

# Origin and establishment of the introduced Cuban Blue Anole, *Anolis allisoni*, in Florida

Dolores G. Morris<sup>1</sup>, Kathleen Morris<sup>2</sup>, Christopher J. Thawley<sup>3\*</sup> , Jason J. Kolbe<sup>3</sup>, and Sozos N. Michaelides<sup>3,4\*</sup> 

<sup>1</sup>Department of Philosophy, University of South Florida, Tampa, FL 33620, USA.

<sup>2</sup>Tampa, Florida, USA.

<sup>3</sup>Department of Biological Sciences, University of Rhode Island, Kingston, RI 02881, USA.

<sup>4</sup>Department of Biology, Concordia University, Montreal H4B 1R6, QC, Canada

\*Corresponding author (cthawley@gmail.com, msozos@gmail.com)

**Edited by:** R. Graham Reynolds. **Date of publication:** 21 September 2021.

**Citation:** Morris DG, Morris K, Thawley CJ, Kolbe JJ, Michaelides SN (2021) Origin and establishment of the introduced Cuban Blue Anole, *Anolis allisoni*, in Florida. *Caribbean Herpetology*, 78, 1–7.

**DOI:** <https://doi.org/10.31611/ch.78>

## Abstract

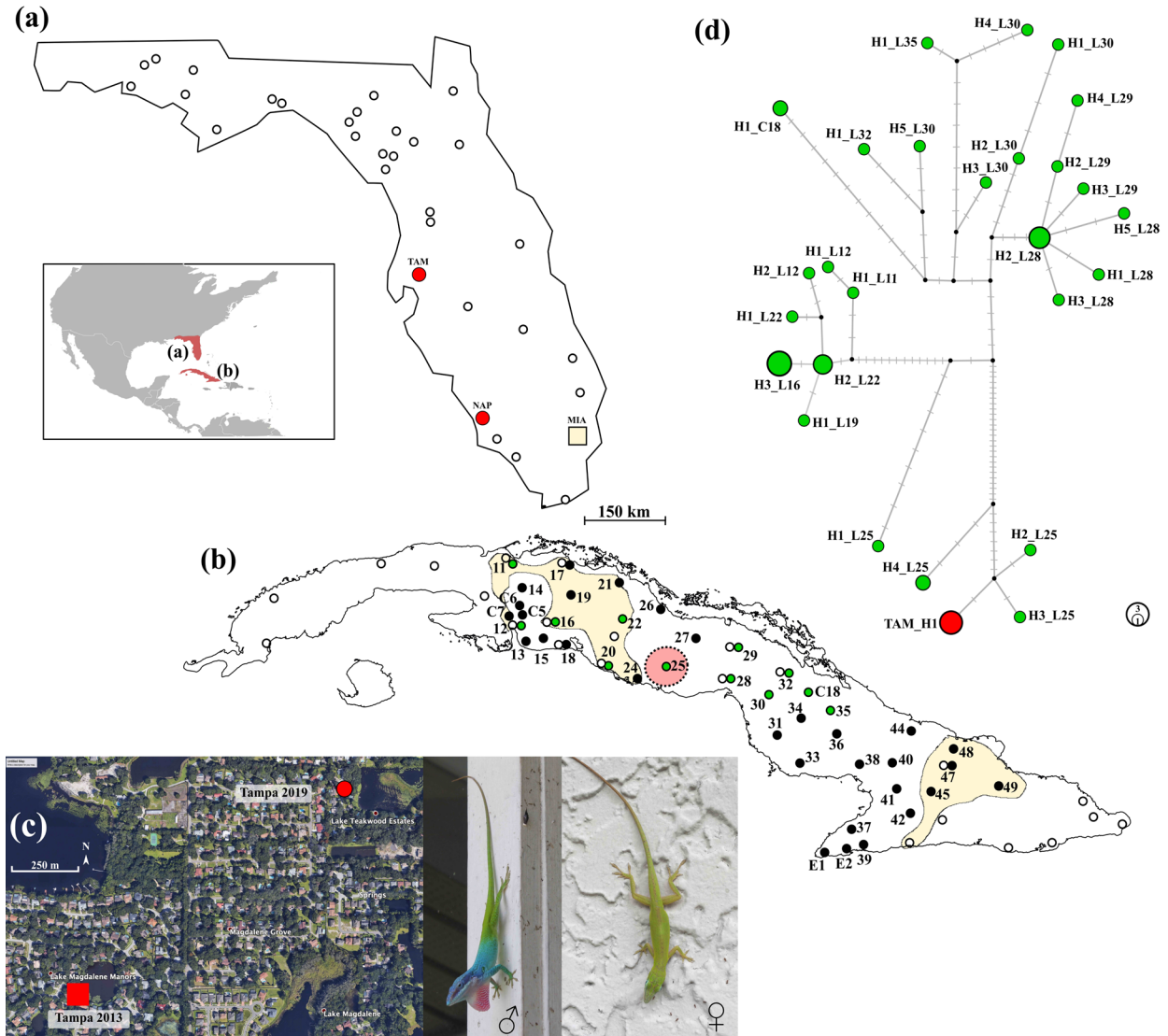
In the state of Florida, USA, lizards of the genus *Anolis* are well represented with at least nine established non-native species and a single native species, *A. carolinensis*. The most recently introduced species is *A. allisoni*, a close relative to both the native *A. carolinensis* and one of the introduced species (*A. porcatius*). *Anolis allisoni* is thought to have been present in two locations in Florida since at least 2013 based on photographic evidence. Here, we analyzed mitochondrial DNA (mtDNA) sequences from these three closely related *Anolis* species to infer the most likely region of origin in the native range and confirm the establishment of the recent invader in Tampa, Florida. We found a single haplotype belonging to *A. allisoni*, which was closely related to native sequences from east-central Cuba. The most likely geographic origin is a tourist destination in the province of Sancti Spiritus, suggesting the potential for human-mediated introduction of *A. allisoni* to Florida. Given the evidence of hybridization within the *carolinensis* subgroup, the presence and establishment of the phylogenetically related and ecomorphologically similar *A. allisoni* may create novel opportunities for interspecific genetic exchange.

