Genetic evidence for invasive rat-caused vegetation damage has implications for endemic Caribbean mammal management

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Abstract

1. Invasive murid rodents have disrupted native biodiversity, including vegetation composition and structure, across island systems such as the Caribbean ecoregion. However, translocations of the Bahamian hutia (*Geocapromys ingrahami*), a threatened Caribbean rodent, have also prompted concerns about vegetation damage, raising complex challenges for management of this species.

2. Extensive vegetation damage reported on John Higgs Cay (Turks and Caicos Islands), along with the presence of abundant large faecal pellets and local traditions of large-bodied rodents called "hootees", was suggestive of possible survival of a remnant hutia population. Fieldwork was conducted to document vegetation damage and collect faecal samples for genetic analysis, which was carried out using ancient DNA protocols for degraded specimens.

3. Extensive areas of damaged shrubs exhibiting stripped vegetation and gnawed branches were present on John Higgs Cay, with damage to 15 species including the highly toxic *Metopium toxiferum*. Although observed vegetation damage differed somewhat from a Bahamian cay exhibiting damage reportedly made by hutias, differences in local ecology and plant diversity between islands could influence rodent food selection and plant survival.

4. An ancient DNA approach designed to remove PCR inhibitors provided robust identification of faecal pellets as being from black rats (*Rattus rattus*) based upon mitochondrial and nuclear genomic data, indicating that vegetation damage on John Higgs Cay was caused by this invasive species rather than by hutias. Local respondent descriptions of "hootees" were found to refer to invasive brown rats (*Rattus norvegicus*) that nested in mangroves.

5. *Practical implication.* Our findings highlight the potential for species misidentification when using indirect signs to survey small mammals in ecologically novel landscapes, providing an important note of caution when assessing unverified reports of species survival. Our study also demonstrates that invasive rodents can cause extensive disruption to native vegetation on tropical islands, highlighting the possibility that damage previously blamed upon hutias may instead be made by rats. Invasive rodents have been present in Caribbean ecosystems for centuries, and the vegetation damage they cause may now be overlooked and perceived as "natural", raising important questions about interpreting native biodiversity states and defining management targets.

Keywords: ancient DNA, Bahamian hutia, conservation translocation, faecal DNA, invasive species, name transference, native vegetation states, shifting baselines

Introduction

Islands represent novel ecosystems, and their unique environmental conditions and biotic communities have often promoted evolutionary diversification and ecological shifts in both native and introduced species (Lugo et al., 2012; Radeloff et al., 2015; Cuthbert et al., 2016; Álvarez-Castañeda & Nájera-Cortazar, 2020). However, island biodiversity has been severely disrupted at a global scale by the human-mediated movement of invasive rodents (Harper & Bunbury, 2015). The introduction of non-native rodent species, especially black rats (*Rattus rattus*), brown rats (*R. norvegicus*), Pacific rats (*R. exulans*) and house mice (*Mus musculus*), has led to extensive population extirpations and extinctions of insular animal taxa around the world through predation, competition and disease transfer (Blackburn et al., 2004; Wyatt et al., 2008; McCreless et al., 2016), and disruption of island ecosystem composition and structure through consumption of seeds, seedlings and adult plants (Drake & Hunt, 2008; Athens, 2009; Wolf et al., 2018). These biotic changes often transform island environments and drive further indirect impacts on ecosystem processes, such as shifts in nutrient cycling (Graham et al., 2018; Benkwitt et al., 2021). Rats may now be the most widely introduced vertebrates (Drake & Hunt, 2008), and rat eradication represents a key global strategy needed to halt biodiversity loss and restore island ecosystems (Russell & Holmes, 2015; Duron et al., 2017).

The biota of the insular Caribbean has been shaped by anthropogenic movement of animals between islands and from neighbouring continental regions for millennia (Newsom & Wing, 2003; Kemp et al., 2020). Several species of hutias, regionally endemic large-bodied capromyine rodents that constituted an important component of prehistoric Amerindian diets, were moved widely between islands and may have been locally managed or domesticated as a food resource (Newsom & Wing, 2003; Shev &

Laffoon, 2022). Following European arrival *c*.500 years ago, black rats and subsequently brown rats were accidentally introduced, with both species now established throughout the Caribbean (Espino et al., 2022). Black rats are widely distributed across a broad range of habitats, whereas brown rats are more closely associated with urban settings (Borroto-Páez, 2009; Borroto-Páez & Woods, 2012b; Shiels & Ramirez de Arellano, 2018). Invasive rats exhibited trophic niche overlap with hutias and other Caribbean rodents (Cooke & Crowley, 2018), as well as with other invasive murids (Witmer et al., 2007), and their arrival is associated with numerous endemic vertebrate extinctions (Cooke et al., 2017).

The Lucayan Archipelago, comprising the Commonwealth of The Bahamas and the British Overseas Territory of the Turks and Caicos Islands (hereafter "TCI"), has experienced human-caused environmental change and biodiversity loss following first human arrival and subsequent European arrival (Watts, 1987; Keegan, 1992; Steadman et al., 2014, 2017). The archipelago's endemic mammal, the Bahamian hutia (*Geocapromys ingrahami*), is probably only native to islands of the Great Bahama Bank (Oswald et al., 2020), but was translocated widely by the Lucayan people, the archipelago's first inhabitants, and is present in archaeological sites across the Bahamas and TCI (LeFebvre et al., 2019; Oswald et al., 2020; Turvey et al., 2021). However, both native and prehistorically introduced populations have been extirpated through hunting and/or invasive mammal introduction (Clough, 1972), and the species was restricted to a single known population on East Plana Cay in the eastern Bahamas by the mid twentieth century (Clough, 1969, 1972; Buden, 1986). Additional translocated populations were established for conservation purposes in the 1970s and 1980s on two further Bahamian islands, Little Wax Cay and Warderick Wells Cay in the Exuma Cays (Clough, 1974, 1985; Jordan, 1989), but the Little Wax Cay population is probably now extinct. The species is now assessed as Critically Endangered on the IUCN Red List (Cartwright et al., 2024).

Hutias are generalist herbivores (Borroto-Páez & Woods, 2012a), and Bahamian hutias forage on leaves, twigs, bark and fruit from numerous herb, shrub and tree species (Clough, 1972; Jordan, 1989; Campbell et al., 1991). It is suggested that hutia browsing may have been responsible for a decline in wild pawpaw trees on East Plana Cay between the nineteenth and twentieth centuries (Clough, 1972), and the disappearance of seven plant species on Little Way Cay following hutia translocation in 1973 (Jordan, 1989; Campbell et al., 1991). Surveys of Little Wax Cay when this island still supported a high-density introduced hutia population also documented obvious perturbation of the island's vegetation, including the presence of numerous dead, defoliated, girdled and stripped trees and shrubs, and with common surviving plant species now mainly cytotoxic to rodents (Jordan, 1989; Campbell et al., 1991). This vegetation damage prompted concerns that hutia introduction may have had associated detrimental impacts on the local herpetofauna (Franz et al., 1983). Although hutias are historically native to the Exuma Cays, which form part of the Great Bahama Bank (Oswald et al., 2020), attitudes toward their reintroduction are complex, with local decision-makers and civil society viewing them not only as a threatened species and the region's only endemic mammal, but also as a problematic, potentially invasive pest that needs to be managed to maintain ecological integrity (e.g. Powers, 2015).

