A Journal of Conservation Biogeography

Diversity and Distributions

BIODIVERSITY RESEARCH

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

Samuel T. Turvey[1], Stuart Peters[2]*, Selina Brace[3]*, Richard P. Young[4], Nick Crumpton[3,5], James Hansford[1,6], Jose M. Nuñez-Miño[4], Gemma King[7], Katrina Tsalikidis[7], José A. Ottenwalder[8], Adrian Timpson[9], Stephan M. Funk[10], Jorge L. Brocca[11], Mark G. Thomas[2] and Ian Barnes[3]

[1]*Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK,* [2]*Research Department of Genetics, Evolution and Environment, University College London, Gower Street, London WC1E 6BT, UK,* [3]*Natural History Museum, Cromwell Road, London SW7 5BD, UK,* [4]*Durrell Wildlife Conservation Trust, Les Augrès Manor, Trinity, Jersey JE3 5BP, Channel Islands,* [5]*Research Department of Cell and Developmental Biology, University College London, Gower Street, London WC1E 6BT, UK,* [6]*Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton Waterfront Campus, European Way, Southampton, UK,* [7]*School of Biological Sciences, Royal Holloway University of London, Egham Hill, Egham TW20 OEX, UK,* [8]*Mahatma Gandhi 254, Gazcue, Santo Domingo, Dominican Republic,* [9]*Institute of Archaeology, University College London, Gordon Square, London WC1H 0PY, UK,* [10]*Nature Heritage, St. Lawrence, Jersey, Channel Islands,* [11]*Sociedad Ornitológica de la Hispaniola, Parque Zoologico Nacional, Avenida de la Vega Real, Arroyo Hondo, Santo Domingo, Dominican Republic*

*Correspondence: Stuart Peters, Research Department of Genetics, Evolution and Environment, University College London, Gower Street, London WC1E 6BT, UK.
E-mail: stuart.peters.13@ucl.ac.uk
and
Selina Brace, Natural History Museum, Cromwell Road, London SW7 5BD, UK.
E-mail: S.Brace@nhm.ac.uk

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 spatio-temporal 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, south-eastern and south-western 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, south-eastern and south-western 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 south-western and south-eastern 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 19th 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).
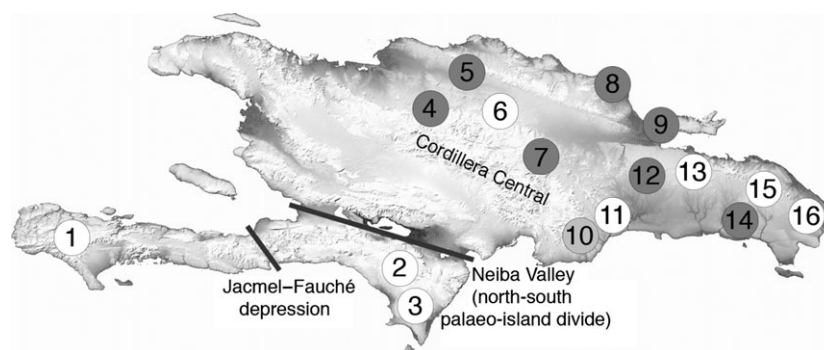

Figure 1 Map of Hispaniola, showing geotectonic boundaries and collection localities for solenodon samples used in this study. Key: 1, Massif de la Hotte; 2, Sierra de Bahoruco; 3, Oviedo/Parque Nacional Jaragua; 4, Santiago Rodríguez; 5, Valverde; 6, Santiago; 7, La Vega; 8, María Trinidad Sánchez; 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.

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

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	1	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	0	1
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

