

Preliminary genetic assessment of the geographic origin of non-native Green Iguanas, *Iguana iguana* (Linnaeus, 1758), in Taiwan

Matthijs P. van den Burg^{1,*}, Ko-Huan Lee², Ren-Jay Wang³, Peter Kuperus⁴, and Adolphe O. Debrot⁵

The Green Iguana, *Iguana iguana* (Linnaeus, 1758), is a large, long-lived reptile that occurs throughout Central and South America (Bock et al., 2022). Given the high intraspecific genetic diversity across its native range, *I. iguana* is regarded as a species complex (Stephen et al., 2013; van den Burg et al., 2026). In addition to its native distribution, *I. iguana* has a large non-native distribution that includes numerous populations in the Caribbean (e.g., Knapp et al., 2021; Uetz et al., 2025). However, non-native populations are also present in countries outside the Neotropics, such as Fiji (Shah et al., 2020), Taiwan (Lee et al., 2019), and some mainland areas of Asia (van den Burg et al., 2020). To understand the origin and dispersal of non-native *I. iguana* populations, numerous studies have utilised available genetic data from native populations (e.g., De Jesús Villanueva et al., 2021; van den Burg et al., 2023). However, genetic assessments of geographic origins have not been performed for all non-native *I. iguana* populations.

Iguana iguana is a popular reptilian pet in Taiwan, with 101,646 individuals that have been shipped there to date (see CITES exporter reported numbers in Table 1; CITES, 2025). Although only few *I. iguana* were found

in the wild during 2004, nowadays, large free-ranging *I. iguana* populations are present (Lee et al., 2019). The species continues to spread and can reach high local densities (Wan, 2023; Chen et al., 2025). Given the negative impact to agriculture and natural ecosystems, Taiwan's Ministry of Agriculture initiated a campaign to reduce the number of wild *I. iguana* in Taiwan (Ministry of Agriculture, 2025); in 2025 over 36,000 iguanas were culled. Whilst pathogens of captive and free ranging *I. iguana* have been genetically assessed (Sun et al., 2022; Chao et al., 2023), no effort has yet been taken to assess the genetic origin of the free-ranging *I. iguana* themselves. Here we generate genetic data from free-ranging *I. iguana* in Taiwan to assess their geographic origin.

Materials and Methods

Tissue samples from a total of seven iguanas were collected during 2022 within a project aimed at understanding the range and number of free-roaming *I. iguana* in eastern Taiwan (Taitung County). Iguanas were captured between Doulan and Xinlan by hand, noosing or shooting. Captured iguanas were euthanised by brain pithing through the parietal eye (see permits in the Acknowledgments); the iguana specimens were not collected. At the University of Amsterdam, we amplified a region of the mtDNA cytochrome c oxidase subunit 1 (*COX1*) using the standard HLO/LCO primers and published PCR program by Folmer et al. (1994). We used Sanger sequencing to generate the genetic data from PCR products that were assessed using gel electrophoresis. Hereafter, we visually assessed and concatenated the generated sequences to remove low-quality base pairs. We used Geneious Prime (Kearse et al., 2012) to generate uncorrected similarities of the quality-checked sequences compared to those in georeferenced datasets of native samples from multiple manuscripts (Stephen et al., 2013; Breuil et al., 2019; van den Burg et al., 2021, 2026). Quality-checked

¹ International Union for Conservation of Nature Species Survival Commission Iguana Specialist Group, Gland 1196, Switzerland; and independent researcher, The Hague, 2565 BW Zuid Holland, The Netherlands.

² School of Life Science, National Taiwan Normal University, No. 88, Tingzhou Road Section 4, Taipei 116, Taiwan.

³ Society for Nature and Humanities in Taitung County, Taitung 950, Taiwan; and independent researcher, Pingtung, Taiwan.

⁴ Institute of Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, 1090 GE Noord Holland, The Netherlands.

⁵ Wageningen Marine Research, Den Helder, 1780 AB Noord Holland, The Netherlands.

* Corresponding author. E-mail: thijs.burg@gmail.com

sequences were submitted to GenBank; haplotype T1, PZ859238; T2, PZ859239; T3, PZ859240.

