

Inquilines highlight overlooked keystone species role for *Iguana delicatissima* Laurenti, 1768 as ecosystem engineer

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Due to their critical impact on other species in local ecosystems, keystone species play a special role in the conservation of global biodiversity (Mills et al., 1993; Bond, 1994; Power et al., 1996; Valencia-Aguilar et al., 2013; de Miranda, 2017). For example, their decline or extinction can have cascading effects and lead to extinctions of other coexisting species (Paine, 1966; Power et al., 1996; Mittelbach et al., 1995; Borrrval et al., 2000; Valencia-Aguilar et al., 2013; de Miranda, 2017). In light of the global decline in biodiversity, it is therefore imperative to identify keystone species and understand their interactions with and functions for other species, and to predict and possibly take remedial actions to prevent larger extinction cascades (Wake and Vredenburg, 2008; Pereira et al., 2010). This is especially true for island ecosystems which are particularly vulnerable to species extinction (e.g., Simberloff, 2000).

Iguanids are large, long-lived reptiles native to the Americas, and a few South Pacific islands, with keystone roles having been described for several. Their consumption of plant seeds benefits both endo- and episaurochorous dispersal (Iverson, 1985; de A. Moura et al., 2015; Lasso and Barrientos, 2015; Burgos-Rodríguez et al., 2016; Traveset et al., 2016), seed germination (Lasso and Barrientos, 2015; Vásquez-Contreras and Ariano-Sánchez, 2016), and shielding of seeds (Salinas and Reynoso, 2023). Excavated burrows used for daily retreat are used by a range of invertebrate taxa, presumably as thermal refugia (Iverson, 1979).

Annual (communal) nesting leads to subsequent large numbers of hatchling iguanas that are a nutrient-rich food source for a wide range of predators (Christian and Tracy, 1981; Knapp et al., 2010; Ortiz-Catedral et al., 2021). Furthermore, during nesting, the excavation of deeper, nutrient-rich soil leads to the enrichment of the otherwise less nutrient-rich topsoil (Eldridge and Myers, 1998; Platt et al., 2016). In addition, the consumption of leaves, fruits, and flowers alters plant phenology through defoliation, and can trigger plant growth and flowering (Auffenberg, 1982; Carlo and García-Quijano, 2008). Lastly, Tapia and Gibbs (2022) highlighted the ecosystem engineering role of Galapagos Land Iguanas, *Conolophus subcristatus* (Gray, 1831), which have a large-scale impact on vegetation structure. Although 80% of IUCN-assessed iguanids fall within a threatened conservation status (IUCN, 2023), the abovementioned interactions demonstrate iguanids as impactful keystone species, contributing to a wide range of diverse and heterogeneous ecosystems. Nevertheless, it is likely that other keystone roles for iguanas have been overlooked and under-appreciated. We here report on opportunistic observations made on nesting sites of the critically endangered Lesser Antillean Iguana, *Iguana delicatissima* Laurenti, 1768 (van den Burg et al. 2018), as obtained during our studies on its reproduction on the Caribbean Lesser Antillean island of Sint Eustatius (21 km²). These observations suggest that *I. delicatissima* has a potential role as ecosystem engineer in the island's terrestrial environment.

Iguana delicatissima is the largest native extant terrestrial animal throughout its historic range, which has recently been drastically reduced in area by 86% (van den Burg et al., 2018). This decline is mainly caused by still-ongoing competitive hybridisation with non-native Green Iguanas (*Iguana iguana* (Linnaeus, 1758) species complex), ecosystem degradation due to free-ranging livestock, and coastal development (Knapp et al., 2014; Vuillaume et al., 2015; van den Burg et al., 2018; Debrot et al., 2022). Similar to most iguana species (e.g., *Iguana* (Rand, 1968), *Cyclura*

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(Iverson, et al. 2004), *Ctenosaura* (Mora, 1989); for an overview see Wiewandt, 1982), *I. delicatissima* lay eggs in underground nests that consist of an entrance, tunnel, and chamber. Nests are often dug either in a singular or communal (“complex”) nesting site where females can create a network of entrances, tunnels, and chambers (Wiewandt, 1982; Rand and Dugan, 1983; Knapp et al., 2016). The nesting behaviour of *I. delicatissima* remains relatively unknown, and published descriptions on nest details are very limited (Knapp et al., 2016).

