A biogeographical profile of the sand cockroach *Arenivaga floridensis* and its bearing on origin hypotheses for Florida scrub biota

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**Abstract**

Florida scrub is a xeric ecosystem associated with the peninsula's sand ridges, whose intermittent Pliocene–Pleistocene isolation is considered key to scrub endemism. One scrub origin hypothesis posits endemics were sourced by the Pliocene dispersal of arid-adapted taxa from southwestern North America; a second invokes Pleistocene migration within eastern North America. Only one study to date has explicitly tested these competing hypotheses, supporting an eastern origin for certain scrub angiosperms. For further perspective, we conducted a genetic analysis of an endemic arthropod, the Florida sand cockroach (*Arenivaga floridensis*), with two aims: (1) to reconstruct the peninsular colonization and residence history of *A. floridensis* and (2) determine whether its biogeographic profile favors either origin hypothesis. We sequenced the *cox2* mitochondrial gene for 237 specimens (65 populations) as well as additional loci (*cox1*, nuclear *H3*) for a subset of Florida roaches and congeners. Using Network and Bayesian inference methods, we identified three major lineages whose genetic differentiation and phylogeographical structure correspond with late Pliocene peninsula insularization, indicating *Arenivaga* was present and broadly distributed in Florida at that time. Stem and crown divergence estimates (6.36 Ma; 2.78 Ma) between *A. floridensis* and western sister taxa span a period of extensive dispersal by western biota along an arid Gulf Coast corridor. These phylogeographical and phylogenetic results yield a biogeographic profile consistent with the western origin hypothesis. Moreover, age estimates for the roach’s peninsular residence complement those of several other endemics, favoring a Pliocene (or earlier) inception of the scrub ecosystem. We argue that eastern versus western hypotheses are not mutually exclusive; rather, a composite history of colonization involving disparate biotas better explains the diverse endemism of Florida scrub.

**Keywords**

*Arenivaga*, dispersal, endemism, Florida platform, Gulf Coast corridor
INTRODUCTION

Florida scrub is a fragmented xeric ecosystem largely confined to peninsular Florida (Menges, 1999), where it is partitioned across a series of relict beach ridges that formed sequentially during the Miocene, Pliocene, and Pleistocene epochs (Scott, 1997; Figure 1). Older ridges occupy the central peninsula, whereas the youngest corresponds roughly with present shorelines (Opydyke, Spangler, Smith, Jones, & Lindquist, 1984). Following inception, most ridges experienced rounds of inundation and isolation associated with sea level fluctuation (Webb, 1990). Today, these ridges retain scrub and related sandhill ecosystems, which were considered to have been widespread on the peninsula in the late Pleistocene (Myers, 1990) but experienced significant contraction to the ridges proper under more mesic conditions of the Holocene (Watts & Hansen, 1994).

Florida’s sand ridges are characterized by quartzipsamment soils, providing porosity and drainage necessary to support the xeromorphic plant community that defines scrub—a shrubland composed of small evergreen oaks (Quercus chapmanii Sargent, Q. geminata Small, Q. inopina Ashe, Q. myrtilifolia Willdenow) interspersed with Florida rosemary (Ceratiola ericoides Michaux) and maintained by low-frequency, high-intensity fires (Menges, 1999). Scrub is inherently patchy, spatially and temporally, and its historical flux, with attendant opportunities for isolation, is considered to have promoted speciation within this ecosystem. Indeed, Florida scrub is distinguished by high levels of endemism, which includes some 40 species of plants (Christman & Judd, 1990), four vertebrates (Moler, 1992; Rodgers, Kale, & Smith, 1996), and over 50 arthropods (Deyrup, 1989). Scrub endemics vary widely in overall distribution, with some species being confined locally within a single ridge and others occupying multiple ridges.

The origin of Florida scrub biota has been variously ascribed to Pliocene or Pleistocene epochs (Hubbell, 1961; Kurz, 1942; Neill, 1957), involving a “combination of both historical and edaphic factors” (Huck et al., 1989). One long-held hypothesis invoking eastward range expansions of arid-adapted biota into peninsular Florida (Myers, 1990) is based on a rich Pliocene fossil record representing numerous extralimital species with western or tropical affinities (Meylan, 1982; Morgan & Emslie, 2010). Western taxa purportedly dispersed along a recurrent Gulf Coast corridor—a broad belt of sand scrub and savanna established by the increased aridity and lowered sea levels associated with Pliocene glaciation (Morgan & Emslie, 2010). Conversely, interglacial periods reduced corridor width, generated more mesic climatic conditions, and initiated Gulf Coast vicariance with regard to arid-adapted species. Sundered from their western lineages, Florida populations underwent allopatric speciation in xeric peninsular settings. An alternative scrub origin hypothesis, detailed in Germain-Aubrey et al. (2014), invokes southward dispersal events within eastern North America during Pleistocene glacial advances. Under this scenario, eastern taxa colonized the peninsula and, following local adaptation to xeric ridge environments, experienced ecological/spatial isolation sufficient for speciation (Swenson & Howard, 2005; Watts, 1975).

