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Geographic distribution of *Strumigenys louisianae* (Hymenoptera: Formicidae)

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Summary

Strumigenys spp. are tiny predatory ants that feed on soil arthropods. *Strumigenys louisianae* has the broadest geographic distribution of any New World *Strumigenys*. Here, I compiled >700 site records of *S. louisianae* to document its biogeography. The known range of *Strumigenys louisianae* is largely continuous from Argentina to North Carolina (and possibly Virginia and Illinois) and on most major West Indian islands. The occurrence of *S. louisianae* throughout this region in a wide diversity of habitats makes it difficult to distinguish where it is native and where it has been introduced. The possibility remains that *S. louisianae* has a very broad native range, but no introduced populations. Alternatively, some isolated *S. louisianae* populations may be exotic, such as those on the Galapagos Islands, Cocos Island, many West Indian islands, and in Arizona. Genetic analyses are needed to determine where *S. louisianae* is native and where it is exotic.

Keywords

Biogeography; island fauna; native range; West Indies

Introduction

Strumigenys spp. are tiny, cryptically colored ants. *Strumigenys* ants are slow moving and typically become motionless when disturbed. As a result, most people, including field biologists, remain unaware of their presence even in areas where *Strumigenys* ants are common. Several Old World *Strumigenys* are tramp species, spread around the world through human commerce, including *Strumigenys rogeri* (Emery), *Strumigenys membranifera* Emery, *Strumigenys emmae* (Emery), and *Strumigenys hexamera* (Brown) (Wetterer, 2011, 2012 a, b, MacGown and Wetterer, 2012). In addition, one New World species, *Strumigenys silvestrii* Emery, has begun to spread in the Old World (MacGown et al., 2012). Here, I examine the geographic distribution of *Strumigenys louisianae* Roger.

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Strumigenys louisianae is only known from the New World, but among the New World *Strumigenys*, *S. louisianae* has the widest geographic distribution and perhaps the broadest ecological tolerances. In the present study, I document the known range of *S. louisianae*, and speculate on its original native range and where it may have spread via human commerce.

When evaluating the native and exotic ranges of a species, researchers may consider a spectrum of distributional, historical, evolutionary, ecological, and genetic information (see Chapman and Carlton, 1991). Evidence considered indicative of a species' native range includes: 1) proximity to the ranges of closely related species, 2) records largely confined to a single continuous region, 3) occurrence in inland native communities, and 4) high genetic diversity. In contrast, evidence indicative of a species' exotic range includes: 1) geographic isolation from closely related species, 2) sudden appearance and spread of the species through an area discontinuous with other known populations, 3) occurrence exclusively in coastal and highly disturbed environments, and 4) low genetic diversity due to a founder effect.

Strumigenys louisianae is one of the better studied of *Strumigenys* species. Smith (1931) found that *S. louisianae* had the largest colony size of any *Strumigenys* he observed, with up to 120 workers. Creighton (1937) studied the feeding habits of *S. louisianae* and was the first to demonstrate that *Strumigenys* ants are predators. Wilson (1950, 1953) found that *S. louisianae* preferentially feed on certain Collembola. Wilson (1953) described the predatory behavior of *S. louisianae*: "When approaching a collembolan, the worker *Strumigenys* moves slowly and cautiously spreading its mandibles to the maximum angle and exposing two long hairs which arise from the paired labral lobes. These hairs extend far forward of the ant's head and apparently serve as tactile range finders for the mandibles. When they first touch the prey, its body is well within reach of the apical teeth. A sudden and convulsive snap of the mandibles literally impales it on the teeth, and drops of haemolymph often well out of the punctures... all but the largest Collembola are quickly immobilized by this action, and struggling is feeble and short-lived."

