Reintroducing species when threats still exist: assessing the suitability of contemporary landscapes for island endemics

NICOLE FRANCES ANGELI and LEE AUSTIN FITZGERALD

Abstract Reintroducing species into landscapes with persistent threats is a conservation challenge. Although historic threats may not be eliminated, they should be understood in the context of contemporary landscapes. Regenerating landscapes often contain newly emergent habitat, creating opportunities for reintroductions. The Endangered St Croix ground lizard *Pholidoscelis polops* was extirpated from the main island of St Croix, U.S. Virgin Islands, as a result of habitat conversion to agriculture and predation by the small Indian mongoose *Herpestes auropunctatus*. The species survived on two small cays and was later translocated to two islands. Since the 1950s, new land-cover types have emerged on St Croix, creating a matrix of suitable habitat throughout the island. Here we examined whether the new habitat is sufficient for a successful reintroduction of the St Croix ground lizard, utilizing three complementary approaches. Firstly, we compared a map from 1750 to the current landscape of St Croix and found statistical similarity of land-cover types. Secondly, we determined habitat suitability based on a binomial mixture population model developed as part of the programme monitoring the largest extant population of the St Croix ground lizard. We estimated the habitat to be sufficient for $>$ 142,000 lizards to inhabit St Croix. Thirdly, we prioritized potential reintroduction sites and planned for reintroductions to take place during 2020–2023. Our case study demonstrates how changing landscapes alter the spatial configuration of threats to species, which can create opportunities for reintroduction. Presuming that areas of degraded habitat may never again be habitable could fail to consider how regenerating landscapes can support species recovery. When contemporary landscapes are taken into account, opportunities for reintroducing threatened species can emerge.

Keywords Conservation planning, landscape regeneration, *Pholidoscelis polops*, reintroduction biology, rewilding, species repatriation, St Croix ground lizard, Teiidae: *Ameiva*

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Introduction

The majority of island endemics lost to invasive exotic mammals over the past 500 years have been reptiles, amphibians and birds (Sax & Gaines, 2008). Many endemic species were lost relatively quickly from small islands, and have often persisted only on small offshore islands and in captive colonies (Manne et al., 1999). A conservation goal is to reintroduce species to the islands from which they were extirpated. Even where threats such as invasive predators continue to persist on islands, reintroduction may be possible. The Guidelines to Reintroductions and Other Conservation Translocations (IUCN, 2013, p. 4) state 'There should generally be strong evidence that the threat(s) that caused any previous extinction have been correctly identified and removed or sufficiently reduced'. Original threats need to be addressed, but they should be understood in the present context. Often original threats such as the presence of mongooses on large islands cannot be completely eliminated with current technologies. The Guideline's phrasing 'sufficiently reduced' implies that large-scale restoration efforts are a prerequisite for reintroductions. However, an alternative way of addressing persistent threats is to understand them in the context of contemporary landscapes that have emerged since losses originally occurred. Extinction/extirpation takes place in a landscape context, and changes of those landscapes over time result in altered threats to biodiversity. Restoration efforts in newly developing ecosystems will thus benefit from fresh approaches and new norms (Hobbs et al., 2009). There may be opportunities for reintroductions into emergent habitats and natural refugia that were not present during historic extirpation events. This can apply to islands where landscapes are regenerating, even when some historic drivers of extinction such as invasive predators are still present.

Human land use changes the configuration of landscape features, influencing species' distributions. Changing political and economic factors also alter prospects for landscape restoration (Wintle et al., 2011). In eastern North America, reduction in agricultural activities allowed regeneration of forests that sustain populations of numerous species, including the red wolf *Canis rufus* and red-legged salamander

Plethodon shermani (Connette & Semlitsch, 2013; Karlin et al., 2016). Recovery of large carnivores such as the lynx *Lynx lynx*, grey wolf *Canis lupus lupus* and wolverine *Gulo gulo* in Europe is largely a result of advances in the management of functional landscapes (Chapron et al., 2014). Successional forests are allowing previously overexploited animals that suffered habitat loss, such as the Puerto Rican parrot *Amazona vittata* and white-crowned pigeon *Patagioenas leucocephala*, to recover in Puerto Rico and throughout the Caribbean (Earnhardt et al., 2014; Rivera-Milán et al., 2016). Networks of suitable habitat have been modelled for the Iberian ibex *Capra pyrenaica* in western Iberia (Torres et al., 2016) and for the North Island robin *Petroica longipes* in New Zealand (Armstrong & Davidson, 2006). These cases highlight how landscape change over time can support species reintroduction and recovery.

