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Author(s): Ivan Prates, Leyla Hernandez, Ricardo R. Samelo, Ana C. Carnaval

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Molecular Identification and Geographic Origin of an Exotic Anole Lizard Introduced to Brazil, with Remarks on Its Natural History

Ivan Prates[1,2,*], Leyla Hernandez[1], Ricardo R. Samelo[3], Ana C. Carnaval[1,2]

[1] *Department of Biology, City College of New York. New York, New York 10031, USA.*
[2] *Department of Biology, Graduate Center, City University of New York. New York, New York 10016, USA.*
[3] *Campus Santos-Rangel, Instituto de Ciências da Saúde, Universidade Paulista. CEP 11045-300, Santos, SP, Brazil.*
* *Corresponding author. Email: ivanprates@gmail.com*

Abstract. Introduced species are major drivers of biodiversity loss worldwide. Several squamate taxa have become established outside of their native ranges after human-mediated transportation, becoming a conservation concern. We report on the occurrence of an exotic anole lizard in the Baixada Santista region in coastal Brazil. To clarify the species' identity and examine the geographic source of its introduction, we generated sequences of one mitochondrial DNA marker. The anole is genetically closest to species in the *Anolis carolinensis* group (Dactyloidae), which does not occur naturally in South America. Phylogenetic analyses found that samples from Brazil nest within *A. porcatus,* a Cuban species that has also been introduced into Florida and the Dominican Republic. Results indicate that Brazilian *A. porcatus* are nested among samples from La Habana, Matanzas, and Pinar del Río, which may suggest a western Cuban source of introduction. Nevertheless, Brazilian samples also cluster closely with a sample from Florida, which may suggest that the Brazilian population originated from lizards exotic elsewhere. High densities of adults and juveniles suggest that it comprises a well-established reproductive population in Brazil, thriving in urban and industrial areas. Introduction of *A. porcatus* may be related to the presence of a major seaport in the study region. Further assessments are needed to uncover whether this species will be able to expand into the surrounding Atlantic Rainforest, and whether it will impact the local communities, including native anoles. This study demonstrates the usefulness of molecular approaches for proper species identification in a group of aggressive invaders characterized by morphological conservatism, hybridization, and convoluted taxonomy.

Keywords. *Anolis;* Atlantic Forest; Green anole; Invasive species; Phylogeography.

Resumo. Espécies introduzidas são um dos principais fatores que levam à perda de biodiversidade em nível global. Vários répteis Squamata se estabeleceram fora de sua área de ocorrência natural após transporte mediado pelo ser humano, tornando-se motivos de preocupação em termos de conservação biológica. Relatamos a ocorrência de um lagarto exótico na região da Baixada Santista, na costa sudeste do Brasil. Para clarificar a identidade da espécie e examinar a origem geográfica de sua introdução no Brasil, foram geradas sequências de DNA de um marcador mitocondrial. O lagarto é geneticamente mais próximo de espécies do grupo *Anolis carolinensis* (Dactyloidae), que não ocorre naturalmente na América do Sul. Análises filogenéticas revelam que as amostras do Brasil se inserem dentro de *A. porcatus,* uma espécie de Cuba que também foi introduzida na Flórida e na República Dominicana. Os resultados indicam que *A. porcatus* brasileiros se inserem próximos à amostras de La Habana, Matanzas e Pinar del Río, o que pode sugerir uma origem no oeste da ilha de Cuba. Entretanto, as amostras do Brasil também se agrupam proximamente à uma amostra da Flórida, o que pode sugerir que esses lagartos se originaram de uma população também exótica de *A. porcatus.* Altas densidades de adultos e jovens sugerem que se trata de uma população reprodutiva bem estabelecida no Brasil, que prospera em áreas urbanas e industriais. A introdução de *A. porcatus* pode estar relacionada com a presença de um porto marítimo na região de estudo. Avaliações posteriores serão necessárias para esclarecer se a espécie será capaz de expandir sua distribuição para a Mata Atlântica ao redor, bem como se ela impactará as comunidades ecológicas locais, incluindo as espécies nativas de *Anolis.* Este estudo demonstra o papel fundamental das abordagens moleculares para identificação adequada de espécies em um grupo de invasores agressivos caracterizados por morfologia conservada, hibridização e taxonomia complexa.