(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, south-eastern and south-western), 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 and 10^6 per population and sampled on a log-scale. In models 2, 3 and 4, migration rate (m) was set between 0 and 0.004 per 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 (Pacifici *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 and 10% per million years
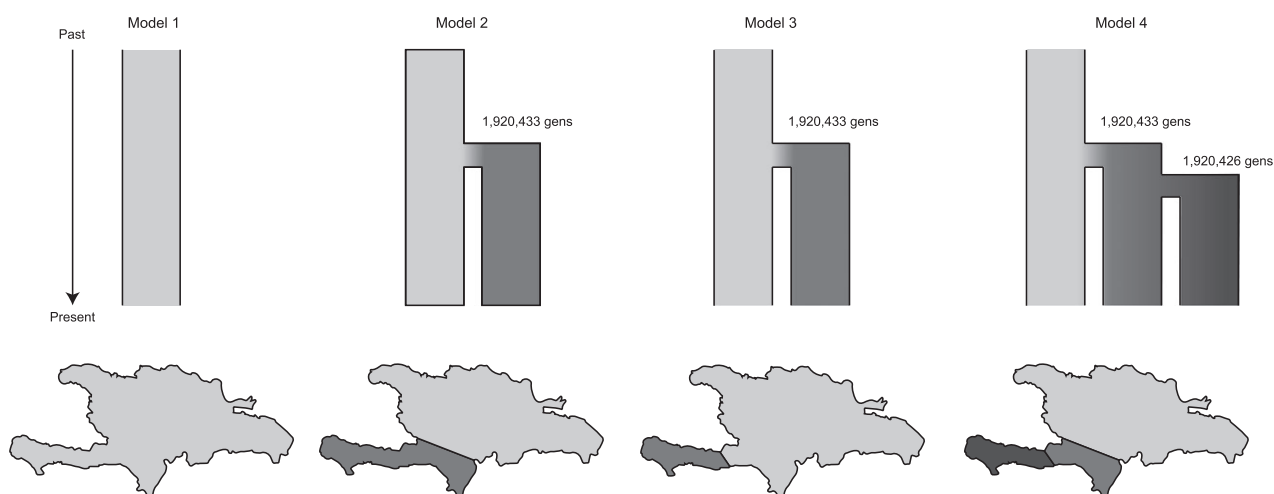

Figure 2 Summary of models used in coalescent simulation analysis. Parameters between branches represent migration rates between populations. The short time between lineage splits represents rapid colonization of different regions of Hispaniola following formation of the island.

(Ma) were explored, and for control region simulations, rates between 1 and 15% per 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 south-western Hispaniola, 16 individuals from south-eastern 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 model values. While the Tajima's *D* statistic (Tajima, 1989) is a derivative of θ S and θ π, 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 with 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; Tables 2 & S3). Eighty-two craniodental measurements (46 cranial, 36 mandibular) were taken using dial calipers accurate to 0.02 mm (Table S4). Data were analysed using analysis of variance (ANOVA), principal component analysis (PCA) and generalized linear models

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

(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 and S4.