New ideas are emerging for the reintroduction of species to their historic ranges when threats are still perceived to be present (Stier et al., 2016). For example, the milu *Elaphurus davidianus* became extirpated as a result of hunting and habitat conversion for land reclamation in China in the early 20th century, but a wild population became established in 1998 from 36 animals that escaped from a nature reserve during a flooding event. Now, > 500 milu descended from those founders persist in the wild (Yang et al., 2016). The Formosan clouded leopard *Neofelis nebulosa*, considered extinct in Taiwan, is now thought to be a candidate for reintroductions in regenerating forests with rebounding prey bases (Chiang et al., 2015). A reported sighting in 2019 and other unconfirmed sightings strengthen the case for reintroductions (Everington, 2019).

We suggest that suitable habitats and networks of refugia may exist as a result of landscape regeneration on Caribbean islands that historically lost 30–97% of native land cover to agricultural conversion. This historic land-cover change, since the 1740s, coincided with introductions of invasive species, creating multiple drivers for island extinctions (Lugo & Helmer, 2004). We studied the Endangered St Croix ground lizard *Pholidoscelis polops* (historically known as *Ameiva polops*), which was extirpated from 99.97% of its historic range on the main island of St Croix (217 km²) after the 1884 introduction of the small Indian mongoose *Herpestes auropunctatus*. The extirpation is thought to be a result of both the conversion of 90% of the island to agricultural pastures and predation by mongooses (Henderson, 1992). Recent translocations (1989 and 2008) to two additional small islands without mongooses were successful (Fitzgerald et al., 2015). Reintroduction to the main island was not recommended historically because the presence of mongooses on St Croix was perceived to prevent population establishment (Meier et al., 1990). Here we explore the alternate view, suggesting that even though mongooses are still present on St Croix, regenerating landscapes in the post-agricultural period create new opportunities for the reintroduction of the St Croix ground lizard.

We predicted that areas appropriate for reintroduction exist based on similarities between the historic (1750) and re-emergent (2016) land-cover types on St Croix. We assessed the suitability of potential lizard habitat using landscape parameters (topography, land cover, elevation) developed with data collected from the largest extant population on an offshore island (Angeli et al., 2018). We collected data on the distribution of mongooses across St Croix, and used a prioritization scheme to rank suitable reintroduction areas (Dawson et al., 2015). Our work demonstrates how changing landscapes present new opportunities for restoration in historic ranges, especially on islands, even when threats still exist on a broader landscape scale.

Study area and species

St Croix is a 218 km² island in the Caribbean Sea and one of the U.S. Virgin Islands. It is a single land bank, erupting from the ocean where tectonic plates merged, surrounded by trenches > 1,000 m deep (Case & Holcombe, 1980). The island is covered by subtropical dry coastal forest, with annual rainfall of 1,250 mm in the west and 750 mm in the east (Bowden, 1968). Easterly trade winds blow across the island throughout the year. In addition to the main island, there are four small offshore islands, with a total area of 85 ha, off the north and south shores: Protestant Cay, Green Cay, Ruth Island and Buck Island.

The main island has been mapped since 1750, but only one land-cover map from 1750 still exists (Hopkins, 1989). The acreage of plantations increased island-wide during 1742–1754 (Westergaard, 1938), transitioning from cotton to sugar cane during 1754–1800 (Tyson, 1992). Mongooses were introduced to control rats *Rattus rattus* and *Rattus norvegicus* in sugar cane fields in 1884. By 1917, nearly 90% of native forests and woodlands had been cleared for agriculture or logged (Ward et al., 2000). Sugar cane cultivation virtually ceased by the late 1950s (Atkinson & Marín-Spiotta, 2015). Since then, secondary subtropical forests have developed on St Croix, with naturalized tree species and novel assemblages colonizing former agricultural lands (Atkinson & Marín-Spiotta, 2015).

