not always used, and trees were saved every 1000 generations in MrBayes.

Species	Number of specimens	Number of localities	Number of generations	Trees eliminated as burn-in
Selenops bifurcatus	44	14	$10^6 \times 2$	12.5^6
Selenops mexicanus	43	17	$15^6 \times 2$	10^6
Selenops insularis	140	33	$75^6 \times 2$	90^6
Selenops lindborgi	136	43	43.5^6	32^6
Selenops 'n. sp. 1'	41	10	$15^6 \times 2$	19^6
Selenops 'n. sp. 2'	38	10	$15^6 \times 2$	12.5^6
Selenops micropalpus	64	13	$15^6 \times 2$	20^6

thus both datasets were combined and the results of the concatenated analyses are shown in Fig. 3A–G. The gene trees of each species are all different from one another, displaying varying degrees of divergence.

Fig. 3. Gene trees from Bayesian analyses of concatenated datasets. Two numbers are shown at tips. The first number corresponds to the unique specimen numbers found in Appendix 1 and the second number corresponds to the localities shown in Fig. 2A–D and to the localities numbered in Appendix 1. Stars along branches indicate posterior probabilities $\geqslant 0.95$. (A) Consensus tree for *S. bifurcatus* from 12,500 trees. (B) Consensus tree for *S. mexicanus* from 10,000 trees. Sample sel_1003 is marked with an asterisk as the precise locality in Mexico where this specimen originated is unknown. (C) Consensus tree for *S. insularis* from 90,000 trees. The tree has been separated for clarity, with the portion to the right detached from the branch at the top on the portion from the left side. (D) Consensus tree for *S. lindborgi* from 32,000 trees. (E) Consensus tree for *S. 'n. sp. 1'* from 19,000 trees. (F) Consensus tree for *S. 'n. sp. 2'* from 12,500 trees. Sample sel_780 and sel_782 are marked with asterisks as they are the only samples which deviate from within-island monophyly. (G) Consensus tree for *S. micropalpus* from 20,000 trees.

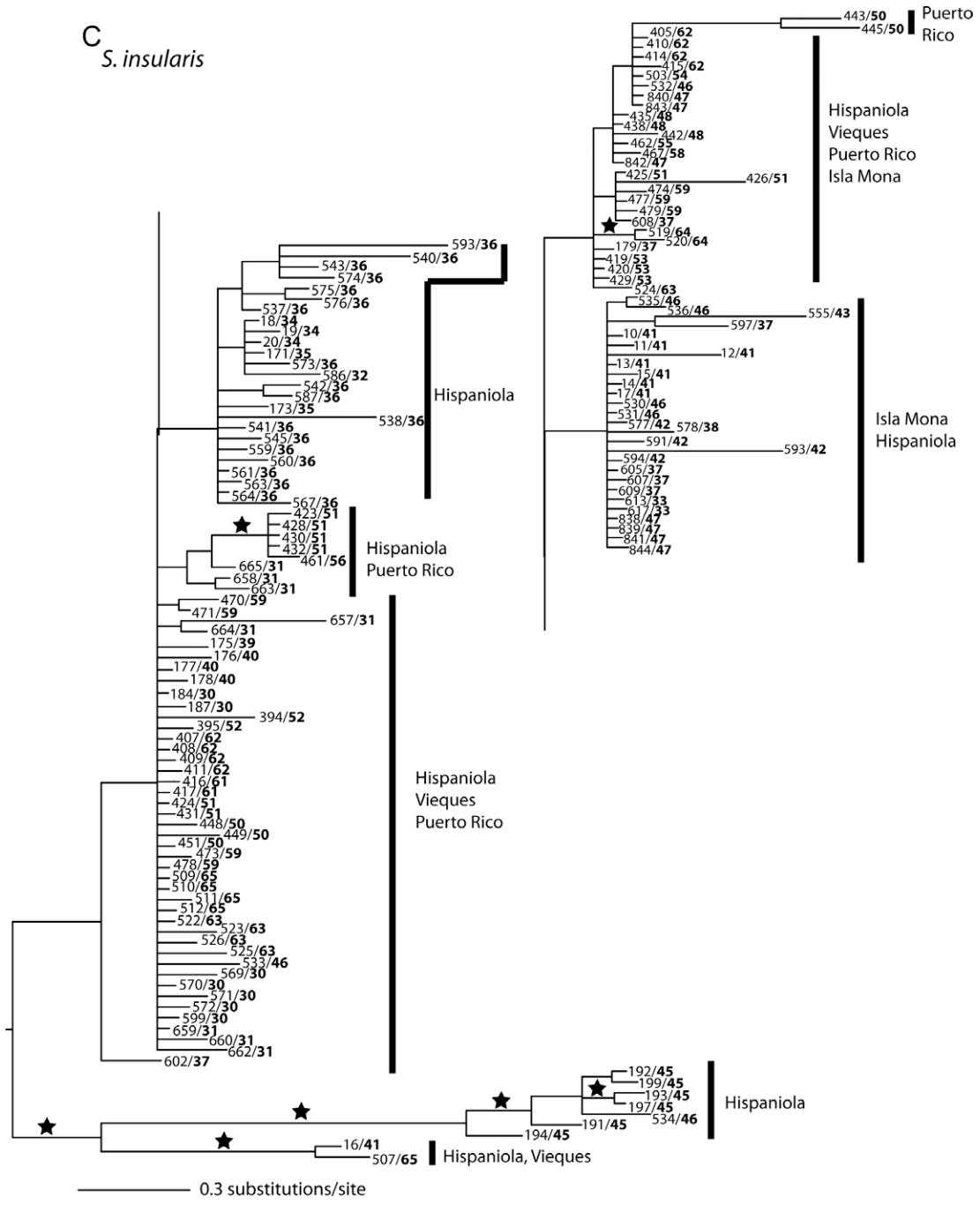

Fig. 3 (*continued*)

