Where the wild things were: intrinsic and extrinsic extinction predictors in the world's most depleted mammal fauna

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Abstract. Preventing extinctions requires understanding macroecological patterns of vulnerability or persistence. However, correlates of risk can be non-linear, within-species risk varies geographically, and current-day threats cannot reveal drivers of past losses. We investigated factors that regulated survival or extinction in Caribbean mammals, which have experienced the globally highest level of human-caused postglacial mammalian extinctions, and included all extinct and extant Holocene island populations of non-volant species (219 survivals or extinctions across 118 islands). Extinction selectivity shows a statistically detectable and complex body mass effect, with survival probability decreasing for both mass extremes, indicating that intermediate-sized species have been more resilient. A strong interaction between mass and age of first human arrival provides quantitative evidence of larger mammals going extinct on the earliest islands colonized, revealing an extinction filter caused by past human activities. Survival probability increases on islands with lower mean elevation (mostly small cays acting as offshore refugia) and decreases with more frequent hurricanes, highlighting the risk of extreme weather events and rising sea levels to surviving species on low-lying cays. These findings demonstrate the interplay between intrinsic biology, regional ecology and specific local threats, providing insights for understanding drivers of biodiversity loss across island systems and fragmented habitats worldwide.

Keywords: Caribbean, extinction risk, Holocene, island extinctions, late Quaternary, West Indies

1. Introduction

Establishing the factors associated with variation in species vulnerability or survival is a key goal for conservation science, both to inform practical management and to predict future extinctions [1, 2]. Large-scale macroecological analyses incorporating data on current-day mammalian species biology, ecology, and phylogenetic relationships have identified intrinsic and extrinsic correlates of extinction risk associated with anthropogenic pressures, which can interact to generate extensive and synergistic variation across species and geographic regions [3]. Body mass in particular shows a strong positive correlation with extinction risk, as larger-bodied species are disproportionately exploited by humans and tend to have lower population densities and intrinsic rates of increase [4, 5]. However, more complex patterns of body mass selectivity associated with differential risk have also been proposed. Recent global analyses have suggested that risk is higher for both the largest and smallest vertebrates [6], whereas at a regional scale, Australian mammals of intermediate body mass (within a proposed "critical weight range" of 35 g-5.5 kg) have been suggested to show elevated extinctions and declines due to increased predation by invasive species [7]. However, in both cases varying survivorship of intermediate-sized species has been challenged [8, 9], for example with Australian mammal size-selectivity possibly varying instead with species ecology and local environmental conditions [10, 11].

Although most extinction risk analyses have been conducted at the species-level, risk can vary substantially across a species' range because of geographic variation in environmental conditions or anthropogenic pressures [12, 13]. Most studies have also focused only on extant species or populations and are thus limited by an "extinction filter" which excludes taxa that are already extinct due to past human activities, potentially providing only incomplete or biased insights into predictors of decline and

extinction [14]. There is increasing recognition of the need to incorporate historical baselines of past biodiversity and faunal turnover, available from long-term environmental archives such as the archaeological and recent fossil records, into analyses of extinction dynamics and conservation planning [15, 16].

The insular Caribbean (the Greater and Lesser Antilles and Bahamian Archipelago) is one of the few "oceanic-type" (non-continental shelf) island groups colonized by numerous land mammal lineages, and had a diverse late Quaternary non-volant fauna including megalonychid sloths, primates, eulipotyphlan insectivores, and caviomorph and muroid rodents [17, 18]. However, this region experienced the world's highest level of mammalian extinctions during both the Holocene and the post-1500 CE historical period [18-21]. Only 13 species (11 rodents, two eulipotyphlans) probably survive today, most of which are threatened [19] and are recognized as global conservation priorities based upon evolutionary history [22]. Whereas a few species might have become extinct during the Pleistocene, and radiometric data to determine species-specific extinction chronologies remain relatively limited, representatives of all groups definitely survived into the Holocene [18]. Recent assessments recognize 55 extinct non-volant Holocene species, extinct taxa continue to be described from the region's rich paleontological and zooarchaeological records, and extinct island populations potentially representing additional species still await formal description (electronic supplementary material, table S1). Sixteen Caribbean bat species have also become extinct [18, 23]. Hunting, landscape transformation, and invasive mammal introduction by successive waves of colonists following human arrival ~6000 years ago are considered the primary drivers of Caribbean mammal loss [18, 20]. The Caribbean is therefore a global priority area for researching mammalian extinction dynamics, with wider implications for making hypotheses about human-caused extinction risk [24].