Brown (1962) wrote that *S. louisianae* was: "widespread in the Americas from Virginia and Tennessee south at least to the Tucumán area of Argentina; northward in Mexico to sheltered canyons and cultivated areas of southern Arizona; Greater Antilles (except Jamaica). Unaccountably absent from certain well-collected areas within this range, such as parts of the Canal Zone, Trinidad, and British Guiana, although plentiful in Costa Rica and at least some localities in Colombia. This species tolerates much drier conditions and will live in plantations and other cultivated situations, so perhaps it is found mostly in habitats outside the primary forest in the central parts of its range." Brown (1962) concluded that: "its range and ecological amplitude are greater than those of any other New World *Strumigenys*."

Concerning the gaps in the distribution of *S. louisianae*, Brown (1953) wrote, "The total absence of this species in collections of dacetines from Barro Colorado Island, British Guinea and Brasil is rather surprising. Perhaps it is really absent or very rare in the true rain-forest belts." In addition, there are large gaps in the known distribution of *S. louisianae* in the West Indies, where there are published records only from Puerto Rico, Haiti, Cuba, and the Bahamas.

In Florida, Deyrup (1997) usually found *S. louisianae* "in mesic forest, swamp forest, or even the edges of salt marshes," and Deyrup and Cover (2009) classified *S. louisianae* as native to Florida. In some locales, however, *S. louisianae* has been considered exotic species, introduced through human commerce. For example, Deyrup et al. (1998) categorized *S. louisianae* as an exotic in the Bahamas, writing that it was "probably introduced from the mainland Neotropics." Wittenborn and Jeschke (2011) included *S. louisianae* on their list of exotic ants that have established populations in North America. Miravete et al. (2013), in their analyses of "which ant species are being accidentally moved around the world," listed *S. louisianae* as a Nearctic species that has become introduced and established in the US. Lubin (1984) considered *S. louisianae* to be a recent introduction to the Galapagos Islands. Solomon and Mikheyev (2005) classified *S. louisianae* on Cocos Islands as "unknown origin, likely tramp species."

Taxonomy and identification

Roger (1863) described *Strumigenys louisianae* from Louisiana. Junior synonyms of *S. louisianae* include *Strumigenys unidentata* Mayr (from Brazil), *Strumigenys unispinulosa* Emery (from Costa Rica), *Strumigenys fusca* Emery (from Brazil), *Strumigenys unispinulosa longicornis* Emery (from Bolivia), *Strumigenys bruchi* Forel (from Argentina), *Strumigenys louisianae obscuriventris* Wheeler (from Puerto Rico), *Strumigenys eggersi cubaensis* Mann (from Cuba), *Strumigenys louisianae laticephala* Smith (from Mississippi), *Strumigenys louisianae costaricensis* Weber (from Costa Rica), *Strumigenys louisianae guatemalensis* Weber (from Guatemala), *Strumigenys louisianae soledadensis* Weber (from Cuba), *Strumigenys clasmospongia* Brown (from Brazil), *Strumigenys producta* Brown (from Bolivia), and *Pyramica wani* Makhan (described from Surinam). Brown (1953, 1962) analyzed the intraspecific geographic variation within *S. louisianae*. Brown (1962) concluded that for *S. louisianae*, "the long list of synonyms reflects in part the rather extreme variation shown by this species on the South American continent. More peripheral populations (North and Central America, West Indies, Argentina) tend to be more uniform both within and among themselves." Bolton (2000) wrote that *S. louisianae* "is extremely variable as regards colour, sculpture and size... The variation remains impenetrable and I strongly suspect that more than one, and maybe several, genuine species are currently concealed in *louisianae*."

Bolton (2000) placed *S. louisianae* in the *louisianae* species-group, along with *Strumigenys dubitata* Bolton (known from Costa Rica), *Strumigenys infidelis* Santschi (known from Argentina, Bolivia, Brazil, and Venezuela), and *Strumigenys mixta* Brown (known from Guatemala).