Haplotype networks of rapidly evolving mtDNA were constructed using statistical parsimony in order to determine whether a stronger geographic pattern of genetic relatedness emerged. In many cases, haplotypes were too divergent to be connected using a standard cut off of 95%, and therefore are not shown. Also, if there were fewer than five connections (i.e., if only two, three or four samples were connected), these are also not shown.

The results of the AMOVAs and the Mantel tests are shown in Tables 2 and 3, respectively. The details of these results are discussed below. Standard diversity indices are shown in Appendix 3. The number of unique haplotypes varied between species and was highest in *S. lindborgi* (72.6%) and lowest in *S. micropalpus* (50%), but was comparable to that found for other spiders (Crews and Hedin, 2006). Pairwise percent differences are shown in Table 4. The lowest average divergence (0.40%) occurs within the NLA species, *S. 'n. sp. 1'*, and the highest average divergence (1.39%) occurs within *S. bifurcatus*, a mainland species. A summary and comparison of results is shown in Table 5.

3.1. Mainland species — *S. bifurcatus* and *S. mexicanus*

The *S. bifurcatus* gene tree consists of many well-supported clades with short tips, each separated by fairly long branches (Fig. 3A). There is some site fidelity within clades, but there is no obvious pattern of geographic association as genetic breaks do not appear to correspond with any known geographic breaks.

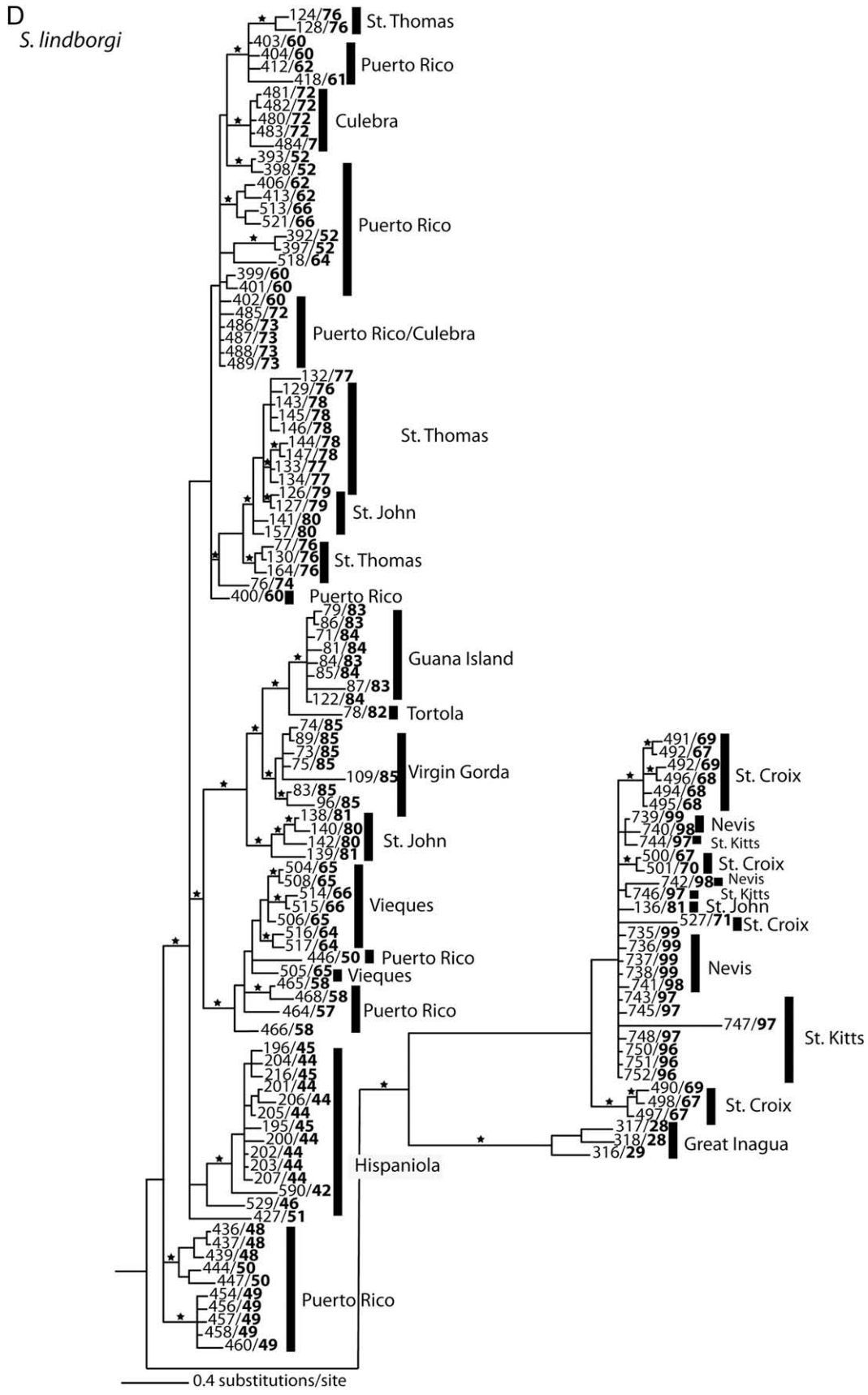

Fig. 3 (*continued*)