RESULTS

Phylogenetic analyses

From the 41 solenodon individuals sampled, 34 successfully yielded mtDNA (GenBank accession numbers: LN994539–LN994605), 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 south-eastern Hispaniola and one from south-western 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 shows 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 (Figs 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–south-eastern migration rate $\leq 1.50 \times 10^{-3}$; modal south-eastern–south-western 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 south-western and south-eastern 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 recognized 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 vs. south-eastern, $T = 9.569$, $P < 0.001$; northern vs. south-western, $T = 5.628$, $P < 0.001$; south-eastern vs. south-western, $T = -4.057$, $P < 0.001$). 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 south-eastern solenodon populations reported by Ottenwalder (2001), and further support previous suggestions that the geographically isolated south-western population in the Massif de la Hotte is also distinct (Woods & Ottenwalder, 1992; Ottenwalder, 2001; Turvey *et al.*, 2008). Ottenwalder (2001) suggested that the south-western population was most closely related to other southern palaeo-island solenodons
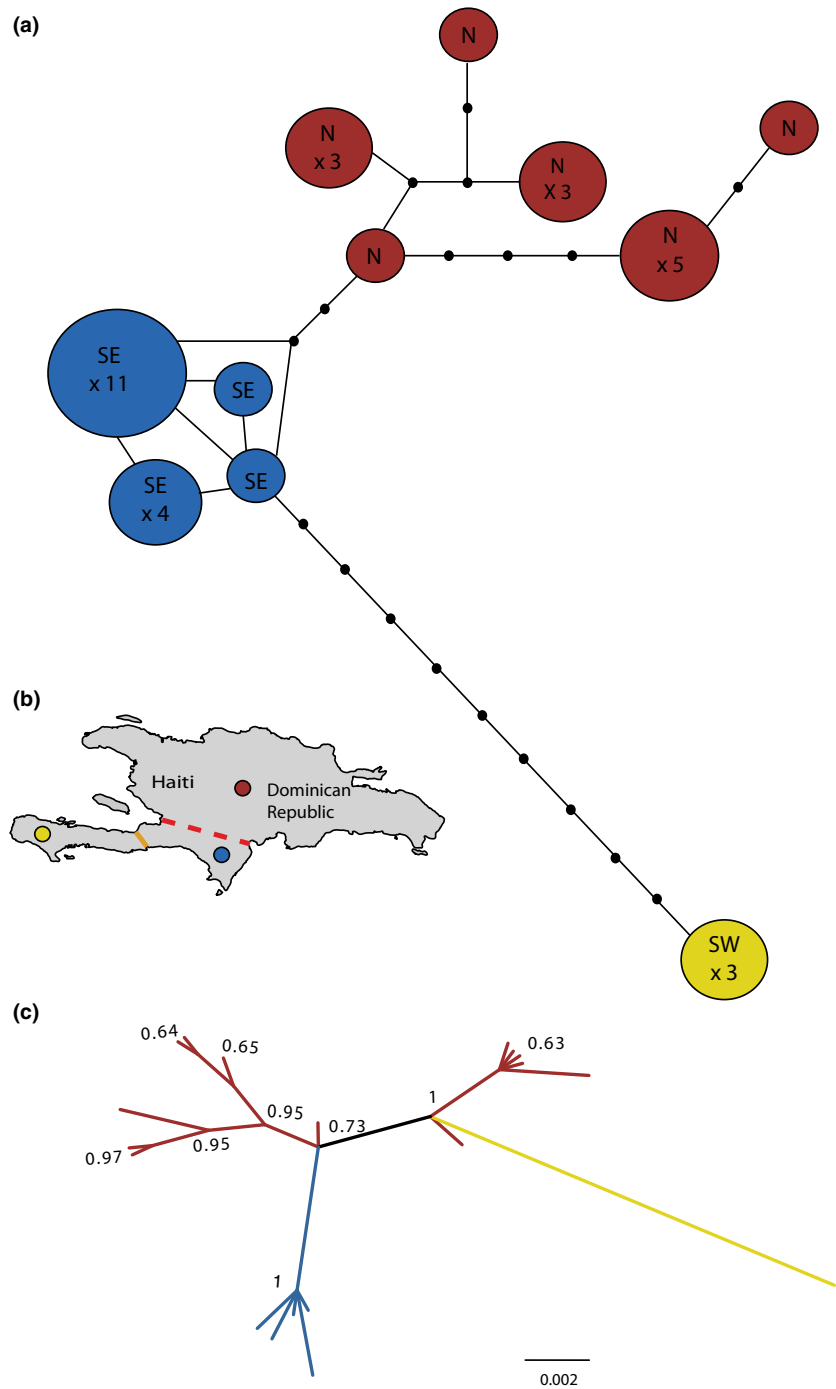
Figure 3 (a) Hispaniolan solenodon mitochondrial haplotype network, using combined control region and cyt *b* data; large coloured circles represent haplotypes, numbers within circles show total numbers of samples represented by each haplotype, and small black circles within network represent single 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.

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

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

	South-west	South-east
1. cyt *b* data, %		
South-east	2.20	
North	1.70	1.10
2. control region data, %		
South-east	1.80	
North	1.70	0.50

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; Sly *et al.*, 2011; Brace *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 (Esselstyn & 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 south-western 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.*,