Strumigenys louisianae workers can be distinguished from most other *Strumigenys* by the regular pattern of bent-spoon-shaped hairs on their heads (Fig. 1). The long mandibles of *S. louisianae* end with an apical fork consisting of two long teeth separated by two much smaller ones. Each mandible also has one preapical tooth. Bolton (2000) includes additional characteristics to distinguish *S. louisianae* from other members of the *louisianae* species-group in Central and South America.

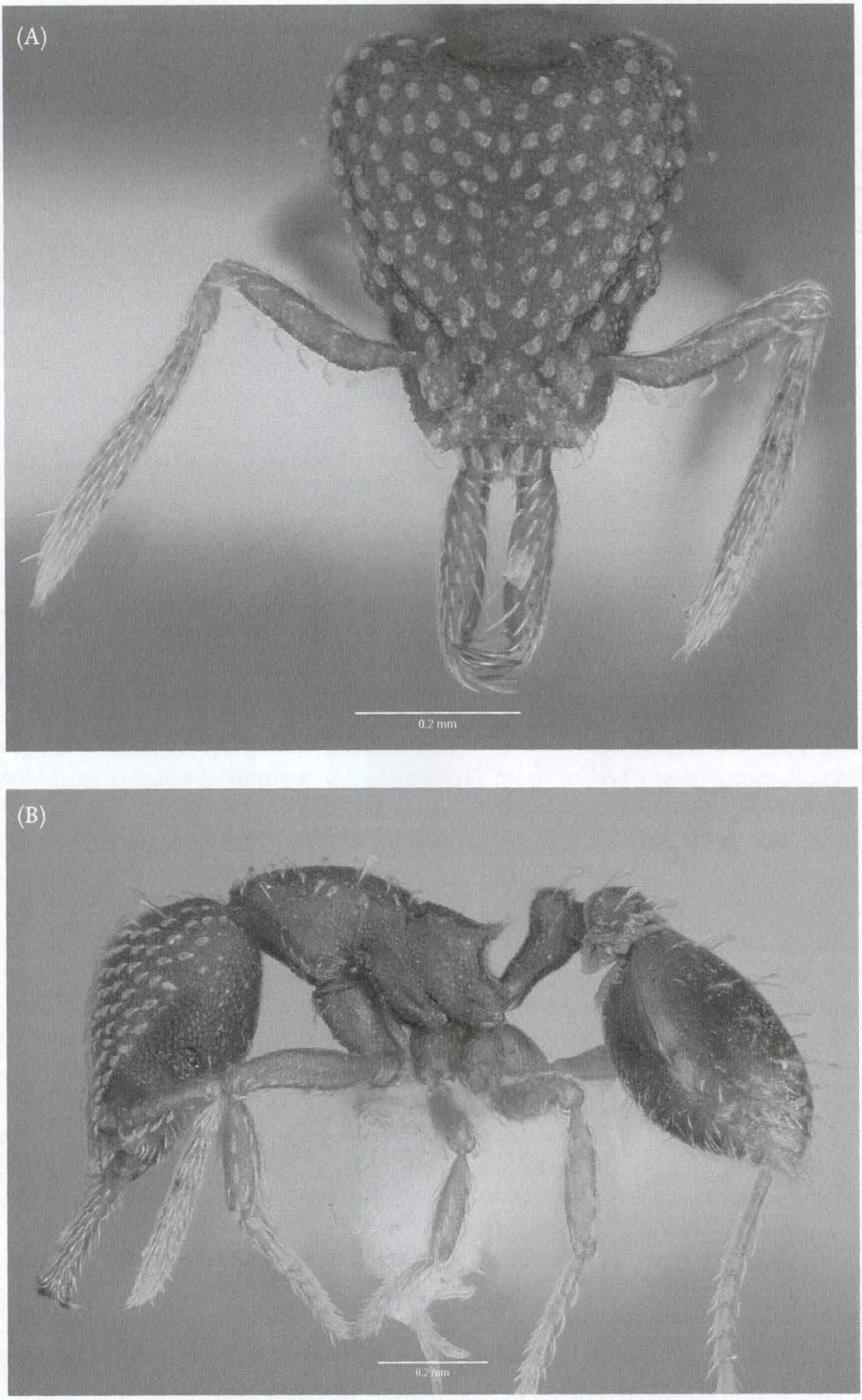

Figure 1. *Strumigenys louisianae*. (A) head, (B) lateral view, and (C) dorsal view of worker from Plantation, Florida (S.P. Cover leg.; photos by A. Nobile). This figure is published in color in the online version.