Results and Discussion

We performed a preliminary genetic assessment of an Asian non-native *I. iguana* population to identify the native geographic origin of free-roaming *I. iguana* in Taiwan. We obtained *COX1* fragments of 669 base pairs from all seven individuals, resulting in three unique haplotypes, the comparisons of which to the native *I. iguana* database indicate origins from mtDNA Clade II and III (see van den Burg et al., 2026; Table 2). This concerns Central America through to Colombia (see van den Burg et al., 2021 for approximations of the clade ranges), areas from where the highest numbers of *I. iguana* were imported to Taiwan (Table 1).

How does this result of multiple geographic sources relate to other non-native *I. iguana* populations? Overall, data from genetic assessments of non-native *I. iguana* populations from elsewhere mostly reveal populations with haplotypes that origin from multiple mtDNA clades from the native *I. iguana* range, e.g., on Anguilla (Pounder et al., 2020), the Dutch Windward islands (van den Burg et al., 2018, 2023), and in Florida (De Jesús Villanueva et al., 2021). However, there are some non-native populations that appear to consist of individuals from only a single mtDNA clade, e.g., Fiji (De Jesús Villanueva et al., 2021) and Antigua (van den Burg et al., 2024). Considering Clades II and III that we identified to be present on Taiwan, non-native populations with a presence of at least these two clades concern those of Puerto Rico, Florida, St. Croix, Dominican Republic, and the Dutch Windward islands (van den Burg et al., 2018, 2023; De Jesús Villanueva et al., 2021).

High genetic diversity is not essential for successful invasion (Uller and Leimu, 2011; Rollins et al., 2013) because following the predictable introduction bottleneck, genetic diversity will typically rebound (Kamuk et al., 2021). However, a recent review of 120 studies on the genomics of successful invasions found

Table 1. Total numbers of *Iguana iguana* exported to Taiwan, as reported by exporters since 1992 (CITES, 2025).

Country of origin	Individuals exported to Taiwan
El Salvador	64,174
Colombia	34,780
Suriname	1620
Guatemala	550
Guyana	200
Nicaragua	300
Ukraine	10
United States	10
Ukraine	10
Peru	2

that admixture of non-native individuals from different origins appears to be the main factor underlying the successful invasiveness of non-native species (Kołodziejczyk et al., 2025), which also increases the potential rate of range expansion (Wagner et al., 2017).

Differences in invasiveness of non-native *I. iguana* populations have not yet been studied, nor have population and life-history characteristics that could be under selection when members from different native mtDNA clades hybridise. Given the high intraspecific genetic variation within the *I. iguana* species complex (e.g., van den Burg et al., 2026), theoretically, non-native populations could be a mixture of a multitude of different sources. Whilst genetic assessments of numerous non-native *I. iguana* populations have been performed, these studies generally analysed a limited number of samples, and more research is needed. In the case of invasions like for *I. iguana* in Taiwan, involving a combination multiple introductions of large numbers of animals from different geographic sources, the stage seems set for a highly successful and persistent invasion

Table 2. Minimum and maximum similarities of the mtDNA *COX1* gene between Taiwan *Iguana iguana* samples and *I. iguana* samples from the native range. Clade numbers follow van den Burg et al. (2026).

Samples (haplotype)	Clade I	Clade II	Clade III	Clade IV
T1 and 3 (T1)	95.07	97.91–100	93.42–93.87	93.87
T2, 4–7 (T2 and T3)	92.98–93.12	93.27–94.17	98.95–100	92.08–92.53

which will be very hard to reverse (Stepien et al., 2005; Dlugosch and Parker, 2008; Facon et al., 2008; Crawford and Whitney, 2010; Blackburn et al., 2016). In the future, it will be interesting to follow how the species' genetic composition may evolve over time as it settles into its new environment.

Acknowledgments. This work was partly made possible through the Wageningen University BO research program (BO-43-117-006) and by finances from the Ministry of Agriculture, Fisheries, Food Security and Nature (LVVN) under project number 4318100346-1. All procedures for capturing and euthanising animals were conducted under the permit for the project: Monitoring and investigating the distribution of invasive species in Taitung County (110-Forest-014). We thank Ren-Jay Wang (Society for Nature and Humanities in Taitung County) for subsampling the tissues from the captured lizards. We also thank Tsui-Wen Li and Si-Min Lin (National Taiwan Normal University, NTNU) for preparing and shipping the tissue samples. We are grateful to Ko-Huan Lee (NTNU) for coordinating sample transportation and for his contributions to the first draft of this manuscript. Samples were shipped under a permit of the Taiwan Ministry of Economic Affairs (FTS512W0055466).