Hutias are recorded from archaeological middens on multiple islands in the TCI (Figure 1), including Middle Caicos (Wing & Wing, 1995) and Providenciales, the site of the largest known concentration of prehistoric hutia remains in the Lucayan Archipelago (LeFebvre et al., 2019). There are no confirmed records of hutia survival into the post-Columbian historical period within the TCI, but some older fishers and farmers are known to currently refer to large rodents locally called "hootee" that reportedly nest in mangroves, suggestive of living memory of hutias and their possible local persistence. In June-July 2014, a seven-week biodiversity survey of the East Bay Islands National Park off North Caicos documented the presence of seagrape (*Coccoloba uvifera*) trees with heavily gnawed bark on John Higgs Cay, together with numerous large rodent faecal pellets. Seagrape is one of the species thought to have been extirpated by hutias through preferential overbrowsing on Little Way Cay (Jordan, 1989; Campbell et al., 1991). Bahamian hutias also leave abundant faecal pellets and can be detected and surveyed using these indirect signs (Clough, 1974, 1985; Jordan, 1989). These findings led to the suggestion that a previously unknown hutia population might survive on John Higgs Cay (Turvey et al., 2017).

Here, we report the findings of follow-up fieldwork on John Higgs Cay to document damage to vegetation caused by rodents, and the outcome of genetic analysis of faecal pellets collected during fieldwork. Our findings provide new perspectives for interpreting the potential impacts of hutias and other species on vegetation in the Lucayan Archipelago, with wider implications for conservation management of native and introduced faunas and vegetation communities in island ecosystems.

Materials and methods

Study site

John Higgs Cay (21°55'17"-21°54'41"N, 71°53'41"-71°53'09"W) is a relatively high (2-4m asl) rocky limestone cay, comprised of limestone pavement and large broken limestone slabs in rocky outcroppings with limited pockets of sandy soil or humus, and surrounded by red mangrove flats that are mostly exposed at low tide. It is separated from other cays and mangrove flats within the East Bay Islands National Park by a network of shallow marine channels 100-250 m wide, and is flanked on its southeast coast by a deeper channel. It is shaped like a capital T, with one branch 1000m long and 230m wide, and the other 750m long and 45m wide. The cay supports a population of the Endangered Turks and Caicos rock iguana (*Cyclura carinata*), but no signs of cats or other feral mammals have been documented by previous researchers.

An initial visit was made to John Higgs Cay in May 2015 to document reported vegetation damage and look for potential hutia pellets. Following observation of large faecal pellets and extensive rodent damage to vegetation, two Maginon WK-3 HD Wildlife Cameras were employed in an initial attempt to detect hutias. One was pointed at a large *Coccoloba uvifera* with heavily and freshly gnawed boughs, and the other was pointed at a heavily and recently gnawed cinnecord (*Vachellia acuifera*) beside a similarly damaged poisonwood (*Metopium toxiferum*). Cameras were baited with ears of partially shucked corn and slices of papaya on long sticks. They were programmed to begin motion detection at 19:00 and stop at 07:00, and to take two still photos followed by a ten-second video, with a minimum interval of one minute between end of video and next motion trigger. Cameras were retrieved after two weeks.

A follow-up visit to collect faecal samples for genetic analysis was conducted in February 2018. During this second trip, the authors also spoke opportunistically with several local residents on North Caicos about their knowledge and observations of large rodents, following a snowball sampling approach that identified individuals considered locally knowledgeable about these animals (Newing, 2011).

Fieldwork was conducted under Scientific Research Permit 18-01-03-03 issued by the Department of Environment and Coastal Resources of the Turks and Caicos Islands under the auspices of the Fisheries Protection Ordinance. Export of samples for genetic analysis was also approved under the Fisheries Protection Ordinance.

Genetic analysis

Faecal samples were preserved in 95% ethanol in the field and stored at -20°C, with the largest and best-preserved pellets selected for analysis. Due to the likely degraded nature of the sample DNA, all pre-amplification work was carried out in the dedicated ancient DNA laboratory at the Natural History Museum, London (NHM). A sterile scalpel was used to slice samples into smaller pieces to increase exposed surface area. Extractions were initially conducted on four pellets (samples 1-4) using a standard protocol for degraded DNA established by Dabney et al. (2013); this was modified for tissue material with lysis based on the Qiagen Blood and Tissue kit (Qiagen), lysing sample fragments with 180ul buffer ATL and 20ul proteinase K and incubating with rotation at 56°C for 24 hours. Due to mixed results with the modified Dabney protocol, a second set of extractions was conducted on three of the previous samples (samples 2-4) and two additional pellets (samples 5-6) using the PowerSoil kit (Qiagen). For both extraction methods (i.e., nine libraries for six samples), dual-indexed double-stranded libraries were constructed based on Meyer and Kircher (2010), amplified for 20 cycles, quantified for DNA and fragment size distribution on an Agilent Tapestation 2200, and pooled for sequencing. Samples were screened on a NextSeq500 paired-end run using a mid-output kit at the NHM.

Raw reads were quality-checked using FastQC v.0.12.0 (www.bioinformatics.babraham.ac.uk/projects/fastqc). Adapter sequences were bioinformatically removed from raw sequenced reads using AdapterRemoval v.2.2.2 (Schubert et al., 2016), with settings to remove sequences shorter than 25 base pairs, allow maximum mismatch rate of 1/3, trim ambiguous bases at read ends, and trim bases at read ends with Phred scores below the default value.

Taxonomic identification of samples was conducted through sequential alignment of reads to a reference panel of nuclear genomes using FastQ Screen v.0.13.0 (https://www.bioinformatics.babraham.ac.uk/projects/fastq_screen/). Reference genomes included *Homo sapiens* (NCBI accession: GCF_000001405.39), *Rattus rattus* (GCF_011064425.1), *R. norvegicus* (GCF_036323735.1), *Mus musculus* (GCF_000001635.26), and *Capromys pilorides* (GCA_004027915.1), which represents the only available capromyine nuclear genome and is the phylogenetically closest stand-in for *Geocapromys ingrahami*. For samples extracted using both protocols (samples 2-4), analysis was conducted using PowerSoil-generated libraries, which yielded the greatest number of reads. Entire FastQ files were used instead of default sampling of 100,000 reads. Further taxonomic identification of samples through alignment with three mitochondrial gene sequences and five nuclear gene sequences previously generated for *G. ingrahami* (Fabre et al., 2014) was not attempted, because alignment of low-quality samples to a reference panel of complete genomes provides a much more robust phylogenetic signal, and because initial mapping showed greatest similarity to *R. rattus* rather than to a hutia species (see below).

As FastqScreen analysis revealed some samples contained considerable human contamination, a competitive alignment was conducted to investigate the proportion of reads that mapped to the nuclear genomes of either *H. sapiens* or *R. rattus*. Competitive mapping was conducted using bwa v.0.7.17-r1188 (Li & Durbin, 2009), with seeding disabled (-l 1024) and allowing maximum edit distance of 1% (-n 0.01) and two gap openings (-o 2), following Pečnerová et al. (2017). Because fragmentation length distributions resulted in considerable unmerged reads, both merged and QC-checked unmerged reads were aligned, with mapping data combined for downstream analysis. Reads mapping to the human genome were discarded. Samtools v.1.10 (Li et al., 2009) was used to remove duplicate reads, with a mapping quality filter of 25 applied to minimise reference bias following Koptekin et al. (2025). Degradation statistics (fragmentation and deamination) were examined with MapDamage2 (Jónsonn et al., 2013).