INTRODUCTION

Introduced species are one of the main drivers of biodiversity loss worldwide. Exotic organisms modify local environments, introduce pathogens, and impose new competition and predation pressures upon native taxa, which may decline to the point of extinction (Mack et al., 2000; Blackburn et al., 2014). A number of squamate species have become successfully established outside of their native ranges as a result of human-mediated transportation and release, often becoming a major conservation concern (Kraus, 2015). Several of these introductions involve anole lizards, genus *Anolis* Daudin, 1802 (Dactyloidae), an ecologically diverse group composed of approximately 400 species originally distributed in the Caribbean islands and mainland Americas (Losos, 2009). Exotic anoles have been introduced into Japan, Singapore, Taiwan, Hawaii, the continental U.S., and beyond (e.g., Goldberg and Bursey, 2000; Kolbe et al., 2007; Huang et al., 2008; Toda et al., 2010; Tan and Kim, 2012). Because the biogeographic history of the *Anolis* clade is characterized by recurrent long-distance dispersal, anole lizards have been regarded as physiologically and ecologically hardwired for colonization (Williams, 1969).

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Anoles can significantly impact local ecological communities once they become invasive (Kraus, 2015). For instance, *Anolis carolinensis* Voigt, 1832, native to the southeastern U.S., and *A. sagrei* Duméril and Bibron, 1837, originally from Cuba, led to decreased abundance and local extinction of arthropod taxa in Japan and Taiwan, respectively (Huang et al., 2008; Toda et al., 2010). Exotic anoles can also displace native ones, as in the case of *A. sagrei,* which led to microhabitat shifts by *A. carolinensis* in Florida (Stuart et al., 2014). Eradicating invasive anoles has proven to be a significant challenge, sometimes with devastating consequences for native lizard species (Ishikawa et al., 2012). It is therefore key to detect and report instances of introduction by these potentially aggressive invaders, as well as to document their geographic spread in colonized regions.

Recently, an exotic anole lizard (Fig. 1) was recorded in the city of Santos in the Baixada Santista region of coastal southeastern Brazil (Samelo and Barrella, 2016). It has been tentatively identified as the Cuban green anole, *Anolis porcatus* Gray, 1840, a member of the *A. carolinensis* species group. However, species identification in this group is complicated by morphological conservatism, instances of hybridization, and cases of paraphyly among species (Glor et al., 2004, 2005). For instance, it is unclear whether *A. porcatus* is morphologically distinguishable from the North American green anole, *A. carolinensis* (Kolbe et al., 2007). Molecular studies indicate that *A. carolinensis* is phylogenetically nested within *A. porcatus,* suggesting that the North American populations descend from *A. porcatus* from western Cuba (Glor et al., 2005; Campbell-Staton et al., 2012). Moreover, populations of *A. porcatus* in western and eastern Cuba do not form a clade, indicating that the eastern group may represent an undescribed species (Glor et al., 2004, 2005; Campbell-Staton et al., 2012). Lastly, *A. porcatus* can hybridize with *A. allisoni* Barbour, 1928 in Cuba (Glor et al., 2004, 2005).

In the face of these sources of taxonomic uncertainty, we performed a study based on DNA sequences to test the proposed identification of the anole species introduced in Brazil and to identify the geographic source of this introduction. To examine whether the exotic lizard is established more broadly, we also sampled additional sites in the Baixada Santista. Based on these results, and in the light of available natural history data, we discuss this lizard's potential for range expansion and impact on native taxa.