The St Croix ground lizard is a small diurnal ectotherm that uses a variety of vegetation cover as habitat. It forages in leaf litter for small invertebrate prey (Fitzgerald et al., 2015). The earliest records of the species' loss are from the 1930s. It was completely extirpated from the eastern end of St Croix by 1920, and the last individuals were observed in Frederiksted on the western end of St Croix in 1969 (Dodd, 1978). Fortunately, two populations persisted on Protestant Cay (2.6 ha; 150 m offshore) and Green Cay

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(4.3 ha; 400 m offshore) because mongooses were absent there (Dodd, 1980; Thomas & Joglar, 1996).

Two successful introductions indicate St Croix ground lizards are relatively easy to establish in new areas. A population was established on Ruth Island (9.7 ha; 430 m offshore), a dredge-spoil island, with only nine founders from Protestant Cay in 1989. A translocation of 57 founders from Green Cay to Buck Island (69 ha; 2.6 km offshore) in 2008 was successful (Treglia & Fitzgerald, 2011; Fitzgerald et al., 2015). An estimated total of c. 3,000 individuals now occur on these four islands, with $> 2{,}000$ on Buck Island. Green Cay, Protestant Cay and Ruth Island each harbour 100–400 individuals (Fitzgerald et al., 2015; Angeli et al., 2018). All of these islands are small (total area 85 ha), leaving the lizard populations vulnerable to stochastic events such as hurricanes, predator invasion and habitat degradation.

Methods

Analysing landscape change

We compiled data on protected areas, the predicted distribution of mongooses and land-cover types, and predicted the carrying capacity for lizards in each 30 m^2 cell in a grid covering the entire island of St Croix. We digitized the land-cover map from 1750 (Hopkins, 1989) using the *Georeferencer* plugin tool in *QGIS 2.14.0* (Open Source Geospatial Foundation, Beaverton, USA). Maps from 1950 showed that at that time 97% of land was urban or agricultural pasture (Ward et al., 2000). We obtained land-cover data for 2016 from Landsat 2016 (Angeli et al., 2018). Because the maps from 1750 and 2016 showed landscapes with a heterogeneous mix of land-cover types that were not dominated by agriculture and urban development such as in 1950, we compared the area occupied by different land-cover types in 1750 and 2016 using a paired Welch's t test.

Estimating lizard carrying capacity

We created a map layer for St Croix ground lizard carrying capacity using the results of a mechanistic binomial mixture model developed for Buck Island (Angeli et al., 2018), which accounted for latent abundance and low detection of the species. In that model, we found significant associations of lizard abundance with areas identified by operative temperature models as optimal for the species' thermoregulation (see model description in Supplementary Material 1, and description of the full modelling process in Angeli et al., 2018 and Fitzgerald et al., 2015). We scored the final data set for mean lizard abundance per grid cell as: 1–6 lizards = not suitable, 7–12 lizards = potentially suitable, 13–20 lizards = suitable, and 21–25 = most suitable (Supplementary Fig. 1). These estimates were summed to obtain an estimate of lizard habitat *A* across all areas (Table 1) for the presently dispersing population and the future population (Supplementary Fig. 2).

Prioritizing suitable sites for reintroduction

We considered protected areas on both public and private land for reintroduction. We prioritized potential reintroduction areas by considering the total area of the site and suitable habitat for St Croix ground lizards in the site. We also gave higher priority to sites where the threat of predation by mongooses was mitigated through management. Mongoose management was in place at some sites (e.g. Sandy Point); at other sites there was capacity for land managers to control mongoose populations.

Capacity to control mongooses was assessed based on reports from staff engaged in the trapping of mongooses to protect nesting marine turtles (Angeli, 2017). We also took into account the threat of predation at individual sites based on the distribution of mongooses on St Croix. Mongooses are not evenly distributed across St Croix; their population density varies. We used a species distribution model created by Gould (2007) to visualize overlap between priority reintroduction areas and mongoose presence. Mongooses were absent from 7.96 km^2 (3.65%) of St Croix, most notably in the south of the island where the carrying capacity of St Croix ground lizards was thus predicted to be greater.