To test the two competing hypotheses, Germain-Aubrey et al. (2014) generated molecular phylogenies for four angiosperm genera, focusing on the topological placement and sister taxon relationships of respective scrub endemics. Their results were ambiguous for one plant, the scrub plum (Prunus geniculata Harper), but they identified eastern origins for the remaining three species: Lewton’s milkwort (Polygala lewtonii Small), scrub holly (Ilex opaca var. arenicola (Ashe) Ashe), and silk bay (Persea humilis Nash). However, age estimates for all four angiosperms dated to the Pliocene (or Miocene), a timeframe inconsistent with a Pleistocene colonization predicated by the eastern hypothesis. Additional reports have offered distributional data supporting eastern biogeographical sources for certain scrub taxa (Huck et al., 1989) and western sources for others (Hubbell, 1961; Zona & Judd, 1986), which suggests that eastern versus western origin hypotheses need not be mutually exclusive. With some 90 endemic species yet to be examined, a prevailing colonization pattern for Florida scrub has yet to be vetted.

Here, we examine the biogeography of a scrub arthropod, the Florida sand cockroach, Arenivaga floridensis Caudell (family Corydiidae). This species is the eastern representative of a genus otherwise distributed in arid settings from central Texas westward into California and Mexico (Hopkins, 2014a). As is characteristic of the genus, A. floridensis is fossorial and sexually dimorphic (females are wingless; Figure 1). Inhabiting scrub as well as adjacent sandhills communities, the species requires patches of open sand (Deyrup, 1994) and demonstrates a strong preference for loose substrate beneath light leaf litter of sand live oaks, Quercus geminata (Lamb, Justice, & Justice, 2006). Males occasionally engage in low, erratic flight at dusk, but juveniles and females appear to be completely fossorial (Deyrup, 1994). With populations documented from 11 peninsular ridges, A. floridensis ranks as Florida scrub’s most geographically widespread faunal endemic (Lamb, Justice, & Justice, 2006).

The overall geographic distribution of Arenivaga appears consistent with expectations of the western origin hypothesis, underscoring...
the potential of *A. floridensis* to provide additional biogeographical perspective on scrub colonization and endemism. Support for the western origin hypothesis (with concomitant rejection of the eastern origin hypothesis) would require *A. floridensis* to meet the following predictions: (1) Pliocene colonization of the Florida peninsula, (2) a derived topological placement within a phylogeny of the genus (its basal placement could potentially negate a western origin of *Arenivaga*), and (3) a nodal divergence estimate for *A. floridensis* and its sister species approximating a late Miocene–early Pliocene timeframe. To distinguish between hypotheses, we present a detailed intraspecific phylogeography for *A. floridensis* in conjunction with a phylogeny for the species and selected congeners. We compare spatiotemporal patterns of our results with the aforementioned predictions to assess support or refutation of the western origin hypothesis.

## METHODS

### 2.1 Sampling and sequencing regimens

To examine genetic variation in *Arenivaga floridensis*, we pursued a dense intra- and inter-ridge sampling survey that yielded 237 roaches representing 65 localities throughout the species’ range (Appendix). Most specimens were captured by sifting sand samples through a two-tier wire-mesh (7.0 and 3.0 mm) sieve, which retains all but the smallest nymphs. Roaches were preserved in 95% ethanol, and a rear leg of each was processed for genomic DNA using Qiagen’s DNeasy kit. We selected the mitochondrial gene cytochrome oxidase I (cox1) and nuclear histone 3 (H3), amplified as detailed in Larkin et al. (2007) and translated to ensure correct reading frames. GeneCodex, Ann Arbor, MI, were aligned in CLUSTALX ver. 2.0 using the MRBAYES “sump” command and the program TRACER (Leigh & Bryant, 2015). We used Bayesian inference (BI) analysis to estimate phylogenetic relationships within *A. floridensis* (cox2 dataset) and, subsequently, among species (multilocus dataset). Best-fit codon partitioning schemes and nucleotide substitution models were selected using the Bayesian information criterion (PartitionFinder v.1.1.0; Lanfear, Calcott, Ho, & Guindon, 2012). We used MRBAYES v.3.2.3 (Ronquist et al., 2012) to execute two concurrent runs involving four simultaneous chains of 20 million Markov chain Monte Carlo generations, sampling trees every 1,000 generations. The first 25% of the posterior distribution were discarded as burn-in. Likelihood values for postanalysis trees and parameters were evaluated for convergence using the MRBAYES “sumt” command and the program TRACER v. 1.6 (http://evolve.zoo.ox.ac.uk/software.html?id=tracer). We used the MRBAYES “sumt” command to generate a majority-rule consensus tree and calculate posterior probabilities (PP) for consensus nodes.