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Previous research into Caribbean extinctions has focused on establishing last-occurrence dates for extinct species, and correlating these dates with the timing of different historical threat processes [18, 21]. However, in addition to ongoing problems with preservation of organic biomolecules for radiometric dating in tropical environments, this approach can be confounded by the complexity of recognizing cause and effect in systems that have experienced multiple stressors, whereby populations might experience protracted declines to extinction following the appearance of particular threats, and with extinction drivers potentially interacting synchronously or synergistically [25]. Although Caribbean mammal body masses spanned several orders of magnitude, all surviving non-volant species fall within a range of $c.$0.5-3.0 kg; this pattern has prompted the 'Goldilocks Hypothesis', which suggests that intermediate-sized species were large enough to be resilient to invasive mammals yet small enough to be resilient to human offtake, and so their size was 'just right' [26]. However, fauna-wide patterns of vulnerability and survival in relation to biological parameters have not been investigated across Caribbean mammals within a rigorous statistical and phylogenetically explicit framework; it is possible that this pattern of survival is instead random with respect to body mass, as the region's late Quaternary fauna consisted of more intermediate-sized species to begin with [18]. Huge variation also exists across different Caribbean islands in extrinsic environmental conditions, levels of natural perturbation, and magnitude and duration of direct and indirect anthropogenic impacts (e.g. human population density, habitat conversion, introduction of invasive predators), all of which might further regulate local biodiversity loss or persistence [1, 27, 28]. Whether regional human activities caused rapid extinction of naïve island faunas, or whether colonists instead coexisted with now-extinct taxa for lengthy periods, is also

debated [29]. Extinction patterns in the Caribbean mammal fauna therefore require critical evaluation across both space and time.

To understand key factors that regulate mammalian survival or extinction in response to human activity through time, we conducted fauna-wide investigation of intrinsic and extrinsic correlates of risk across the diverse non-volant Caribbean land mammal fauna, while accounting for phylogenetic non-independence in the data. To overcome the extinction filter effect, we incorporated a historical baseline and included all Holocene representatives of this fauna in our analyses. We also conducted analyses considering separate island populations of the same species as having varying potential survivorship trajectories that could be influenced by differing island conditions. Our findings provide new insights into the relationships between extinction risk, body mass and environmental conditions, and the contribution of both biological and external factors to species vulnerability or survival, with important predictive implications for regional and global conservation.

2. Material and Methods

(a) Data collection

We compiled a dataset containing 219 records of non-volant mammal species survival or extinction across 118 Caribbean islands, representing 67 described species, 11 described subspecies, and 11 currently undescribed island populations (potentially distinct species/subspecies) (figure 1; electronic supplementary material, table S1). We excluded non-oceanic Caribbean islands associated with the South American continental shelf, which are characterized by continental biotas (e.g. Aruba, Bonaire, Curaçao, Margarita, Tobago, Trinidad). Some extinct Caribbean mammal populations (e.g. of *Geocapromys ingrahami* and *Isolobodon portoricensis*) represent prehistoric

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Amerindian-mediated translocations to islands outside their native range, but are inferred to have become established as wild populations and so represent comparable extinction records [30, 31]; however, we excluded extant populations that have recently been translocated to new islands, often for conservation management [19, 32]. We also excluded *Amblyrhiza inundata* and *Puertoricomys corozalus*, which are inferred to have become extinct before the Holocene [18]. Extinction status was defined in two ways: (i) binary (0=extinct, 1=extant), with species listed as Critically Endangered (Possibly Extinct) by ref. 19 considered extant; (ii) ranked (0-4), where 0=extinct, pre-European (no good evidence for survival until close to European arrival); 1=extinct, last-occurrence date close to European arrival ~CE 1500 (evidence from direct/indirect ^{14}C dates, probabilistic statistical analysis, historical observation, or archaeological context post-dating CE 1000); 2=extinct, 19th century onwards (historical observation); 3=extant, threatened; 4=extant, non-threatened (categories 3 and 4 based on ref. 19 or population-specific information reported in literature).

