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Independent evolutionary histories in allopatric populations of a threatened Caribbean land mammal

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ABSTRACT

Aim To determine the evolutionary history, relationships and distinctiveness of allopatric populations of Hispaniolan solenodon (*Solenodon paradoxus*), a highly threatened Caribbean “relict” mammal, to understand spatiotemporal patterns of gene flow and the distribution of diversity across complex large island landscapes and inform spatial conservation prioritization.

Location Historical and modern-day solenodon specimens were analysed from sampling localities across Hispaniola, representing this geotectonically complex island’s distinct northern, southeastern and southwestern biogeographic provinces.

Methods We successfully amplified mitochondrial cytochrome *b* and control region sequences from 34 solenodon samples. Bayesian phylogenetic analyses were applied to assess the relationship between these sequence data, and coalescent simulation and approximate Bayesian computation were used to identify which model of solenodon intra-island demographic history best explains the observed patterns of variation. We also conducted morphometric analysis of 110 solenodon specimens to investigate whether allopatric Hispaniolan populations can be differentiated using craniodental characteristics.

Results Unique haplotypes were identified in solenodon samples from each biogeographic region, with no haplotype sharing between regions. Higher marginal posterior probability values were found for a three-population model

comprising allopatric northern, southeastern and southwestern Hispaniolan populations, with exceptionally low migration rates inferred between all populations, indicating that they are genetically isolated. Modal estimates of long-term effective female population size are extremely low for southwestern and southeastern populations. Morphometric differentiation is observed between all three populations.

Main conclusions Evolutionary differentiation of Hispaniolan solenodons into three distinct populations is congruent with phylogenetic patterns observed in several other Hispaniolan species, with population isolation possibly associated with past marine transgression. We interpret these populations as distinct subspecies, with the two genetically impoverished southern subspecies particularly vulnerable to environmental change. Our improved understanding of Hispaniolan solenodon evolutionary history provides an important baseline for identifying wider patterns of intra-island diversification, and prioritizing conservation attention for evolutionarily significant populations.

Keywords

Coalescent modelling, conservation genetics, Hispaniolan solenodon, historical biogeography, palaeo-islands, *Solenodon paradoxus*

INTRODUCTION

Island systems such as the Caribbean have been the focus of research into evolutionary patterns, processes and dynamics since the nineteenth century (Wallace, 1880; Ricklefs & Bermingham, 2008; Helmus *et al.*, 2014). Islands also often preserve “relict” clades that have disappeared elsewhere, and their role as repositories of ancient biodiversity provides important conservation implications for understanding the evolutionary history of insular biotas, especially as many island taxa are particularly vulnerable to human pressures. Such research has often aimed to reconstruct colonization histories and adaptive radiations at an island-wide level, or compare inter-island diversity patterns to identify general evolutionary or biogeographic principles (Schluter, 2000; Losos & Ricklefs, 2009; Yoder *et al.*, 2010). However, the increasingly heterogeneous environments of larger islands may also be associated with modern or historical barriers to gene flow that can drive allopatric speciation, and diversification rates in insular taxa are positively correlated with island size (Kisel & Barraclough, 2010). Determining the distribution of diversity across complex large island landscapes therefore constitutes an important area of research in insular evolution, to analyse gene flow in relation to geography and understand its ecological determinants, and inform local-scale spatial conservation prioritization of island taxa (Heads, 2002; Brown *et al.*, 2014).

The insular Caribbean is one of the only oceanic-type island systems to have been colonized by non-volant land mammals, which diversified into >100 endemic species before human-caused extinction of most of this fauna during the Holocene and recent historical era (Turvey, 2009). The extant fauna includes two surviving representatives of the Solenodontidae, the Hispaniolan solenodon

(*Solenodon paradoxus*) and Cuban solenodon (*Atopogale cubana*), large-bodied lipotyphlan insectivores which are the only living mammals with dental venom delivery systems (Folinsbee, 2013), and which constitute an ancient lineage that diverged from other living mammals c.76 million years ago (Mya) (Roca *et al.*, 2004). Solenodons have frequently been considered extremely rare if not already extinct (Verrill, 1907; Bridges, 1936; Allen, 1942; Fisher & Blomberg, 2011), and this combination of evolutionary distinctiveness and severe threat has led to both species being identified as global priorities for mammal conservation (Collen *et al.*, 2011).