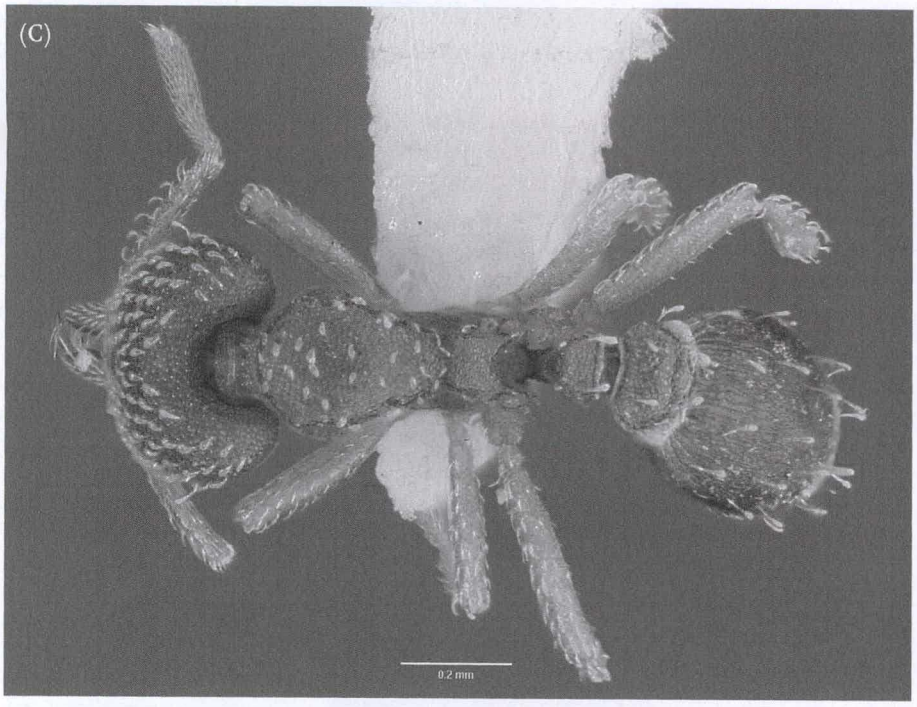

Figure 1. (*Cont.*)

The genus *Strumigenys* was formerly classified in the Tribe Dacetini. Ward & al. (2014), however, found Dacetini to be polyphyletic and instead included *Strumigenys* in the greatly expanded Tribe Attini.

Materials and methods

Using published and unpublished records, I documented the worldwide range of *S. louisianae*. I obtained unpublished site records from museum specimens in the collections of Archbold Biological Station (ABS, identified by Mark Deyrup), the Museum of Comparative Zoology (MCZ, identified by Stefan Cover), and the Smithsonian Institution (SI, identified by Barry Bolton). In addition, I used the on-line databases of Antweb (www.antweb.org), and the Global Biodiversity Information Facility (www.gbif.org). Thiago S. Ranzani da Silva sent me collection information of *S. louisianae* specimens from 32 sites in Brazil in the Museu de Zoologia da Universidade de São Paulo (MZSP, identified by C.R.F. Brandão).

I obtained geo-coordinates for collection sites from published references, specimen labels, maps, or geography web sites (e.g., earth.google.com, www.tageo.com, and www.fallingrain.com). If a site record listed a geographic region rather than a 'point locale,' and I had no other record for this region, I used the coordinates of the largest town within the region or, in the case of small islands and natural areas, the center of the region. Published records usually included collection dates. In a number of cases,

publications did not include the collection dates for specimens, but I was able to determine the approximate date based on information on the collector's travel dates or the publication date.