References

- Blackburn, T.M., Lockwood, J.L., Cassey, P. (2016): The influence of numbers on invasion success. In: *Invasion genetics: The Baker and Stebbins Legacy*, p. 25–39. Barrett, S.C.H., Colautti, R.I., Dlugosch, K.M., Riesenberger, L.H., Eds., New Jersey, USA, John Wiley & Sons, Ltd.
- Bock, B., Malone, C.L., Knapp, C., Aparicio, J., Avila-Pires, T.C.S., Cacciali, P., et al. (2022): *Iguana iguana* (amended version of 2020 assessment). The IUCN Red List of Threatened Species **2022**: e.T174481A218317281. Accessed on 27 October 2025.
- Breuil, M., Vuillaume, B., Schikorski, D., Krauss, U., Morton, M.N., Haynes, P., et al. (2019): A story of nasal horns: two new subspecies of *Iguana* Laurenti, 1768 (Squamata, Iguanidae) in Saint Lucia, St Vincent & the Grenadines, and Grenada (southern Lesser Antilles). *Zootaxa* **4608**(2): 201–232.
- Chao, L.L., Chen, T.H., Shih, C.M. (2023): First report and molecular identification of a reptilian tick, *Amblyomma helvolum* (Acari: Ixodidae), infesting wild green iguanas, *Iguana iguana* (Reptilia: Iguanidae), in southern Taiwan. *Experimental and Applied Acarology* **90**(3): 375–387.
- Chen, M.T., Chen, C.H., Lin, C.T., Chang, Y.Y. (2025): Enhancing YOLOv8 by Adding Global Attention Mechanism to Identify Targets in Complex Backgrounds. *Sensors & Materials* **37**: 2935–2948.
- CITES [Convention on International Trade in Endangered Species] (2025): CITES trade statistics derived from the CITES Trade Database. Cambridge, UK: UNEP World Conservation Monitoring Centre.
- Crawford, K.M., Whitney, K.D. (2010): Population genetic diversity influences colonization success. *Molecular Ecology* **19**(6): 1253–1263.
- De Jesús Villanueva, C.N., Falcón, W., Velez-Zuazo, X., Papa, R., Malone, C.L. (2021): Origin of the green iguana (*Iguana iguana*) invasion in the greater Caribbean Region and Fiji. *Biological Invasions* **23**(8): 2591–2610.
- Dlugosch, K.M., Parker, I.M. (2008): Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. *Molecular Ecology* **17**(1), 431–449.
- Facon, B., Pointier, J.P., Jarne, P., Sarda, V., David, P. (2008): High genetic variance in life-history strategies within invasive populations by way of multiple introductions. *Current Biology* **18**(5): 363–367.
- Folmer, O., Black, M., Hoeh, W., Lutz, R., Vrijenhoek, R. (1994): DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology & Biotechnology* **3**: 294–299.
- Kañuch, P., Berggren, Å., Cassel-Lundhagen, A. (2021): A clue to invasion success: genetic diversity quickly rebounds after introduction bottlenecks. *Biological Invasions* **23**(4): 1141–1156.
- Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., et al. (2012): Geneious basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* **28**: 1647–1649.
- Knapp, C.R., Grant, T.D., Pasachnik, S.A., Angin, B., Boman, E., Brisbane, J., et al. (2021): The global need to address threats from invasive alien iguanas. *Animal Conservation* **24**: 717–719.
- Kołodziejczyk, J., Fijarczyk, A., Porth, I., Robakowski, P., Vella, N., Vella, A., et al. (2025): Genomic investigations of successful invasions: the picture emerging from recent studies. *Biological Reviews* **100**(3): 1396–1418.
- Lee, K.H., Chen, T.H., Shang, G., Clulow, S., Yang, Y.J., Lin, S.M. (2019): A check list and population trends of invasive amphibians and reptiles in Taiwan. *ZooKeys* **829**: 85.
- Ministry of Agriculture (2025): Instant Updates on Green Iguana Prevention and Control: Upgraded Crop Natural Disaster Reporting System Launched. Available at: <https://www.forest.gov.tw/en/news/0076006>.
- Pounder, K.C., Mukhida, F., Brown, R.P., Carter, D., Daltry, J.C., Fleming, T., et al. (2020): Testing for hybridisation of the Critically Endangered *Iguana delicatissima* on Anguilla to inform conservation efforts. *Conservation Genetics* **21**(3): 405–420.
- Rollins, L.A., Moles, A.T., Lam, S., Buitenwerf, R., Buswell, J.M., Brandenburger, C.R., et al. (2013): High genetic diversity is not essential for successful introduction. *Ecology and evolution*, **3**(13): 4501–4517.
- Shah, S., Dayal, S.R., Bhat, J.A., Ravuiwasa, K. (2020): Green iguanas: a threat to man and wild in Fiji islands?. *International Journal of Conservation Science* **11**(3): 765–782.
- Stephen, C.L., Reynoso, V.H., Collett, W.S., Hasbun, C.R., Breinholt, J.W. (2013): Geographical structure and cryptic lineages within common Green iguanas, *Iguana iguana*. *Journal of Biogeography* **40**: 50–62.
- Stepien, C.A., Brown, J.E., Neilson, M.E., Tumeo, M.A. (2005): Genetic diversity of invasive species in the Great Lakes versus their Eurasian source populations: insights for risk analysis. *Risk Analysis: An International Journal* **25**(4): 1043–1060.
- Sun, P.L., Yang, C.K., Li, W.T., Lai, W.Y., Fan, Y.C., Huang, H.C.,