MATERIALS AND METHODS

Sampling of specimens

We began our survey by identifying sites potentially occupied by the alien anole, based on interviews with residents of the Baixada Santista area, state of São Paulo. Because these lizards perform conspicuous dewlap displays, they have become easily recognized by local residents. Guided by these informal reports, we performed fieldwork in the municipalities of Santos, São Vicente and Guarujá in September of 2015 (Fig. 2).

Our surveys were performed during the day and involved two researchers (IP and RRS). At each site, we recorded the number of lizard observations and collected voucher specimens for identification in the laboratory. Animals were euthanized with an intraperitoneal

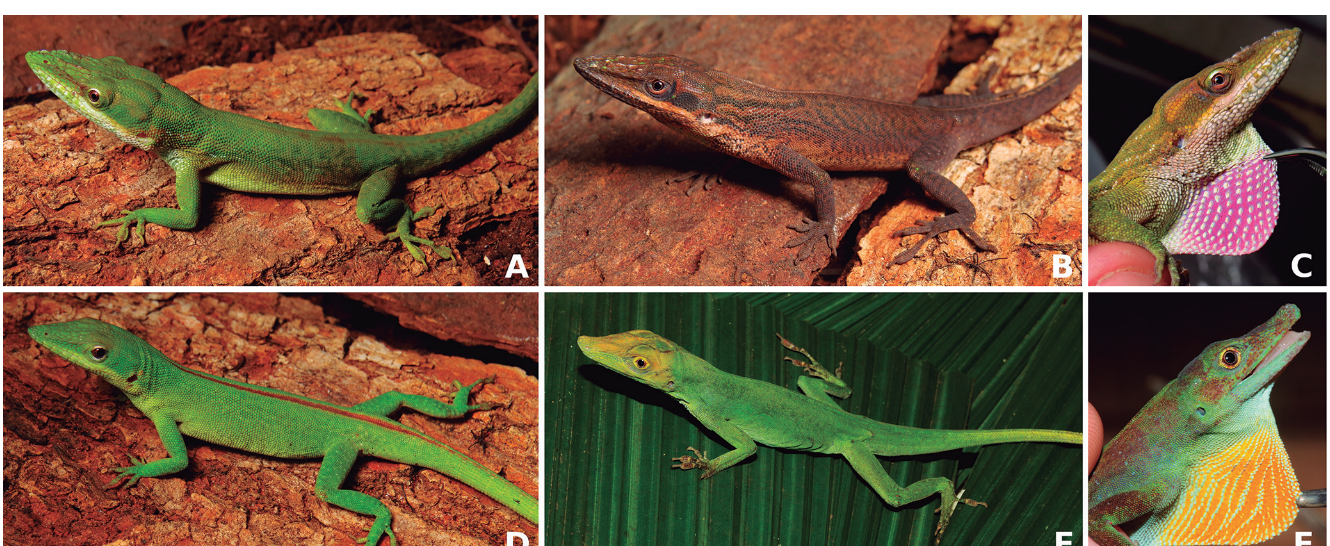

Figure 1. *Anolis porcatus* collected in Brazil, and comparison with the native anole *A. punctatus.* **(A)** male *A. porcatus* showing green coloration. **(B)** male *A. porcatus* showing brown coloration. **(C)** the pink dewlap of male *A. porcatus.* **(D)** female *A. porcatus.* **(E)** male *A. punctatus,* a native anole species. **(F)** the yellow dewlap of male *A. punctatus.* Photo credits: A–D, Mauro Teixeira Jr.; E, Renato Recoder.

injection of pentobarbital. Liver tissue samples were harvested and preserved in 100% ethanol for genetic analyses, while individuals were fixed in 4% formaldehyde and later preserved in 70% ethanol. Specimens were deposited in the collection of the Laboratório de Herpetologia, Departmento de Zoologia, Instituto de Biociências, Universidade de São Paulo (USP), under voucher numbers MTR 33485–33499.