Evolutionary research into Caribbean land mammals has almost exclusively investigated mainland sister-group relationships and the timing and number of colonization events for different clades, mainly within the context of the competing mechanistic hypotheses of vicariance and overwater dispersal (MacFadden, 1980; Roca *et al.*, 2004; Fabre *et al.*, 2014; Brace *et al.*, 2015). However, Cuba and Hispaniola, the largest Caribbean islands, have also experienced within-island radiations of several mammal clades into allopatrically distributed populations that are genetically and morphologically differentiated (e.g. *Capromys* and *Mysateles* hutias in Cuba; Borroto-Páez *et al.*, 2005). Hispaniola, divided politically into the Dominican Republic and Haiti, has a complex geotectonic history that has shaped local patterns of endemic biodiversity. It consists of independent northern and southern palaeo-islands that docked tectonically during the middle-late Miocene (Mann *et al.*, 1991; Graham, 2003) but remained separated by the Neiba Valley, a prominent depression periodically or continually inundated by a narrow seaway until the Late Pleistocene (Maurrasse *et al.*, 1980). The southern palaeo-island is further

subdivided into two major physiographic provinces (western Massif de la Hotte, eastern Massif de la Selle-Sierra de Bahoruco) separated by the Jacmel-Fauché depression, which bisects the peninsula and was also inundated during some or all of the Plio-Pleistocene (Maurrasse *et al.*, 1980) (Fig. 1). Regional ecological differentiation may also have been effected by Pleistocene climate fluctuations and associated vegetational changes (Pregill & Olson, 1981). All three regions are biogeographically distinct and characterized by substantial endemism in many terrestrial taxa (Williams, 1961; Schwartz, 1980; Hedges, 1999).

Combined molecular and morphometric research on the Hispaniolan hutia (*Plagiodontia aedium*), Hispaniola's other surviving non-volant land mammal, has demonstrated that distinct hutia subspecies are distributed allopatrically across all of the island's biogeographic regions (Brace *et al.*, 2012; Hansford *et al.*, 2012; Turvey *et al.*, 2015). Hispaniolan solenodons are also distributed across all three biogeographic regions (Ottenwalder, 1999, 2001), but research into the evolutionary history of solenodon populations across Hispaniola has so far been limited. Ottenwalder (2001) used a series of single-measurement morphometric analyses to differentiate two distinct northern and southern subspecies. The only previous molecular investigation of within-island solenodon genetic diversity, an analysis of the 5' end of the mitochondrial control region in three samples by Allard *et al.* (2001), concluded on the basis of relatively high observed nucleotide diversity that different Hispaniolan populations might be geographically or reproductively isolated, but provided no insights into spatial structuring or between-population relationships.

Establishing an improved understanding of the structure and evolutionary relationships of solenodon populations across Hispaniola is

essential to determine whether different species exhibited similar evolutionary responses to historical allopatric barriers on this geotectonically complex island, or whether the significance of these barriers in regulating gene flow has been affected by ecological or other factors. As solenodon populations across Hispaniola are experiencing different levels of anthropogenic threat (Turvey *et al.*, 2008, 2014), assessing their evolutionary distinctiveness is also of urgent importance to inform optimal conservation management and resource allocation. We therefore conducted combined molecular and morphological analyses on a sample of solenodons comprising both recent field-caught individuals and historical museum specimens from each of Hispaniola's biogeographic regions, to reconstruct the evolutionary history of allopatric solenodon populations and test whether they show evidence of major lineage divergence across the island, and determine whether this history is congruent with evolutionary patterns inferred for other endemic Hispaniolan taxa.

METHODS

Genetic samples

We obtained 41 solenodon samples with known geographic provenance within Hispaniola, comprising 23 samples from museum collections and 18 archived hair/soft tissue samples originally from live-caught and dead individuals encountered during fieldwork in 2009-2013 (Table 1; see also Table S1 in Supporting Information), as part of a long-term research programme on Hispaniola's endemic mammals (Young, 2012). These samples represent collection localities distributed widely across both palaeo-islands, and east and

west of the Jacmel-Fauché depression (Fig. 1).

DNA extraction and amplification

Due to variation in sample preservation and quality of highly degraded field-collected and museum tissues, all DNA extractions were conducted in a dedicated ancient DNA laboratory (Royal Holloway, University of London), following protocols described in Brace *et al.* (2012). We amplified mitochondrial DNA (mtDNA) using short overlapping fragments to more easily identify potential contamination and miscoding lesions, targeting 534 base pairs (bp) of the control region and 411 bp of the cytochrome *b* (*cyt b*) region. Four primer pairs were designed for this study (Table S2). PCR reactions, amplicon purification, sequencing, and protocols to prevent contamination that include negative controls and repeated PCR amplification, were performed as described in Brace *et al.* (2012) with primer-specific annealing temperatures of 50/52°C.

Phylogenetic analyses

Solenodon sequences were aligned manually. DNA substitution model and partition fit were selected under Bayesian information criterion using PARTITIONFINDER 1 (Lanfear *et al.*, 2012). For control region data, Hasegawa-Kishino-Yano (HKY) (Hasegawa *et al.*, 1985) plus gamma (G) was then selected. For *cyt b* sequence data, three partitions were selected: codon position 1 Jukes Cantor (JC) (Jukes & Cantor, 1969), position 2 (HKY+G), and position 3 (HKY). Phylogenetic trees were inferred using MRBAYES 3.2 (Ronquist & Huelsenbeck, 2003), using four chains (three heated, one cold) run for 1×10^6 generations, and sampling every 1×10^3 generations with a burn-in period of 250 trees. Nodal

support was determined by approximate posterior probabilities performed in MrBayes. In the absence of a recent sister taxon for this species (Hispaniolan and Cuban solenodons are estimated to have diverged c.25 Mya; Roca *et al.*, 2004), no outgroup was used. A network was constructed using TCS (Clement *et al.*, 2000) with maximum connections set at 95% and all gaps treated as missing data. Pairwise sequence divergence estimates were calculated in MEGA 5.1 (Tamura *et al.*, 2011) using the Kimura-2 parameter (K2P) model (Kimura, 1980).