**Keywords:** *Anolis* lizards, Florida, invasions, mtDNA, Cuba

## Introduction

The state of Florida in the southeastern USA is a center for non-native species introductions of reptiles and amphibians (Krysko *et al.* 2011). Among lizards, the genus *Anolis* is the most represented with nine established species in addition to the sole native species, *A. carolinensis*, which is found throughout Florida and the southeastern USA (Kolbe *et al.* 2007; Krysko *et al.* 2011). When introduced, closely related taxa with similar habitat use and ecology to the native species have the potential to interact strongly with and even drive evolutionary change in affected native species. For example, the invasion of the Cuban brown anole (*A. sagrei*) in Florida has forced *A. carolinensis* to move to higher perches, leading to the evolution of larger toepads in just 20 generations (Stuart *et al.* 2014). In another example, the introduction of the Cuban green anole, *A. porcatius*, has led to hybridization with the native species followed by genetic distinctiveness of the hybrid population in South Miami (Wegener *et al.* 2019). In the latter case, both species (*A. carolinensis* and *A. porcatius*) are members of the *carolinensis* subgroup, which includes nine species of canopy-dwelling anoles with similar coloration and morphology (Glor *et al.* 2005). Despite considerable divergence time between these two species, reproductive isolation between *A. carolinensis* and *A. porcatius* appears to be weak.

The latest introduction of an *Anolis* species in the continental USA is *A. allisoni* (Krysko *et al.* 2015). The Cuban Blue Anole, native to Cuba and islands off the coast of Honduras, Belize, and Mexico (Schwartz *et al.* 1991), is another member of the *carolinensis* subgroup. In Florida, the species is known from two locations (Fig. 1a). In 2013,



**Figure 1.** Sampling locations and mtDNA haplotype network. The inset map of North America shows Florida (a) and Cuba (b) shaded in red. (a) Map of Florida showing the two known introduced populations of *A. allisoni* in Tampa (TAM) and Naples (NAP) in red circles. Open circles represent sampling locations of mtDNA sequences for *A. carolinensis*, and the yellow square in South Miami (MIA) denotes a hybrid population derived from introduced WC *A. porcatius* and native *A. carolinensis*. (b) Map of Cuba showing sampling locations (filled circles) for native *A. allisoni*. Green circles represent locations of *A. allisoni* sequences used in the network analysis. The dotted pink-shaded area around location 25 indicates the likely geographic origin in Cuba of the *A. allisoni* introduced to Tampa. Open circles represent sampling locations of mtDNA sequences of *A. porcatius*, and the two yellow-shaded regions denote parts in eastern and western Cuba where introgression between *A. porcatius* and *A. allisoni* was previously detected. Location numbers follow Glor *et al.* (2005) and Cadiz *et al.* (2018). (c) Close-up aerial image of a portion of Tampa showing the location of the first description of *A. allisoni* in 2013 (red square) and the new location in 2019 (red circle) along with photos of a male and female *A. allisoni* (photos taken by Dolores Morris). (d) Median-joining network of 37 *A. allisoni* sequences belonging to the east-central subclade. The size of each circle corresponds to the number of individuals sharing that haplotype. Dashes denote mutation steps. The sequences from *A. allisoni* collected in Tampa are identical (TAM-H1, red circle) and most closely related to haplotypes from location 25 in Cuba.