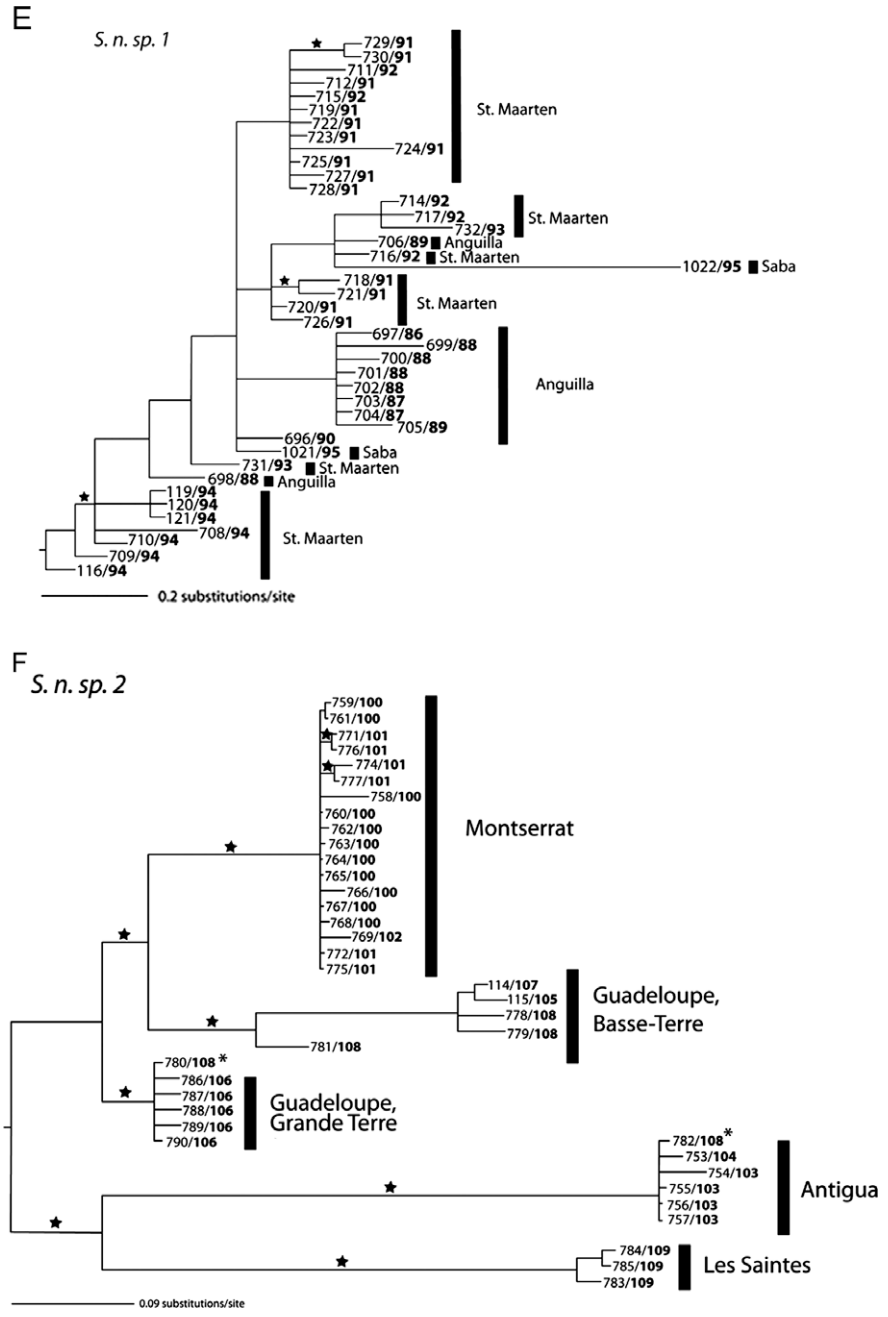

Fig. 3 (*continued*)

The gene tree for the other mainland species, *S. mexicanus*, is similar to that of *S. bifurcatus*, with many well-supported deep clades (Fig. 3B). In both of the ML species, *S. bifurcatus* and *S. mexicanus*, there were no networks consisting of more than five sample sites, and thus no haplotype networks are shown for these species. Neither mainland species displays a pattern consistent with isolation by distance.