Coalescent modelling

We considered four plausible models of solenodon demographic history since Hispaniola formed from separate palaeo-islands (Fig. 2), and used coalescent simulation (Wakeley, 2009) and approximate Bayesian computation (ABC; Beaumont *et al.*, 2002) to test which model best explains the observed mtDNA data. The first model assumes that solenodons belong to a single panmictic population with no subdivision. The second assumes that they are subdivided into two populations (northern, southern) separated by the Neiba Valley but connected by migration. The third model is similar to the second, except that northern and southern populations are separated by the Jacmel-Fauché depression. The fourth model assumes that solenodons are subdivided into three populations (northern, southeastern, southwestern), but connected by migration across the Neiba Valley and Jacmel-Fauché depression.

We performed 1×10^8 coalescent simulations for each model, choosing parameter values at random from their prior distributions. In all models, female effective population size (N_{ef}) prior distribution was set between 10^5 - 10^6 /population, and sampled on a log-scale. In models 2, 3 and 4, migration rate

(m) was set between 0-0.004/generation after exploratory analysis with wider ranges produced very high rejection rates for $m > 0.004$. A published generation time of 1901.92 days was assumed (Pacifi *et al.*, 2013).

Datasets for each model were simulated using Fastsimcoal 2 (FSC; Excoffier *et al.*, 2013) separately for each sequenced mtDNA region. For *cyt b* simulations, mutation rates sampled from a flat prior between 1-10%/million years (Ma) were explored, and for control region simulations, rates between 1-15%/Ma were explored, based on reported rates in lipotyphlans and other mammals (Stewart & Baker, 1994; Pesole *et al.*, 1999; Hope *et al.*, 2011). Simulations were run assuming 0.71422 of substitutions as transitions for *cyt b* and all substitutions as transitions for control region; transition/transversion ratios were estimated from sample data using Arlequin ver. 3.11 (Excoffier *et al.*, 2005). For each mtDNA region, 1×10^8 simulations were performed separately. We assumed that populations north and south of the Neiba Valley diverged from a common ancestral population 1,920,433 generations ago, i.e. equivalent to 10 Mya, reflecting approximate timing of docking of palaeo-islands during the middle-late Miocene and thus the earliest timing for possible dispersal across Hispaniola. Populations east and west of the Jacmel-Fauché depression were assumed to have diverged 1,920,426 generations ago, seven generations (36 years) after docking of the palaeo-islands. While uncertainty remains over the exact date of palaeo-island docking (Mann *et al.* 1991; Graham 2003), in practice these assumed dates make no difference to our results, because in the vast majority of our coalescent simulations all lineages coalesce to a single lineage in a markedly shorter time than 10 Ma. Sequences were sampled from coalescent simulations in three groups, to mimic the actual number and location of samples

collected for the observed data: three individuals from southwestern Hispaniola, 16 individuals from southeastern Hispaniola, and 11 individuals (cyt *b*) or 13 individuals (control region) from northern Hispaniola.

Within-sample summary statistics (number of haplotypes, number of segregating sites, average pairwise difference, haplotype diversity (biased by $n/n-1$), Tajima's *D*) and between-sample summary statistics (number of haplotypes private to each sample, average pairwise difference, F_{ST}) were calculated from observed data and simulated data using bespoke code written in R 2.10.1 (R Development Core Team 2011). Between-model comparisons were made by calculating Euclidean distances (Ray *et al.*, 2010) between observed and simulated summary statistics for all models separately for control region and cyt *b* sequences. Summary statistics were normalized using means and standard deviations computed by pooling all model simulations together (4×10^8 simulations for each sequenced region); simulations were then ordered by increasing Euclidean distance, and the top 1% retained. Relative proportions of simulations from each model within the *n*-smallest Euclidean distances gave estimates of marginal posterior probabilities for each model (Estoup *et al.*, 2004; Ray *et al.*, 2010). We plotted the posterior probability of each model by calculating the number of each model in the top *n* closest simulations. We then assessed the number of top-sliced simulations required to clearly differentiate support for the best model by generating 10^6 random draws from a Dirichlet distribution under a null prior, with parameters equal to the number of simulations from each model at each top-slice. The top 1%, 0.5% and 0.1% of simulations with smallest Euclidean distances from the model with highest posterior probability were then used to estimate marginal posterior

probabilities for model parameters by ABC (Beaumont *et al.*, 2002), using a rejection-only approach. Posterior probability distributions were plotted by kernel density estimation. The 95% highest posterior density intervals for model parameters N_{ef} and m were estimated along with their modal values. While the Tajima's D statistic (Tajima, 1989) is a derivative of θS and $\theta \pi$, the ABC algorithm results in additional conditioning information from inclusion of this statistic.