Results

Landscape change

In 1750, 42% of St Croix was forested, $< 11\%$ was devoted to pasture or agriculture and $< 5\%$ was urban. According to the historic map, the remaining 42% consisted of woodland, shrubland, and edge forest. The 2016 map showed 32% pasture and agriculture, 31% forest cover and 12% urban areas. Succession of fallow fields to shrubland, woodland and edge forest comprised the remaining 25% of land cover in 2016. We found no statistical differences in land-cover area between the 1750 and 2016 maps (Fig. 1; $t = 0.013$, df = 4.26, $P = 0.989$). The model of mongoose occurrence on St Croix showed numerous areas where mongooses are predicted to be absent that overlapped with priority areas for reintroduction of the St Croix ground lizard (Hoagland et al., 1989; Gould et al., 2007; Fig. 2).

Lizard carrying capacity

The models estimated that St Croix could potentially support 142,421 lizards across 1,169 ha. We identified 19 protected areas, with 2.4—100% suitable habitat (Table 1, Fig. 2). Population models estimated 21,469 St Croix ground lizards

TABLE 1 A ranked list of the proposed areas for potential reintroduction of the St Croix ground lizard *Pholidoscelis polops*, based on combined scores of habitat suitability, mongoose presence, and mongoose control measures.

Protected area	Area (km^2)	Habitat (km^2)	Suitable habitat (%)[1]	Predicted carrying capacity[2]	Priority
Existing populations					
Ruth Cay Wildlife Sanctuary	0.097	0.097	100.0	461	Extant
Protestant Cay Wildlife Sanctuary	0.026	0.025	95.4	151	Extant
Green Cay National Wildlife Refuge	0.043	0.030	70.2	499	Extant
Buck Island Reef National Monument	0.695	0.620	90.0	2,150	Extant
Ranked reintroduction sites					
Sandy Point National Wildlife Refuge	1.555	0.434	28.2	1,273	Highest
Altoona Lagoon Beach Recreation Area	0.068	0.068	100.0	488	Highest
Southgate Coastal Preserve	0.419	0.193	46.1	1,722	Highest
East End Marine Park	0.551	0.146	26.6	1,941	High
Salt River Bay National Historic Park & Ecological Preserve	1.623	0.663	40.9	8,193	High
East Bay & Point Udall	0.535	0.031	5.8	1,829	High
Estate Little Princess	0.194	0.158	81.5	847	High
U.S. Virgin Islands Wetlands	0.350	0.068	19.4	1,130	High
Derick O. Steinmann Memorial Beach	0.008	0.001	16.1	52	Low
Manning Bay Wetlands	0.299	0.292	97.6	1,835	Low
Long Point Bay	0.078	0.022	27.9	258	Low
Estate Great Pond	0.129	0.021	16.4	478	Low
Jack & Isaacs Bays Preserve	1.208	0.028	2.4	1,423	Low
Total for reintroduction sites	7.017	2.125	30.3	21,469	
Entirety of St Croix	217.500	11.690	5.0	142,421	

[1]Per cent of the total habitat in the categories: potentially suitable, suitable, most suitable.
[2]Carrying capacity was estimated from the model, and summed to obtain an estimate for the entire area.

could be supported in protected areas on St Croix, based on a mean of 8.2 ± SD 4.1 (range 0.0–24.0) lizards per 30 m^2 grid cell. Based on the model results and ranking of potential sites, we prioritized reintroduction sites that contained suitable lizard habitat and reduced threat from mongooses (Fig. 3). Eight of the 30 protected areas with lizard habitat already have some mongoose control measures in place, specifically trapping to reduce mongoose density. Mongoose-proof barriers do not currently exist on St Croix, but could be constructed at some sites with < 3 km of fencing. We included this information in the ranking should managers decide to build barriers.

The three most suitable reintroduction sites are: (1) The Sandy Point National Wildlife Refuge, which is located on the south-west end of St Croix and contains 43.4 ha of suitable habitat. The mongoose population in the Refuge has been monitored and reduced through trapping. Lizard reintroductions can occur without fencing, but a 2.9 km mongoose exclusion fence proposed to benefit nesting marine turtles would also reduce mongoose predation on the St Croix ground lizard in this area. (2) Altoona Lagoon, which is managed by the Government of the Virgin Islands, with 6.8 ha of habitat. Our model showed the entire area as suitable habitat for the St Croix ground lizard. The site is protected and is equal in size to Protestant Cay and Green Cay combined, where the lizards persisted after extirpation from St Croix. A wetland adjacent to coastal forest and beach is an important area for migratory birds. This would be a good site to study effects of mongoose control on St Croix ground lizard density. (3) The Southgate Coastal Reserve, which contains 19.3 ha of suitable habitat and is managed by the St Croix Environmental Association. Southgate has a large salt pond supporting birds, and a beach used by nesting marine turtles on the north shore of St Croix. A birding trail is used for environmental education, and outreach activities for the St Croix ground lizard could be included. The reserve is currently fenced with stainless steel chain link, which can potentially be modified to exclude mongooses if deemed necessary.