We compiled body mass data for extant taxa using published direct measurements, and for extinct taxa using: (i) published estimates calculated using predictive regression equations based on skeletal measurements; (ii) estimates newly calculated for this study using published regression equations for different taxonomic groups and published or newly measured skeletal morphometric data; (iii) genus-level means from the PanTHERIA database [33]; or (iv) imputation whereby the posterior mean of missing observations were used to replace missing data in the predictors. For *Isolobodon portoricensis*, we calculated one body mass estimate for its native population (Hispaniola and associated islands) and a separate estimate for all introduced populations, which are known to have been larger possibly due to domestication [30]. For other taxa with multiple island populations, we calculated mean estimates for

populations lacking specific body mass data using all available population-specific estimates (electronic supplementary material, table S2).

For each island, we calculated area, maximum and mean elevation, proportional forest cover in 2000 relative to island area, and two metrics of human environmental impact: proportional forest loss in 2000-2014 relative to cover in 2000, and mean Human Footprint Index (HFI) [34]. We sourced island spatial data from GADM [35], and calculated areas using WGS 84 World Mercator (ESPG:3395)-projected GADM shapefiles in QGIS v.2.16.2 [36]. All further geospatial analyses were conducted in R v.3.2.5 [37]. We calculated maximum and mean island elevation across all intersecting pixels in WGS 84 World Mercator-projected Shuttle Radar Topography Mission Digital Elevation Model data (30m resolution; downloaded from https://earthengine.google.com) [38]. We used 30m resolution datasets of percentage forest cover (2000) and pixel-specific forest loss (2000-2014) [39]. We cropped a mosaicked WGS 84 World Mercator-projected forest-cover raster to the GADM boundaries of each island and extracted total forest cover (km^2) by multiplication of pixel area by pixel-specific percentage forest cover. We extracted forest cover loss by multiplying pixel area by pixel-specific percentage forest cover for all pixels identified as deforested by 2014 (forest cover loss 2000-2014 raster pixel value=1) [39]. We also collected island-specific data on the following additional variables: presence/absence of active Holocene volcano (http://www.volcano.si.edu/, http://caribbeanvolcanoes.com); hurricane frequency (number of tropical systems passing within 60 nautical miles of island from 1851-2011, with mean values used for islands with multiple reported values: http://stormcarib.com/climatology/); presence/absence of introduced mongoose [17]; and date of first human arrival [18]. It was not possible to obtain all values for all islands (table 1; electronic supplementary material, table S1).

(b) *Statistical analyses*

Analyses were conducted in R v.3.6.2 [37]. We investigated covariates of mammalian

population survival probability (species traits and island variables) using our two

measures of extinction status as response variables in different analyses (table 1). To

test the Goldilocks Hypothesis, we first scaled log_{10}-transformed mass values, which

made mass center on 0 with a standard deviation of 1, and then squared these values.

This made all mass^2 values positive, with both low and high mass extremes having

higher and positive values. To investigate the potential for multicollinearity among

island predictors, we calculated correlation coefficients on variables for individual

islands using the *cor* and *cor.test* routines in R. Although low correlation coefficients can

distort inference [40], we adopted a cut-off of absolute 0.70 for significant correlation

coefficients (i.e. $R^2 \cong 0.50$) for excluding collinear predictors. This cut-off partially reflects

the robustness of Bayesian regression to imperfectly collinear predictors compared to

approaches based on null hypothesis-testing [41].