Results

Overall, I compiled and mapped *S. louisianae* specimen records from >700 sites (Fig. 2). I documented the earliest known records for 61 geographic areas (countries, island groups, West Indian islands, and US states), including 27 for which I found

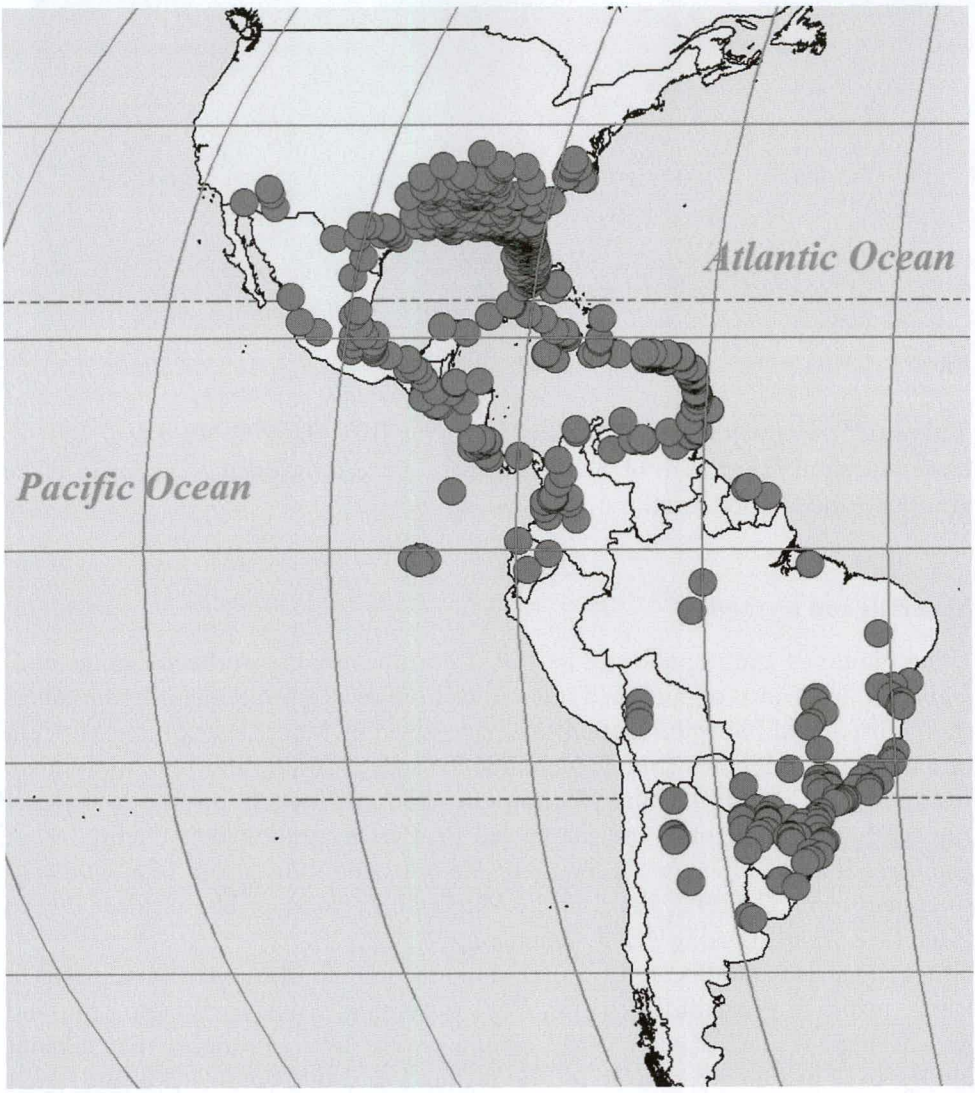

Figure 2. Geographic distribution of *Strumigenys louisianae* records. This figure is published in color in the online version.

no previously published records (Tables 1-2): Anguilla, Antigua, Barbados, Belize, Culebra, Curaçao, Dominican Republic, El Salvador, Grenada, Guadeloupe, Honduras, Jamaica, Marie Galante, Martinique, Montserrat, Providenciales, St Croix, St John, St Kitts, St Martin, St Thomas, St Vincent, St. Lucia, Tobago, Tortola, Trinidad, and Vieques.