As mapping statistics for samples 1 and 5 showed sufficient mitochondrial reads, mitochondrial genomes were assembled for these samples through iterative de-novo assembly with MITObim (Hahn et al., 2013), using a mitochondrial genome of *R. rattus* (NC_012374) as seed and default options. The final iteration .maf files were converted to .sam format, and downstream filtering for duplicate reads was conducted using samtools. Consensus fasta sequences were called with majority calling, without trimming read ends as no deamination was detected. A coverage of 3× per site was used for sample 5, and 2× per site for sample 1 to increase the amount of called bases for this sample with fewer reads. Whole-mitochondrial genome Bayesian phylogenetic analysis was conducted, including available mitochondrial genomes for *Rattus rattus* from multiple locations, all other *Rattus* species with mitochondrial genomes, and using *Mus musculus* as an outgroup (Table S1). Sequences were aligned with mafft v7.453 (Katoh & Stanley, 2013), with a GTR+I+G substitution model determined using PartitionFinder v.2 (Lanfear et al., 2017). Phylogenetic analysis was run using MrBayes v.3.2.7a (Ronquist et al., 2012), with eight MCMC processes for 1 million generations.

Results

Vegetation survey

Reconnaissance of John Higgs Cay observed extensive areas of damaged shrubs exhibiting stripped vegetation and severely gnawed boughs (Figure 2), with damage documented in 15 plant species (Table 1). The most heavily damaged species was *Vachellia acuifera*, with nearly all individual trees largely or completely defoliated, showing heavy browsing and gnawing on newer twigs and deep scaring on trunks and older limbs, and with no remaining reproductive parts. Seagrape also showed intense damage, with many limbs gnawed right through, including some up to 4cm in diameter; much of the gnawed material on larger boughs had dropped to the ground instead of being eaten, as piles of shredded bark and wood were present under many gnawed spots. *Metopium toxiferum* was also a favoured browse tree, with slender twigs and small branches gnawed right through and leafy twigs left on the ground under trees, and saplings gnawed almost completely to the stump.

Old and fresh rodent faecal pellets were found in abundance. These were *c.*12-15mm in length, rounded and slightly curved, and appeared morphologically very similar to *Geocapromys* pellets (Figure 1).

Camera trapping

Both cameras recorded multiple images and videos of rats (*Rattus* sp.) engaging with the bait during the first night they were set, after which both memory cards became full. No other mammal species were detected.

Genetic analysis

Libraries generated from Dabney-adapted protocol extracts yielded 120-229,930 reads, reduced to 28-213,109 reads after adapter-removal and collapsing read pairs (NCBI, 2025; Table 2). Overall, 0-30.76% of reads mapped to the reference panel genomes.

Only sample 1 yielded DNA identifiable as rodent, with 1.63% of reads mapping uniquely to *R. rattus*, 0.44% to *R. norvegicus*, and <0.01% to each of *M. musculus*, *C. pilorides* or *H. sapiens* (Table 3). Other samples had fewer than 3,000 total reads, with no reads uniquely assigned to the reference panel genomes (Figure S1, Tables S2-S3).

Libraries generated from PowerSoil kit extracts yielded 3.49-10.89 million reads, reduced to 1.44-6.73 million reads after adapter-removal and collapsing read pairs (NCBI, 2025; Table 2). Overall, 0.14-47.74% of reads mapped to the reference panel genomes. For sample 5, 1.69% of reads mapped uniquely to *R. rattus*, followed by 0.54% to *R. norvegicus*, and <0.01% to each of *H. sapiens*, *C. pilorides* or *M. musculus* (Table 3). Results were less clear for other samples, for which the highest proportion of uniquely mapping reads aligned to *H. sapiens* (0.51-4.15%), indicative of poor sample preservation and human contamination, followed by *R. rattus* (0.018-0.031%), and with minimal alignment to other genomes (0.002-0.010%) (Figure S1, Table S2).

When reads were competitively mapped to *R. rattus*, samples 1 and 5 yielded endogenous proportions of 27.96% and 51.33% of sequenced DNA, respectively, whereas samples 2, 3, 4 and 6 had endogenous proportions of 0.14-0.15% (Table S3). Recovered mitochondrial genomes had average coverages of 1.66× for sample 1 and 26.78× for sample 5 (NCBI, 2025). Bayesian phylogenetic analysis showed that samples 1 and 5 cluster monophyletically within *R. rattus*, with high support for all branches (probabilities >92%) (Figure 3).

Local knowledge and opportunistic observations of rodents

Informal conversations with ten respondents on North Caicos provided accounts of an animal locally referred to as “hutia” or “mangrove rat”, described as a brown rodent larger than a black rat that constructed nests in mangroves and was sometimes encountered by people when they were fishing. During a boat trip into an area of mangroves off the coast of North Caicos, the authors observed a *c*.70cm diameter spherical nest made of sticks built around the lower branches of a mangrove. This nest was said to have been made by a "hutia" and was found to contain a family of brown rats.

Discussion

Our study of rodent damage to vegetation on John Higgs Cay was prompted by the possibility that a previously overlooked population of the Critically Endangered Bahamian hutia might persist in the TCI (Turvey et al., 2017). However, our investigations found no evidence of continued hutia survival, and instead revealed only genetic evidence of black rats on John Higgs Cay, and observations of brown rats in mangroves elsewhere around North Caicos. Whilst this result is disappointing for hutia conservation, it provides a new baseline for understanding the impacts of invasive rats on native vegetation in the Caribbean, with important implications for conservation management across this region.

Although camera trapping detected only rats on John Higgs Cay, the large faecal pellets present on the cay were suggestive of a larger rodent, and our limited camera-trapping survey effort may have failed to detect a remnant population of hutias that could also be present. Further genetic investigation of the pellets was thus conducted. An ancient DNA approach was adopted due to the degraded and likely low-quality nature of the collected genetic material (Ando et al., 2020), combined with the tropical depositional environment and uncertain time since faecal deposition, which are not conducive to DNA preservation (Brace et al., 2016). Two of the pellets selected for analysis showed good preservation, permitting robust identification as *R. rattus*. The other PowerSoil-extracted samples displayed a lower number of unique reads mapping to *R. rattus* (12-38%), but still aligned much more closely with *R. rattus* than with other murid genomes or a comparative hutia genome. If these samples had been processed in a non-ancient DNA laboratory, inferences about their taxonomic identity would likely incur greater uncertainty. The samples extracted with the Dabney-adapted protocol did not yield as much amplifiable DNA, probably due to increased presence of PCR inhibitors in faeces (Poinar et al., 1998) compared with the degraded tissue material for which this protocol is designed. In contrast, the PowerSoil kit is designed to remove PCR inhibitors from soil and faecal samples during extraction, and is also used in ancient DNA analysis of faecal material (Cano et al., 2014; Boast et al., 2018). Our results thus indicate that addressing the specific chemical properties of faecal samples is necessary to improve likelihood of successful extraction and taxonomic identification.

Faecal pellets of many rodents can show intraspecific variation depending upon diet and other conditions (Borroto-Páez & Mancina, 2011; McCleery et al., 2021). Black rat pellets in Caribbean environments are typically 7-14mm long, with a narrow, tapered shape, and their length approximately four or five times their width (Morton & Cole, 2013). Hutia pellets vary in size between species (Borroto-Páez & Mancina, 2011) but are typically much larger and more rounded than rat pellets, and often have a distinctive curved shape, leading to some hutias being known as “banana rats” (Parker et al., 2020). The pellets from John Higgs Cay are thus markedly larger and morphologically different to black rat pellets in many other landscapes, potentially due to a trophic shift in this species associated with the depauperate environmental conditions on this small cay (e.g., lack of competitors, limited food plants). This variation highlights the potential for species misidentification when using indirect signs to survey small mammals in ecologically novel island landscapes, especially if multiple species might be present (McCleery et al., 2021). Relatively subtle differences in pellet morphology have been proposed as a diagnostic method for differentiating hutia species in Cuba (Garrido, 1971; Borroto-Páez & Mancina, 2011), and have even been used to suggest the continued survival of the possibly extinct hutia *Mesocapromys nanus* (Garrido, 1980). We encourage critical assessment of intraspecific variation in faecal morphology for native and invasive rodents in Caribbean ecosystems, and the factors that underpin such variation.