Genetic analyses

To guide species identification, we followed the protocols of Jeskova et al. (2009) to generate sequences of the *NADH dehydrogenase subunit 2* (ND2) and the flanking *tryptophan transfer RNA* (tRNA-Trp) genes from four collected specimens. Sequences were edited with Geneious Pro 6 (Biomatters, Auckland), deposited in GenBank (accession numbers KY311808-KY311811), and aligned with the Geneious algorithm. Based on GenBank's nucleotide collection, we identified the five species that are genetically most similar to our samples using the BLASTn program (Benson et al. 2013). We then downloaded four sequences from each of these five species and also from 15 other representative species of *Anolis* and two species of *Polychrus* Cuvier, 1817 as outgroups. In the case of *A. porcatus,* we included 11 sequences spanning the native range of this species in Cuba, as well as three samples from Florida and the Dominican Republic where this species is also invasive (Powell et al., 1990; Kolbe et al., 2007; Stuart et al., 2012).

Phylogenetic inference was performed under a Bayesian framework using MrBayes 3.2.1 (Ronquist et al., 2012), implementing three independent runs of four Markov chains of 20 million generations each, sampling every 1,000 steps. Models of nucleotide substitution were estimated in JmodelTest 2.1 (Darriba et al., 2012). We assessed convergence and stationarity of model parameters using Tracer 1.5, combined runs in LogCombiner 1.8.3 (with 10% discarded as burn-in), and summarized a maximum clade credibility tree in TreeAnnotator 1.8.3 (Drummond et al., 2012). Results were visualized in FigTree 1.4 (Rambaut, 2014). Lastly, we estimated pairwise uncorrected genetic distances across species using the APE 3.1 package (Paradis et al., 2004) of the R platform (R Core Team, 2016).