| Gene | Primer | Sequence (5′–3′) | Anneal. temp. (°C) | Cycles | Reference |
|------|--------|-----------------|--------------------|--------|-----------|
| cox1 | C1-J-2183 | CAA CAT TTA TTT TGA TTT TTT G | 50 | 32 | Simon et al. (1994) |
| | Roach-t-Leucine⁄ | TCC ATT GCA CTA ATC TGC CA | | | This study |
| cox2 | TL2-J-3037 | ATG GCA GAT TAG TGC AAT GG | 50 | 32 | Simon et al. (1994) |
| | TK-N-3785 | GTT TAA GAG ACC AGT ACT TG | | | |
| H3 | HexAF | ATG GCT ACC AAG CAG ACG GC | 61.5 | 45 | Ogden and Whiting (2003) |
| | HexAR | ATA TCC TTG GGC ATG ATG GTG AC | | | |

| TABLE 1 | Primers and cycling conditions used for DNA amplification |

*‡A version of Simon et al.’s (1994) TL2-N-3014, modified slightly for roaches.*
2.3 | Divergence time estimations

Divergence time estimates between the Florida lineages and between A. floridensis and western roach species were calculated using BEAST 1.8.2 (Drummond, Suchard, Xie, & Rambaut, 2012). Without fossil calibrations for Arenivaga, we used a substitution rate estimated across 15 beetle species for cox2 (Pons, Ribera, Bertranpetit, & Balke, 2010) and an average of rates estimated for Hawaiian katydids (Shapiro, Strazanac, & Roderick, 2006) and beetles (Andújar, Serrano, & Gómez-Zurita, 2012; Papadopoulou, Anastasiou, & Vogler, 2010; Pons et al., 2010) for cox1. Three partitions were analyzed (cox1, cox2, and H3; each separated by codon position) under PartitionFinder chosen substitution models and a birth–death speciation prior. Runs comprised 50 million generations and were sampled every 1,000 generations. To date the nodes, we used the following rates of substitution: cox2 = 0.02610 substitutions per site per million yrs per lineage (subs/s/My/l) and cox1 = 0.03605 subs/s/My/l. Under each model, the two nonfixed rates were estimated under a LogNormal relaxed clock. Two independent BEAST analyses were conducted and combined using LOGCOMBINER, with the first 10% of each run discarded as burn-in. Convergence of analyses were conducted and combined using LOGCOMBINER, subs/s/My/l. Under each model, the two nonfixed rates were estimated under a LogNormal relaxed clock. Two independent BEAST analyses were conducted and combined using LOGCOMBINER, with the first 10% of each run discarded as burn-in. Convergence of parameters was accessed using TRACER, and trees were summed using TREEANNOTATOR.

In light of potential issues with concatenated gene data, we also produced a time-calibrated species tree using StarBEAST2 (Ogilvie, Bouckaert, & Drummond, 2016) in BEAST2 v2.4.5 (Bouckaert et al., 2014). Site models, clock models, and topologies were unlinked between the mitochondrial and nuclear loci; ploidy assignments for cox1 and cox2 were designated haploid, and H3 was designated diploid. The population model was set as “Analytical Population Size Integration.” Topologies and divergence times were estimated as in BEAST analysis above, using the cox2 calibration rate.

3 | RESULTS

3.1 | Haplotype distribution, phylogeography, and phylogenetics

We obtained a 684-bp fragment—effectively, the entire cox2 gene—for all 237 specimens; sequence comparisons revealed 91 unique haplotypes (Appendix). Haplotype distribution was extremely localized, with 88 of the 91 haplotypes (97%) being observed at single localities. Three haplotypes (Fp2, SB1, Vl) representing more than one locality were limited to proximate sites 2–12 km apart. No haplotypes were shared between ridges despite the fact that certain inter-ridge populations were within 5 km of each other. Such localized spatial distribution, in part a function of scrub patchiness, may also reflect the species’ limited vagility: Arenivaga floridensis is restricted to friable, sandy soils (Deyrup, 1994), and the wingless females may impose additional dispersal constraints.