It is possible that our four simple models of historical biogeographic structuring of solenodon populations are misspecified, which would lead to misleading inferences. To examine this possibility, Fisher's method (Fisher, 1925) was used to combine two-tailed probabilities of observed conditioning statistics, obtained by comparison to the top 100,000 simulations for the best model. The resultant chi statistic was compared to a distribution of chi statistics obtained by comparing each simulation against the set of all other simulations (Voight *et al.*, 2005) in the top 100,000, to obtain a two-tailed p -value for the combined observed statistics under the best model and best joint estimates of model parameter values. This was performed separately for *cyt b* and control region sequences.

Morphometric analyses

We studied 110 crania and/or mandibles of adult solenodons (individuals showing complete dental eruption) from known localities across Hispaniola, including specimens from all three biogeographic regions, as well as eight Cuban solenodon specimens (Fig. 1; Table 2; Table S3). Eighty-two craniodental measurements (46 cranial, 36 mandibular) were taken using dial calipers

accurate to 0.02mm (Table S4). Data were analyzed using Analysis of Variance (ANOVA), Principal Component Analysis (PCA), and Generalized Linear Models (GLM) in R 2.10.1, to investigate whether solenodon populations from Hispaniola's three biogeographic regions and from Cuba could be differentiated morphometrically from each other using craniodental characteristics. The full morphometric dataset was used for all individual ANOVAs, but due to minor damage to some specimens it was not possible to use the full measurement or specimen series for PCA of the total Hispaniolan or Hispaniolan+Cuban datasets. It was also not possible to perform a GLM to compare different Hispaniolan populations using the entire measurement dataset, as the number of dependent variables is greater than the overall sample size, thus violating statistical assumptions. Dataset reduction, involving sequential elimination of measurements and specimens based on levels of missing data, was performed to maximize both number of measurements and number of specimens from each comparative population retained in analyses, whilst maintaining a greater number of specimens to measurements so as to not violate PCA/GLM assumptions. Reduced datasets used for these analyses are shown in Tables S3-S4.

RESULTS

Phylogenetic analyses

From the 41 solenodon individuals sampled, 34 successfully yielded mtDNA, with 32 samples unambiguously yielding amplicons for the entire targeted area of control region, and 29 samples yielding amplicons for the entire targeted area

of *cyt b*. Six unique haplotypes were identified from northern Hispaniola, four from southeastern Hispaniola, and one from southwestern Hispaniola, with no haplotype sharing across these regions (Fig. 3). We report strong posterior probability values (1) for monophyly of haplotypes found east of the Jacmel-Fauché depression and the distinct haplotype west of this biogeographic barrier. The clustering of groups of sequences from northern Hispaniola also show good support, with posterior probability values of 0.63-0.97. Pairwise sequence divergence estimates between samples are shown in Table 3.

Coalescent-based analyses

Higher marginal posterior probability values were found for the three-population model compared with other models, using both *cyt b* and control region sequences separately (Fig. S1-S2). The three-population model with parameter values from the top 100,000 simulations taken as posterior estimates was not rejected by the method of Voight *et al.* (2005), returning two-tailed *p*-values of 0.211 and 0.515 for *cyt b* and control region sequences respectively. Exceptionally low levels of migration (individual migrants/generation) were inferred between all three populations (modal northern-southeastern migration rate $\leq 1.50 \times 10^{-3}$; modal southeastern-southwestern migration rate $\leq 9.43 \times 10^{-4}$; all 95% confidence intervals $\leq 3.00 \times 10^{-3}$), indicating that they are almost certainly all highly isolated (Table 4). Whereas modal estimates of N_{ef} are reasonably high for the northern population (*cyt b*-based modal estimate=2584, control region-based modal estimate=3218), they are extremely low for southwestern and southeastern populations (*cyt b* estimates=32 and 34; control region-based estimates=32 for both populations) (Table 4).

Morphometric analyses

Analysis of Hispaniolan and Cuban specimens shows significant between-sample morphological differentiation ($F=290.86$, $p<0.001$). There is clear separation between solenodons from different islands, which are uncontroversially recognised as representing separate species, on PCA axis 2, explaining 14.17% of variation. However, solenodons from different Hispaniolan populations are distributed across PCA axis 1, explaining 47.54% of variation and therefore indicating considerable morphometric differentiation between these populations (Fig. 4a).

Analysis of Hispaniolan specimens shows that the three population samples exhibit differentiation in morphospace along PCA axis 1 (Fig. 4b), with statistically significant separation seen between all three samples in a GLM of residuals of PCA 1 (northern versus southeastern, $T=9.569$, $p<0.001$; northern versus southwestern, $T=5.628$, $p<0.001$; southeastern versus southwestern, $T=-4.057$, $p<0.001$). Craniodental measurements showing statistically significant population-level differences in ANOVA are listed in Table S4.