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) cyt *b*			
N_{ef}			
North	2584	102	999,487
South-east	32	10	618
South-west	34	10	211,104
Migration rate			
North–south-east	1.37×10^{-3}	1.20×10^{-6}	3.57×10^{-3}
South-east–south-west	9.43×10^{-4}	1.13×10^{-7}	3.23×10^{-3}
(b) Control region			
N_{ef}			
North	3218	128	999,622
South-east	32	10	2032
South-west	32	10	3700
Migration rate			
North–south-east	1.50×10^{-3}	3.32×10^{-6}	3.59×10^{-3}
South-east–south-west	7.63×10^{-4}	1.86×10^{-7}	3.00×10^{-3}
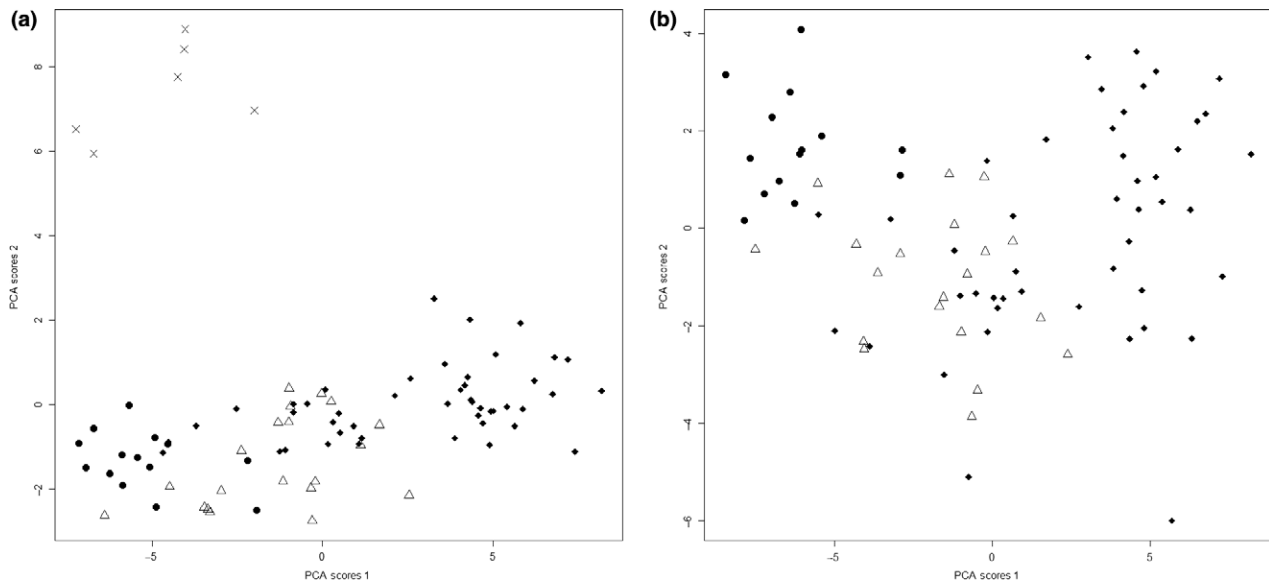
Figure 4 PCA for solenodon craniodental measurements. (a) Hispaniola+Cuba dataset. Percentage variation explained by PCA: axis 1, 44.65%; axis 2, 13.65%. (b) Hispaniola-only dataset. Percentage variation explained by PCA: axis 1, 51.07%; axis 2, 9.45%. Key: northern Hispaniola (filled diamonds), southwestern Hispaniola (open triangles), southeastern Hispaniola (filled circles), Cuba (crosses).

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*, vs. 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 recognizing the northern subspecies *Solenodon paradoxus paradoxus* and the south-eastern subspecies *Solenodon paradoxus woodi*, and we describe the currently unnamed south-western 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 south-western and south-eastern 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 south-western and south-eastern 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 utilizing 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 south-western 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 south-eastern 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 south-eastern 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 south-eastern 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 south-western sample, our south-eastern 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 south-eastern 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 south-eastern 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 south-western 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 100 km^2, 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.

ACKNOWLEDGEMENTS

REFERENCES

Allard, M.W., Baker, S.D., Emerson, G.L., Ottenwalder, J.A. & Kilpatrick, C.W. (2001) Characterization of the mitochondrial control region in *Solenodon paradoxus* from Hispaniola and the implications for biogeography, systematics, and conservation management. *Biogeography of the West Indies: patterns and perspectives* (ed. by C.A. Woods and F.E. Sergile), pp. 331–334. CRC Press, Boca Raton, FL.

Allen, G.M. (1942) *Extinct and vanishing mammals of the western hemisphere with the marine species of all the oceans*. American Committee for International Wild Life Protection, Washington, DC.

Beaumont, M.A., Zhang, W.Y. & Balding, D.J. (2002) Approximate Bayesian computation in population genetics. *Genetics*, **162**, 2025–2035.

Borroto-Páez, R., Woods, C.A. & Kilpatrick, C.W. (2005) Sistemática de las jutías de las Antillas (Rodentia, Capromyidae). *Monografies de la Societat d'Història Natural de les Balears*, **12**, 33–50.