The BI consensus tree for cox 2 identified three strongly supported lineages (PP > 0.99), with evident phylogeographical structure observed within and across lineages (Figures 2 and 3). The largest lineage, genetically and geographically, is designated the Atlantic-Central Lineage. Comprising 50 haplotypes, it encompasses four major (Atlantic Coastal, Mount Dora, Northern Brooksville, and Trail) and five minor (Bell, Crescent City, DeLand, Orlando, and Winter Haven) ridges and as well as adjacent sandy uplands. This lineage also includes a five-member haplogroup (CI1, CI2, LL1, LL2, and PR) from the northern end of Lake Wales Ridge. However, the 18 remaining Lake Wales localities, which span the southern 140 km of the ridge’s 186 km north–south axis, constitute a second distinct lineage of 29 haplotypes, appropriately termed the Lake Wales Lineage. The third lineage is distributed across a single major (Southern Brooksville) and minor ridge (Cotton Plant) and two disjunct scrub parcels (Cedar Key, Tampa Bay). With just 13 haplotypes, this, the Southern Brooksville Lineage, is the smallest but most genetically distinct lineage, constituting the sister group to the Atlantic-Central/Lake Wales clade. These three major lineages were also identified in both SPLITSTREE (Figure 3) and TCS haplotype networks (not illustrated), the latter providing finer details of phylogeographic structure less pertinent to the predictions being tested.

The three lineages were again recovered (all PP = 1.0) in the concatenated BI analysis but with higher nodal support for the Atlantic-Central/Lake Wales clade (PP = 0.98; Figure 4) than in the cox2 tree (PP = 0.79). The concatenated tree also reveals strongly supported interspecific relationships (all PP = 1.0), which are topologically congruent with Hopkins and Giernakowski’s (2014) molecular–morphological phylogeny for the genus. Namely, Arenivaga floridensis is recovered as the sister taxon to an A. erratica + A. tonkawa clade, whereas the species A. gumperzae, A. gaiophanes, and A. bolianna represent increasingly divergent clades.

3.2 | Divergence dating

Cox2 divergence time estimates within A. floridensis and among species are depicted in Figure 5. The nodal age between the Lake Wales and Atlantic-Central lineages is estimated to be 2.27 Ma (95% highest posterior density [HPD]: 2.92–1.71), whereas coalescence of all three roach lineages dates to 2.78 Ma (HPD: 3.61–2.08). The nodal age estimated for the floridensis–erratica+tonkawa clade is 6.36 Ma (HPD: 8.39–4.69). The species tree generated in StarBEAST2 yielded an identical topology (Figure S3), though with weaker nodal support (a function of limited variation in H3) and a slightly younger age estimate for floridensis–erratica+tonkawa clade (cox2 = 4.02 Ma; HPD: 5.40–2.26). In turn, cox1 divergence time estimates are older (BEAST consensus tree; Figure S4), with the Lake Wales and Atlantic-Central clade dating to 3.17 Ma (HPD: 3.98–2.47), lineage coalescence for A. floridensis to 3.88 Ma (HPD: 4.89–2.99) and the floridensis–erratica+tonkawa clade to 8.84 Ma (HPD: 11.33–6.61). Although the Arenivaga age estimates should be interpreted with caution in the absence of fossil calibration, we note that cox2 and cox1 HPD intervals exhibit substantial overlap for each of the three nodes. Furthermore, both genes offer general timeframes for peninsular colonization (late Miocene–Pliocene) and ridge population isolation (Pliocene) that clearly predate the Pleistocene.
DISCUSSION