a photographic voucher of a single male *A. allisoni* (UF-Herpetology 170513) was obtained in Tampa (TAM), Florida (Krysko *et al.* 2015). Mature male *A. allisoni* are readily distinguished by the distinctive blue coloration of the front half of their bodies, and *A. allisoni* may also be distinguished from *A. carolinensis* by the teardrop-like shape of their ear opening. However, subsequent surveys in Tampa by Krysko *et al.* (2015) failed to find other individuals of

*A. allisoni*. Mitochondrial DNA (mtDNA) analyses of juvenile green anoles in the area, which are difficult to assign to species using morphology, were ascribed to *A. carolinensis* (Krysko *et al.* 2015). As such, it has been unclear whether an established population of *A. allisoni* has persisted in the area. A separate reproducing population, which has been present since at least 2014, is restricted to an outdoor courtyard in Naples (NAP; Fig. 1c), Florida (Donini *et al.* 2017). Nevertheless, neither of these previous studies characterized the details of the introduction(s) of *A. allisoni* in Florida. For instance, we do not know the geographic source(s) of introductions, likely introduction pathway, and whether sightings were due to single or multiple introductions. Genetic tools are particularly useful to address these questions which are important for management, but also for the detection and characterization of hybridization between native and introduced species (Fitzpatrick *et al.* 2012). In this study, we verified ongoing presence and used a mtDNA marker to confirm the phylogenetic identity and infer the most likely native-range source location(s) of *A. allisoni* in Tampa.

## Materials and Methods

**Sampling and genetic analyses.** We caught three male lizards with *A. allisoni* phenotype from the Lake Teakwood Estates neighborhood in Tampa in 2019 (Fig. 1c). This population is  $\approx 1$  km from the sighting reported in Krysko *et al.* (2015). We extracted DNA from tail tips stored in 95% ethanol using the Isolate II Genomic DNA Kit (Bioline, USA) with overnight lysis. We sequenced approximately 800 base pairs (bp) of the mtDNA ND2 gene with the forward primer H5730 (5'- AGCGAATRGAAGCCCGCTGG-3'; Glor *et al.* 2004) and the reverse L4437a (5'- AAGCTTTCGGGC-CCATACC-3'; Macey *et al.* 1997). Amplifications were carried out in a total volume of 30  $\mu$ l consisting of 15  $\mu$ l of

**Table 1.** Mean pairwise mtDNA (ND2 gene) divergence (Tamura-Nei, %) between native *A. carolinensis* and each introduced *Anolis* species in Florida with available genetic data. Ecomorph category is from Losos (2009). Introduced *A. porcatius* originated from western Cuban (WC) populations and *A. allisoni* from east-central Cuban (ECC) populations.

Species	Ecomorph	mtDNA divergence (%)
WC <i>A. porcatius</i>	Trunk-crown	9.6
ECC <i>A. allisoni</i>	Trunk-crown	16.2
<i>A. equestris</i>	Crown-giant	28.8
<i>A. chlorocyanus</i>	Trunk-crown	30.0
<i>A. cristatellus</i>	Trunk-ground	30.9
<i>A. garmani</i>	Crown-giant	31.0
<i>A. sagrei</i>	Trunk-ground	33.4
<i>A. cybotes</i>	Trunk-ground	34.5
<i>A. distichus</i>	Trunk	35.3

MyTaq HS Mix (Bioline), 1.2  $\mu$ l (0.4 mM) of each primer, 10.6  $\mu$ l PCR grade H<sub>2</sub>O and 2  $\mu$ l template DNA (20 ng). PCR conditions were as follows: an initial denaturation step at 95°C for 1 min, followed by 30 cycles at 95°C for 1 min, 53°C for 35 sec and 72°C for 80 sec, and a final extension step at 72°C for 5 min. PCR products were purified using the Isolate II PCR Kit (Bioline), and sequencing reactions were performed on the ABI 3130xl genetic analyzer at the University of Rhode Island (URI) Genomics and Sequencing Center.