We employed a hierarchical Bayesian approach to simultaneously estimate

coefficients for species and island covariates; we use the terms "cluster-specific" instead

of "random" and "sample-wide" instead of "fixed" to avoid confusion [42]. Following refs

43 and 44, we modelled each observation *i* (i.e. a mammal population on a particular

island) as a single-trial binomial response of the probability of survival by island given

by pr_i such that:

$$y_i \sim dbern(pr_i)$$

$$logit(pr_i) = \beta_0 + \beta_1 X_i + b_0 + b_1 X_{species} + b_{islands}$$

Wherein β_0 and β_1 are sample-wide effects. Independent species-specific intercepts

are given by:

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$$b_0 \sim Gaussian(0, \sigma_0^2 I_{species})$$

Species-specific effects on predictor variables x assumed to depend on the phylogenetic variance-covariance matrix $V_{species}$ are given by:

$$b_1 \sim Gaussian(0, \sigma_0^2 V_{species})$$

And independent island-specific intercepts are given by:

$$b_{islands} \sim Gaussian(0, \sigma_2^2 I_{islands})$$

As the binomial distribution has no error associated with observations, we did not specify a Gaussian error term in this model [45]. We used an automated complexity-penalizing prior-setting procedure to set priors [46].

Many Caribbean mammal species are included in the recent phylogeny of ref. 47, from which we randomly sampled 100 published trees to account for phylogenetic uncertainty (downloaded from http://vertlife.org/phylosubsets/). Some species, including all undescribed taxa (n=42), were missing, so were grafted to these trees inside taxonomic constraints using *bind.tip* in the R package phytools [48] followed by *multi2di* in the R package ape [49]. Arbitrarily short branch lengths of 0.0001 were added to the resolved polytomies of the grafted internodes to meet Bayesian model assumptions. We pruned the trees to match the dataset and used them as inputs in phylogenetic regressions.

We used an approximate Bayesian approach to accommodate the hierarchical data structure (i.e. individual observations cluster by species *and* by islands) and phylogenetic uncertainty in relationships among species (electronic supplementary material, text S1). We employed the Phylogenetic Generalized Linear Mixed Model for Community Data (*pglmm*) routine implemented in the R package phyr [50], which uses integrated nested Laplacian approximations implemented in the INLA package [51]. INLA enables estimation of coefficients despite missing values for individual responses,

and imputation of covariate values using the posterior means of missing covariates from an initial model [52]. We first implemented a model including all covariates and missing data with a single phylogeny. We then included the posterior means of missing covariates or imputed values into the predictors and reran the model. Next, we ran three sets of models across the sample of 100 trees: (1) all covariates and missing data; (2) only those covariates with posterior coefficients excluding 0 and missing data; (3) same as 2 but with imputed data.

To summarize results across models with variance-covariance structures from each of the 100 trees, we extracted summaries of the posteriors of sample-wide coefficients as well as independent species-specific (b_0) and island-specific ($b_{islands}$) intercepts comprising the median and 95% high-probability intervals (from 2.5% to 97.5% of the posterior marginals). We summarized variation by computing medians of summary values across all sampled phylogenies.

3. Results

Observed or estimated Caribbean mammal body masses varied by several orders of magnitude (for all described species and undescribed island taxa: mean=8.59 kg; range=0.01–101.5 kg; SD=20.98). Islands varied between 0.05 and >123,000 km^2 in area, between 3 and >3000 m in maximum elevation, and between <1 and 406 m in mean elevation. Our dataset included 32 species with >1 island population; most of these had only 2 (n=17) or 3 (n=8) populations, but three species had many more populations (*Capromys pilorides*, n=71 with 8 extinct; *Geocapromys ingrahami*, n=15 with 14 extinct; *Isolobodon portoricensis*, n=14 with all extinct). Multicollinearity estimates revealed mean elevation was strongly positively correlated with mongoose presence (r = -0.71, p<0.001) and with maximum elevation (r = 0.93, p<0.001), and the

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latter was also positively correlated with island area (r = 0.74, p<0.001) (electronic supplementary material, figure S1). We excluded maximum elevation from further analyses, and ran models including either mean elevation or mongoose presence to explore the relative effect of each variable; we present results below for models that included mean elevation (continuous variable) instead of mongoose presence (binary variable).