- Yu, P.H. (2022): Infection with *Nannizziopsis guarroi* and *Ophidiomyces ophiodiicola* in reptiles in Taiwan. *Transboundary and Emerging Diseases* **69**(2): 764–775.
- Uetz, P., Freed, P., Aguilar, R., Reyes, F., Kudera, J., Hošek, J. (eds.) (2025): The Reptile Database, <http://www.reptile-database.org>, accessed on 27 October 2025.
- Uller, T., Leimu, R. (2011): Founder events predict changes in genetic diversity during human-mediated range expansions. *Global Change Biology* **17**(11): 3478–3485.
- van den Burg, M.P., Meirns, P.G., van Wagensveld, T.P., Kluskens, B., Madden, H., Welch, M.E., Breeuwer, J.A. (2018): The Lesser Antillean Iguana (*Iguana delicatissima*) on St. Eustatius: genetically depauperate and threatened by ongoing hybridization. *Journal of Heredity* **109**(4): 426–437.
- van den Burg, M.P., Van Belleghem, S.M., De Jesus Villanueva, C.N. (2020): The continuing march of Common Green Iguanas: arrival on mainland Asia. *Journal for Nature Conservation* **57**: 125888.
- van den Burg, M.P., Grandjean, F., Schikorski, D., Breuil, M., Malone, C.L. (2021): A genus-wide analysis of genetic variation to guide population management, hybrid identification, and monitoring of invasions and illegal trade in *Iguana* (Reptilia: Iguanidae). *Conservation Genetics Resources* **13**(4): 435–445.
- van den Burg, M.P., Goetz, M., Brannon, L., Weekes, T.S., Ryan, K.V., Debrot, A.O. (2023): An integrative approach to assess non-native iguana presence on Saba and Montserrat: are we losing all native *Iguana* populations in the Lesser Antilles? *Animal Conservation* **26**: 813–825.
- van den Burg, M.P., Lindsay, K., Kappelhof, J., Debrot, A.O. (2024): Reassessing the status of a data-deficient insular population of a critically endangered species. *Caribbean Journal of Science* **54**(2): 443–450.
- van den Burg, M.P., de Queiroz, K., Ventayol, M., Debrot, A.O., Malone, C.L. (2026): Consideration of range-wide variation is critical when splitting widely distributed species: the case of the proposed *Iguana melanoderma*. *Zootaxa* **5748**(3): 387–399.
- Wagner, N.K., Ochocki, B.M., Crawford, K.M., Compagnoni, A., Miller, T.E. (2017): Genetic mixture of multiple source populations accelerates invasive range expansion. *Journal of Animal Ecology* **86**(1): 21–34.
- Wan, B.-L. (2023): 屏東縣綠鬣蜥 (*Iguana iguana*) 主要入侵範圍族群監測: 密度與體型變化 [Monitoring the invasive Green Iguana populations in Pingtung: Changes in density and body size]. pp.1–50. Unpublished PhD thesis, Institute of Wildlife Conservation, Pingtung University of Science and Technology, Pingtung, Taiwan.