Mitochondrial DNA sequences from both directions were corrected by eye and aligned to obtain a consensus sequence. All sequences were then aligned using MAFFT (Kato *et al.* 2002) implemented in Geneious 8 (Kearse *et al.* 2012) and trimmed to a uniform length of 798 bp. A unique sequence was submitted to GenBank under the accession number MZ475900.

**Phylogenetic analyses.** We used phylogenetic analyses to reconstruct relationships among haplotypes and to determine the genetic origin of the introduced haplotypes. We combined our sequences with 348 sequences (of varying lengths) obtained from GenBank representing native range *A. allisoni* from Cuba (Glor *et al.* 2004; Cádiz *et al.* 2018), *A. porcatius* from Cuba (Glor *et al.* 2004), *A. allisoni* x *A. porcatius* hybrids from Cuba (Glor *et al.* 2004),

**Table 2.** Mean pairwise mtDNA (ND2 gene) divergence between pairs of *Anolis* species with genetic evidence of hybridization and introgression. The abbreviations denote sequences sampled from western (WC) and eastern (EC) Cuban populations.

Species pair	mtDNA divergence (%)	Study
<i>A. carolinensis</i> x WC <i>A. porcatius</i>	9.6	Wegener <i>et al.</i> 2019
EC <i>A. allisoni</i> x EC <i>A. porcatius</i>	10.0	Glor <i>et al.</i> 2004; 2005
WC <i>A. sagrei</i> x <i>A. quadricellifer</i>	10.2	Kolbe <i>et al.</i> 2004; (Reynolds <i>et al.</i> 2020)
WC <i>A. allisoni</i> x WC <i>A. porcatius</i>	14.3	Glor <i>et al.</i> 2004; 2005
<i>A. krugi</i> x <i>A. pulchellus</i>	15.4	Jezkova <i>et al.</i> 2013

native *A. carolinensis* from Florida (Kolbe *et al.* 2007; Tollis *et al.* 2012; Campbell-Staton *et al.* 2012), *A. carolinensis* x *A. porcatius* hybrids from South Miami, FL (Wegener *et al.* 2019), and sequences of green anoles previously sampled from Tampa, FL and ascribed to *A. carolinensis* (Krysko *et al.* 2015). We also obtained from GenBank three sequences belonging to the Cuban species *A. oporinus*, *A. isolepis* and *A. altitudinalis* (Glor *et al.* 2004) to use as outgroups.

We constructed the phylogenetic tree using a Bayesian inference (BI) with the add-on plugin of MrBayes (Huelsenbeck *et al.* 2001), implemented in Geneious 8 (Kearse *et al.* 2012). The GTR + G + I substitution model was selected based on the lowest BIC criterion in MEGA X (Stecher *et al.* 2020), and the BI analysis was run with four chains of 2,000,000 generations sampling every 500 trees. We discarded (burn-in-length) the first 10% of trees after checking for convergence of the chains (trace viewer within Geneious 8), and posterior probability branch support was estimated from the 50% majority-rule consensus tree. To assess and visualize better the phylogenetic relationships among haplotypes, we also constructed a median-joining network in NETWORK v10 (Bandelt *et al.* 1999) using a subset of sequences (n = 37) belonging to the east-central *A. allisoni* subclade (see Results). This method uses median vectors as a hypothetical ancestral sequence required to connect existing sequences within the network with maximum parsimony. For this analysis, all sequences were trimmed to 798 bp to match the newly-generated sequence lengths.

In addition, we gathered unique sequences (introduced haplotypes of the ND2 gene only) from established non-native anoles in Florida from GenBank (Kolbe *et al.* 2007) and calculated mean pairwise mtDNA divergence between these and the native haplotypes of *A. carolinensis* using MEGA X (Stecher *et al.* 2020). Combined with ecomorphological categorization (i.e., habitat specialist group, Losos 2009), we discuss how human-mediated introductions may create opportunities for hybridization between the native (*A. carolinensis*) and the introduced *Anolis* species as well as among introduced *Anolis* species in Florida.