Discussion

Two successful conservation introductions showed the St Croix ground lizard can be established on small offshore cays where mongooses have been eradicated, such as on Buck Island. However, all four existing populations are vulnerable. Continued recovery of this Endangered endemic species depends on reintroducing it to the main island of St Croix. The short-term risk of reintroduction to the survival of the extant populations is low, because the new population on Buck Island has $> 2{,}000$ individuals and can serve as source of individuals for reintroductions. Two successful translocations of the St Croix ground lizard to Ruth Island

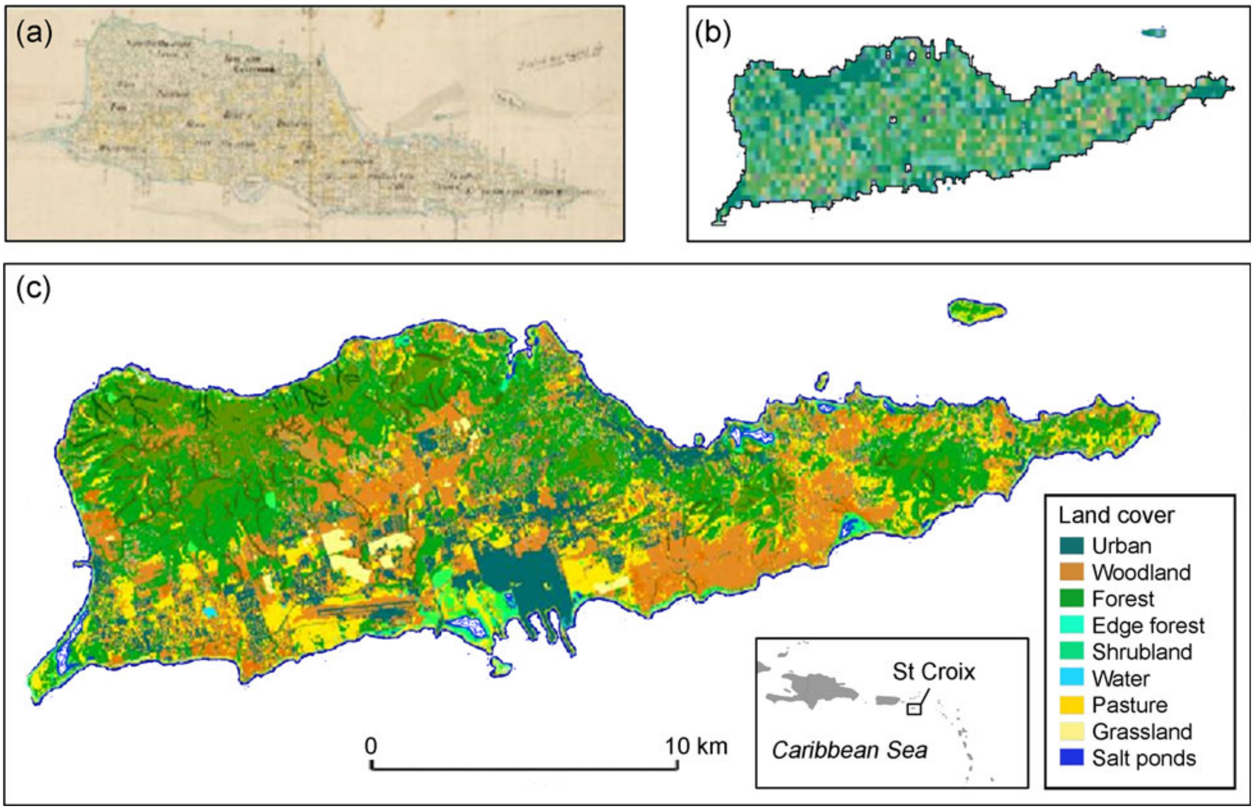

FIG. 1 Historic and recent land cover in St Croix, U.S. Virgin Islands. (a) The historic map from 1750 was created by J. Cronenberg and J. von Jaegersber (reproduced with permission of Copenhagen Archives). (b) This map was digitized to show historic land-cover types. Landscape transformation and introduction of mongooses led to the extirpation of the now Endangered St Croix ground lizard *Pholidoscelis polops*. (c) Land-cover classifications of 2016, matched to the digitized historic land-cover types. Establishment of protected areas, land spared from agriculture, and suburban development resulted in emergent land-cover types, which now include potential habitats for the St Croix ground lizard.

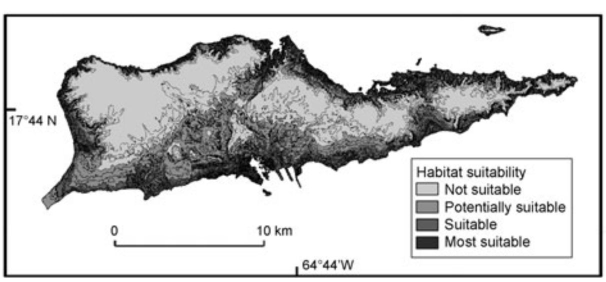

FIG. 2 Suitable habitat for the St Croix ground lizard on St Croix, U.S. Virgin Islands. We used a predictive habitat suitability model, with suitability categories based on threats, land-cover types and ongoing conservation efforts.