We implemented both binary and ordinal extinction response models, but only binary models (population = extinct/extant) could recover sufficient signal to estimate non-zero covariate coefficients. Species traits and island variables were both associated with differential population survival, and the intercept indicates that survival probability for the average Caribbean land mammal is very low (figures 2-3, table S3). Results for body mass were similar in analyses based on imputed and non-imputed data: body mass was mostly positively correlated with survival probability but the coefficient of square mass was always negative, indicating that smaller and larger mammals both had lower survival probabilities than intermediate-sized mammals (figure 3, table S3). This effect was compounded by the negative coefficient on the interaction between mass and time of human arrival; greater age of human colonization events elevated extinction risk in an increasing, mass-dependent manner. Using these estimated coefficients, we infer a highest mass-dependent survival probability of ~25% between 1.4-3.6 kg, but only for the most recently colonized islands. For mammals on islands with the oldest histories of colonization, survival probability peaks at only 0.38% and ~2 kg, with a 4.7% peak in survival probability for species on islands colonized at the archipelago-wide median (figure 3).

Conversely, results for sample-wide island covariates differed among analyses. Mean island elevation and the interaction between age of human colonization and mass

were always negatively correlated with survival probability, but hurricane frequency was negatively correlated with survival probability in the all-data models only (figures 2-3, table S3). Mongoose presence was not correlated with survival probability in models that excluded mean island elevation (results not shown). No species-specific or island-specific intercepts were different from zero in any analysis.

4. Discussion

Our study provides the first quantitative investigation of intrinsic and extrinsic extinction risk predictors in a diverse mammal fauna that has experienced the world's greatest number and proportion of postglacial losses. While most extinction risk analyses focus on the species level, we conducted our analyses at a population level to account for variation in vulnerability with differing environmental conditions between islands. This enabled us to test longstanding but hitherto unquantified hypotheses about the interactions between species traits and island characteristics. To overcome potential biases in interpretation of risk associated with extinction filters, we also incorporated information on both extant and extinct populations by integrating ecological, archaeological, and paleontological datasets. By applying techniques from phylogenetic community ecology, we then modeled species and their traits within islands as 'communities' with island-level covariates. This comprehensive approach represents a technical innovation in macroecology and extinction research, and provides insights for understanding drivers of biodiversity loss across island systems and fragmented habitats worldwide.

Caribbean mammal extinction selectivity shows a significant and complex body mass effect, with both mass extremes negatively correlated with survival probability across all models. We therefore confirm the 'Goldilocks Hypothesis' proposed for the

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Caribbean non-volant mammal fauna [26]. Instead of survivorship representing a random subset of the pre-human fauna, or a probabilistic outcome of extinctions in a fauna containing more intermediate-sized species, we demonstrate that Caribbean medium-bodied rodents and solenodontid eulipotyphlans have been less sensitive to extinction compared to their smaller and larger non-volant counterparts.

It is challenging to investigate the influence of specific life-history or ecological parameters because such traits cannot be inferred confidently for many extinct Caribbean species, most of which were only distantly related to living species [53-54]. However, body mass is strongly correlated with many key traits such as home range and reproductive rate [55, 56], and is thus a useful proxy for understanding broader patterns of intrinsic risk. Bats were not included in our analyses because their ecology differs radically from that of non-volant land mammals; most bats exhibit slow life histories, but their large ranges and long dispersal distances reduce extinction risk compared to other mammals [57]. While our analyses thus exclude the lowest end of the mammalian mass range, future studies can model taxon-specific differences in risk between volant and non-volant species using our approach.