I collected *S. louisianae* at 119 sites on 25 of 30 major West Indian islands I surveyed, including Puerto Rico, New Providence, and 23 islands for which there are no previously published records (Table 2). I also collected *S. louisianae* at three sites in El

Table 1. Earliest known records for *Strumigenys louisianae* from North, Central, and South America. Site and museum data included for specimen records. ABS: Archbold Biological Station. FM: Field Museum (from antweb.org). MCZ: Museum of Comparative Zoology. SI: Smithsonian Institution. +: no previously published records.

	Earliest record		
	Year	Reference	Locality
Louisiana	≤1863	Roger, 1863	
Costa Rica	1889	Emery, 1890 as *S. unispinulosa*	
Bolivia	1891	Emery, 1894 as *S. unispinulosa longicornis*	
Brazil	≤1887	Mayr, 1887 as *S. unidentata*	
Texas	≤1900	Wheeler, 1900	
Florida	≤1908	Wheeler, 1908	
Guatemala	1911	Weber, 1934 as *S. louisianae guatemalensis*	
Argentina	1911	Forel, 1912 as *S. bruchi*	
Mississippi	1920	Smith, 1931 as *S. louisianae laticephala*	
Arizona	1926	H. S. Barber and E. A. Schwarz; SI	Hot Springs
Mexico	1928	W.M. Mann, SI	St Lucrecia
Alabama	1929	Smith, 1931 as *S. louisianae laticephala*	
South Carolina	1932	D.E. Read, SI	Charleston
Arkansas	1936	c.u., SI	Lafayette Co.
North Carolina	≤1937	Creighton, 1937 as *S. louisianae laticephala*	
Tennessee	≤1938	Dennis, 1938	
Colombia	1938	Brown, 1953	
Georgia	1949	H.T. Vanderford, SI	Savannah
Panama	1959	H.S. Dybas, FM	Madden Forest Preserve
Surinam	1959	Kempf, 1961	
Virginia	≤1962	Brown, 1962	
Oklahoma	1962	W.G. Carter, MCZ	McCurtin Co.
Ecuador	1969	M. Deyrup, MCZ	Piedrero
Illinois	≤1971	Ross et al., 1971	
Honduras+	1979	W.L. Brown, MCZ	Lancetilla
Paraguay	≤1980	Fowler, 1981	
Venezuela	1980	P.F. Kukuk, MCZ	Parque Laguna Grande
Galapagos	≤1982	Lubin, 1984	
Nicaragua	≤1989	Bolton, 2000	
Belize+	2006	J. Mangold, ABS	Mayflower NP
French Guiana	≤2010	Dejean et al., 2011	
El Salvador+	2012	J.K. Wetterer, MCZ	La Libertad

Table 2. Earliest known records of *Strumigenys louisianae* on West Indian islands. Symbols and abbreviations as in Table 1.