Brace, S., Barnes, I., Powell, A., Pearson, R., Woolaver, L.G., Thomas, M.G. & Turvey, S.T. (2012) Population history of the Hispaniolan hutia *Plagiodontia aedium* (Rodentia: Capromyidae): testing the model of ancient differentiation on a geotectonically complex Caribbean island. *Molecular Ecology*, **21**, 2239–2253.

Brace, S., Turvey, S.T., Weksler, M., Hoogland, M.L.P. & Barnes, I. (2015) Unexpected evolutionary diversity in a recently extinct Caribbean mammal radiation. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20142371.

Bridges, W. (1936) The Haitian solenodon. *New York Zoological Society Bulletin*, **39**, 13–18.

Brown, J.L., Cameron, A., Yoder, A.D. & Vences, M. (2014) A necessarily complex model to explain the biogeography of the amphibians and reptiles of Madagascar. *Nature Communications*, **5**, e5046.

Clement, M., Posada, D. & Crandall, K.A. (2000) TCS: a computer program to estimate gene genealogies. *Molecular Ecology*, **9**, 1657–1660.

Collen, B., Turvey, S.T., Waterman, C., Meredith, H.M.R., Kuhn, T., Baillie, J.E.M. & Isaac, N.J.B. (2011) Investing in evolutionary history: implementing a phylogenetic approach for mammal conservation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**, 2611–2622.

Cooke, S.B., Rosenberger, A.L. & Turvey, S.T. (2011) An extinct monkey from Haiti and the origins of the Greater Antillean primates. *Proceedings of the National Academy of Sciences USA*, **108**, 2699–2704.

Drummond, A.J., Rambaut, A., Shapiro, B. & Pybus, O.G. (2005) Bayesian coalescent inference of past population dynamics from molecular sequences. *Molecular Biology and Evolution*, **22**, 1185–1192.

Eldredge, M.D.B., Meek, P.D. & Johnson, R.N. (2013) Taxonomic uncertainty and the loss of biodiversity on Christmas Island, Indian Ocean. *Conservation Biology*, **28**, 572–579.

Esselstyn, J.A. & Brown, R.M. (2009) The role of repeated sea-level fluctuations in the generation of shrew (Soricidae: *Crocidura*) diversity in the Philippine Archipelago. *Molecular Phylogenetics and Evolution*, **53**, 171–181.

Estoup, A., Beaumont, M., Sennedot, F., Moritz, C. & Cornuet, J.-M. (2004) Genetic analysis of complex demographic scenarios: spatially expanding populations of the cane toad, *Bufo marinus*. *Evolution*, **58**, 2021–2036.

Excoffier, L., Laval, G. & Schneider, S. (2005) Arlequin version 3.0: an integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online*, **1**, 47–50.

Excoffier, L., Dupanloup, I., Huerta-Sánchez, E., Sousa, V.C. & Foll, M. (2013) Robust demographic inference from genomic and SNP data. *PLOS Genetics*, **9**, e1003905.

Fabre, P.-H., Vilstrup, J.T., Raghavan, M., Der Sarkissian, C., Willerslev, E., Douzery, E.J.P. & Orlando, L. (2014) Rodents of the Caribbean: origin and diversification of hutias unraveled by next-generation museomics. *Biology Letters*, **10**, 20140266.

Fisher, R.A. (1925). *Statistical methods for research workers*. Oliver and Boyd, Edinburgh.

Fisher, D.O. & Blomberg, S.P. (2011) Correlates of rediscovery and the detectability of extinction in mammals. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 1090–1097.

Folinsbee, K.E. (2013) Evolution of venom across extant and extinct eulipotyphlans. *Comptes Rendus Palevol*, **12**, 531–542.

Frankham, R. (1995) Effective population size/adult population size ratios in wildlife: a review. *Genetical Research*, **66**, 95–107.

Frankham, R., Bradshaw, C.J.A. & Brook, B.W. (2014) Genetics in conservation management: revised recommendations for the 50/500 rules, Red List criteria and population viability analyses. *Biological Conservation*, **170**, 56–63.

Getty, S.R., Asmerom, Y., Quinn, T.M. & Budd, A.F. (2001) Accelerated Pleistocene coral extinctions in the Caribbean Basin shown by uranium-lead (U-Pb) dating. *Geology*, **29**, 639–642.