Black and brown rats have successfully invaded many ecosystems on tropical islands and are both documented from the TCI (Masseti, 2011; Borroto-Páez & Woods, 2012b). Whereas black rats are recorded widely from mangroves (Harper et al., 2014; Harper & Bunbury, 2015; Ringler et al., 2021), brown rats are also documented from this habitat on several islands (Phillips et al., 2007; Dencer-Brown et al., 2020). However, there has been little research into brown rat distribution and ecology in mangroves, with further work needed to understand their ecological impacts and potential eradication (Harper & Bunbury, 2015; Keitt et al., 2015). Our record of brown rats from mangroves in the TCI therefore constitutes an important observation for regional environmental planning.

The local interpretation of brown rats as "hutias" or "hootees" also provides an interesting example of name transference. The English-language word "hutia" is derived from the Indigenous pre-Columbian Taíno name for this animal (Granberry & Vescelius, 2004). Local communities might therefore have retained this word following hutia extinction and used it to refer instead to large invasive rats. This etymological phenomenon, an example of shifting baseline syndrome (Papworth et al., 2009), is also documented following extinctions in other regions (Cheke, 2006). However, "hutia" or local variations are sometimes used to refer generically to native small mammals and even iguanas elsewhere in the Caribbean (de la Fuente, 1982; Woods & Ottenwalder, 1992; Turvey et al., 2008, 2014), and may therefore have been introduced more recently to the TCI through socio-cultural interactions with the Bahamas, Cuba, or Hispaniola. Confusion over the identity of animals known as "hutias" thus provides an important note of caution when assessing unverified reports of survival of other Caribbean mammals (e.g. Woods et al., 1985).

Observed vegetation damage differs between Little Wax Cay and John Higgs Cay, although direct comparisons are not straightforward because of differences in local ecology and plant diversity between these islands, which could influence rodent food selection and plant survival. Some species heavily damaged on Little Wax Cay (*Manilkara jaimiqui*, *Phyllanthus epiphyllanthus*, *Strumpfia maritima*; Campbell et al., 1991) were present but unaffected on John Higgs Cay. Campbell et al. (1991) also documented the extinction of one palm species (*Pseudophoenix sargentii*) and severe damage to another palm (*Coccothrinax argentata*) on Little Wax Cay; neither species occurs on John Higgs Cay, but the palm present on this island (*Leucothrinax morrisii*) showed no sign of damage. Conversely, the highly toxic species *Metopium toxiferum* was heavily damaged on John Higgs Cay, whereas this species had become the most conspicuous woody plant in parts of Little Wax Cay and was considered inedible to rodents by Campbell et al. (1991).

Vegetation damage blamed on hutias at Little Wax Cay has led to extensive debate about potential control measures, which conflict with the species' global-priority conservation status and generate complexities around management decision-making. However, although we document some differences in vegetation damage between Little Wax Cay and John Higgs Cay, our study demonstrates that comparable damage on other islands in the Lucayan Archipelago is produced by black rats. Importantly, although invasive rats were not mentioned by Campbell et al. (1991) in their study of vegetation damage on Little Wax Cay, black rats are also present on this island (Clough, 1985; Jordan, 1989). Indeed, they were initially considered "numerous" by Clough (1985), although subsequent studies recorded them less regularly (Jordan 1989).

In contrast to concerns around hutia damage on Little Wax Cay, research into disruption to Caribbean plant communities by invasive rats has been relatively limited (e.g., Harper & Bunbury, 2015; Figuerola-Hernández et al., 2017). Given our evidence for extensive rat-caused damage on John Higgs Cay, we recommend that wider attention is paid to this important ecological impact, as well as to deleterious effects of rats on native faunas (Borroto-Páez, 2009; Borroto-Páez & Woods, 2012b; Daltry et al., 2017; Donihue et al., 2021). In particular, it is crucial to determine whether vegetation damage on Little Wax Cay may have been caused by rats rather than hutias. Hutias are also locally blamed for vegetation damage elsewhere in the Caribbean, including damage to crops grown by low-income Indigenous communities within landscapes that also support rats (Turvey et al., 2008, 2014, 2024). Whereas this damage is often associated with perceived hutia population increases caused by strengthened conservation, rats have been present in Caribbean ecosystems for several centuries, with invasive murids introduced across this region on multiple occasions in association with historical human movement and trade (Atkinson, 1985; Shiels et al., 2020). It is thus possible that vegetation damage by rats may be overlooked and perceived as "natural" (constituting another example of shifting baseline syndrome; Papworth et al., 2009). These issues raise important wider questions around interpreting biodiversity baselines, and defining native vegetation states and management or restoration targets for islands that historically supported now-lost hutia populations. It is essential to evaluate patterns and magnitude of damage caused by both hutias and rats across other islands (e.g. the

Exuma Cays), to support an evidence-based approach to conservation that benefits both native biodiversity and local community livelihoods and needs.

Author contributions

Bryan Naqqi Manco, Samuel T. Turvey, Selina Brace and Rosalind J. Kennerley conceived ideas and designed methodology; Bryan Naqqi Manco, Junel Blaise, Rosalind J. Kennerley, Samuel T. Turvey, Selina Brace and Ian Barnes collected data; Maria H. Zicos and Selina Brace analysed data; Samuel T. Turvey and Maria H. Zicos led writing of manuscript. All authors contributed critically to drafts and gave final approval for publication.

Statement on inclusion

Our study brings together authors from different countries, including conservationists based in the territory where the study was carried out, who initiated the research. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent was considered from the onset. Whenever relevant, literature published by scientists from the region was cited, including work published in local languages across the Caribbean.

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Conflict of interest

We declare no conflict of interest.

Data availability statement

Genetic data generated in this study are available on the Sequence Read Archive at the NCBI database (www.ncbi.nlm.nih.gov/sra) under project number PRJNA1322284.

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Table 1. Plant species on John Higgs Cay and observed rodent damage.