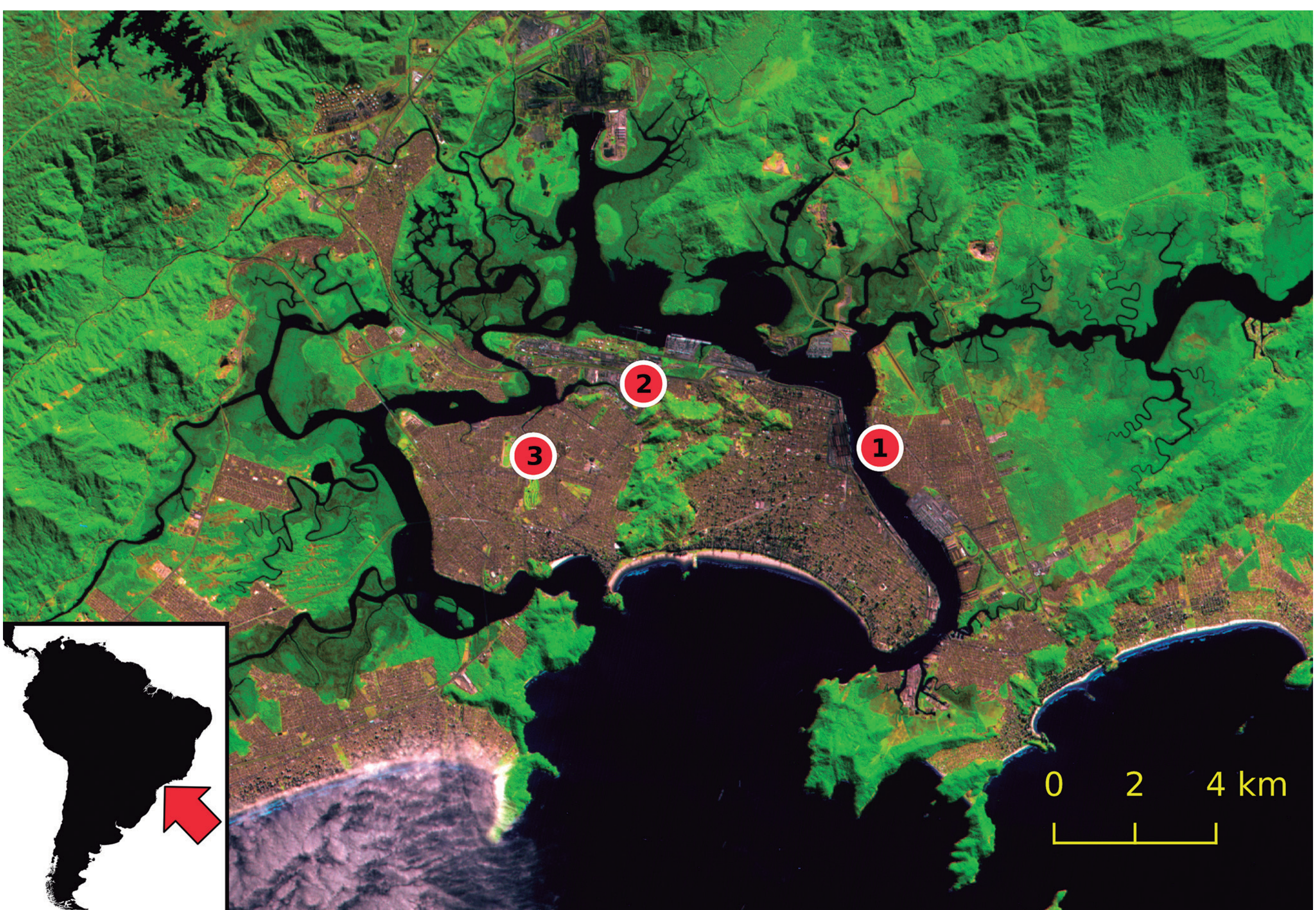

Figure 2. Localities in the Baixada Santista in southeastern coastal Brazil where introduced *Anolis porcatus* were detected. 1, Guarujá. 2, Santos. 3, São Vicente. Green indicates Atlantic Forest cover; gray indicates urban areas; black indicates water bodies.

RESULTS

Species identification

The exotic lizard is readily distinguished from all five native Atlantic Forest anoles (*Anolis fuscoauratus* D'Orbigny in Duméril and Bibron, 1837), *A. nasofrontalis* Amaral, 1933, *A. ortonii* Cope, 1868, *A. pseudotigrinus* Amaral, 1933, and *A. punctatus* Daudin, 1802) by having a head with pronounced frontal and canthal ridges, strong sexual dimorphism in size (males larger), and pink dewlap in males (Fig. 1). The exotic species can be distinguished from *A. fuscoauratus, A. nasofrontalis, A. ortonii,* and *A. pseudotigrinus* by a very elongated rostrum, and from *A. fuscoauratus* and *A. ortonii* by its green body color (which can be behaviorally changed to brown), with darker reticulations. Being active during the day, and having conspicuous habits, this species is usually promptly detected in the field.

The four specimens sampled for genetic data (from Alemoa and Chico de Paula in Santos) share the same mitochondrial haplotype. Hits from a BLAST search found highest similarity to published sequences of *Anolis porcatus* and *A. allisoni* native from Cuba, *A. carolinensis* native from the southeastern Unites States, and *A. smaragdinus* Barbour and Shreve, 1935 and *A. brunneus* Cope, 1894 native from the Bahamas, in this order. All of these species belong to the *A. carolinensis* species group, which does not have representatives native to South America (Nicholson et al., 2012).

A phylogenetic analysis indicates that samples collected in Brazil are nested within the clade of *Anolis porcatus* from western Cuba, with high support (Fig. 3). Brazilian samples form a clade with samples from La Habana, Pinar del Río, and Matanzas in western Cuba, as well as with one sample from Coral Gables in Florida. This clade is sister to a clade composed of two samples from Florida and the Dominican Republic, where *A. porcatus* is also invasive. Similar to previous studies (Glor et al., 2004, 2005; Campbell-Staton et al., 2012), we found that samples of *A. porcatus* in eastern Cuba form a distinct clade from the western Cuban *A. porcatus,* which may indicate an undescribed species. We also found *A. carolinensis* to be nested within the western Cuban *A. porcatus* clade. Brazilian samples of *A. porcatus* are only distantly related to the native Atlantic Forest anoles (Fig. 3).