3.2. Large island species — *S. insularis* and *S. lindborgi*

Selenops insularis and *S. lindborgi*, both widespread throughout the Greater Antilles, show contrasting patterns of genetic structure. The gene tree for *S. insularis* (Fig. 3C) has very little support at basal nodes and the structure is essentially comb-like. The tree displays little-to-no site or island fidelity, with the only exception being a clade of well-differentiated haplotypes, primarily from localities in eastern Hispaniola. The gene tree for *S. lindborgi* (Fig. 3D) reveals three extremely divergent clades, one from the Bahaman island of Great Inagua, one from the islands of St. Kitts, Nevis and St. Croix, and one from the Greater Antilles and Virgin Islands (VI). The GA-VI clade comprises several structured subclades while the St. Kitts–Nevis–St. Croix clade shows little population differentiation. Fig. 4A shows haplotype networks from *S. insularis* from the GA. Most of the networks constructed from this dataset show both star-like patterns and deep divergence of haplogroups within each network. The centers of each of the star-like structures are made up of haplotypes primarily from Puerto Rico and Vieques, while the tips mainly comprise Hispaniolan haplotypes. Fig. 4B depicts three haplotype networks from the *S. lindborgi* dataset. One consists primarily of divergent haplotypes from

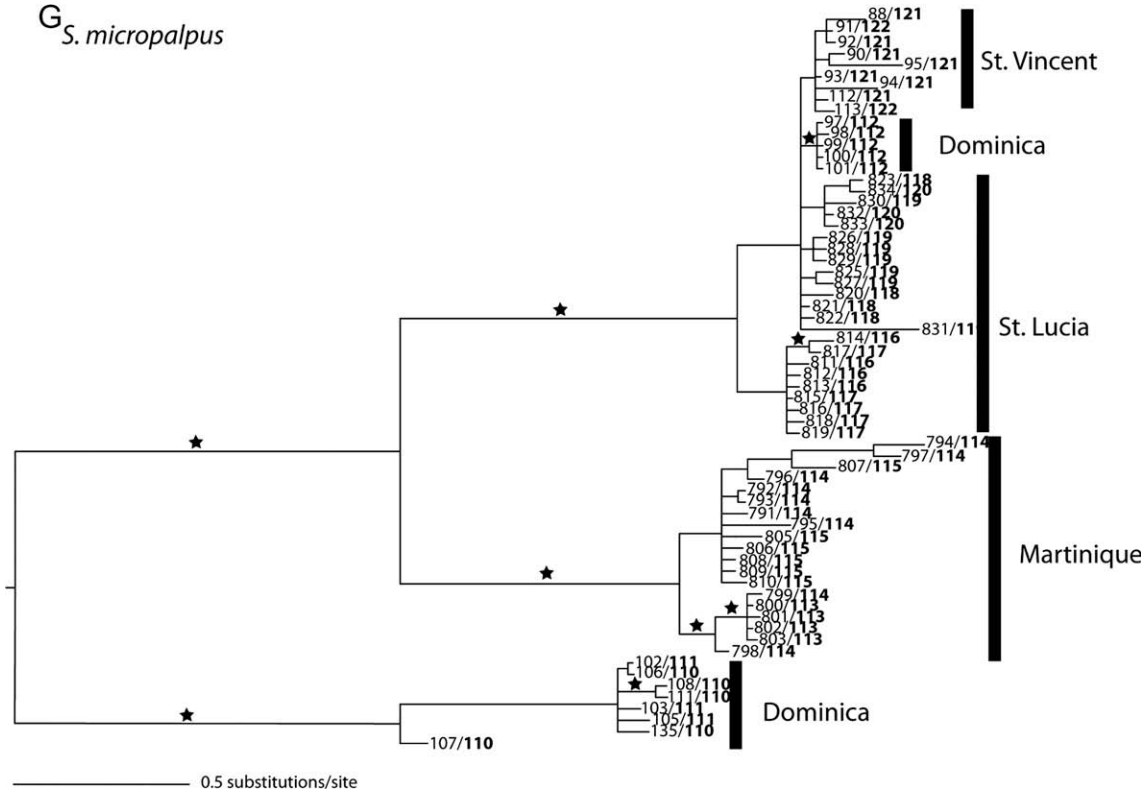

Fig. 3 (*continued*)

Table 2
Results of the AMOVA analyses for each species, showing degrees of freedom (d.f.), sum of squares (SS), variance components, percent of variation (% of variation) and the values for the different hierarchies of *F* followed by the *P*-values in parentheses.

	d.f.	SS	Variance components	% of variation	Values of *F*
S. insularis					
Among islands	3	86.42	0.37	3.88	$F_{CT}(P)$ 0.04 ($P < 0.00$)
Among populations within islands	23	367.37	3.52	36.76	$F_{SC}(P)$ 0.41 ($P < 0.00$)
Among individuals within islands	59	335.59	5.69	59.36	$F_{ST}(P)$ 0.41 ($P < 0.16$)
S. lindborgi					
Among islands	11	1507.46	13.26	67.79	$F_{CT}(P)$ 0.68 ($P < 0.00$)
Among populations within islands	27	291.60	3.09	15.77	$F_{SC}(P)$ 0.49 ($P < 0.00$)
Among individuals within islands	74	238.01	3.22	16.44	$F_{ST}(P)$ 0.84 ($P < 0.00$)
S. 'n. sp. 1'					
Among islands	1	7.35	−0.85	−10.75	$F_{CT}(P)$ 0.11 ($P < 0.01$)
Among populations within islands	3	41.17	3.70	46.44	$F_{SC}(P)$ 0.42 ($P < 0.02$)
Among individuals within islands	6	30.67	5.11	64.31	$F_{ST}(P)$ 0.36 ($P < 0.64$)
S. 'n. sp. 2'					
Among islands	2	248.51	13.20	67.52	$F_{CT}(P)$ 0.68 ($P < 0.00$)
Among populations within islands	6	56.80	2.13	10.88	$F_{SC}(P)$ 0.34 ($P < 0.48$)
Among individuals within islands	20	84.44	4.22	21.60	$F_{ST}(P)$ 0.78 ($P < 0.00$)
S. micropalpus					
Among islands	3	187.47	5.31	52.45	$F_{CT}(P)$ 0.52 ($P < 0.00$)
Among populations within islands	9	95.74	3.43	33.90	$F_{SC}(P)$ 0.71 ($P < 0.00$)
Among individuals within islands	25	34.58	1.39	13.65	$F_{ST}(P)$ 0.86 ($P < 0.00$)