Gifford, M.E., Powell, R., Larson, A. & Gutberlet, R.L. Jr (2004) Population structure and history of a phenotypically variable teiid lizard (*Ameiva chrysolaema*) from Hispaniola: the influence of a geologically complex island. *Molecular Phylogenetics and Evolution*, **32**, 735–748.

Graham, A. (2003) Geohistory models and Cenozoic pale-oenvironments of the Caribbean region. *Systematic Botany*, **28**, 378–386.

Hansford, J., Nuñez-Miño, J.M., Young, R.P., Brace, S., Brocca, J.L. & Turvey, S.T. (2012) Taxonomy-testing and the 'Goldilocks Hypothesis': morphometric analysis of species diversity in living and extinct Hispaniolan hutias. *Systematics and Biodiversity*, **10**, 491–507.

Hasegawa, M., Kishino, H. & Yano, T. (1985) Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution*, **22**, 160–174.

Hawkins, B.A., McCain, C.M., Davies, T.J., Buckley, L.B., Anacker, B.L., Cornell, H.V., Damschen, E.I., Grytnes, J.-A., Harrison, S., Holt, R.D., Kraft, N.J.B. & Stephens, P.R. (2012) Different evolutionary histories underlie congruent species richness gradients of birds and mammals. *Journal of Biogeography*, **39**, 825–841.

Heads, M. (2002) Regional patterns of biodiversity in New Guinea animals. *Journal of Biogeography*, **29**, 285–294.

Hedges, S.B. (1999) Distribution patterns of amphibians in the West Indies. *Patterns of distribution of amphibians: a global perspective* (ed. by W.E. Duellman), pp. 211–254. Johns Hopkins University Press, Baltimore, MD.

Helmus, M.R., Mahler, D.L. & Losos, J.B. (2014) Island biogeography of the Anthropocene. *Nature*, **513**, 543–546.

Henry, P., Miquelle, D., Sugimoto, T., McCullough, D.R., Caccone, A. & Russello, M.A. (2009) *In situ* population structure and *ex situ* representation of the endangered Amur tiger. *Molecular Ecology*, **18**, 3173–3184.

Hope, A.G., Waltari, E., Fedorov, V.B., Goropashnaya, A.V., Talbot, S.L. & Cook, J.A. (2011) Persistence and diversification in the Holarctic shrew, *Sorex tundrensis* (Family Soricidae), in response to climate change. *Molecular Ecology*, **20**, 4346–4370.

Iturralde-Vinent, M.A. & MacPhee, R.D.E. (1999) Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History*, **238**, 1–95.

IUCN (2001) *IUCN Red List categories and criteria: version 3.1*. IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, UK.

Jukes, J.C. & Cantor, T.H. (1969) Evolution of protein molecules. *Mammalian protein metabolism*, pp. 21–132. Academic Press, New York.

Kimura, M. (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, **16**, 111–120.

Kisel, Y. & Barraclough, T.G. (2010) Speciation has a spatial scale that depends on levels of gene flow. *The American Naturalist*, **175**, 316–334.

Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, **29**, 1695–1701.

Li, H. & Durbin, R. (2011) Inference of human population history from individual whole-genome sequences. *Nature*, **475**, 493–496.

Losos, J.B. & Ricklefs, R.E. (2009) Adaptation and diversification on islands. *Nature*, **457**, 830–836.

MacFadden, B.J. (1980) Rafting mammals or drifting islands?: biogeography of the Greater Antillean insectivores *Nesophontes* and *Solenodon*. *Journal of Biogeography*, **7**, 11–22.

MacPhee, R.D.E. & Grimaldi, D.A. (1996) Mammal bones in Dominican amber. *Nature*, **380**, 489–490.

Mann, P., Draper, G. & Lewis, J.F. (1991) An overview of the geologic and tectonic development of Hispaniola. *Geologic and tectonic development of the North America – Caribbean Plate boundary in Hispaniola* (ed. by P. Mann, G. Draper and J.F. Lewis), pp. 1–51. Geological Society of America Special Publication 262, Boulder, CO.

Martínez, P., Nuñez Miño, J., Brocca, J.L., Young, R., Turvey, S., Grasela, K., Ottenwalder, J. & Polonia, A. (2013) *Plan de acción para la conservación de los mamíferos terrestres endémicos de la Hispaniola, Solenodon paradoxus y Plagiodontia aedium, 2013–2018*. Ministerio de Medio Ambiente y Recursos Naturales/Sociedad Ornitológica de la Hispaniola, Santo Domingo.