and Buck Island indicate that once established, populations grow rapidly and disperse into unoccupied available habitat (Fitzgerald et al., 2015). On Buck Island, the newly established population expanded rapidly, with a marked dispersal front emanating from the point of introduction (Angeli et al., 2018). This indicates high potential for dispersal on mainland St Croix once founder populations are established.

Lindenmayer et al. (2008, p. 134) suggested, 'novel ecosystems present major challenges to traditional thinking in conservation ecology, such as the focus on species extinctions as the usual response to landscape transformation.' Understanding the landscape of threats and using that knowledge to adjust conservation actions can present positive opportunities for restoration of species and rewilding ecosystems (Jordan, 2000). We examined land-cover change on St Croix spanning 250 years and documented landscape transformations that led to extirpation of the St Croix ground lizard. The primary factors in this extirpation were deforestation, land conversion for agriculture, and introduction of mongooses. In recent decades land has been spared from agriculture, protected areas have been established, and invasive species including mongooses are increasingly managed. This recent transformation of land use in St Croix has facilitated emergence of land cover that includes suitable habitat for the St Croix ground lizard. Using a prioritization scheme, we identified potential reintroduction sites that could increase the area occupied by the St Croix ground lizard by 180%. In previous studies, a predictive approach using demographic data demonstrated that sufficiently low levels of threats could allow reintroductions of the Iberian ibex in western Iberia, and the North Island robin