4.1 | Phylogeographical structure and lineage ages

Our genetic survey of *Arenivaga floridensis* reveals a scrub endemic characterized by pronounced phylogeographical structure, much of it partitioned by sand ridges. Genetic differentiation among the three major lineages is likely attributable to isolation imposed by episodic marine transgressions, which inundated substantial portions of Florida during the Pliocene and Pleistocene epochs. Estimated lineage ages correspond closely with peninsular fragmentation during the Pliocene warm period (3.2–2.7 Ma) when sea levels rose significantly, with a peak some 22 m higher than present day (Miller et al., 2012). Nonetheless, peninsular uplands emergent at this time were likely limited to portions of the Lake Wales, Mount Dora, Trail, and Southern Brooksville ridges, which offer striking geographical congruence with the Lake Wales, Central-Atlantic, and Southern Brooksville lineages (Figure 3). The older age observed for the Southern Brooksville Lineage suggests a longer isolation history, which is consistent with the presence of specific Southern Brooksville endemics (Deyrup, 2005; Neill, 1957; Squitier, Deyrup, & Capinera, 1998) and notable absence of more widespread scrub species, for example, the Florida sand skink, *Plestiodon reynoldsi* (Stejneger), and Florida scrub lizard, *Sceloporus woodi* Stejneger. Uniquely, the Lake Wales Ridge is inhabited by populations representing two major lineages: the Lake Wales Lineage, present from the ridge’s central portion to its southern terminus, and the Atlantic-Central Lineage, represented by a 5-member haplogroup confined to the ridge’s northernmost sector. The presence of Atlantic-Central haplotypes on the Lake Wales Ridge could reflect dispersal from the adjacent Mount Dora.
Ridge. However, phylogeographical structuring in a second scrub endemic, the aforementioned Florida sand skink, provides a more compelling interpretation. Substantive mtDNA divergence (cob, 4.5%) between skink populations from northern Lake Wales and those further south (Richmond, Reid, Ashton, & Zamudio, 2009) exhibits precise geographical congruence and a similar level of divergence (cox2, 5.5%) with roach haplotypes. Their genealogical concordance suggests a shared history whereby codistributed ancestral populations experienced vicariant separation in the northern Lake Wales Ridge. Overall, the phylogeography of *A. floridensis* reveals the combined influences of relatively early colonization (2.78 Ma), close edaphic ties to peninsular ridges, and an episodic flux of scrub habitat under the climatic oscillations of Plio-Pleistocene glaciation. Divergence levels detected for the three major lineages clearly support prediction 1 of the western origin hypothesis: *Arenivaga floridensis* has been present on the Florida peninsula since the Pliocene. Moreover, the roach’s fidelity to Florida scrub and persistence through rounds of ecosystem expansion/fragmentation are aptly reflected in its phylogeographical complexity.

### 4.2 A western origin for *Arenivaga floridensis*

*Arenivaga* comprises a desert-dwelling clade of roaches distributed largely within southwestern North America. The genus is now recognized as being far more species rich (48 vs. 9 spp) than traditionally perceived, with its highest levels of diversity centered in northern Mexico (Hopkins, 2014a). Although *A. floridensis* is considered to be the only species native to the southeastern United States, we note that two male specimens of *A. bolliana* have been collected in Florida (from the cities of Gainesville and Seminole). Otherwise, the eastern range boundary of *A. bolliana* terminates in Texas (some 1,400 km west); if viable populations do occur in Florida, they were probably
recently introduced and remain extremely localized. Hopkins and Giermakowski’s (2014) phylogeny of *Arenivaga* (24 of the 48 species) identified *A. erratica* as the sister species to *A. floridensis*, providing consistency with an earlier morphological interpretation that placed *A. floridensis* in the “erratica group” (Hebard, 1920). Our phylogeny differs slightly, recovering a sister group relationship between *A. floridensis* and *A. erratica* + *A. tonkawa*. This topological discrepancy probably reflects the influence of morphological characters in Hopkins and Giermakowski’s (2014) integrated dataset. Hopkins’ (2014b) BI consensus trees for DNA sequence data, generated separately for *cox1*, *12S*, and *H3* genes, depict slightly different relationships among these three species, although all are invariably recovered in the same clade.

Topological placement of *A. floridensis*, relative to other congeners, reveals a derived position within the genus, both in our BI tree and in Hopkins and Giermakowski’s (2014) phylogeny. As well, their phylogeny depicts a Baja California endemic, *Arenivaga diaphana* Hopkins, as the sister taxon to the remaining 23 species surveyed, which corroborates southwestern North America as the center of origin for *Arenivaga*. Our estimated dates for the most recent common ancestor of *A. floridensis* and *A. erratica* + *A. tonkawa* (6.36 Ma) provide a
timeframe spanning the late Miocene to early Pliocene epochs. Arid conditions linking Florida and southwestern North America at this time facilitated biotic interchange and account for a strong western influence on the peninsula’s Plio-Pleistocene faunas (Krysko, Nuñez, Lippi, Smith, & Granatosky, 2016; Morgan & Emslie, 2010). Complementary patterns in diversity, distribution, and phylogenetic relationships for *Arenivaga*, together with nodal estimates for the *eratica-floridensis-tonkawa* clade, provide spatiotemporal consistency with an eastward migration from southwestern North America. These results satisfy predictions 2 (derived topological placement) and 3 (appropriate sister taxon divergence estimate) of the western origin hypothesis.