DISCUSSION

Evolutionary relationships and distinctiveness

Our combined molecular-morphological study constitutes the most thorough investigation to date into the evolutionary history of Hispaniolan solenodons, and provides strong evidence that three evolutionarily distinct allopatric solenodon populations are present on this geotectonically complex island, with

minimal levels of historical gene flow between populations. Evolutionary differentiation into distinct populations associated with each of Hispaniola's major physiographic provinces is congruent with the pattern observed in Hispaniolan hutias, the only other extant native non-volant small mammal present on the island (Brace *et al.*, 2012), and supports the suggestion of geographic structuring of solenodon populations across Hispaniola proposed on the basis of more limited genetic data by Allard *et al.* (2001). Our analyses support the major distinction between northern and southeastern solenodon populations reported by Ottenwalder (2001), and further support previous suggestions that the geographically isolated southwestern population in the Massif de la Hotte is also distinct (Woods & Ottenwalder, 1992; Ottenwalder, 2001; Turvey *et al.*, 2008). Ottenwalder (2001) suggested that the southwestern population was most closely related to other southern palaeo-island solenodons, and would share a sister-taxon relationship with the southeastern population if recognized as distinct. Such a pattern is also observed in Hispaniolan hutias (Brace *et al.*, 2012). However, a contrasting pattern is evident when comparing solenodon and hutia phylogenetic networks, with a greatly reduced number of mutational steps differentiating northern and southern solenodon samples (2) compared to northern and southern hutia samples (32). Given that single-loci phylogenetic trees are only weakly constrained by population histories, we advise caution when interpreting these networks. However, the pattern of evolutionary relationships observed between allopatric solenodon populations is not necessarily congruent with that seen in hutias, raising the possibility that these species may have experienced different geographic patterns of historical gene flow and isolation shaping population differentiation.

The inferred distinction between allopatric solenodon populations across Hispaniola may have resulted from an originally geographically localized population that secondarily dispersed across environmental barriers separating the island's physiographic provinces. As southern Hispaniola only became fully exposed above sea level during the Plio-Pleistocene, whereas northern Hispaniola has a longer subaerial history and until c.20-25 Mya was connected to Cuba, the other Caribbean island where solenodons occur (Iturralde-Vinent & MacPhee, 1999; Graham, 2003), this suggests a longer evolutionary history for solenodons in this region. Alternately, the observed phylogeographic structure may have resulted from a formerly island-wide population that was secondarily subdivided by formation of barriers to gene flow. The almost complete lack of a pre-Quaternary Caribbean lipotyphlan fossil record (MacPhee & Grimaldi, 1996) makes it challenging to investigate these contrasting hypotheses further. Inundation of the Neiba Valley and Jacmel-Fauché depression during the Plio-Pleistocene has previously been inferred as a likely biogeographic mechanism driving intra-island population isolation for several Hispaniolan taxa, with periodic dispersal events across these barriers occurring throughout the Neogene and Quaternary via intermittent regional marine transgression or stochastic overwater dispersal (Gifford *et al.*, 2004; Townsend *et al.*, 2007; Brace *et al.*, 2012; Sly *et al.*, 2012); potential differences in genetic structuring of population relationships between solenodons and hutias may therefore be the product of chance historical events. Repeated sea-level fluctuations have also driven lipotyphlan evolutionary diversification in other island systems (Esseltyne & Brown, 2009). Increasing climatic fluctuation throughout the Quaternary may

also have driven population fragmentation in many Caribbean taxa (Getty *et al.*, 2001).

The evolutionary distinctiveness inferred for the southwestern solenodon population is consistent with higher-order taxonomic differentiation seen in some other locally endemic extinct Quaternary mammal taxa also restricted to the Massif de la Hotte (the primate genus *Insulacebus* and the rodent genus *Rhizoplagiodontia*; Woods, 1989; Cooke *et al.*, 2011), and with extreme levels of range-restricted endemism shown by other groups (e.g. *Eleutherodactylus* frogs) in this global biodiversity hotspot (Ricketts *et al.*, 2005). This substantial regional evolutionary distinctiveness across multiple taxa suggests that local geographic and/or ecological characteristics that have supported extensive evolutionary diversification in the Massif de la Hotte may also have driven population isolation and differentiation in solenodons, irrespective of the mechanism by which solenodon population subdivision occurred on Hispaniola.

As the three solenodon populations identified in this study are morphologically differentiated on the basis of substantial sample series for each population ($n \geq 20$; Table S3) and also highly genetically differentiated on the basis of multiple analyses of available genetic samples, we interpret them as taxonomically distinct from each other. Levels of between-population sequence divergence (Table 3) are comparable in magnitude to those observed between allopatric hutia subspecies occurring across Hispaniola (1.03-2.86%; Brace *et al.*, 2012), and are closer to levels of intraspecific rather than interspecific variation in *cyt b* data for well-diagnosed related species of other lipotyphlan taxa (e.g. maximum 8.9% in *Crocidura russula* and maximum 8.4% in *C. suaveolens*, versus 14.3-20.6% between European *Crocidura* species; Vogel *et al.*, 2003).