Analyses of pairwise genetic distances indicate low distances between our sequences and published data from the western Cuban *Anolis porcatus,* ranging from 0.5–8.2%, with the lowest genetic distance to a sample from Pinar del Río. Genetic distances between samples from Brazil and the Dominican Republic were 2% and distances between samples from Brazil and Florida were 1.1–2.3%. Genetic distances were 7.9–8.6% to *A. carolinensis,* 12.6–13.1% to *A. smaragdinus,* 12.7–13.4% to the eastern *A. "porcatus"*, 13.2–13.8% to *A. allisoni;* and 14–14.5% to *A. brunneus*. The exotic specimens showed even greater genetic distances, between 26.5–27.4%, to the native Atlantic Forest anoles for which genetic data are available (*A. fuscoauratus, A. ortonii,* and *A. punctatus*).

Distribution and habits

We found *Anolis porcatus* at three nearby sites in the Alemoa and Chico de Paula districts in Santos (23°55′48.3″S, 46°21′36.5″W; 23°56′1.2″S, 46°21′33″W; 23°55′56.8″S, 46°21′25.7″W), at one site in the Sambaiatuba district in São Vicente (23°56′45.4″S, 46°23′13.2″W), and one site in the Paecara district in Guarujá (23°56′41.6″S, 46°18′10.4″W; all coordinates in WGS 1984 datum).

Male and female adults, as well as juveniles, were spotted in urban and industrial areas characterized by strong human presence. Lizards occupied building walls, light posts, fences, debris, trees, shrubs, and lawn in residential yards, abandoned lots, and alongside streets and sewage canals. A high density of individuals was observed at all sites. For instance, in Santos, 30 *Anolis porcatus* were spotted within 2.5 h of active search (10:00–12:30 h). In São Vicente, 24 individuals were observed within 3 h of active search (10:00–13:00 h). Lastly, in Guarujá, three individuals were spotted within a 20-min interval. Several males were observed performing dewlap displays to conspecifics.

DISCUSSION

This study confirms the presence of the Cuban green anole, *Anolis porcatus,* as an introduced species in the Baixada Santista region of Brazil's southeastern coast. The high density of individuals across multiple sites, as well as the presence of juveniles with various body sizes, provides evidence that these lizards currently comprise at least one well-established, reproductive population. Our investigation demonstrates the usefulness of molecular approaches for proper species identification in a group of potentially aggressive invaders (Powell et al., 1990; Toda et al., 2010; Kraus, 2015) that is characterized by morphological conservatism, hybridization, and a convoluted taxonomy (Glor et al., 2004, 2005; Campbell-Staton et al., 2012).

The origin of *Anolis porcatus* in southeastern Brazil is unknown, but it might be related to the presence of the country's largest seaport complex, the Porto de Santos, in this region. Numerous storage lots for intermodal shipping containers are situated near sites where the lizards were detected. In one instance, multiple specimens were found sheltered inside an open container. It is therefore possible