Vieques and southwestern Puerto Rico. A second consists of divergent samples from the Virgin Islands excluding St. Croix with a few samples from northern Puerto Rico. The third network has star-like features with centers in St. Croix and St. Kitts, as well as divergent haplotypes. Samples from southwestern Puerto Rico could not be grouped with these haplotypes.

Selenops insularis shows a pattern of isolation by distance with the raw data only, while *S. lindborgi* shows a pattern of isolation by distance only in the analysis where log(genetic distance) was used. Among-island population variance is significant in both *S. insularis* and *S. lindborgi*, providing evidence for geographic structuring in these two species.

3.3. Small island species — S. 'n. sp. 1', S. 'n. sp. 2' and S. micropalpus

The gene tree for *Selenops 'n. sp. 1'*, a species endemic to the islands of the northernmost inner and outer arcs of the Lesser Antilles (Anguilla, St. Maarten, Saba), is shown in Fig. 3E. There is evidence

Table 3
Results of the IBDWS analyses for each species.

Species	Raw data			Log (genetic distance)		
	Z	*r*	*P*	*Z*	*r*	*P*
S. bifurcatus	4543.19	0.08	0.31	42.03	0.02	0.47
S. mexicanus	58,296.34	0.06	0.39	204.47	0.08	0.29
S. insularis	51,7781.25	0.07	0.05*	363.48	0.04	0.13
S. lindborgi	69,443.62	0.13	0.17	528.42	0.17	0.05*
S. 'n. sp. 1'	216.48	0.02	0.34	10.38	−0.04	0.50
S. 'n. sp. 2'	2123.67	0.16	0.02*	45.79	0.27	0.00*
S. micropalpus	21,931.98	−0.01	0.52	34.00	0.14	0.13

Significant *P*-values are noted with an asterisk.

Table 4
Uncorrected pairwise percent mtDNA sequence divergence for each species.

Species	Avg. (Min.–Max.)
Selenops bifurcatus	1.39 (0–8.40)
Selenops mexicanus	0.92 (0–5.31)
Selenops insularis	0.42 (0–4.27)
Selenops lindborgi	1.11 (0–6.04)
S. 'n. sp. 1'	0.40 (0–3.31)
S. 'n. sp. 2'	0.88 (0–5.31)
Selenops micropalpus	1.15 (0–9.49)

of clade differentiation, but little-to-no support and little evidence of within island monophyly, however some site monophyly is evident. Fig. 3F illustrates the gene tree from *S. 'n. sp. 2'*, a species found in the Central Lesser Antilles. Branch lengths are much shorter in this tree than in any of the other trees (note scale); however the relative differentiation between major clades is among the highest of all species examined. Similar to other species there are some deeply divergent, well-supported major clades with little-to-no substructure within these clades. There is a nearly complete pattern of within-island monophyly, except for two samples from Trois-Rivieres in Basse-Terre. One of these is shown to group with samples from Antigua and the other groups with specimens from Grande Terre. These are marked with asterisks in Fig. 3F.

Fig. 3G shows the gene tree from *S. micropalpus* from the Southern Lesser Antilles. This gene tree displays the deepest between-clade divergences of all species analyzed. Similar to most of the other island species, there are several well-separated deeply divergent clades with little to no within clade substructure. Populations of *S. micropalpus* are monophyletic on each of the islands on which it occurs except for Dominica in which there are two distinct and well-supported clades.

The haplotype network from *S. 'n. sp. 1'* depicts only divergent samples, with no star-like features (Fig. 4C). Only a single, small haplotype network was constructed from the mtDNA dataset of *S. 'n. sp. 2'* (Fig. 4D). It is star-like, with the center as a 'missing' haplotype. The samples in this network are from Grande Terre (Guadeloupe), and two sites in Montserrat. Fig. 4E shows haplotype networks from the mtDNA dataset of *S. micropalpus*. These are the only networks that correspond well to the gene tree. The first network consists only of individuals from Martinique, the second only of individuals from St. Lucia and the third, which is slightly star-like, has individuals from multiple islands with a center of Dominica (Roseau) and with divergent haplotypes from St. Lucia and St. Vincent. Haplotypes from other Dominican locales are very divergent and not connected to any network.

Selenops 'n. sp. 2' is the only one of the small island species that displays a pattern of isolation by distance in both analyses. Among-island population variance is significant in all three species, providing evidence of geographic structuring in these species.