Maurrasse, F., Pierre-Louis, R. & Rigaud, J.-G. (1980) Cenozoic facies distribution in the southern peninsula of Haiti and the Barahona Peninsula, Dominican Republic, and its relations concerning tectonic evolution of the La Selle-Baoruco block. *Caribbean Geology, Collected Contributions*, **9**, 1–24.

May, R.M. (1990) Taxonomy as destiny. *Nature*, **347**, 129–130.

Ottenwalder, J.A. (1999) Observations on the habitat and ecology of the Hispaniolan solenodon (*Solenodon paradoxus*) in the Dominican Republic. *Monografies de la Societat d'Història Natural de les Balears*, **6**, 123–168.

Ottenwalder, J.A. (2001) Systematics and biogeography of the West Indian genus *Solenodon*. *Biogeography of the West Indies: patterns and perspectives* (ed. by C.A. Woods and F.E. Sergile), pp. 253–329. CRC Press, Boca Raton, FL.

Pacifici, M., Santini, L., Di Marco, M., Baisero, D., Francucci, L., Grottolo Marasini, G., Visconti, P. & Rondinini, C. (2013) Generation length for mammals. *Nature Conservation*, **5**, 89–94.

Palstra, F.P. & Fraser, D.J. (2012) Effective/census population size ratio estimation: a compendium and appraisal. *Ecology and Evolution*, **2**, 2357–2365.

Pesole, G., Gissi, C., De Chirico, A. & Saccone, C. (1999) Nucleotide substitution rate of mammalian mitochondrial genomes. *Journal of Molecular Evolution*, **48**, 427–434.

Pregill, G.K. & Olson, S.L. (1981) Zoogeography of West Indian vertebrates in relation to Pleistocene climatic cycles. *Annual Review of Ecology and Systematics*, **12**, 75–98.

R Development Core Team (2011) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.

Ray, N., Wegmann, D., Fagundes, N.J.R., Wang, S., Ruiz-Linares, A. & Excoffier, L. (2010) A statistical evaluation of

models for the initial settlement of the American continent emphasizes the importance of gene flow with Asia. *Molecular Biology and Evolution*, **27**, 337–345.

Ricketts, T.H., Dinerstein, E., Boucher, T. *et al.* (2005) Pinpointing and preventing imminent extinctions. *Proceedings of the National Academy of Sciences USA*, **51**, 18497–18501.

Ricklefs, R. & Bermingham, E. (2008) The West Indies as a laboratory of biogeography and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363**, 2393–2413.

Roca, A.L., Bar-Gal, G.K., Eizirik, E., Helgen, K.M., Maria, R., Springer, M.S., O'Brien, S.J. & Murphy, W.J. (2004) Mesozoic origin for West Indian insectivores. *Nature*, **429**, 649–651.

Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, **19**, 1572–1574.

Schluter, D. (2000) *The ecology of adaptive radiation*. Oxford University Press, Oxford.

Schubert, C. & Medina, E. (1982) Evidence of Quaternary glaciation in the Dominican Republic: some implications for Caribbean paleoclimatology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **39**, 281–294.

Schwartz, A. (1980) The herpetogeography of Hispaniola, West Indies. *Studies on the fauna of Curaçao and other Caribbean Islands*, **61**, 86–127.

Sly, N.D., Townsend, A.K., Rimmer, C.C., Townsend, J.M., Latta, S.C. & Lovette, I.J. (2011) Ancient islands and modern invasions: disparate phylogeographic histories among Hispaniola's endemic birds. *Molecular Ecology*, **20**, 5012–5024.

Stewart, D.T. & Baker, A.J. (1994) Patterns of sequence variation in the mitochondrial D-loop region of shrews. *Molecular Biology and Evolution*, **11**, 9–21.

Tajima, F. (1989) Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics*, **123**, 585–595.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution*, **28**, 2731–2739.

Townsend, A.K., Rimmer, C.C., Latta, S.C. & Lovette, I.J. (2007) Ancient differentiation in the single-island endemic radiation of endemic Hispaniolan chat-tanagers (Aves: *Calytophilus*). *Molecular Ecology*, **16**, 3634–3642.

Turvey, S.T. (2009) *Holocene extinctions*. Oxford University Press, Oxford.