### 4.3 | Reevaluating scrub origin hypotheses

Our phylogeographical and phylogenetic results for *Arenivaga* support a different scrub origin hypothesis than Germain-Aubrey et al.’s (2014) angiosperm phylogenies but, importantly, indicate that the two hypotheses are not mutually exclusive. Although no other studies have actually tested either hypothesis, it is possible to infer eastern versus western origins for additional scrub endemics (or near endemics) from published phylogenies. For example, the evolutionary history of the Florida scrub-jay exhibits remarkable parallels with that of *Arenivaga floridensis*. The Florida scrub-jay—also the sole eastern representative of its genus—is sister taxon to four western species that form the ‘scrub-jay group’ within *Aphelocoma* jays (McCormack et al., 2011). Sequence divergence (mitochondrial *cob* and *nad2*) between the Florida and western scrub-jays, at 8.0%, with a nodal estimate of ~6.0 Ma (McCormack et al., 2011), corresponds with our observed *cox2* divergence and age estimate between *Arenivaga floridensis* and *A. erratica* + *A. tonkawa* (8.6%, 6.36 Ma). This case, together with phylogenies for additional taxa (Table 2), reveal unequivocal eastern and western contributions to Florida scrub biota. The eastern origin hypothesis advocates a Pleistocene inception of Florida scrub, invoking dispersal of eastern North American species onto the peninsula in response to glacial advances between 2.56 Ma and 10 ka. Compiling Germain-Aubrey et al.’s (2014) phylogenetic results with those of others, we identified eight scrub endemics with sister species from eastern North America (Table 2). However, only two cases appear indicative of Pleistocene speciation. The first involves silk bay, *Persea humilis*, and closely related taxa, *Persea borbonia* (L.) Sprengel and *Persea palustris* (Rafinesque) Sargent, which form a clade dating to near the Pliocene–Pleistocene interface (Germain-Aubrey et al., 2014). The second example involves the grasshopper *Schistocerca ceratiola* Hubbell and Walker, an obligate, sedentary specialist on Florida rosemary that exhibits minimal genetic distance across ridges (0.16%–0.3%; Lamb & Justice, 2005) and recent divergence (~0.6 Ma) from its sister species (Song, Moulton, Hiatt, & Whiting, 2013). If the western origin cases are also considered, then age estimates for nine of ten scrub endemics date to peninsular residence times of Pliocene age or older. Although Pleistocene glaciation unquestionably influenced intraspecific phylogeography in eastern North America (Avise, 2000; Soltis et al., 2006), its role in scrub speciation appears to have

### Table 2 | Geographic origins and epoch age assignments for selected Florida scrub endemics

| Taxon | Hypothesis support | Sister taxon range | Epoch age assignment | Reference |
|-------|--------------------|-------------------|---------------------|-----------|
| **Plants** |                     |                   |                     |           |
| Florida rosemary (*Ceratiola ericoides*) | Eastern | NE | Miocene | Li, Alexander, Ward, Del Tredici, and Nicholson (2002) and Trapnell, Schmidt, Quintana-Ascencio, and Hamrick (2007) |
| Scrub holly (*Ilex opaca* var. *arenicola*) | Eastern | E | Pliocene | Germain-Aubrey et al. (2014) |
| Lewton’s polygala (*Polygala lewtonii*) | Eastern | E | Miocene | Germain-Aubrey et al. (2014) |
| Silk bay (*Persea humilis*) | Eastern | SE | Pleistocene | Germain-Aubrey et al. (2014) |
| Scrub plum (*Prunus geniculata*) | Ambiguous | NA | Mi- Pliocene interface | Germain-Aubrey et al. (2014) |
| Scrub hickory (*Carya floridana*) | Eastern | SE | Pliocene | Zhang et al. (2013) |
| Florida jujube (*Condalia celata*) | Western | SW | _ | Islam and Guralnick (2015) |
| **Animals** |                     |                   |                     |           |
| Florida scrub-jay (*Aphelocoma coerulescens*) | Western | SW | Mi- Pliocene interface | McCormack, Heled, Delaney, Peterson, and Knowles (2011) |
| Florida sand skink (*Plestiodon reynoldsi*) | Eastern | SE | Miocene | Brandley et al. (2011) |
| Florida scrub lizard (*Sceloporus woodi*) | Eastern | SE | _ | Wiens, Kuczynski, Arif, and Reeder (2010) |
| Rosemary grasshopper (*Schistocerca ceratiola*) | Eastern | SE | Pleistocene | Song (2004) and Song et al. (2013) |