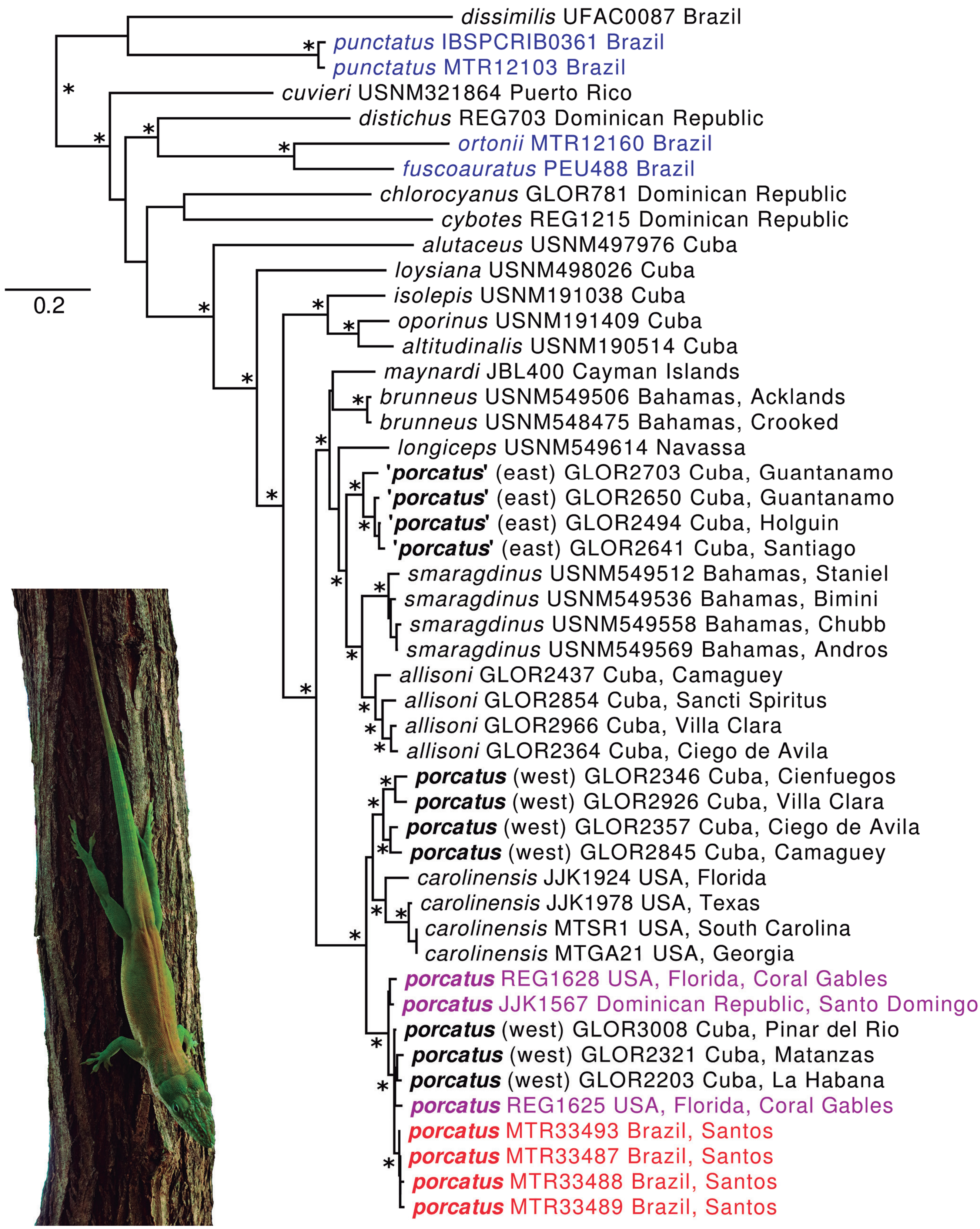

Figure 3. Phylogenetic relationships of *Anolis porcatus* introduced in Brazil (indicated in red), inferred using MrBayes based on a mitochondrial DNA locus. Purple indicates samples of *A. porcatus* invasive elsewhere (Florida and the Dominican Republic). Blue indicates native Atlantic Forest anole species. Asterisks indicate posterior probability > 0.95. Photograph shows a male *A. porcatus* collected in São Vicente, Brazil.

that *A. porcatus* reached Brazil after being unintentionally transported by ships bringing goods from overseas.