Global analysis of vertebrate extinction risk suggests the largest species are mostly threatened by direct overexploitation, while the smallest species are more vulnerable because they may have restricted ranges threatened by habitat degradation [6]. However, this global model is unlikely to explain increased vulnerability of Caribbean small mammals because island area (a proxy for range) has no effect in predicting extinction risk, and many of the smallest Caribbean species (nesophontid island-shrews, heteropsomyine rodents) were distributed widely across the largest islands [58]. Unfortunately it is difficult to compare our Caribbean data directly with patterns of mammalian extinction vulnerability and survival for many other insular systems, given

the ongoing lack of Quaternary baseline data to enable reconstruction of former regional species diversity and loss [59, 60]. However, variation in Caribbean mammal vulnerability with respect to mass differs from patterns in some other heavily depleted insular mammal faunas for which historical baselines are available, such as Flores rodents [61], Madagascar mammals [62] or "island-continent" Australian mammals [7, 8], and represents a region-specific response to particular anthropogenic threats.

Ecological attributes such as arboreality are associated with lower risk in Australian mammals [10], and all surviving Caribbean rodents exhibit varying degrees of arboreality, although several probably arboreal species (e.g. primates, smaller sloths) are now extinct [63]. Other comparisons between Australian and Caribbean faunas highlight the varying interplay between intrinsic biology, regional ecology, and different threats. Australia has numerous native murid rodents including native *Rattus* species, and its native fauna is threatened by invasive feral cats and foxes, which prey on relatively large-bodied native species. The smallest Australian mammals are considered more resilient to these invasive predators because of higher population growth rates [7]. In contrast, the Caribbean fauna lacks native murids and its biodiversity is threatened by invasive murids, notably black rats (*Rattus rattus*), as well as mongooses [19], and the timing of rat and mongoose introduction is closely correlated with last-sighting dates for several now-extinct small Caribbean mammals [21, 64]. Interestingly, mongoose presence/absence did not correlate with survival probability in our models, possibly because mongooses are present not only on islands that have lost their native mammals, but also on larger islands that retain surviving species (Cuba, Hispaniola, Jamaica). Comparative investigation of mongoose and native mammal distributions at higher spatial resolutions across island landscapes may therefore be required to assess their impact. Unfortunately, other specific invasive mammals could not be included in

our analyses; island presence/absence data are patchy for most species, and black rats are now ubiquitous across the region, so minimal across-island variation exists to detect an effect using our approach.

Although some threatened Caribbean mammals survive today only in mountain regions (e.g. *Solenodon cubanus*; [32]), our analyses show mammals were more likely to survive on islands with lower mean elevation. This finding contradicts studies of environmental risk correlates in other systems, which typically show persistence in high-elevation refugia where anthropogenic habitat conversion or hunting are reduced [13, 65]. Our contrasting results are likely driven by numerous extinctions on Hispaniola, the highest-elevation island, and the survival of several populations on low-elevation cays in Cuba and the Bahamas [19, 32]. Many other threatened or now-extinct species in other regions also survived longest as remnant populations on small islands on the periphery of their former ranges [12, 66]. While finer-scale within-island analyses demonstrate the importance of higher elevations for persistence of some (but not all) surviving mammals on larger Caribbean islands [67], our results emphasize the importance of low-elevation offshore refugia for conservation of Caribbean mammals and other regionally endemic vertebrates [68].

Hurricane frequency was negatively correlated with survival probability in our full model, highlighting a further important factor for regional conservation. Caribbean biodiversity has evolved in a system regularly impacted by hurricanes, suggesting that its biota might be resilient to perturbation [14]. However, the effects of such extreme events are exacerbated by habitat fragmentation and in declining populations vulnerable to stochastic impacts [28]. Multiple drivers may therefore have acted synergistically in this system, with faunas on hurricane-prone islands inherently less resilient when perturbed by other factors. Tropical storms are now increasing in

frequency and intensity [69], with several range-restricted Caribbean mammals occurring in landscapes recently impacted by severe hurricanes (e.g. Massif de la Hotte, Haiti; [70]). Low-lying cays identified in our analyses as high-priority sites for surviving species are at increased risk of inundation by storm surges and rising sea levels [71]. Our results highlight the importance and urgency of increasing resilience to extreme weather events, for example by establishing voucher populations for surviving taxa, and assessing population vulnerability to such events [28].