Turvey, S.T., Meredith, H.M.R. & Scofield, R.P. (2008) Continued survival of Hispaniolan solenodon *Solenodon paradoxus* in Haiti. *Oryx*, **42**, 611–614.

Turvey, S.T., Fernández-Secades, C., Nuñez-Miño, J.M., Hart, T., Martinez, P., Brocca, J.L. & Young, R.P. (2014) Is local ecological knowledge a useful conservation tool for small mammals in a Caribbean multicultural landscape? *Biological Conservation*, **169**, 189–197.

Turvey, S.T., Hansford, J., Kennerley, R.J., Nuñez-Miño, J.M., Brocca, J.L. & Young, R.P. (2015) A new subspecies of hutia (*Plagiodontia*, Capromyidae, Rodentia) from southern Hispaniola. *Zootaxa*, **3957**, 201–214.

Verrill, A.H. (1907) Notes on the habits and external characters of the solenodon of San Domingo (*Solenodon paradoxus*). *American Journal of Science, 4th Series*, **24**, 55–57.

Vogel, P., Cosson, J.-F. & Jurado, L.F.L. (2003) Taxonomic status and origin of the shrews (Soricidae) from the Canary islands inferred from a mtDNA comparison with the European *Crocidura* species. *Molecular Phylogenetics and Evolution*, **27**, 271–282.

Voight, B.F., Adams, A.M., Frisse, L.A., Qian, Y., Hudson, R.R. & Di Rienzo, A. (2005) Interrogating multiple aspects of variation in a full resequencing data set to infer human population size changes. *Proceedings of the National Academy of Sciences USA*, **102**, 18508–18513.

Wakeley, J. (2009) *Coalescent theory: an introduction*. Roberts and Company Publishers, Greenwood Village, Colorado.

Wallace, A.R. (1880) *Island life*. Macmillan & Co., London.

Williams, E.E. (1961) Notes on Hispaniolan herpetology. 3. The evolution and relationships of the *Anolis semilineatus* group. *Museum of Comparative Zoology, Breviora*, **136**, 1–8.

Woods, C.A. (1981) Last endemic mammals in Hispaniola. *Oryx*, **16**, 146–152.

Woods, C.A. (1986) *Mammals of the national parks of Haiti*. Unpublished report, prepared for USAID/Haiti under contract number 521-0169-C-00-3083-00.

Woods, C.A. (1989) A new capromyid rodent from Haiti: the origin, evolution, and extinction of West Indian rodents, and their bearing on the origin of New World hystricognaths. *Natural History Museum of Los Angeles County, Science Series*, **33**, 59–90.

Woods, C.A. & Ottenwalder, J.A. (1992) *The natural history of southern Haiti*. Florida Museum of Natural History, Gainesville, FL.

Yoder, J.B., Clancey, E., Des Roches, S., Eastman, J.M., Gentry, L., Godsoe, W., Hagey, T.J., Jochimsen, D., Oswald, B.P., Robertson, J., Sarver, B.A.J., Schenk, J.J., Spear, S.F. & Harmon, L.J. (2010) Ecological opportunity and the origin of adaptive radiations. *Journal of Evolutionary Biology*, **23**, 1581–1596.

Young, R. (2012) *Building evidence and capacity to conserve Hispaniola's endemic land mammals*. Unpublished final report to Darwin Initiative. Available at: http://www.darwininitiative.org.uk/project/17025/ (Downloaded 4 June 2015.) (accessed 4 June 2015).

Zachos, F.E., Apollonio, M., Bärmann, E.V., Festa-Bianchet, M., Göhlich, U., Habel, J.C., Haring, E., Kruckenhauser, L., Lovari, S., McDevitt, A.D., Pertoldi, C., Rössner, G.E., Sánchez-Villagra, M.R., Scandura, M. & Suchentrunk, F. (2013) Species inflation and taxonomic artefacts – a critical comment on recent trends in mammalian classification. *Mammalian Biology*, **78**, 1–6.

SUPPORTING INFORMATION

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

Figure S1 Posterior model probabilities for mtDNA data.

Figure S2 Posterior distributions for mtDNA data.

Figure S3 Type specimen of *Solenodon paradoxus haitiensis*.

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.

Appendix S1 Systematic taxonomy.

BIOSKETCH

Samuel T. 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.

Editor: Jeremy Austin