## Results and Discussion

Genetic samples from all three presumptive *A. allisoni* individuals sampled from Tampa were nested in the *A. allisoni* clade, providing conclusive evidence that they are indeed *A. allisoni* or hybrids with *A. allisoni* maternal mtDNA. More than 50 adult *A. allisoni* of both sexes were observed in our focal area (*DM and KM personal observation*) covering several residences and landscaped vegetation over an area of approximately 0.02 km<sup>2</sup>. We observed individuals conducting dewlap displays, engaging in combat, and mating, supporting their establishment success. Anecdotal interviews with local residents and photographic evidence indicate that *A. allisoni* has been in the area since at least 2017. It seems likely that the previous sighting in this area ( $\approx 1$  km distance, Krysko *et al.* 2015) is from the same population. This population has also survived through multiple winters (*DM and KM personal observation, spring 2021*), suggesting that cold temperatures and potential associated mortality have not impacted its establishment.

All three individuals sampled in Tampa shared the same haplotype (TAM-H1). The overall topology of our phylogenetic tree (not shown) is similar to the one described by Glor *et al.* (2004) supporting two subclades for *A. allisoni* (western and east-central), which are sister to *A. porcatius* from eastern Cuba. The haplotype sampled in

this study clusters within the east-central *A. allisoni* subclade, and the median-joining network (Fig. 1d) shows that the TAM-H1 haplotype is genetically similar (three nucleotides different) to haplotypes from the province of Sancti Spiritus in Cuba (location 25 in Fig. 1b as described in Glor *et al.* 2004).

Our finding is the first verification of the genetic Cuban origin of *A. allisoni* in Florida. The fact that this species was observed in 2013 (Krysko *et al.* 2015) and that we recently collected it, provides evidence that the species is reproducing, established, and likely dispersing across the urban landscape of Tampa. The province of Sancti Spiritus, the likely geographic origin in east-central Cuba, has many attractions for tourists (e.g., UNESCO World Heritage sites), suggesting a human-mediated introduction. Whether the introduction was deliberate, such as via the pet-trade, or accidental, is unknown. The species has also been introduced to Quintana Roo, Mexico as well as the island of Utila and city of La Ceiba, both in Honduras (McCranie *et al.* 2015). In the latter case, both locations (Utila and La Ceiba) are connected via ferry to the island of Roatan, where *A. allisoni* is native (McCranie *et al.* 2015), suggesting a nearby source for introductions.

When introduced and native species are phylogenetically related with similar habitat use and ecology, the native species may face both ecological and evolutionary pressure through competitive exclusion, niche displacement, hybridization, and introgression (Blackburn *et al.* 2014). Three introduced *Anolis* species in Florida (*A. porcatulus*, *A. allisoni* and *A. chlorocyanus*) occupy the same structural habitat as the native *A. carolinensis* (all belong to the trunk-crown ecomorph, Table 1) and are similar in morphology and behavior (Losos 2009). Furthermore, two of these species, *A. porcatulus* and *A. allisoni*, are closely related phylogenetically to the native anole with 9.6% (western Cuban haplotypes) and 16.2% mtDNA sequence divergence, respectively (Table 1). Specifically, within the *carolinensis* subgroup, hybridization events suggest that species boundaries and reproductive isolation might be weak. In western and eastern parts of Cuba where *A. allisoni* and *A. porcatulus* occur sympatrically and have a mean pairwise mtDNA divergence of 10.0 – 14.3% (Glor *et al.* 2005), introgression is bidirectional (Figure 1; Glor *et al.* 2004). In Florida, introduced western Cuban (WC) *A. porcatulus* in South Miami hybridizes with *A. carolinensis*; these taxa have a mean pairwise mtDNA divergence of 9.6% (Wegener *et al.* 2019). In comparison, the mean pairwise mtDNA divergence between *A. carolinensis* and eastern Cuban (EC) *A. porcatulus* is 15.9% (Glor *et al.* 2005). Thus, given the phylogenetic and ecological similarity of *A. allisoni* to the native green anole in Florida (Table 1), the potential for hybridization exists.