Here we report on observations of multiple other taxa utilising *I. delicatissima* nests during our study of nesting in this species on St. Eustatius in December of 2022 and 2023 (Table 1; Fig. 1). As part of a study to characterise nesting areas and communal nesting behaviour in *I. delicatissima*, we studied and mapped the detailed structure of iguana nests and nest complexes. We used the absence-presence of new hatchling emergence holes as a proxy for nest presence, as well as to avoid

disturbance of active nests. Out of 29 nest sites with hatching activity, we randomly selected 14 nests that we excavated by hand, at least five days after occurrence of new emergence holes. Excavated nests were distributed across nine sites; three communal and six individual nesting sites. Communal nesting sites were only partially excavated to limit further disturbance of those sites. Nests were measured and mapped in detail along with characteristics of the sites, in terms of slope, terrain, nest depth, and chamber, the results of which are to be reported elsewhere. During excavations we recorded all taxa that were encountered, and collected invertebrates for subsequent identification by users of the citizen science platform iNaturalist.org.

We here report on “other” taxa encountered within emergence holes, tunnels, and egg chambers across the nine nest sites. The deepest two nest chambers were 1.65 m below the surface, and the longest tunnel had a horizontal distance of 6 m. Observed animals consisted

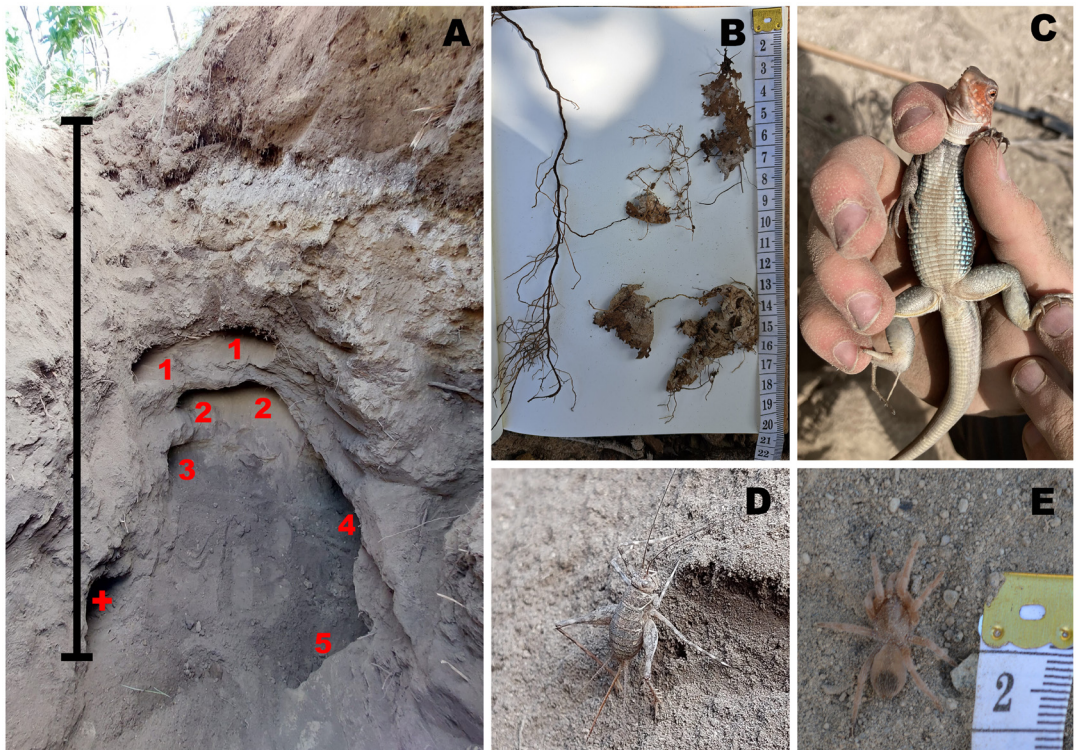


Figure 1. Photos of a partially excavated complex nesting site and encountered taxa on Sint Eustatius: (A) Multiple old tunnels (numbered) and one nest chamber (plus sign), with scale bar indicating a depth of 1.20 m; (B) roots of the *Bourreria succulenta* tree that grew among egg shells in an old nest chamber; (C) *Pholidoscelis erythrocephalus* encountered in a closed tunnel at 72 cm depth; (D) *Gryllobates sigillatus* found at 50 cm depth in a closed tunnel; and, (E) juvenile *Cyrtopholis* sp. tarantula at 110 cm depth in a closed tunnel. Photos by Julian Thibaudier and Matthijs van den Burg.