4. Discussion

4.1. Coincidence of geographic and genetic breaks

4.1.1. Mainland

Several studies of disparate taxa have demonstrated concordance of genetic structure with geographic boundaries among populations of species that occur in México and Central America (Demastes et al., 1996; Sullivan et al., 1997; Parkinson et al., 2000; Flores-Villela and Goyenechea, 2001; Cavers et al., 2003; Novick et al., 2003; Devitt, 2006; Hasbún et al., 2005). The two mainland species examined in this study, *S. bifurcatus* and *S. mexicanus*, show no concordance with geographic barriers. Closely-related haplotypes are widespread over hundreds of kilometers, and any deep genetic breaks do not correspond to known geographic breaks. Moreover, there is no pattern of isolation by distance in either mainland species, a feature that has also been found in butterflies in which there is little genetic differentiation over huge geographic distances on the mainland (Davies and Bermingham, 2002). The lack of any genetic signature of isolation could indicate that these species are good dispersers. However, we found that the spiders within any one locality do, in general, share similar haplotypes, suggesting that the spiders are not broadly dispersive. If *S. bifurcatus* and *S. mexicanus* were actively dispersing, we would expect genetic distance to increase with distance between populations. Instead the results indicate that the genetic distance between localities has no relationship to geographic distance. A

Table 5
Summary table of results for all species. GT = gene tree.

Species	*S. bifurcatus*	*S. mexicanus*	*S. insularis*	*S. lindborgi*	*S. n. sp. 1*	*S. n. sp. 2*	*S. micropalpus*
Locality	Contiguous landmasses (ML)		Large island (GA)		Small islands (NLA)	(CLA)	(CLA)
Gene tree	Clades with short tips separated by long branches		Comb-like	Structured by island	Not structured by island		Structured by island
Site fidelity (GT)	Some	Some	No	Yes	Some	No	Some
Within-clade substructure (GT)	Low	High	Low	High	Low	Low	Low
Genetic/geographic breaks (GT)	No association			Associated by island	No association	Associated by island	
Haplotype network description	No network consisting of more than 5 sites		Star-like[a]	Separated by island[b]	Divergent samples	Star-like[c]	Corresponds to gene tree
Geog. structuring by island (AMOVA)	—	—	Yes	Yes	Yes	Yes	Yes
Assoc. genetic & geog. distance (IBD)	No	No	Yes	Yes	No	Yes	No

[a] Centers are smaller islands (Vieques, Puerto Rico), tips are larger islands (Hispaniola).
[b] Centers are smaller islands (Vieques, Puerto Rico).
[c] Center is 'missing' haplotype.