Morphometric differentiation between solenodon samples from different regions of Hispaniola is also comparable to that between allopatric hutia subspecies (Hansford *et al.*, 2012). Increased use of the phylogenetic species concept in mammalian taxonomy has led to recent elevation of many subspecies to species rank; however, this approach has been widely criticized as promoting artificial taxonomic inflation (Zachos *et al.*, 2013), and pending future reassessment of species concepts across the Lipotyphla we therefore interpret these solenodon populations as distinct from each other at the subspecies level. We follow Ottenwalder (2001) in recognising the northern subspecies *Solenodon paradoxus paradoxus* and the southeastern subspecies *Solenodon paradoxus woodi*, and we describe the currently unnamed southwestern Hispaniolan population here as the new subspecies *Solenodon paradoxus haitiensis* (Appendix S1, Fig. S3).

Conservation implications of evolutionary history

Our most unexpected finding is the extremely low modal estimate of long-term N_{ef} for both the southwestern and southeastern solenodon populations (Table 4). Confidence intervals on our N_{ef} estimates are mostly quite wide, reflecting the somewhat limited information content of our data; our population inferences are therefore made with these stated confidence intervals. There is also both variation and uncertainty around the relationship between N_{ef} and adult census population size (Palstra & Fraser, 2012). However, comprehensive estimates of the ratio of effective:actual population size have averaged 0.10-0.11 (Frankham, 1995), suggesting that southwestern and southeastern populations are likely to have small long-term effective population sizes, or have experienced severe demographic contraction that has left them genetically impoverished. Indeed,

estimated modal N_{ef} levels for these solenodon populations are similar to those seen in critically endangered taxa such as Amur tiger (*Panthera tigris altaica*) that are reduced to tiny remnant wild populations and require intensive conservation management (Henry *et al.*, 2009). Differentiating between recent population collapse and long-term small effective population size is probably beyond the information content of our mtDNA data. However, future analyses utilising larger mtDNA sample sizes (Drummond *et al.*, 2005) or whole-genome sequencing (e.g. Li & Durbin, 2011) may be able to resolve this question.

Only three solenodon samples were analysed from southwestern Hispaniola, providing limited information on effective population size (as reflected in the wide 95% highest posterior density interval for N_{ef}). However, these samples were collected several kilometres apart, across an area of the Massif de la Hotte representing a substantial part of the known surviving distribution of this population (Turvey *et al.*, 2008; Appendix S1), and hutias sampled across exactly the same area show an N_{ef} estimate that is several orders of magnitude higher (mode=18,086, 95% credibility interval=5849-66,407; Brace *et al.*, 2012), indicating a very different population status for these two mammals in this region. Although both solenodons and hutias are now largely restricted in the Massif de la Hotte to a small area of karstic plateau to the east of Pic Macaya (Woods, 1981, 1986; Woods & Ottenwalder, 1992), hutias are well-known to local informants and are reportedly encountered relatively frequently and often considered crop pests, whereas solenodons are reportedly much rarer and lack a consistent well-known local name (Turvey *et al.*, 2008). Whereas past field surveys have only attempted to determine continued survival of solenodons in the Massif de la Hotte rather than estimate local population size, it is certainly

conceivable that this population is in the low hundreds of surviving individuals, suggesting that our N_{ef} estimate reflects its current status rather than long-term effective population size. We encourage further research into the genetic history of this newly described subspecies.

In contrast, the southeastern population, whilst not abundant, has been recorded across a greater geographic area comprising multiple habitat types and including the medium-high elevation Sierra de Bahoruco and low-elevation Parque Nacional Jaragua in the Dominican Republic (Ottenwalder 1999, 2001; Martínez *et al.*, 2013) and the Massif de la Selle in southeastern Haiti (Turvey *et al.*, 2014). Whilst meaningful estimates of current population size are again unavailable, recent field studies have confirmed continued solenodon occurrence across much of this region (Young, 2012), and we were able to include a much greater number of samples from this population in our genetic analyses, covering widely-distributed collection localities (Table 1). We consider it very unlikely that only a few hundred solenodons remain in the sampling area of southeastern Hispaniola, suggesting that our N_{ef} estimate may instead reflect long-term effective population size, which is typically the harmonic mean of population size through time, and thus preferentially weighted towards bottlenecks. As with the southwestern sample, our southeastern mtDNA data are unlikely to contain sufficient information to resolve population oscillations through time.

Nonetheless, we speculate that past regional solenodon population crash may have been associated with European arrival c.500 years ago and/or historical-era human-caused environmental changes, with mid-late Holocene pressures on local environments by Amerindians, or with Late Pleistocene climatic fluctuations, which are all likely to have driven other Caribbean mammal

extinctions (Turvey, 2009). The higher N_{ef} estimate for the northern solenodon population suggests that any such historical demographic event was likely driven by factors local to southeastern Hispaniola, such as potentially severe Pleistocene-Holocene environmental shifts in the high-elevation Massif de la Selle-Sierra de Bahoruco region (cf. Schubert & Medina, 1982). Our N_{ef} estimate for hutias from this region, despite being based on a smaller number of samples ($n=5$), is again markedly higher (mode=6509, 95% credibility interval=1650-56,207; Brace *et al.*, 2012), and the low solenodon N_{ef} estimate warns that this genetically impoverished population may have reduced viability and adaptive potential and may be particularly vulnerable to future environmental change (Frankham *et al.*, 2014).