*North American sectors abbreviated as: E = eastern, NA = North America, NE = northeastern, SE = southeastern, SW = southwestern.*
been minimal. Germain-Aubrey et al. (2014) noted a Miocene cooling trend in eastern North American (Foster, Lunt, & Parrish, 2010) that may have elicited earlier southward migrations, which would provide greater temporal consistency with observed genetic differentiation between scrub endemics and their sister taxa. We have provided the first molecular phylogenetic evidence used to test and confirm the western origin hypothesis for a Florida scrub endemic and have compiled additional molecular phylogenies identifying both eastern and western progenitors to scrub species. These cases reveal more examples of eastern origin than western, and proximity alone would seem to favor eastern contribution potential over intermittent dispersal from the southwest. Still, we hesitate to endorse a prevailing eastern assembly when the evolutionary histories for most scrub species have yet to be determined. It is clear now, however, that arguments for a single regional source leading to the inception of this ecosystem can be rightly dismissed; rather, a composite biogeographical history involving disparate biotas better explains Florida scrub origins and endemism.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

TL conceived the project; TJ, PM, TL, and JB collected specimens; TJ and TL generated/analyzed sequence data; MB and JB conducted network and phylogenetic analyses; HH provided material and sequence data for the western Arenivaga; TL wrote the manuscript; MB generated figures and contributed to the text.

DATA ACCESSIBILITY

DNA sequences: GenBank accession numbers—DQ873966.1, DQ874280.1, FJ830540.1, KP986405.1, MG761831–MG761994.

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found online in the supporting information tab for this article.

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**APPENDIX**

Localities, coordinates, sample sizes, and *cox2* haplotype designations (derived from locality abbreviations) for populations of *Arenivaga floridensis*, partitioned by ridges, from north to south

| Ridge                          | Coordinates         | \( n \) | Haplotype (\( n \)) |
|-------------------------------|---------------------|--------|---------------------|
| Trail                         |                     |        |                     |
| Gold Head State Park          | 29.82782, –81.94990 | 4      | GH (4)              |
| Ordway Preserve               | 29.72840, –81.97990 | 2      | Od (2)              |
| Interlachen                   | 29.6243, –81.9198   | 2      | It (2)              |
| Atlantic Coastal              |                     | 35     |                     |
| Roseland                      | 27.82842, –80.47814 | 2      | Ro1 (1), Ro2 (1)    |
| Viking                        | 27.54285, –80.36295 | 3      | Vi (3)              |
| Ft. Pierce                    | 27.47035, –80.33381 | 5      | Vi (5)              |
| Savannas State Preserve       | 27.29906, –80.25837 | 4      | Sa (4)              |
| Hobe Sound A                  | 27.10840, –80.16827 | 3      | HS1 (3)             |
| Hobe Sound B                  | 27.05972, –80.14045 | 5      | HS2(4), HS3 (1)     |
| Jonathan Dickinson State Park | 27.01693, –80.11015 | 3      | JD (3)              |
| Jupiter Ridge Natural Area    | 26.91608, –80.07305 | 4      | JR (4)              |
| Juno Beach                    | 26.87847, –80.05540 | 6      | JB (6)              |
| Bell                          |                     | 4      |                     |
| Bell                          | 29.79037, –82.85362 | 6      | Be1(3), Be2 (1)     |
| Northern Brooksville          |                     | 15     |                     |
| Archer                        | 29.50267, –82.57250 | 5      | Ar1 (2), Ar2 (3)    |
| Newberry                      | 29.6313, –82.7050   | 5      | Ne (5)              |
| Northern Brooksville Ridge (south) | 29.11872, –82.44727 | 1      | NB                  |
| Williston                     | 29.3314, –82.5367   | 4      | WI1 (3), WI2 (1)    |
| Crescent City                 |                     | 11     |                     |
| Pomona Park                   | 29.49041, –81.58434 | 5      | PP1 (4), PP2 (1)    |
| Como Lake A                   | 29.46995, –81.60461 | 5      | Co1 (3), Co2 (2)    |
| Como Lake B                   | 29.47275, –81.59063 | 1      | Co3 (1)             |