Species	**Common name**	**Plant type**	**Rodent damage**
Agave millspaughii	Wild sisal	Succulent perennial	—
Caesalpinia bahamensis	Brasiletto	Shrub or small tree	Lightly gnawed
Chamaecrista lineata	Popcorn	Subshrub or shrub	—
Coccoloba diversifolia	Pigeonplum	Shrub or small tree	—
Coccoloba uvifera	Seagrape	Small tree	Heavily gnawed
Conocarpus erectus	Buttonwood	Mangrove shrub	—
Crossopetalum rhacoma	Bird cherry	Shrub or small tree	—
Dodonaea viscosa	Dogwood	Shrub or small tree	Gnawed
Elaeodendron xylocarpum	Whitewood	Shrub or small tree	Lightly gnawed
Encyclia altissima	Tall orchid	Perennial epiphyte/lithophyte	Heavily gnawed, only this year's leaves present
Encyclia caicensis	Caicos orchid	Perennial epiphyte/lithophyte	Heavily gnawed, only this year's leaves present
Encyclia inaguensis	Inagua orchid	Perennial epiphyte/lithophyte	Heavily gnawed, only this year's leaves present
Erithalis fruticosa	Black torch	Shrub or small tree	—
Guapira discolor	Donkey bread	Shrub or small tree	Gnawed
Jacquinia keyensis	Joe wood	Shrub or small tree	Some twigs defoliated
Lepidaploa arbuscula	Bumbo bush	Shrub	—
Leucothrinax morrisii	Buffalo-top	Small palm	—
Manilkara jaimiqui	Wild dilly	Shrub or small tree	—
Maytenus buxifolia	Whitewood	Shrub or small tree	—
Metopium toxiferum	Poisonwood	Small tree	Heavily gnawed, branches cropped, saplings eaten
Opuntia nashii	Horse pear	Perennial cactus	—
Opuntia stricta	Prickly pear	Perennial cactus	Lightly gnawed
Phyllanthus epiphyllanthus	Sword bush	Shrub	—
Pilosocereus royenii	Dildo cactus	Perennial cactus	Heavily gnawed where freshly broken
Reynosia septentrionalis	Darling plum	Shrub or small tree	Gnawed
Rhachicallis americana	Sandfly bush	Shrub	—
Rhizophora mangle	Red mangrove	Mangrove tree	—
Sarcomphalus taylorii	Wild jujube	Shrub	Gnawed
Schizachirium gracile	Slender beard-grass	Perennial grass	—
Senna mexicana var. *chapmanii*	Popcorn	Shrub	—
Sophora tomentosa	Necklace pod	Shrub or small tree	—
Strumpfia maritima	Mosquito-bush	Shrub	—
Vachellia acuifera	Cinnecord	Shrub or small tree	Defoliated 95-100%, heavily gnawed

Table 2. Sequenced samples from John Higgs Cay and read numbers after bioinformatic pre-processing.

Specimen number	Raw reads	Merged reads
A. *Extractions using Dabney-adapted protocol for degraded DNA*		
1	229,930	213,109
2	120	28
3	3,625	2,948
4	5,108	1,323
B. *Extractions using Qiagen PowerSoil kit*		
2	10,891,234	6,645,351
3	6,870,508	2,687,355
4	3,489,661	1,442,287
5	8,519,290	6,734,539
6	6,246,706	2,350,350

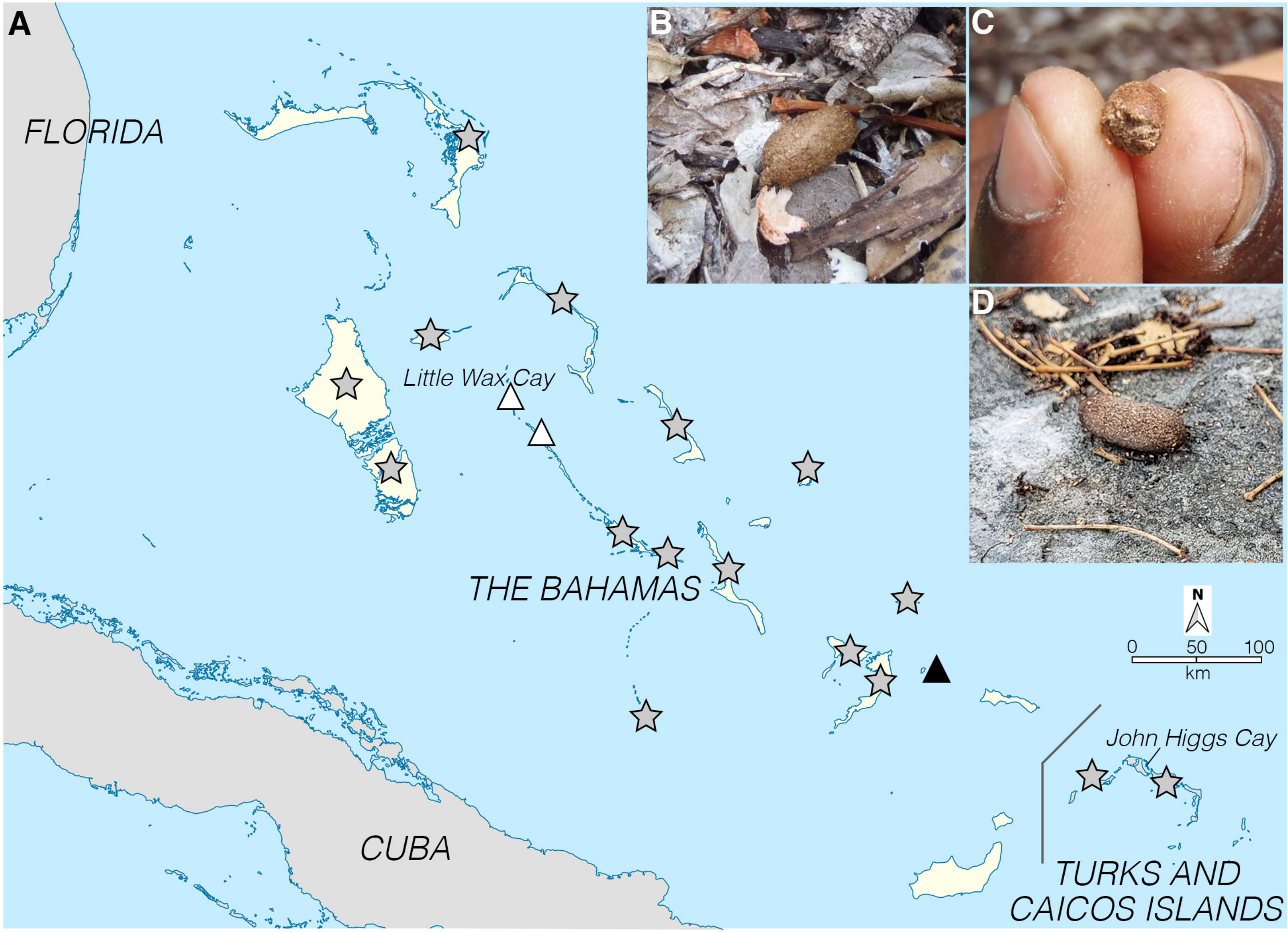
Table 3. Taxonomic identification of John Higgs Cay samples through sequential alignment of reads to nuclear genome reference panel. Values for "% reads mapped" include reads mapping to multiple genomes (conserved regions) or multiple locations within genome (repeats), so are greater than values for "% unique reads".

Sample	**Comparative nuclear genome**	**% reads mapped**	**Unique reads**	**% unique reads**	**Ratio to *R. rattus***
1	*Homo sapiens*	1.597	5	0.002	0.001
	Mus musculus	10.130	14	0.007	0.004
	Rattus norvegicus	29.259	934	0.438	0.269
	Rattus rattus	30.762	3,478	1.632	1
	Capromys pilorides	1.458	1	0	0
2	*Homo sapiens*	0.643	33,808	0.509	16.573
	Mus musculus	0.189	412	0.006	0.202
	Rattus norvegicus	0.270	575	0.009	0.282
	Rattus rattus	0.301	2,040	0.031	1
	Capromys pilorides	0.143	388	0.006	0.190
3	*Homo sapiens*	4.302	97,651	4.155	225.002
	Mus musculus	0.142	144	0.006	0.332
	Rattus norvegicus	0.147	165	0.007	0.380
	Rattus rattus	0.163	434	0.018	1
	Capromys pilorides	0.145	114	0.005	0.263
4	*Homo sapiens*	2.340	30,664	2.126	70.654
	Mus musculus	0.235	143	0.010	0.329
	Rattus norvegicus	0.240	121	0.008	0.279
	Rattus rattus	0.268	434	0.030	1
	Capromys pilorides	0.224	100	0.007	0.230
5	*Homo sapiens*	3.105	587	0.009	0.005
	Mus musculus	19.122	516	0.008	0.005
	Rattus norvegicus	46.369	36,086	0.536	0.317
	Rattus rattus	47.744	113,788	1.690	1
	Capromys pilorides	2.883	131	0.002	0.001
6	*Homo sapiens*	3.524	92,799	3.453	192.929
	Mus musculus	0.055	86	0.003	0.179
	Rattus norvegicus	0.056	81	0.003	0.168
	Rattus rattus	0.077	481	0.018	1
	Capromys pilorides	0.065	60	0.002	0.125