While body mass, elevation and hurricane frequency were important survival covariates, other potential indicators of human activity and environmental disturbance were not statistically associated with risk. For volcanic activity, few replicates limiting sample size and leading to wide credible intervals may explain this result. However, the Human Footprint Index and both forest cover and loss showed negligible coefficients despite region-wide data being available, such that greater statistical power is unlikely to yield strong links with risk, unlike relationships observed in other systems [1, 72]. Although investigation of finer-scale environmental parameters and associated impacts might provide additional insights (e.g. habitat structure; [73]), recent human activities thus appear less important in determining Caribbean mammal extinctions compared to ecological properties of this system. Interestingly, forest cover shows a strong negative correlation with time since first human arrival, corroborating a pattern of land-use transformation documented in archaeological studies [74]. Nevertheless, present-day forest cover or its recent loss dynamics may have little relationship to regional land-use changes or human population densities that affected biodiversity in past centuries or millennia [75, 76].

Whereas systematic data on the regional distribution and intensity of past human activities are unavailable, the anthropogenic causation of past Caribbean extinctions is

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clearly demonstrated by the negative interaction between age of human colonization and species body mass. Available evidence for prehistoric hunting of larger Caribbean mammals (sloths, primates, giant rodents) is limited [30], but these species may have been particularly vulnerable to fire-driven habitat change, and even occasional harvesting could have been unsustainable for slowly-reproducing populations [18]. In contrast, many smaller species might have only become vulnerable with the later introduction of invasive mammalian competitors and predators [21, 26, 77]. As these introductions occurred relatively recently, our model predicts their extinction risk through the square mass variable. Thus, through this interaction term, our models capture the earlier regional extinction of larger species [18] in a systematic manner.

By considering both intrinsic traits and extrinsic extinction drivers, our results have important implications for mammal conservation in the Caribbean and beyond. The vulnerability of island faunas to anthropogenic stressors is well-established [5, 20], but the complex influence of body mass on risk and its potential to interact with site-specific extinction drivers are novel findings. In contrast with traditional overexploitation models that predict risk directly scaling with mass, the additional signal of elevated risk for small-bodied Caribbean species highlights the importance of controlling invasive species to conserve surviving endemics. The strong signal of hurricane frequency in our models further indicates that future risk from climate change (especially for low-lying cays) is greater than implied by island size alone. While neither area nor forest cover indices were associated directly with risk, corridors and habitat restoration will likely become necessary to build environmental resilience as hurricanes increase in intensity and frequency, alongside targeted protection of key Caribbean mammal habitats such as mangroves and intact montane forests. Novel emerging anthropogenic threats may provide further unexpected pressures on

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surviving Caribbean mammals, making it uncertain whether the region's surviving medium-bodied rodents and solenodons will remain resilient to human-caused extinction into the future. Nevertheless, Holocene extinctions dating back to prehistoric human arrival thus provide an invaluable new context and perspective to help inform conservation of island mammals in the Anthropocene.

Data accessibility. All datasets are available in the electronic supplementary material. All code, phylogenies and models are available online at https://github.com/n8upham/CaribbeanExtinctions-WTWTW.

Authors' contributions. S.T.T. and L.M.D. designed research; S.T.T. and C.D. collected data; L.M.D., N.S.U., X.H., C.D. and S.T.T. interpreted and analysed data; and S.T.T. and L.M.D. wrote the paper with support from other authors.

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Table 1. Covariates included in analyses and their transformations.

Covariate	Level	Transformation
Body mass	species	$\log_{10}$ and scale
Body mass^2	species	$\text{mass}_{\text{transformed}}^2$
Island area	island	$\log_{10}$ and scale
Mean island elevation	island	$+1$, $\log_{10}$ and scale
Maximum island elevation	island	$\log_{10}$ and scale
Forest cover (2000)	island	scale
Forest loss (2000–2014)	island	$\log_{10}$
Human Footprint Index	island	none
Active volcano	island	none, binary
Hurricane frequency	island	scale
Mongoose presence/absence	island	none, binary
First human arrival	island	/1000