(Continues)
### Ridge Coordinates

| Ridge                                | Coordinates            | n   | Haplotype (n)                      |
|--------------------------------------|------------------------|-----|-----------------------------------|
| DeLand                               | 4 1                    |     | De (3)                            |
| DeLand                               | 29.01872, −81.23567    |     |                                   |
| Cotton Plant                         | 6 3                    |     |                                   |
| Cotton Plant                         |                        |     |                                   |
| Morriston A                          | 4 1                    |     | Mo1 (3), Mo2 (1)                  |
| Morriston B                          | 2 2                    |     | Mo3 (2)                           |
| Southern Brooksville                  | 15 6                   |     |                                   |
| Dunellon                             | 3 2                    |     | Du1 (2), Du2 (1)                  |
| Weeki Wachee                         | 2 2                    |     | WW (2)                            |
| Weeki Wachee Spring                  | 3 3                    |     | WS (3)                            |
| Withlacoochee State Forest           | 7 7                    |     | WI1 (6), WI2 (1)                  |
| Mount Dora                           | 21 5                   |     |                                   |
| Ocala Natl. Forest, Lake Kerr        | 4 4                    |     | Oc (4)                            |
| Ocala Natl. Forest, firetower        | 6 6                    |     | Oc (6)                            |
| Ocala Natl. Forest, Astor Park       | 2 2                    |     | AP (2)                            |
| Ocala Natl. Forest, Tomahawk Lake   | 5 5                    |     | TL (5)                            |
| Wekiwa Springs State Park            | 4 4                    |     | We1 (3), We2 (1)                  |
| Lake Apopka                          | 2 2                    |     | LA (2)                            |
| Orlando                              | 3 1                    |     |                                   |
| Orlando                              |                        |     |                                   |
| Lake Wales                           | 83 35                  |     |                                   |
| Clermont                             | 3 3                    |     | CI1 (2), CI2 (1)                  |
| Palatlakaha River Park               | 1 1                    |     | PR (1)                            |
| Lake Louisa                          | 5 5                    |     | LL1 (3), LL2 (2)                  |
| Lake Marion                          | 4 4                    |     | LM (4)                            |
| Dundee                               | 2 2                    |     | DD (2)                            |
| Frostproof                           | 3 3                    |     | FP1 (2), FP2 (1)                  |
| Snell Creek                          | 3 3                    |     | SC (3)                            |
| Lake Wales                           | 5 5                    |     | LW1 (3), LW2 (1), LW3 (1)         |
| Warner College                       | 5 5                    |     | WC (5)                            |
| Hickory Lake Scrub Preserve          | 3 3                    |     | HL (1), FP2 (1)                   |
| Lake Streety                         | 4 4                    |     | LS (4)                            |
| Saddle Blanket Scrub Preserve        | 4 4                    |     | SB1 (2), SB2 (2)                  |
| Silver Lake                          | 5 5                    |     | SB1 (1), SL1 (2), SL2 (1), SL3 (1)|
| Carter Creek Scrub Preserve          | 4 4                    |     | CC (4)                            |
| Highlands Hammock State Park         | 4 4                    |     | HH (4)                            |
| Sebring                              | 6 6                    |     | SE1 (4), SE2 (2)                  |
| Josephine Creek                      | 4 4                    |     | JC (4)                            |
| Lake Placid                          | 5 5                    |     | LP1 (1), LP2 (3), LP3 (1)         |
| Placid Lakes                         | 2 2                    |     | PL (2)                            |
| Archbold Biological Station          | 8 8                    |     | ABS1 (5), ABS2 (1), ABS3 (2)      |
| Venus                                | 1 1                    |     | Ve (1)                            |
| Winter Haven                         | 8 5                    |     |                                   |
| Winter Haven                         | 4 4                    |     | WH1 (2), WH2 (2)                  |
| Bartow                               | 2 2                    |     | Ba (2)                            |
| McLeod Lake                          | 2 2                    |     | Mc1 (1), Mc2 (1)                  |

(Continues)
### APPENDIX (Continued)

| Ridge                      | Coordinates       | n  | Haplotype (n)                          |
|----------------------------|-------------------|----|----------------------------------------|
| Unnamed ridges/uplands     |                   |    |                                        |
| Dixie                      | 29.60855, −83.07015 | 5  | Di1 (3), Di2 (1), Wi2 (1)              |
| Indian Lake State Forest   | 29.2835, −82.0539  | 1  | IL                                     |
| Cedar Key                  | 29.18520, −83.01901 | 4  | CK (4)                                 |
| Silver Springs Shores A    | 29.06142, −81.90823 | 5  | SS1 (3), SS2 (2)                       |
| Silver Springs Shores B    | 29.0415, −81.8710  | 2  | SS3 (2)                                |
| Silver Springs Shores C    | 29.0558, −81.8846  | 1  | SS4 (1)                                |
| Tampa                      | 28.0698, −82.3948  | 6  | Ta (6)                                 |