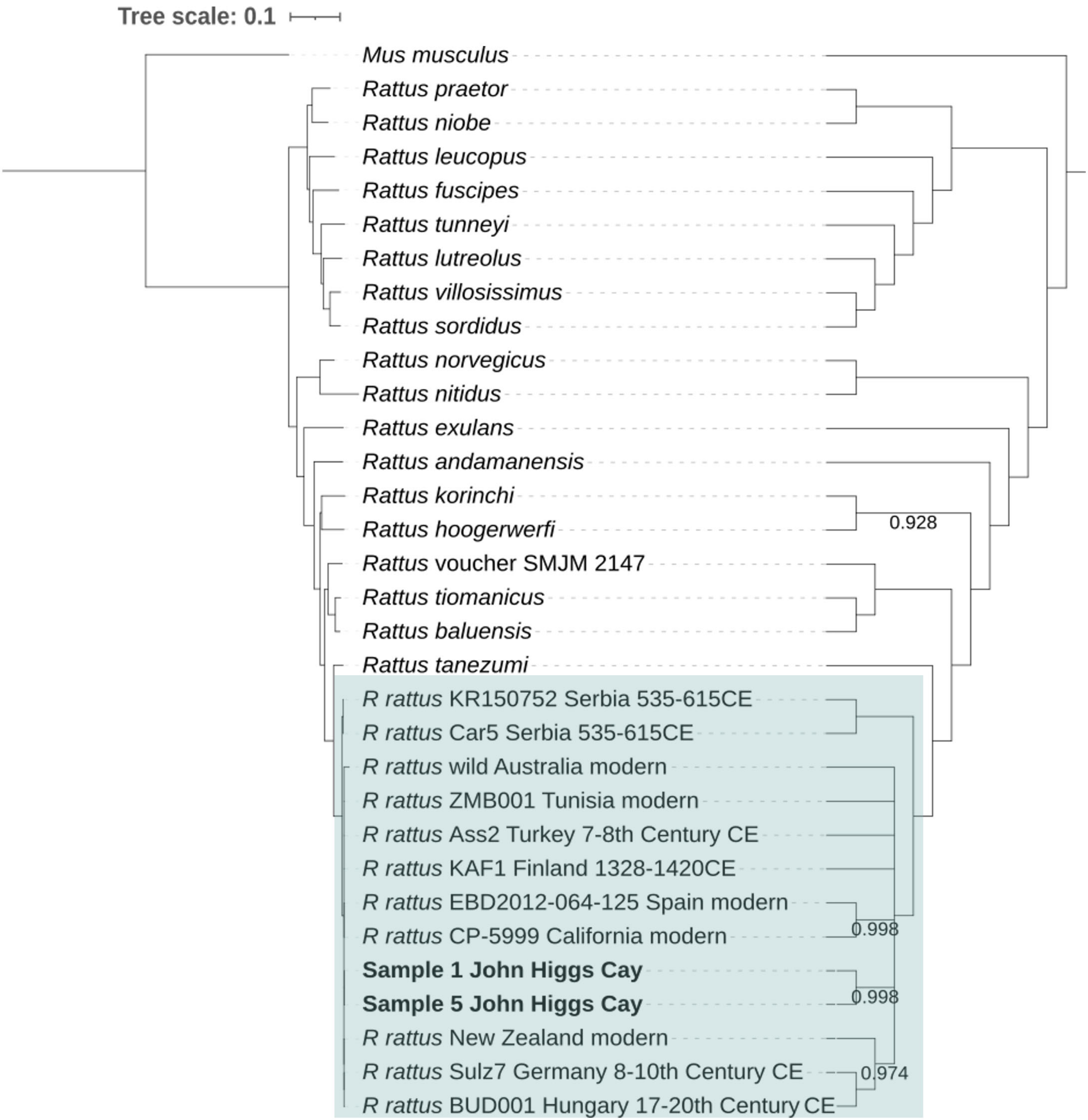
Figure 1. A, Map of Lucayan Archipelago, showing distribution of last surviving (black triangle), translocated (white triangle), and extirpated (grey star) Bahamian hutia populations, and cays with reported vegetation damage (Little Way Cay, John Higgs Cay). Data from LeFebvre et al. (2019) and Turvey et al. (2021). **B-C,** Large rodent faecal pellet on John Higgs Cay. **D,** Faecal pellet of Jamaican hutia (*Geocapromys brownii*), closest extant relative of Bahamian hutia, in similar limestone dry forest habitat in Hellshire Hills, Jamaica (photograph copyright Samuel Turvey/ZSL).

Figure 2. Rodent-caused vegetation damage observed on John Higgs Cay. **A,** Cinnecord (*Vachellia acuifera*), completely defoliated tree. **B-C,** Poisonwood (*Metopium toxiferum*), heavily gnawed sapling and branch. **D-F,** Seagrape (*Coccoloba uvifera*), heavily gnawed sapling and branches, showing rodent incisor marks (**D**) and accumulation of faecal pellets beneath gnawed sapling (**E**).

Figure 3. Whole-mitochondrial genome Bayesian phylogeny of John Higgs Cay samples, other *Rattus rattus* samples, and mitochondrial genomes for other *Rattus* species (outgroup: *Mus musculus*). Highlighted area indicates *R. rattus* clade. **Left,** Phylogeny showing branch lengths. **Right,** Topology without branch lengths, showing support values. Support value equals 1 for nodes lacking values. Sequence accession numbers available in Table S1.


A
B
C
D
FLORIDA
Little Wax Cay
THE BAHAMAS
CUBA
John Higgs Cay
TURKS AND CAICOS ISLANDS
N
0
50
100
km


A
B
C
D
E
F


Tree scale: 0.1
Mus musculus
Rattus praetor
Rattus niobe
Rattus leucopus
Rattus fuscipes
Rattus tunneyi
Rattus lutreolus
Rattus villosissimus
Rattus sordidus
Rattus norvegicus
Rattus nitidus
Rattus exulans
Rattus andamanensis
Rattus korinchi
Rattus hoogerwerfi
0.928
Rattus voucher SMJM 2147
Rattus tiomanicus
Rattus baluensis
Rattus tanezumi
R rattus KR150752 Serbia 535-615CE
R rattus Car5 Serbia 535-615CE
R rattus wild Australia modern
R rattus ZMB001 Tunisia modern
R rattus Ass2 Turkey 7-8th Century CE
R rattus KAF1 Finland 1328-1420CE
R rattus EBD2012-064-125 Spain modern
R rattus CP-5999 California modern
0.998
Sample 1 John Higgs Cay
Sample 5 John Higgs Cay
0.998
R rattus New Zealand modern
R rattus Sulz7 Germany 8-10th Century CE
0.974
R rattus BUD001 Hungary 17-20th Century CE