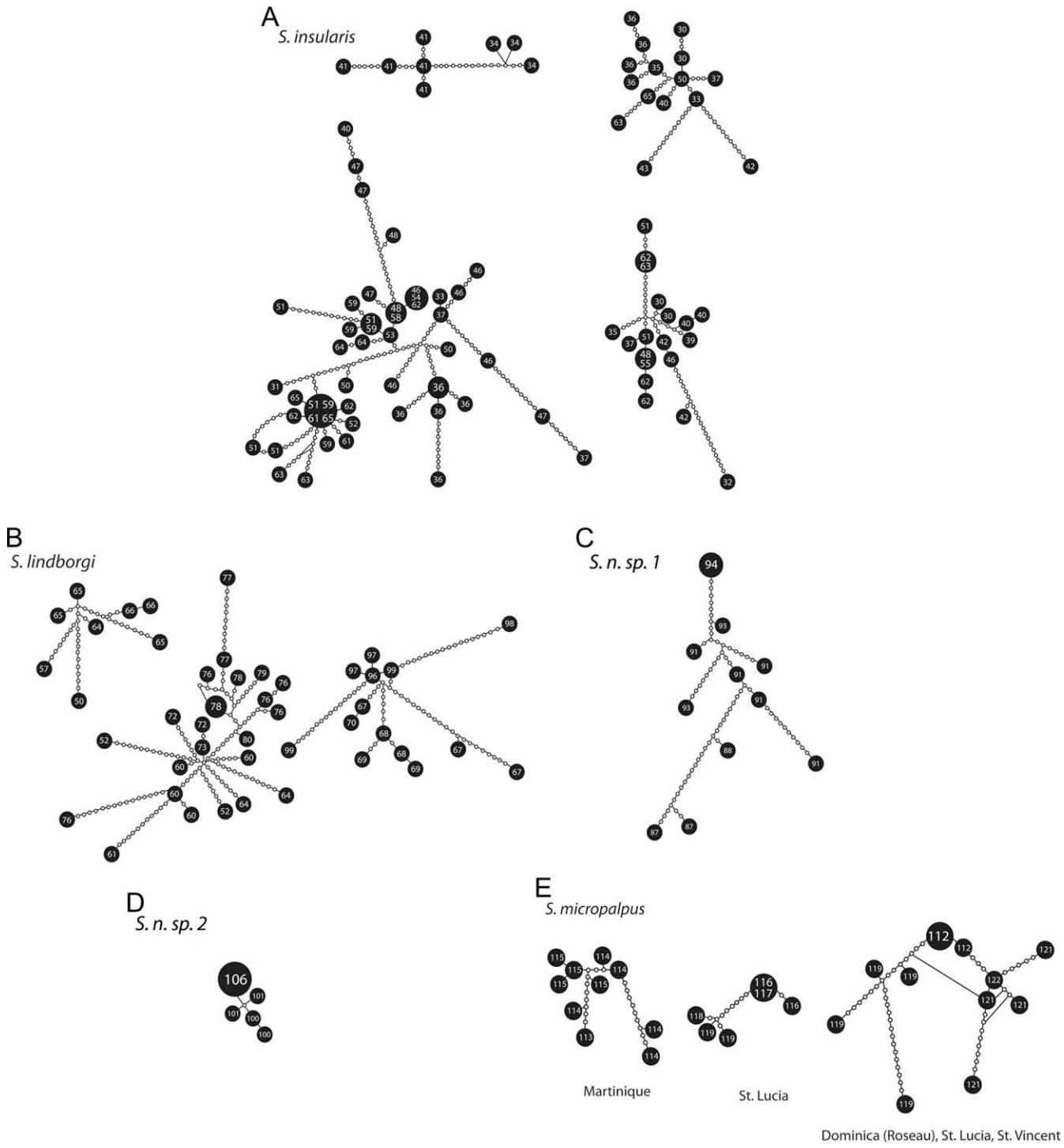

Fig. 4. Haplotype networks assembled using statistical parsimony. Numbers within the black circles correspond to collecting localities shown in Fig. 2 and listed in Appendix 1. The size of the circle is indicative of the number samples of sharing the same haplotype, with larger circles indicating more samples, and smaller circles indicating less samples. Small white circles are representative of 'missing' haplotypes. (A) Haplotype networks from the *S. insularis* mtDNA dataset. (B) Haplotype networks from the *S. lindborgi* mtDNA dataset. (C) Single haplotype network from the *S. 'n. sp. 1'* dataset. (D) Single haplotype network derived from the *S. 'n. sp. 2'* dataset. (E) Three haplotype networks from the *S. micropalpus* mtDNA dataset.

post-hoc test of non-random distribution of haplotypes indicates significant differences between only 3 out of 19 sampled localities (Huixtla, in México with two other localities, Finca El Carmen in El Salvador and Isla Ometepe in Nicaragua) for *S. mexicanus* and in *S. bifurcatus*, only 2 localities out of 13 are shown to be non-random (two localities in El Salvador, San Salvador and Lotificación Amaya).

A likely scenario that might lead to such a pattern, or lack thereof, is that both species are transported by vectors, the most likely agent being humans. Both *S. bifurcatus* and *S. mexicanus* are often collected near human dwellings, particularly in agricultural settings. When no obvious habitat is available, *S. mexicanus* is often found on banana plants, while both species can be found under

rocks and concrete blocks (Crews et al., 2008). Coupled with their preference for anthropogenic structures, these spiders are very elusive so may readily be vectored by humans whether or not cargo is checked. For example, the mainland *S. mexicanus* was collected from Phillipsburg, St. Maarten, on a recently planted palm near the cruise ship dock. Records from the Department of the Environment in St. Maarten showed that these palms had come from a supplier in Dade County, Florida, who recently received the trees from México (A. Caballero, personal communication). The haplotypes of these specimens fall within a group of *S. mexicanus* from Chiapas, suggesting their recent transportation into two different countries. The specimens taken were an adult male and a juvenile female.

However, the large genetic breaks that do occur within the two species may represent divergences that were present before human-mediated intervention. Moreover, examination of the regression plots from the Mantel tests (not shown) do not indicate any particular clustering of points, thus the results are likely not due to a poor fit of the linear equation.

4.1.2. Large islands: Greater Antilles

The two widely distributed primarily Greater Antillean species have contrasting patterns of population structure even though many samples of both species were taken from the same localities. In *S. insularis* there is no correspondence with genetic divergence and geography. There are few closely-related haplotypes widespread throughout the islands. In contrast, specimens of *S. lindborgi* show a marked pattern of within-island monophyly, as several well-supported clades contain species that occur on only one or a few nearby islands. Differences in population structure could be due to different dispersal capabilities, although the similarity between these species in abundance and ecological affinity (Crews et al., 2008) would suggest that their tendencies for movement might also be similar.

The *S. insularis* gene tree suggests some additional points. In particular, the comb-like structure may be a signature of recent range expansion (Excoffier et al., 2009). Also, as in *S. mexicanus*, human-mediated transport could play a role in structuring populations of *S. insularis*. The species is rarely taken from the interior of islands and is occasionally found in human dwellings. It has only once been collected in Jamaica and this specimen was from Kingston, the primary port of entry, and does not seem to be established there. The regression plots from the Mantel tests (not shown) reveal some clustering of points, and thus it may be that the linear equation does not fit well. However, in the analysis using both the log genetic and geographic distances, the points are more dispersed, yet there is still no significant pattern of isolation by distance.

4.2. Within-island monophyly and structure

4.2.1. Large islands: Greater Antilles

Tests of within-island monophyly and partitioning of molecular variation which used both gene trees and AMOVA, revealed no pattern of within-island monophyly from the Bayesian analysis of sequence data in *S. insularis*, though the raw data indicated a significant trend between genetic and geographic distance. *Selenops lindborgi*, on the other hand, showed some within-island monophyly, but with multiple colonizations and subsequent diversifications within islands. It would then seem that there is at least some migration between Puerto Rico and the Virgin Islands, although not enough to create a signature of persistent gene flow. For the remaining populations in Great Inagua, St. Kitts and Nevis (SKN) and St. Croix, there is no apparent gene flow between populations from the Greater Antilles or Virgin Islands. The specimens from SKN seem to be a relatively new group of populations, perhaps originating in St. Croix, as there is little differentiation within SKN, and apparently some unsorted haplotypes from St.Croix. To date, *Selenops* is the only taxon which demonstrates a sister relationship between St. Croix and St. Kitts or these two populations and Great Inagua. The AMOVA showed that there was significant variation among islands in both *S. lindborgi* and *S. insularis*.