Phylogenetic analyses indicate that Brazilian *Anolis porcatus* are nested among samples from La Habana, Matanzas, and Pinar del Río, with the lowest genetic distances between Brazilian *A. porcatus* and a sample from Pinar del Río (0.5%). These results suggest a western Cuban source of colonization for the Brazilian population. Nevertheless, we found that Brazilian samples also cluster closely with a sample from Florida in the continental United States, which could indicate that the Brazilian population originated from a population that is exotic elsewhere. Analyses incorporating large numbers of nuclear markers will be necessary to further refine the geographic source and possible trade routes that have led to the introduction of *A. porcatus* into South America.

Our observations indicate that *Anolis porcatus* thrives in human-modified areas. This pattern was also observed in the species' introduced range in the Dominican Republic (Powell et al., 1990), suggesting that urban and suburban settings offer little resistance to the spread of this anole, and perhaps facilitate it. On the other hand, it is possible that the intense transportation of shipping containers throughout the Baixada Santista might have played a role in the local spread of this species. If this is the case, we expect that the range of *A. porcatus* will continue to increase in this region and that this lizard will soon colonize interior portions of Brazil.

It is currently unclear whether *Anolis porcatus* will be able to expand into the surrounding Atlantic Rainforest, which occurs throughout Brazil's coast. In their native range, these lizards occupy high perches near the canopy in forest settings (Schettino et al., 2010) as well as open vegetation and forest edges (Ruibal and Williams, 1961). As a result, it cannot be ruled out that these heliothermic lizards might also expand into more open natural settings in South America, such as the shrublands in the Cerrado domain.

It is also unknown whether introduced *Anolis porcatus* will have negative impacts on the local ecological communities. Although this lizard feeds mostly on arthropods, it is an opportunistic predator that has been reported to predate a small rodent (Torres and Acosta, 2014). In Brazil, *A. porcatus* might compete with other diurnal arboreal lizards such as *Enyalius* Wagler, 1830, *Polychrus,* and the native *Anolis* species. In some sites in the Dominican Republic, introduced *A. porcatus* seem to have displaced the native anole *A. chlorocyanus* Duméril and Bibron, 1837 (Powell et al., 1990). In Brazil, no native Atlantic Forest anole species is currently known to occur in sympatry with *A. porcatus*. However, the native *A. punctatus* has been reported for a site in Bertioga (Vanzolini, 1972) located only 50 kilometers from the site in Guarujá where we found *A. porcatus.* The possibility of negative interactions between *A. porcatus* and native Brazilian lizards, especially *A. punctatus,* deserves close examination during future surveys.

Prior to this study, an exotic green anole lizard was found in a forest fragment in the coastal city of Salvador, state of Bahia, in Brazil's northeast (Fonseca et al., 2014). That single specimen was identified as *Anolis carolinensis* and the record was tentatively attributed to the release of a specimen imported through the pet trade. Nevertheless, similar to the Baixada Santista region, Salvador hosts a major seaport complex (the Porto de Salvador). Further surveys are necessary to assess whether the presence of this specimen in Bahia represents an isolated occurrence or an independent invasion by *A. porcatus*.

Because of the currently limited data available about the status of *Anolis porcatus* in Brazil, we propose classifying this species as Data Deficient (DD) according to the Environmental Impact Classification for Alien Taxa (Blackburn et al., 2014; Hawkins et al., 2015). Proper classification of the potentially invasive status of *A. porcatus* will require a continuous assessment of the extent of its current distribution and potential for future spread in Brazil, as well as data about whether and how *A. porcatus* impacts the native taxa. These data will also help decide whether the introduced species should be considered in conservation measures, including population management. However, we alert for the potential of mistaking the native *A. punctatus* for *A. porcatus,* as both lizard species are diurnal, arboreal, green, overlap in size, and are superficially similar (Fig. 1).

While we here opt for disclosing the localities where *Anolis porcatus* was found, we urge herpetologists and reptile enthusiasts not to collect and keep individuals as pets, which may favor their spread throughout South America.

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