Our evidence for the existence of genetically and morphometrically distinct Hispaniolan solenodon populations, which we interpret as separate subspecies, has important conservation implications, and we propose that all three populations should be treated as distinct management units. Whereas formal assessment of the threat status of the northern and southeastern populations should await further analysis of recently collected field data on solenodon distribution and abundance across the Dominican Republic (Young, 2012), we emphasize the perilous status of the newly described subspecies *Solenodon paradoxus haitiensis* in southwestern Hispaniola, and stress the urgency of implementing conservation interventions to prevent its imminent extinction. This subspecies probably has an extent of occurrence of less than 100km², is restricted to a single known subpopulation, and is experiencing continuing observed declines in area, extent and quality of habitat due to accelerating forest clearance in the Massif de la Hotte, and probably also in

number of mature individuals due to predation by introduced carnivores and opportunistic exploitation for food by subsistence farmers (Woods & Ottenwalder, 1992; Turvey *et al.*, 2008). We therefore recommend that it should be listed as Critically Endangered under Criterion B1a,biii,v on the IUCN Red List (IUCN 2001).

Conclusions

Our improved understanding of the evolutionary history of Hispaniolan solenodons, and the relationship between allopatric populations across Hispaniola, provides an important new baseline to identify wider patterns of intra-island diversification and to further develop the Caribbean as a unique workshop for studying island evolution. In particular, historical barriers to gene flow have generated broadly consistent patterns of population segregation in solenodons, hutias, and other Hispaniolan taxa, but these congruent patterns of diversity may reflect different evolutionary histories (cf. Hawkins *et al.*, 2012), suggesting that a “one-size-fits-all” biogeographic model for large, environmentally complex islands may not be appropriate (Brown *et al.*, 2014). Our study also clarifies the taxonomic status of solenodon populations, helping ensure that previously unrecognized but distinct taxa can receive appropriate conservation prioritization (May, 1990; Eldredge *et al.*, 2013), and strengthening the evidence-base for protecting this enigmatic, evolutionarily unusual, and highly threatened mammal.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Systematic taxonomy.

Table S1. Solenodon genetic samples.

Table S2. Primer pairs used to amplify mtDNA.

Table S3. Collection details for solenodon specimens in morphometric analyses.

Table S4. Measurement data used in morphometric analyses.

Figure S1. Posterior model probabilities for mtDNA data.

Figure S2. Posterior distributions for mtDNA data.

Figure S3. Type specimen of *Solenodon paradoxus haitiensis*.

BIOSKETCH

Samuel Turvey is a conservation biologist interested in evolution and extinction dynamics in island systems, and in using evolutionary history to inform conservation prioritization. His research focuses on highly threatened mammals in the Caribbean and in eastern and southeast Asia.

Author contributions: S.T.T., R.P.Y. and I.B. conceived the ideas; N.C., J.M.N.M., J.A.O. and J.L.B. collected/provided samples or data; S.P., S.B., I.B., M.G.T., J.H., G.K., K.T., A.T. and S.F. analysed the data; and S.T.T., S.P., S.B. and M.G.T. led the writing.

Table 1. Summary of solenodon samples used for genetic analysis, showing sample source and collection locality within Hispaniola. Key: AMNH, American Museum of Natural History; CPS, Slater Museum of Natural History, University of Puget Sound; FC, field collection; MHND, Museo Nacional de Historia Natural, Santo Domingo; OUM, Oxford University Museum of Natural History; RMNH, Naturalis (Nationaal Natuurhistorisch Museum), Leiden; ZOODOM, Parque Zoológico Nacional, Santo Domingo.

| Country | Palaeo-island | Locality (province/region) | Source | Successfully amplified mtDNA | Failed to amplify mtDNA |
|---------|---------------|--|--------|------------------------------|-------------------------|
| DR | N | Cordillera Central | AMNH | 0 | 3 |
| DR | N | Cordillera Central | ZOODOM | 0 | 1 |
| DR | N | El Seibo | CPS | 4 | 0 |
| DR | N | El Seibo | ZOODOM | 1 | 0 |
| DR | N | Hato Mayor | FC | 1 | 0 |
| DR | N | La Altagracia (Bávaro) | ZOODOM | 2 | 0 |
| DR | N | La Altagracia (Parque Nacional del Este) | FC | 1 | 0 |
| DR | N | San Cristóbal | AMNH | 1 | 0 |
| DR | N | San Cristóbal | CPS | 1 | 0 |
| DR | N | Santiago | CPS | 3 | 0 |
| DR | N | Santiago (La Cuesta) | RMNH | 1 | 0 |
| DR | N | Santo Domingo | AMNH | 1 | 0 |
| DR | SE | Pedernales | MHND | 0 | 1 |
| DR | SE | Pedernales (Parque Nacional Jaragua) | FC | 1 | 0 |
| DR | SE | Sierra de Bahoruco (multiple localities) | FC | 15 | 0 |
| DR | SE | Sierra de Bahoruco | OUM | 1 | 0 |
| Haiti | SW | Massif de la Hotte | OUM | 3 | 0 |