4.2.2. Small islands: Lesser Antilles

Selenops 'n. sp. 1' from the NLA differs from all of the other species in having well-differentiated clades, with little-to-no support and apparently low site fidelity. Because this species is restricted to the northernmost Lesser Antilles and all of the islands on which it occurs are relatively young (>5 to <0.1 My — Powell et al., 2005), it either did occur elsewhere and has since become extinct, or more likely it is a relatively young species. In this case the results may be explained by insufficient time for the development of patterns of site monophyly or isolation by distance.

Within both the CLA and SLA species, there is marked correspondence between genetic and geographic breaks. Interestingly, the depths of the splits in both species differ more than in any other pair of species, with those of *S. micropalpus* being very deep and those of *S. 'n. sp. 2'* being relatively shallow (note scales on Fig. 3F and G). However, *S. micropalpus* shows no pattern of isolation by distance, while *S. 'n. sp. 2'* is the only species that shows a pattern of isolation by distance in both the analysis of the raw data and the analysis of the log (genetic distance).

In both the CLA and SLA species, a pattern of nearly complete island monophyly is present. The two exceptions from the *S. 'n. sp. 2'* data are two specimens, both from Basse-Terre, Guadeloupe, that group with specimens from both Grande Terre and Antigua. In *S. micropalpus* there are two clades from Dominica (Fig. 3G), and one is nested within specimens from St. Lucia and St. Vincent. There is no support for the St. Vincent clade, and the St. Lucia specimens belong to one unsupported clade or are unsorted haplotypes. A Martinique clade is well-supported, as is a second Dominican clade, which consists of more northerly specimens than the first Dominican clade. It would appear that the second Dominican clade may represent a recent colonization to the island. Population differentiation is distributed among islands in both *S. 'n. sp. 2'* and *S. micropalpus*.

4.3. Comparison to other studies

As mentioned previously, few population-level studies have been conducted on Caribbean taxa, particularly in a comparative manner. However, in studies that have been (Davies and Bermingham, 2002; Carstens et al., 2004; Oneal, 2009), contrasting patterns of genetic structure between lineages seem to be the rule. In bats (Carstens et al., 2004), island monophyly was rejected in two species, though not in another. However, molecular variance was not partitioned among islands, as it is in the spiders studied here. Genetic divergence does occur across some ocean passages in anoles, but does not in others (Brandley and de Queiroz, 2004). Therefore, it appears that the identity of barriers to gene flow between islands has varied both within and between taxa.

Patterns of within-island diversification also appear to vary across taxa. In Cuban *Anolis* lizards, there is evidence that intraspecific divergence was caused by past geological events (Glor et al., 2004). Among spiders in the family Pholcidae, extensive within-island diversification is known in the genera *Tainonia* in Hispaniola (Huber and Astrin, 2009) and *Modisimus* in Haiti (Huber et al., in press). These patterns contrast with the results from the *Selenops* data in which there is apparently very little within island diversification that corresponds to any earth history events. Perhaps this is due to the relative ages of the taxa in question, or differences in

niche-utilization and hence competition. Indeed, it has been suggested that the ability of anoles to specialize ecologically may allow structure to develop between populations and may in turn have served as the driving force for subsequent speciation (Ogden and Thorpe, 2002; Stenson et al., 2002; Thorpe and Stenson, 2003; Thorpe et al., 2005). In contrast, the *Selenops* species in this study demonstrate little ecological specialization (Crews et al., 2008).

A more consistent pattern is the tendency for larger islands such as Hispaniola, Puerto Rico, St. Croix and Great Inagua to have served as a source for multiple independent colonization events of smaller islands, such as St. Kitts and Nevis and the Virgin Islands (Ricklefs and Bermingham, 2008). This pattern was found here in *S. lindborgi*, and is expected based on relative island (and hence population) sizes.

5. Conclusions

Population structure of *Selenops* species from the mainland are similar to each other, but differ from those of insular *Selenops* species. Among mainland *Selenops* species, in contrast to data from several other organisms, there is no obvious pattern of population structure. This could be due to human-mediated dispersal in the spider species. It seems that geological events may have played a role in the differentiation of species, but their role is not evident at the population level.

In general, the amount of structuring within species is variable. It appears that differences are not related to whether the species is from the mainland, islands, or a particular group of islands, as the results show similarities and differences between species from each region. Most species display patterns of well-supported deep divergences with varying degrees of support for more terminal samples. An exception to this is in the species *S. insularis*, where the gene tree appears to be, for the most part, comb-like, with one basal division separating specimens from eastern Hispaniola from all other samples.

Overall, *Selenops* appear to disperse readily within large landmasses, such as Mesoamerica or the Greater Antilles. In addition, the spiders may use the larger islands as jumping off points from which they colonize smaller islands. However, the species on smaller islands necessarily have smaller population sizes, which may explain the greater amount of differentiation of small island taxa. Interestingly, in species that show patterns of island monophyly, sister taxa are not necessarily from the most geographically proximate island, indicating island distance has played a relatively minor role in dictating population structure, and thus isolation *per se* is not the most important factor in structuring these populations.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2009.10.012.

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