	Earliest record		
	Year	Reference	Locality
Puerto Rico	1906	Wheeler, 1908 as *S. louisianae obscuriventris*	
Haiti	1912-13	Wheeler and Mann, 1914 as *S. unispinulosa*	
Cuba	1917	Mann, 1920 as *S. cubaensis*	
New Providence	1995	Deyrup et al., 1998	
North Andros	1996	Deyrup et al., 1998	
Trinidad+	2003	J.K. Wetterer, MCZ	St Augustine
Tobago+	2003	J.K. Wetterer, MCZ	Bon Accord
St Lucia+	2003	J.K. Wetterer, MCZ	Boguis
Curaçao+	2004	J.K. Wetterer, MCZ	Punda
St Thomas+	2005	J.K. Wetterer, MCZ	Hope
St Croix+	2005	J.K. Wetterer, MCZ	Frederiksted
St John+	2005	J.K. Wetterer, MCZ	Bordeaux Mtn
Tortola+	2005	J.K. Wetterer, MCZ	Sabbath Hill
Culebra+	2005	J.K. Wetterer, MCZ	South of airport
Anguilla+	2006	J.K. Wetterer, MCZ	Meads Bay
Barbados+	2006	J.K. Wetterer, MCZ	Black Rock
St Martin+	2006	J.K. Wetterer, MCZ	First Stick Hill
St Vincent+	2006	J.K. Wetterer, MCZ	La Soufriere
Vieques+	2006	J.K. Wetterer, MCZ	0.7 km SW of bunker 309
Dominican Rep+	≤2007	Wilson et al., 2007	
St Kitts+	2007	J.K. Wetterer, MCZ	Camp Bay
Antigua+	2007	J.K. Wetterer, MCZ	Seatons
Montserrat+	2007	J.K. Wetterer, MCZ	Brades
Martinique+	2008	J.K. Wetterer, MCZ	Anse Couleuvre
Guadeloupe+	2008	J.K. Wetterer, MCZ	Rivière Corossol
Marie Galante+	2008	J.K. Wetterer, MCZ	Beaurenom
Providenciales+	2010	J.K. Wetterer, MCZ	Club Med
Jamaica+	2010	J.K. Wetterer, MCZ	Montego Bay
Grenada+	2014	J.K. Wetterer, MCZ	Mardigras

Salvador. I found *S. louisianae* in a wide variety of habitats, including urban alleyways, beachfront sea grapes, botanical gardens, agricultural fields, and deep within forest reserves.

I documented site records of *S. louisianae* from every country in Central and South America except Chile, Guyana, Peru, and Uruguay. It seems likely that *S. louisianae* is actually present in all these countries, except Chile, which is isolated from the rest of South America by deserts and high mountains. Site records ranged from La Plata, Argentina (34.9°S; Forel 1912 as *S. bruchi*; Bolton 2000) in the south to Nashville, Tennessee (36.2°N; Bolton 2000) in the north (not including the questionable records from Virginia and Illinois; see below).

Brown (1962) mentioned *S. louisianae* occurring in Virginia, but gave no locale (see Introduction), so I mapped this record to Clarksville (36.6°N) in southernmost Virginia close to the northernmost record from North Carolina (36.0°N). Ross et al. (1971) wrote that *S. louisianae* "occurs in Illinois," but gave no locale, so I mapped this record to Cairo (37.2°N) in southernmost Illinois. I consider the reports of *S. louisianae* from Virginia and Illinois to be questionable because they are not based on documented specimen data and because they come from higher latitudes than that of any specimen-based records (maximum = 36.2°; see above). The Illinois record may have resulted from a misreading of specimen label data: the Global Biodiversity Information Facility (GBIF) currently lists a record of *S. louisianae* from Fisher, Illinois (http://www.gbif.org/occurrence/436431255); James N. Zahniser (pers. comm.), however, re-examined of labels and determined that the specimens actually came from Fisher Island in Florida (Illinois Natural History Survey specimens 281447 and 281448; see http://inhsinsectcollection.speciesfile.org/InsectCollection.aspx).

The oldest record of *S. louisianae* from Arizona is from "Hot Springs." Although there is currently no town by this name in Arizona, when the specimens were collected in the 1920's, a health resort "patronized by notable people from all parts of the world" called the Castle Hot Springs Hotel listed its address as "Hot Springs, Arizona" (Castle Hot Springs Hotel, 1924). The other three Arizona records are from urban areas: from Yuma (1953; E.N. Haga; MCZ), Phoenix (Bang and Faeth, 2011), and Tucson (2006; A. Wild, pers. comm.). I found no records of *S. louisianae* from New Mexico, leaving a sizable distributional gap between West Texas and Arizona (Fig. 2).