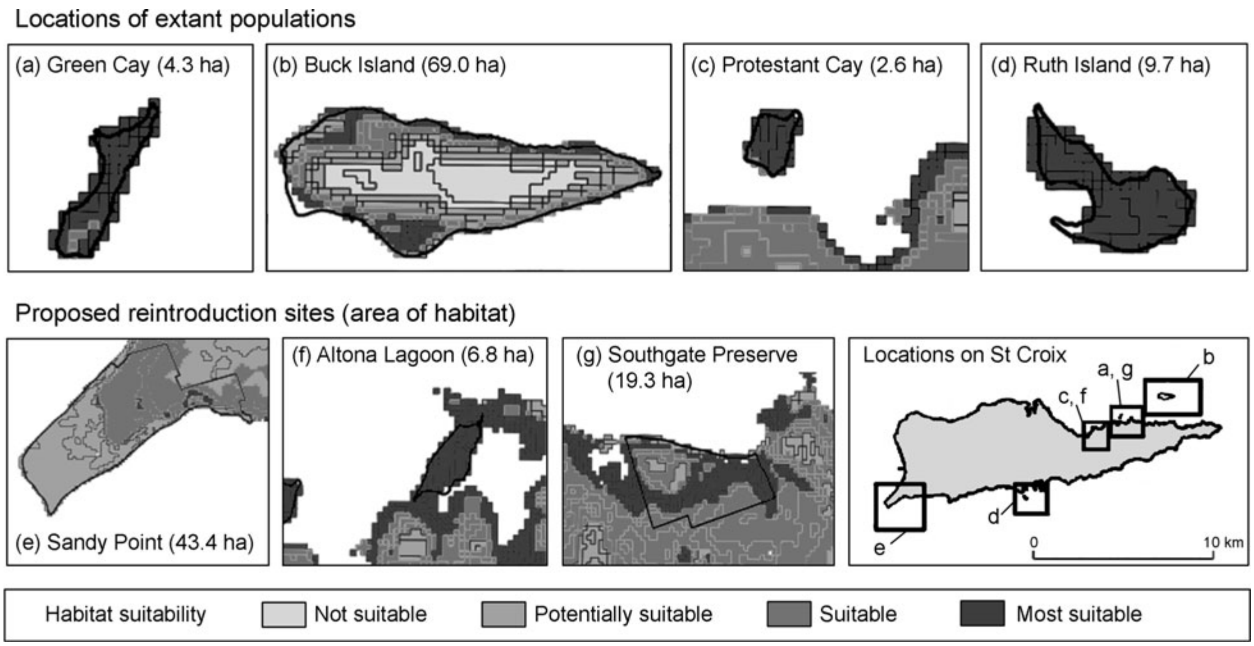

FIG. 3 The St Croix ground lizard occurs in four extant populations, on (a) Green Cay, (b) Buck Island, (c) Protestant Cay and (d) Ruth Island. We propose three reintroduction sites on St Croix, at (e) Sandy Point, (f) Altoona Lagoon and (g) Southgate Coastal Preserve. Area of habitat is shown for each site; they are not drawn to scale. The inset map indicates where each site is located on St Croix.

and North Island saddleback *Philesturnus rufusater* in New Zealand (Armstrong & Davidson, 2006; Parlato & Armstrong, 2012; Torres et al., 2016). Our approach differs in that we evaluated suitability across emergent contemporary landscapes, to determine areas best suited for reintroduction.

Although threat abatement is important for protecting endemic species on islands, and mongoose control on St Croix should be a priority, total eradication of invasive predators on relatively large, human-inhabited islands may not be feasible. Our approach relies on re-emergence of habitat and refugia that will allow the St Croix ground lizards to persist, despite continued presence of mongooses. The decline of the St Croix ground lizard, spanning 95 years, provides some evidence that anthropogenic landscapes created refugia where populations escaped predation. The last stronghold for the species in the 1960s was along the waterfront in the busy town of Frederiksted (Dodd, 1978). St Croix was stripped of native vegetation cover, and mongooses devastated native fauna. In comparison with the pre-extinction landscape, present-day St Croix contains similar amounts of suitable habitat in protected and in urbanized areas.

Reintroduction experiments such as the one we have proposed can be carried out with careful implementation and monitoring, and species recovery can be tracked with frameworks such as the IUCN Green List (Akçakaya et al., 2018). In 2019 we met with ecologists and personnel from U.S. Virgin Islands resource agencies, the U.S. Fish & Wildlife Service and U.S. National Park Service to finalize decisions about the reintroductions. The group planned for reintroductions during 2020–2023 using the prioritization outlined here.

There is a long-term risk associated with not learning how to repatriate endemic species. Small, isolated wildlife populations will remain vulnerable to sea level rise and anthropogenic disturbance. In such conditions, they could increasingly be perceived as only able to persist in refuge locations outside their core range. Taking contemporary landscapes and regeneration of suitable habitat into account could provide new opportunities for reintroducing threatened species to areas from which they were originally extirpated.

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Author contributions Study design, fieldwork, writing: both authors; analysis: NFA.

Conflicts of interest None.

Ethical standards This research was carried out under U.S. Virgin Islands permit (STX 019-13), USFWS permit (TE98000A-0) and Texas A&M University permit IACUC (2013-0011), and otherwise complied with the *Oryx* guidelines on ethical standards.

Data availability Geospatial data layers are available at figshare.com/projects/Repatriation_St_Croix_ground_lizard/28461. Code is available at github.com/nangeli1/repatriation.

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