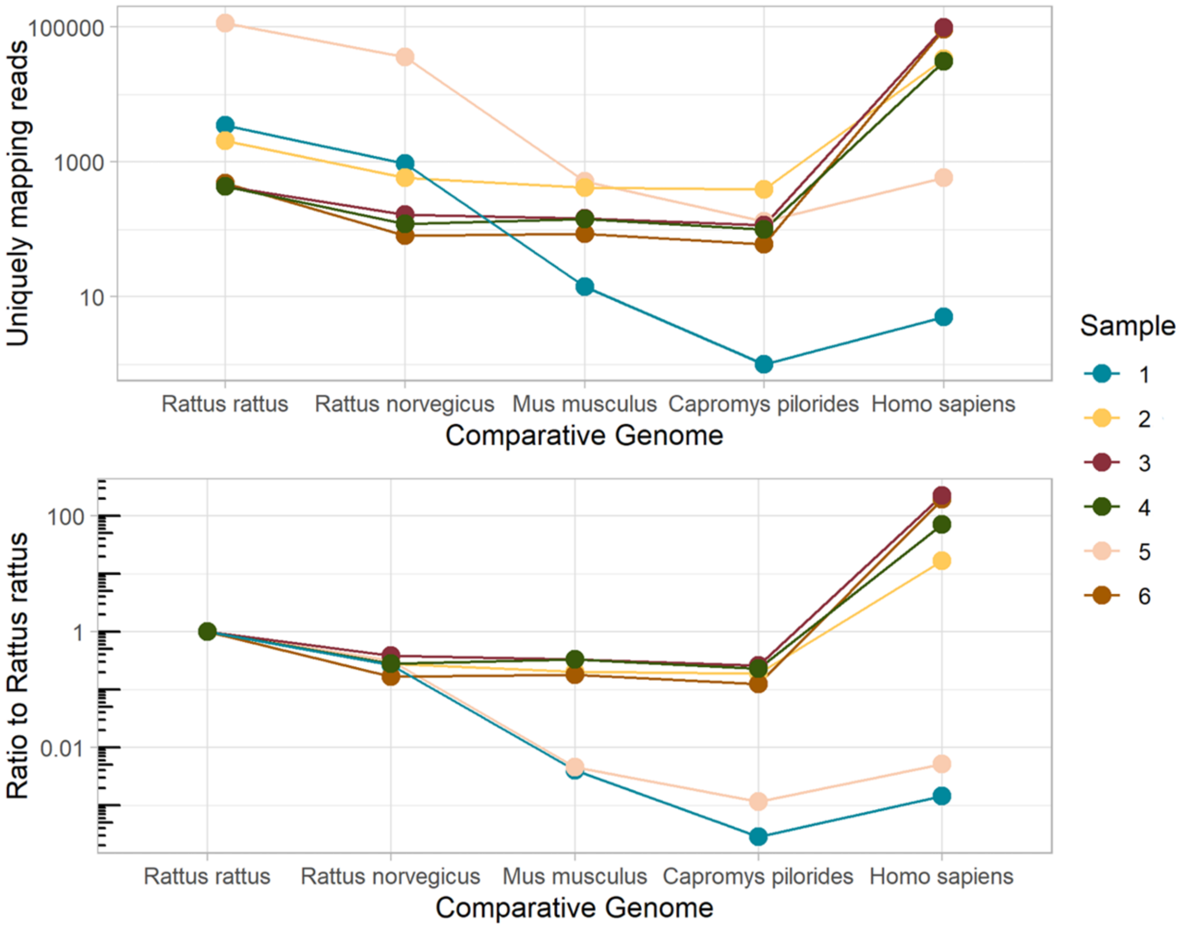


Figure S1. Taxonomic association of samples to reference panel of nuclear genomes. **Top,** Counts of uniquely mapping reads to each reference genome. **Bottom,** Ratio of unique reads mapping to *Rattus rattus* versus other species.

Table S1. Mitochondrial genomes for *Rattus* species and outgrou

Accession number	**Species**
Sample1_1x	John Higgs Cay sample 1
Sample5_3x	John Higgs Cay sample 5
FJ355927.1	*Rattus rattus*
MW209724.1	*Rattus rattus*
OM574940.1	*Rattus rattus*
OM574941.1	*Rattus rattus*
OM574946.1	*Rattus rattus*
OM574951.1	*Rattus rattus*
OM574953.1	*Rattus rattus*
OM574959.1	*Rattus rattus*
OM574960.1	*Rattus rattus*
OM574964.1	*Rattus rattus*
NC_012374.1	*Rattus rattus*
NC_046686.1	*Rattus andamanensis*
NC_035621.1	*Rattus baluensis*
NC_012389.1	*Rattus exulans*
NC_014867.1	*Rattus fuscipes*
NC_049040.1	*Rattus hoogerwerfi*
NC_049042.1	*Rattus korinchi*
NC_014855.1	*Rattus leucopus*
NC_014858.1	*Rattus lutreolus*
NC_023347.1	*Rattus niobe*
NC_040919.1	*Rattus nitidus*
NC_001665.1	*Rattus norvegicus*
NC_012461.1	*Rattus praetor*
NC_014871.1	*Rattus sordidus*
NC_049041.1	*Rattus* sp. (NH 2147 voucher SMJM_2147)
NC_011638.1	*Rattus tanezumi*
NC_029888.1	*Rattus tiomanicus*
NC_014861.1	*Rattus tunneyi*
NC_014864.1	*Rattus villosissimus*
NC_005089.1	*Mus musculus*

p used in Bayesian phylogenetic analysis.

Reference
This study
This study
Nilsson MA et al. 2010. The impact of fossil calibrations, codon positions and relaxed clocks on t
Yu H. et al. 2022. Palaeogenomic analysis of black rat (*Rattus rattus*) reveals multiple European
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Yu H. et al. 2022. Palaeogenomic analysis of black rat (*Rattus rattus*) reveals multiple European
Yu H. et al. 2022. Palaeogenomic analysis of black rat (*Rattus rattus*) reveals multiple European
RefSeq
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he divergence time estimates of the native Australian rodents (Conilurini). *Gene* , **455**, 22-3

introductions associated with human economic history. *Nature Communications* , **13**, 239

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introductions associated with human economic history. *Nature Communications* , **13**, 239

introductions associated with human economic history. *Nature Communications* , **13**, 239

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Table S2. Taxonomic identification of samples through sequential alignment of reac

Sample	Extraction method	Concentration	Genome	#Raw_reads
1	Dabney		*Homo sapiens*	229930
			Mus musculus	
			Rattus norvegicus	
			Rattus rattus	
			Capromys pilorides	
2	Dabney	0.06	*Homo sapiens*	120
			Mus musculus	
			Rattus norvegicus	
			Rattus rattus	
			Capromys pilorides	
	PowerSoil	1.33	*Homo sapiens*	10891234
			Mus musculus	
			Rattus norvegicus	
			Rattus rattus	
			Capromys pilorides	
3	Dabney	0.08	*Homo sapiens*	3625
			Mus musculus	
			Rattus norvegicus	
			Rattus rattus	
			Capromys pilorides	
	PowerSoil	1.97	*Homo sapiens*	6246706
			Mus musculus	
			Rattus norvegicus	
			Rattus rattus	
			Capromys pilorides	
4	Dabney	0.11	*Homo sapiens*	5108
			Mus musculus	
			Rattus norvegicus	
			Rattus rattus	
			Capromys pilorides	
	PowerSoil	0.78	*Homo sapiens*	3489661
			Mus musculus	
			Rattus norvegicus	
			Rattus rattus	
			Capromys pilorides	
5	PowerSoil	21.60	*Homo sapiens*	8519290
			Mus musculus	
			Rattus norvegicus	
			Rattus rattus	
			Capromys pilorides	
6	PowerSoil	2.13	*Homo sapiens*	6870508

			Mus musculus *Rattus norvegicus* *Rattus rattus* *Capromys pilorides*	

ds to nuclear genome reference panel with FastqScreen.