Human-mediated introductions often create opportunities for intra- and inter-specific hybridization by removing spatial barriers between previously allopatric taxa (e.g. Kolbe *et al.* 2004; Michaelides *et al.* 2013; Stephens *et al.* 2020). For the non-native species, such opportunities may facilitate establishment, adaptation, and range expansion through increased diversity, hybrid vigor, and the generation of novel genotypes (Ellstrand *et al.* 2000; Rius *et al.* 2014). For the native species, however, interspecific hybridization with a non-native species could lead to genetic swamping and potentially extinction of local lineages (Todesco *et al.* 2016; Ottenburghs 2021). However, anthropogenic hybridization can also provide opportunities for exchange of adaptive genetic variation and speciation (see review by Ottenburghs 2021). The 16.2% mtDNA sequence divergence between the recently introduced *A. allisoni* and the native *A. carolinensis* is only slightly more than the divergence between successfully hybridizing species in Puerto Rico (Table 2). Hybridization between native *A. carolinensis* and all other introduced *Anolis* species in Florida (besides *A. porcatulus*) is much less likely given the greater mtDNA sequence divergence with these species, all 28.8% or more (Table 1). Among the introduced species, opportunities for hybridization might occur for *A. porcatulus* and *A. allisoni*, however, both are currently established in different locations in Florida. The closest *A. allisoni* population to South Miami, where WC *A. porcatulus* was introduced, is in Naples (200 km to the west). The phylogenetic identity of this population is still unknown, but if this introduction has a WC *A. allisoni* origin then hybridization with WC *A. porcatulus* is very likely upon future secondary contact.

In conclusion, photographic, observational, and genetic evidence suggest that *A. allisoni* is well established in this Tampa neighborhood, having likely dispersed at least 1 km through suburban habitats. Knowledge of the geographic origin of this introduced species in east-central Cuba could guide future sampling (both in the



native and introduced range) and use of bi-parentally inherited nuclear markers to investigate whether hybridization is occurring and the potential consequences thereof.

## Acknowledgements

Funding for the genetic work was provided from the University of Rhode Island.

## Author Contributions

DM and KM initiated the research, collected photographs and specimens, and revised the manuscript; CT coordinated the research, drafted and revised the manuscript; SM conducted the laboratory work, analyses and co-wrote the manuscript; JK provided funding, contributed to the interpretation of data and revised the manuscript. All authors approved the final version.

## References

- Bandelt HJ, Forster P, & Röhl A (1999) Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution* 16, 37–48. **Article**
- Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Marková Z, Mrugała A, Nentwig W, Pergl J, Pyšek P, et al. (2014) A Unified Classification of Alien Species Based on the Magnitude of their Environmental Impacts. *PLoS Biology* 12, e1001850. **Article**
- Cádiz A, Nagata N, Díaz LM, Suzuki-Ohno Y, Echenique-Díaz LM, Akashi HD, Makino T, & Kawata M (2018) Factors affecting interspecific differences in genetic divergence among populations of *Anolis* lizards in Cuba. *Zoological Letters* 4, 1–12. **Article**
- Campbell-Staton SC, Goodman RM, Backström N, Edwards SV, Losos JB, & Kolbe JJ (2012) Out of Florida: mtDNA reveals patterns of migration and Pleistocene range expansion of the Green Anole lizard (*Anolis carolinensis*). *Ecology and Evolution* 2, 2274–2284. **Article**
- Donini J, & Allman P (2017) Geographic distribution: *Anolis allisoni* (Allison's anole). *Herpetological Review* 48, 14
- Ellstrand NC, & Schierenbeck KA (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Sciences* 97, 7043–7050. **Article**
- Fitzpatrick BM, Fordyce JA, Niemiller ML, & Reynolds RG (2012) What can DNA tell us about biological invasions? *Biological Invasions* 14, 245–253. **Article**
- Glor RE, Gifford ME, Larson A, Losos JB, Schettino LR, Lara ARC, & Jackman TR (2004) Partial island submergence and speciation in an adaptive radiation: a multilocus analysis of the Cuban green anoles. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271, 2257–2265. **Article**
- Glor RE, Losos JB, & Larson A (2005) Out of Cuba: overwater dispersal and speciation among lizards in the *Anolis carolinensis* subgroup. *Molecular Ecology* 14, 2419–2432. **Article**
- Huelsenbeck JP, & Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics (Oxford, England)* 17, 754–755. **Article**
- Katoh K, Misawa K, Kuma K, & Miyata T (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30, 3059–3066. **Article**
- Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, et al. (2012) Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28, 1647–1649. **Article**
- Kolbe JJ, Glor RE, Rodríguez Schettino L, Lara AC, Larson A, & Losos JB (2004) Genetic variation increases during biological invasion by a Cuban lizard. *Nature* 431, 177–181. **Article**
- Kolbe JJ, Glor RE, Schettino LR, Lara AC, Larson A, & Losos JB (2007) Multiple Sources, Admixture, and Genetic Variation in Introduced *Anolis* Lizard Populations. *Conservation Biology* 21, 1612–1625. **Article**