Table 1. Encountered individuals of inquiline taxa and their depths during Lesser Antillean iguana nest excavations on St. Eustatius.

Order	Taxa	n	Depth Range (cm)
Squamata	<i>Pholidoscelis erythrocephalus</i> (individual)	4	10–72
	<i>Pholidoscelis erythrocephalus</i> (egg)	5	25–50
	<i>Alsophis rufiventris</i>	1	20
Araneae	<i>Cyrtopholis</i> sp.	4	10–135
	Unidentified Araneae sp.	1	55
Orthoptera	<i>Grylloides sigillatus</i>	3	30–50
Hemiptera	<i>Paratrechina longicornis</i> (nests)	3	0–30
Decapoda	<i>Gecarcinus ruricola</i>	1	50
Scolopendromorpha	<i>Scolopendra alternans</i>	1	35

of nine different invertebrate and vertebrate taxa comprising lizards, crabs, centipedes, ants, crickets, spiders, and a snake (Table 1).

Among vertebrates, Red-faced Ground Lizards, *Pholidoscelis erythrocephalus* (Shaw, 1802), were present in tunnels at four of the nine nesting sites (Fig. 1C). In addition to four individuals, we found five *P. erythrocephalus* eggs within three tunnels, consisting of one single egg and two double-egg clutches (Appendix 1). Besides incubation sites, the presence of adult and subadult *P. erythrocephalus* suggests that the species may also use iguana nests as thermal refugia and for foraging. Previously reported species interactions substantiate foraging as a potential reason for the subterranean presence of *P. erythrocephalus*, explaining the surprising depth of 70 cm at which we found one individual. Besides reported predation on tarantulas by *P. erythrocephalus* (Perez-Rivera and Molina-Opio, 2008), which we also encountered in the iguana nests (Table 1), *Pholidoscelis* species are also known to prey on iguana eggs; although this has only been witnessed above ground (Breuil, 2002; Knapp, 2007; Knapp et al., 2016). On one occasion we witnessed an adult Red-bellied Racer, *Alsophis rufiventris* (Duméril, Bibron & Duméril, 1854), entering an (old) iguana nest. This species is known to consume *P. erythrocephalus* and their eggs (Zobel et al., 2018; Adam Mitchell pers. comm. 2023). Among the encountered species, *A. rufiventris* is presumably the only casually-visiting species instead of an inquiline (Keese, 2011).

Among invertebrates, we encountered native tarantulas (*Cyrtopholis* sp.) in four nests, at a maximum depth of 1.35 m (Fig. 1E). At three nest sites we observed nests of the non-native Longhorn Crazy Ant (*Paratrechina longicornis*) that had used an old hatchling emergence

hole as their nest entrance. At two different nest sites, individuals of the non-native Tropical House Cricket (*Grylloides sigillatus*) were found at depths ranging from 30–50 cm (Fig. 1D). For three additional invertebrates, an unidentified Araneae sp., a Caribbean Giant Centipede (*Scolopendra alternans*), and a Purple Land Crab (*Gecarcinus ruricola*), only one individual was encountered. The ecology of these invertebrate species remains largely unknown, so explanations for their occurrence deep in iguana nests remain speculative. Given the limited number of excavated nests, it is likely that more species will be found to inhabit subterranean iguana nesting sites.

Apart from the above results suggesting multiple animal species make active use of *I. delicatissima* nesting sites, these sites arguably impact local flora species as well. As germination can be triggered by a sudden alteration in light, moisture, or oxygen (Bewley et al., 2006), dormant seeds in the soil seed bank may germinate in excavated soil in and around nest entrances and emergence holes. Furthermore, nesting iguanas also introduce nutrients below ground through the deposition of empty eggshells, egg contents, as well as dead embryos and hatchlings. During one excavation, roots, likely of a nearby Strong Back Tree (*Bourreria succulenta*), were found growing through old decomposing eggs, indicating an overlap between nesting chambers and the rooting depths of plants (Fig. 1B). As little is known about microenvironmental conditions in iguanid nests (such as pH and nutrient deposition; but see Troyer, 1984; Bouchard and Bjorndal, 2000; Marco et al., 2005; de Miranda, 2017), we encourage future studies on these and other conditions. One interesting question to address is whether communal nesting positively affects local microenvironmental conditions for increased

nesting success.