Table 2. Summary of solenodon specimens used for morphometric analysis, showing source and collection locality. Key: AMNH, American Museum of Natural History; JAO, private collection of José Ottenwalder (currently stored at UF); MCZ, Museum of Comparative Zoology, Harvard University; OUM, Oxford University Museum of Natural History; UF, Florida Museum of Natural History; USNM, United States National Museum.

| Collection | Geographic provenance | | | |
|--------------|-----------------------|---------------|---------------|----------|
| | N Hispaniola | SE Hispaniola | SW Hispaniola | Cuba |
| AMNH | 1 | – | – | – |
| JAO | 30 | 18 | – | – |
| MCZ | 27 | – | – | 3 |
| OUM | – | 1 | 2 | – |
| UF | – | – | 27 | – |
| USNM | 3 | 1 | – | 5 |
| Total | 61 | 20 | 29 | 8 |

Table 3. Average pairwise estimates of sequence divergence between regionally sampled solenodon populations from Hispaniola.

| | southwest | southeast |
|-------------------------------|-----------|-----------|
| 1. <i>cyt b</i> data | | |
| southeast | 2.20% | |
| north | 1.70% | 1.10% |
| 2. control region data | | |
| southeast | 1.80% | |
| north | 1.70% | 0.50% |

Table 4. Modal and 95% highest probability density (HPD) values of posterior probability distributions of model parameters for allopatric Hispaniolan solenodon populations based on *cyt b* data and control region data.

| | Mode | 95% HPD | |
|---------------------------|-----------------------|-----------------------|-----------------------|
| | | Lower | Upper |
| (a) <i>cyt b</i> | | | |
| <i>N_{ef}</i> | | | |
| north | 2584 | 102 | 999,487 |
| southeast | 32 | 10 | 618 |
| southwest | 34 | 10 | 211,104 |
| migration rate | | | |
| north–southeast | 1.37×10^{-3} | 1.20×10^{-6} | 3.57×10^{-3} |
| southeast–southwest | 9.43×10^{-4} | 1.13×10^{-7} | 3.23×10^{-3} |
| (b) control region | | | |
| <i>N_{ef}</i> | | | |
| north | 3218 | 128 | 999,622 |
| southeast | 32 | 10 | 2032 |
| southwest | 32 | 10 | 3700 |
| migration rate | | | |
| north–southeast | 1.50×10^{-3} | 3.32×10^{-6} | 3.59×10^{-3} |
| southeast–southwest | 7.63×10^{-4} | 1.86×10^{-7} | 3.00×10^{-3} |

FIGURE LEGENDS

Figure 1. Map of Hispaniola, showing geotectonic boundaries and collection localities for solenodon samples used in this study. Key: 1, Massif de la Hotte; 2, Sierra de Bahoruco; 3, Oviedo/Parque Nacional Jaragua; 4, Santiago Rodríguez; 5, Valverde; 6, Santiago; 7, La Vega; 8, María Trinidad Sánchez; 9, Samaná; 10, San Cristóbal; 11, Santo Domingo; 12, Monte Plata; 13, Hato Mayor; 14, La Romana; 15, El Seibo; 16, La Altagracia. White circle, both genetic and morphometric samples; pale grey circle, genetic sample only; dark grey circle, morphometric sample only.

Figure 2. Summary of models used in coalescent simulation analysis. Parameters between branches represent migration rates between populations. The short time between lineage splits represents rapid colonisation of different regions of Hispaniola following formation of the island.

Figure 3. (a) Hispaniolan solenodon mitochondrial haplotype network, using combined control region and *cyt b* data; large coloured circles represent haplotypes, numbers within circles show total numbers of samples represented by each haplotype, and small black circles within network represent single mutational steps. (b) Map of Hispaniola showing allopatric distribution of different colour-coded solenodon populations. (c) Unrooted Bayesian phylogenetic tree of Hispaniolan solenodon mitochondrial haplotypes; numbers at nodes represent Bayesian posterior probabilities, scale bar represents number

of substitutions per site. Key: red=northern population, blue=southeastern population, yellow=southwestern population.

Figure 4. PCA for solenodon craniodental measurements. (a) Hispaniola+Cuba dataset. Percentage variation explained by PCA: axis 1, 44.65%; axis 2, 13.65%. (b) Hispaniola-only dataset. Percentage variation explained by PCA: axis 1, 51.07%; axis 2, 9.45%. Key: northern Hispaniola (filled diamonds), southwestern Hispaniola (open triangles), southeastern Hispaniola (filled circles), Cuba (crosses).