- Krysko KL, Burgess JP, Rochford MR, Gillette CR, Cueva D, Enge KM, Somma LA, Stabile JL, Smith DC, Wasilewski JA, Kieckhefer Iii GN, Granatosky MC, *et al.* (2011) Verified non-indigenous amphibians and reptiles in Florida from 1863 through 2010: Outlining the invasion process and identifying invasion pathways and stages. *Zootaxa* 3028, 1–64. **Article**
- Krysko KL, MacKenzie-Krysko C, Connor LL, Alfonso YU, & Nunez LP (2015) The Cuban Blue Anole, *Anolis allisoni* Barbour 1928 (Squamata: Dactyloidae), a New Nonnative Lizard Introduced in Florida. *IRCF Reptiles & Amphibians* 22, 128–131. **Article**
- Losos J (2009) Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles. *University of California Press*.
- Macey JR, Larson A, Ananjeva NB, & Papenfuss TJ (1997) Evolutionary Shifts in Three Major Structural Features of the Mitochondrial Genome Among Iguanian Lizards. *Journal of Molecular Evolution* 44, 660–674. **Article**
- McCranie JR, & Köhler G (2015) The Anoles (Reptilia: Squamata: Dactyloidae: *Anolis: Norops*) of Honduras. Systematics, Distribution, and Conservation. *Bulletin of the Museum of Comparative Zoology* 161, 1–280. **Article**
- Michaelides S, While GM, Bell C, & Uller T (2013) Human introductions create opportunities for intra-specific hybridization in an alien lizard. *Biological Invasions* 15, 1101–1112. **Article**
- Ottenburghs J (2021) The genic view of hybridization in the Anthropocene. *Evolutionary Applications* n/a. **Article**
- Reynolds RG, Kolbe JJ, Glor RE, López-Darias M, Gómez Pourroy CV, Harrison AS, Queiroz K, Revell LJ, & Losos JB (2020) Phylogeographic and phenotypic outcomes of brown anole colonization across the Caribbean provide insight into the beginning stages of an adaptive radiation. *Journal of Evolutionary Biology* 33, 468–494. **Article**
- Rius M, & Darling JA (2014) How important is intraspecific genetic admixture to the success of colonising populations? *Trends in Ecology & Evolution* 29, 233–242. **Article**
- Schwartz A, & Henderson RW (1991) Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history. University of Florida Press, Gainesville, Florida, USA.
- Stecher G, Tamura K, & Kumar S (2020) Molecular Evolutionary Genetics Analysis (MEGA) for macOS. *Molecular Biology and Evolution* 37, 1237–1239. **Article**
- Stephens K, Measey J, Reynolds C, & Le Roux JJ (2020) Occurrence and extent of hybridisation between the invasive Mallard Duck and native Yellow-billed Duck in South Africa. *Biological Invasions* 22, 693–707. **Article**
- Stuart YE, Campbell-Staton SC, Hohenlohe PA, Reynolds GR, Revell LJ, & Losos JB (2014) Rapid evolution of a native species following invasion by a congener. *Science* 346. **Article**
- Todesco M, Pascual MA, Owens GL, Ostevik KL, Moyers BT, Hübner S, Heredia SM, Hahn MA, Caseys C, Bock DG, & Rieseberg LH (2016) Hybridization and extinction. *Evolutionary Applications* 9, 892–908. **Article**
- Tollis M, Ausubel G, Ghimire D, & Boissinot S (2012) Multi-Locus Phylogeographic and Population Genetic Analysis of *Anolis carolinensis*: Historical Demography of a Genomic Model Species. *PLOS ONE* 7, e38474. **Article**
- Wegener JE, Pita-Aquino JN, Atutubo J, Moreno A, & Kolbe JJ (2019) Hybridization and rapid differentiation after secondary contact between the native green anole (*Anolis carolinensis*) and the introduced green anole (*Anolis porcatius*). *Ecology and Evolution* 9, 4138–4148. **Article**