Discussion

The closest known relatives of *Strumigenys louisianae* come from tropical South and Central America, suggesting a Neotropical origin for this species (Bolton 2000). The documented range of *Strumigenys louisianae*, however, extends far beyond the tropics with a largely continuous continental distribution from Argentina to North Carolina, and possibly Virginia and Illinois (Fig. 2). The present compilation has filled in some gaps in the distribution of *S. louisianae* in the New World pointed out by Brown (1962), including records from the former Canal Zone (Table 1), Trinidad (Table 1), and 76 site records from Brazil (Fig. 2; primarily from Bolton, 2000 and unpublished records from the MZSP). Still, conspicuous gaps remain, particularly in South America. For example, *S. louisianae* is notably absent from a recent survey of *Strumigenys* and related species in Guyana (Sosa-Calvo et al., 2010), supporting Brown's (1962) contention that this species may be rare or absent in intact tropical rainforest. *Strumigenys louisianae* is also now known from most major islands of the West Indies (Fig. 2). The occurrence of *S. louisianae* throughout this region in a wide diversity of intact and disturbed habitats makes it difficult to distinguish where it is native and where it has been introduced through human commerce.

It is plausible, though far from certain, that the isolated populations of *S. louisianae* found on the Galapagos Islands and the Cocos Island are exotic. There also appears to

be a distributional gap separating the populations of *S. louisianae* in Arizona from the closest populations in Texas. Brown (1953) wrote that a *S. louisianae* specimen collected in 1926 in Hot Springs, Arizona, "was taken under conditions that would lead one to believe that the record does not represent a chance introduction into Arizona. If so, this is a rather remarkable locality, for *louisianae* has not been taken in nature at any other point west of central Texas and north of the Mexican Border, in spite of heavy collecting by myrmecologists and other entomologists in this region." Brown (1953) did not elucidate how the *S. louisianae* specimen from Hot Springs, Colorado was collected, but is seems possible that *S. louisianae* could have been accidentally imported into the area on plants used at the local resort, Castle Hot Springs Hotel, which boasted it "occupies the entire valley" and had its own orchards and gardens, as well as "a sporty nine hole golf course" (Castle Hot Springs Hotel, 1924). The three subsequent Arizona records of *S. louisianae* all came from urban areas (Yuma, Phoenix, and Tucson), a pattern more indicative of a species that is exotic to Arizona.

The possibility remains that *S. louisianae* is a widespread, but often overlooked species, with no exotic populations. Alternatively, some *S. louisianae* populations may have been introduced by humans, such as those on the Galapagos Islands, Cocos Island, many West Indian islands, and in Arizona. Genetic analyses should be useful in determining where *S. louisianae* is native and where it may be exotic, as well as evaluating whether *S. louisianae* is actually a species group with two or more cryptic species rather than a single, highly variable species.

Whereas there is some evidence indicative of exotic spread by *S. louisianae*, and there is no evidence at all that *S. louisianae* is displacing any other species in any part of its range. In fact, Deyrup and al. (2000) suggested that an Old World tramp *Strumigenys*, *S. rogeri*, is displacing native populations of *S. louisianae* in south and central Florida.

Many questions remain concerning the ecology of *S. louisianae.* It occurs in such a wide range of habitats, so one might expect to find this species common almost anywhere in the New World tropics and subtropics, especially in disturbed habitats, but this is not the case. Tolerance for human disturbance would seem to predispose *S. louisianae* to being a tramp species, spread around the world by human commerce. However, to date *S. louisianae* has not been recorded as an exotic in the Old World. It is possible, however, that populations of this tiny, inconspicuous ant have been simply overlooked in the Old World, as was previously true of populations throughout the West Indies.

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