#Reads_processed	#Unmapped	%Mapped	%Unmapped	#One_hit_one_genome
213109	209706	1.60	98.40	5
	191520	10.13	89.87	14
	150755	29.26	70.74	934
	147552	30.76	69.23	3478
	210002	1.46	98.54	1
28	28	0	100	0
	28	0	100	0
	28	0	100	0
	28	0	100	0
	28	0	100	0
6645351	6602645	0.64	99.36	33808
	6632760	0.19	99.81	412
	6627415	0.27	99.73	575
	6625355	0.30	99.70	2040
	6635859	0.14	99.85	388
2948	2937	0.37	99.63	0
	2936	0.41	99.59	0
	2933	0.51	99.49	0
	2934	0.47	99.52	0
	2934	0.47	99.53	0
2350350	2249238	4.30	95.71	97651
	2347007	0.14	99.86	144
	2346884	0.15	99.85	165
	2346526	0.16	99.83	434
	2346944	0.14	99.86	114
1323	1321	0.15	99.85	0
	1320	0.23	99.77	0
	1320	0.23	99.77	0
	1320	0.23	99.77	0
	1320	0.23	99.77	0
1442287	1408532	2.34	97.66	30664
	1438893	0.24	99.76	143
	1438826	0.24	99.76	121
	1438421	0.27	99.74	434
	1439061	0.22	99.78	100
6734539	6525444	3.10	96.90	587
	5446794	19.12	80.88	516
	3611823	46.37	53.64	36086
	3519227	47.74	52.25	113788
	6540355	2.88	97.12	131
2687355	2592658	3.52	96.48	92799

	2685888	0.05	99.95	86
	2685838	0.06	99.95	81
	2685279	0.08	99.92	481
	2685614	0.06	99.94	60

%One_hit_one_genome	**Ratio *Rattus rattus***	**#Multiple_hits_one_genome**
0.002	0.001	1
0.007	0.004	1
0.438	0.269	148
1.632	1.000	738
0.000	<0.001	0
0	Not computed	0
0	Not computed	0
0	Not computed	0
0	Not computed	0
0	Not computed	0
0.509	16.573	108
0.006	0.202	142
0.009	0.282	248
0.031	1	890
0.006	0.190	106
0	Not computed	0
0	Not computed	0
0	Not computed	2
0	Not computed	0
0	Not computed	1
4.155	225.002	89
0.006	0.332	37
0.007	0.380	55
0.018	1	181
0.005	0.263	19
0	Not computed	0
0	Not computed	0
0	Not computed	0
0	Not computed	0
0	Not computed	0
2.126	70.654	58
0.010	0.329	56
0.008	0.279	64
0.030	1	205
0.007	0.230	28
0.009	0.005	45
0.008	0.005	110
0.536	0.317	5701
1.690	1	23317
0.002	0.001	32
3.453	192.929	94

0.003	0.179	20
0.003	0.168	38
0.018	1	202
0.002	0.125	40

%Multiple_hits_one_genome	#One_hit_multiple_genomes	%One_hit_multiple_genomes
0	1121	0.53
0	11107	5.21
0.07	44077	20.68
0.35	45581	21.39
0	890	0.42
0	0	0
0	0	0
0	0	0
0	0	0
0	0	0
0	1351	0.02
0	2524	0.04
0	6773	0.10
0.01	7260	0.11
0	1729	0.03
0	0	0
0	0	0
0.07	1	0.03
0	2	0.07
0.03	2	0.07
0	1039	0.04
0	545	0.02
0	536	0.02
0.01	652	0.03
0	1193	0.05
0	0	0
0	0	0
0	0	0
0	0	0
0	0	0
0	532	0.04
0	382	0.03
0	393	0.03
0.01	420	0.03
0	623	0.04
0	71427	1.06
0	700420	10.40
0.08	2248926	33.39
0.35	2352830	34.94
0	60734	0.90
0	949	0.04

0	330	0.01
0	353	0.01
0.01	375	0.01
0	759	0.03

Multiple_hits_multiple_genomes	%Multiple_hits_multiple_genomes
2276	1.07
10467	4.91
17195	8.07
15760	7.4
2216	1.04
0	0
0	0
0	0
0	0
0	0
7439	0.11
9513	0.14
10340	0.16
9806	0.15
7269	0.11
11	0.37
12	0.41
12	0.41
12	0.41
11	0.37
2333	0.10
2617	0.11
2710	0.12
2557	0.11
2080	0.09
2	0.15
3	0.23
3	0.23
3	0.23
3	0.23
2501	0.17
2813	0.20
2883	0.20
2807	0.19
2475	0.17
137036	2.03
586699	8.71
832003	12.35
725377	10.77
133287	1.98
855	0.03

1031	0.04
1045	0.04
1018	0.04
882	0.03

Table S3. Mapping statistics of samples in competitive alignment to *Rattus rattus* and *Homo sapiens*

Samples, DNA concentrations and sequencing statistics				
Sample	**Library concentration (ng/uL)**	**Raw reads**	**Merged reads**	**Unmerged reads**
1		229930	207835	13427
2	1.33	10891234	6645351	3515507
3	1.97	6246706	2350350	1541160
4	0.78	3489661	1442287	1084621
5	21.60	8519290	6734539	1723196
6	2.13	6870508	2687355	2536478
Extraction blank	0.31	143069	12746	63161
Library blank	0.30	241653	26917	63789

: nuclear references.

Alignment to nu				
Merged reads mapped to both genomes	Unmerged read1 mapped to both genomes	Unmerged read2 mapped to both genomes	Total reads mapped to both genomes	Reads mapped to both genomes as percent of raw reads
64364	4068	4795	73227	31.85
29871	1233	452723	483827	4.44
63577	301	458214	522092	8.36
20322	320	291904	312546	8.96
3067519	484481	524566	4076566	47.85
50336	315	489462	540113	7.86
472	10	56866	57348	40.08
3214	12	56146	59372	24.57

clear genomes of *R. rattus* and *H. sapiens*

Merged reads mapping to *R. rattus* only	Unmerged read1 mapping to *R. rattus* only	Unmerged read2 mapping to *R. rattus* only	Total reads mapped to *R. rattus* genomes	Reads mapped to *R. rattus* as percent of raw reads	Total unique reads mapping to *R. rattus* genome
64094	4060	4748	72902	31.71	63266
16020	1102	450759	467881	4.30	12639
16330	203	456362	472895	7.57	5054
7347	255	290631	298233	8.55	3324
3059585	483946	523471	4067002	47.74	2982497
14909	269	487735	502913	7.32	5527
162	—	—	162	0.11	132
960	—	—	960	0.40	534

		Alignment to *R. rattus* mitogenome			deNovo mitogen
Total unique reads mapping to *R. rattus* genome with mapping quality ≥25	**Endogenous portion of the samples (column Q as percentage of raw reads)**	**Unique reads mapping to *R. rattus* mitochondrial genome at MQ≥25**	**Extent of coverage of mitochondrial genome**	**Average coverage depth of mitochondrial genome**	**Average coverage depth of mitochondrial genome**
58112	27.96	111	34.39	0.47	1.66
10154	0.15	12	0	0	0
3258	0.14	1	0	0	0
2092	0.15	1	0	0	0
3456831	51.33	3811	84.58	21.37	26.78
3670	0.14	0	0	0	0
73	—	0	0	0	0
297	—	0	0	0	0

ome assembly
Missing sites
9167
0
0
0
23
0
0
0