Figure 1. Caribbean islands with Holocene–Recent terrestrial non-volant mammal populations. **Main map,** 1: Cuba; 2: Little Swan Island; 3: Grand Cayman; 4: Little Cayman; 5: Cayman Brac; 6: Jamaica; 7: North Andros; 8: South Andros; 9: New Providence; 10: Great Abaco; 11: Eleuthera; 12: Cat Island; 13: San Salvador; 14: Great Exuma; 15: Little Exuma; 16: Long Island; 17: Samana Cay; 18: East Plana Cay; 19: Crooked Island; 20: Acklins; 21: Ragged Island; 22: Middle Caicos; 23: Hispaniola; 24: Ile de la Gonâve; 25: Ile de la Tortue; 26: Beata; 27: Isla de Mona; 28: Puerto Rico; 29: Vieques; 30: Water Island; 31: St. Croix; 32: St. Thomas; 33: Jost Van Dyke; 34: Guana; 35: Tortola; 36: St. John; 37: Anguilla; 38: Tintamarre; 39: St. Martin; 40: Saba; 41: Sint Eustatius; 42: St. Kitts; 43: Nevis; 44: Barbuda; 45: Antigua; 46: Montserrat; 47: Guadeloupe; 48: La Désirade; 49: Marie-Galante; 50: Martinique; 51: St. Lucia; 52: St. Vincent; 53: Barbados; 54: Carriacou; 55: Grenada. **Inset map,** 1: Cuba; 2: Cayo Juan García; 3: Cayo Real; 4: Isla de la Juventud; 5: Cayo Grande; 6: Cayo El Calvario; 7: Cayo Diego Pérez; 8: Cayo Matias; 9: Cayo Hicacos; 10: Cayo Campo; 11: Cayo Ávalos; 12: Cayo Cantiles; 13: Cayo Rosario; 14: Cayo de la Piedra; 15: Cayo Estopa; 16: Cayo Peraza; 17: Cayo Rico; 18: Cayeria Los Majáes; 19: Cayo Largo del Sur; 20: Cayo Alcatraz; 21: Cayo Bretón; 22: Cayo Cinco Balas; 23: Cayo Alcatracito; 24: Cayo Caballones; 25: Cayos Salinas; 26: Cayo Balandras; 27: Cayo Punta Arenas; 28: Cayo Algodón Grande; 29: Cayo Anclitas-Miraflores; 30: Cayo Piedra Chica; 31: Cayo Piedra Grande; 32: Cayo Las Cruces; 33: Cayo Boca Chica; 34: Cayo Largo; 35: Cayo Juan Grín; 36: Cayo Camposanto; 37: Cayo Las Varas; 38: Cayo Los Chinos; 39: Cayo La Cafetera; 40: Cayo Cotorro; 41: Cayo Caguama; 42: Cayo Cabeza del Este; 43: Cayo Jia; 44: Cayo María Valache; 45: Cayo Guasa; 46: Cayo Macío; 47: Cayo Romero; 48: Cayo Mono; 49: Cayo Blanco; 50: Cayo Macho; 51: Cayo Cruz del Padre; 52: Cayo Mono-Galindo; 53: Cayo Boca Rompida; 54: Cayo Cinco Leguas; 55: Cayo Juan Clarito; 56: Cayo Fragoso; 57: Cayo Lucas; 58: Cayo Frances; 59: Cayo Las Brujas; 60: Cayo Ensenacho; 61: Cayo Santa María; 62: Cayo Guillermo; 63: Cayo Coco; 64: Cayo Romano; 65: Cayo Sabinal; 66: Cayo Ballenatos; 67: Cayo Saetia.

Figure 2. Posterior estimates and high-probability intervals for sample-wide model coefficients including all non-collinear predictor variables.

Figure 3. Survival probability as function of body mass for islands at the most recent quartile (recent), median (intermediate), and top quartile (ancient) of first human arrival, with all other predictors corresponding to their sample means. Bottom ticks show species body masses. Species silhouettes from www.phylopic.org (credits: T. Michael Keesey after Monika Betley; Natasha Vitek; Zimices).