Our observations of diverse subterrestrial commensals and casual visitors of iguana nests suggest that *I. delicatissima* is an *allogenic ecosystem engineer* (Jones et al., 1994). Interestingly, only a few reptile species have so far been considered as ecosystem engineers: tortoises (Gibbs et al., 2010; Kinlaw and Grasmueck, 2012), sea turtles (Madden et al., 2008), crocodylians (Somaweera et al., 2020), one iguanid (Tapia and Gibbs, 2022), and some varanid lizards (Doody et al., 2021; see overview of ecosystem engineers in Coggan et al., 2018). Indeed, large-bodied iguanids (e.g., *Iguana*, *Cyclura* and some *Ctenosaura* sp.) have largely been overlooked, as suggested by Doody et al. (2021), but see Tapia and Gibbs (2022). However, published data suggests their probable eco-engineering role; (1) nesting sites can be large (e.g., Knapp et al. 2016), (2) nests may be up to at least 1.65 m deep (e.g., present study), (3) communal nesting areas may be used by tens- to over hundreds of nesting females (e.g., Carpenter, 1966; Rand, 1968; Bock et al., 1985; Knapp et al., 2016), and (4) nest sites may be used annually (e.g., Iverson et al., 2004; Perez-Buitrago et al., 2016). The highly complex three-dimensional subterranean nest sites that iguanid species can create (Fig. 1A, Appendix 2), which are then used by other organisms (both inquiline commensals and casual visitors), substantiates their role as ecosystem engineers. We urge further study of commensals of iguanid nests and nesting sites to further elucidate their ecological importance and conservation priority, especially since 80% of iguanids are considered threatened (IUCN, 2023).

Since scientific work on *I. delicatissima* has allowed a more acute understanding of the decline and deteriorating population trend of *Iguana delicatissima* (Breuil et al., 1994; Day and Thorpe, 1996; Day et al., 2000; Breuil, 2000), all focus has gone towards understanding underlying actors and the mitigation and removal of threats (e.g., Breuil 2013; Knapp et al., 2014, 2016; Vuillaume et al., 2015; van Wagenveld and van den Burg, 2018; Debrot et al., 2022; van den Burg et al., 2022). Our observations provided here suggest how the regional decline and local extirpations of *I. delicatissima* might have affected or be affecting other sympatric species. These potential effects could ideally be assessed by ecological comparisons between islands with and without *I. delicatissima*. For instance, *P. erythrocephalus* occurs on both St. Eustatius and St. Kitts, with *I. delicatissima* only persisting on St. Eustatius. A study comparing the reproductive ecology of *P. erythrocephalus* between these two islands could

shed light on any significance of *I. delicatissima* nest burrows for its reproduction. Furthermore, considering that *I. delicatissima* is not only disappearing but also being replaced by non-native iguanas on numerous islands (van den Burg et al., 2018, 2023; Knapp et al., 2021), the question arises if and/or how these replacements affect local species, ecosystems, and local functional diversity (Kemp, 2023). While this topic has so far received little attention, assessing ecological differences such as the reproductive ecology of *P. erythrocephalus* between islands with only native iguanas, only non-native iguanas, and complete absence of iguanas, would be a topic for future studies. For example, it appears that *I. delicatissima* may nest deeper (max. depth of 1.65 m in this study) compared to populations of the *Iguana iguana* species complex (max. reported depth of 1.20 m; Haller and Rodrigues, 2005), which could translate into differential functional ecological effects. In conclusion, this report provides first evidence of an ecosystem engineering function and keystone species role of *I. delicatissima*, highlighting the importance of conservation of this species to maintain healthy ecosystem function across the Lesser Antilles.

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Appendix 1. Egg of *Pholidoscelis erythrocephalus* with live embryo found within excavated iguana nest tunnel at 50 cm depth below ground level. Photo by Julian Thibaudier.



Appendix 2. Below-ground image of complex three-dimensional structure of *Iguana delicatissima* communal nesting site. Asterisk indicates nest chamber at 1.20 m depth. Numbers correspond to different tunnels. Photo by Julian Thibaudier.

