Recent extinctions disturb path to equilibrium diversity in Caribbean bats

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Islands are ideal systems to model temporal changes in biodiversity and reveal the influence of humans on natural communities. Although theory predicts biodiversity on islands tends towards an equilibrium value, the recent extinction of large proportions of island biotas complicates testing this model. The well-preserved subfossil record of Caribbean bats—involving multiple insular radiations—provides a rare opportunity to model diversity dynamics in an insular community. Here, we reconstruct the diversity trajectory in noctilionoid bats of the Greater Antilles by applying a dynamic model of colonization, extinction and speciation to phylogenetic and palaeontological data including all known extinct and extant species. We show species richness asymptotes to an equilibrium value, a demonstration of natural equilibrium dynamics across an entire community. However, recent extinctions—many caused by humans—have wiped out nearly a third of island lineages, dragging diversity away from equilibrium. Using a metric to measure island biodiversity loss, we estimate it will take at least eight million years to regain pre-human diversity levels. Our integrative approach reveals how anthropogenic extinctions can drastically alter the natural trajectory of biological communities, resulting in evolutionary disequilibrium.

Whether species diversity is dominated by equilibrium dynamics or is fundamentally non-equilibrial is a crucial, currently unresolved question in biodiversity and conservation research[1,2]. According to equilibrium explanations, biodiversity asymptotes to a constant value[3,4], while under non-equilibrium models species richness has no upper bound[1,2]. The equilibrium theory of island biogeography[5] favours an equilibrium model for diversity on islands, but the potential confounding effect of Quaternary extinctions has been a key obstacle to testing this model[6]. Insular species have evolved in isolation and have proved vulnerable to both Pleistocene climate change[7] and human activities, including the introduction of non-native species, habitat destruction and exploitation[8,9]. As a result, many islands have lost large portions of their biota during the Quaternary and especially following human colonization[10]. By failing to include extinct species, analyses testing for equilibrium dynamics may overlook critical information needed to calculate natural rates of species accumulation[11,12].

Here, we focus on Caribbean noctilionoid bats (Chiroptera: Noctilionoidea), an ideal group to study insular diversification. First, most bats survived the late Pleistocene and Holocene waves of extinction in the West Indies[8,10,13] that drove over 70% of mammal species extinct[14]. Second, the Antillean noctilionoid bat fossil record is well understood and the phylogeny and divergence dates for extinct taxa are available from recent analyses[15]. Finally, although mammals are poorly represented on islands, bats colonize islands more readily than their non-volant relatives[16]. For example, rodents are approximately twice as diverse as bats globally, but tend to have fewer species on islands[17]. Today the West Indies hosts approximately 70 species of bats, including multiple independent *in situ* radiations of noctilionoids[14].

Current knowledge on Caribbean diversity dynamics is limited[6]. Lineage-through-time analyses of extant lizards found evidence for clade-specific equilibria governed by diversity-dependent speciation[4], but community-wide analyses of Cenozoic mammals[14,18] and divergence dates of Lesser Antillean passerines[19] both supported non-equilibrium. No study to date has modelled dynamics on islands including all known extinct and extant species, and at the same time accounted for the three key processes determining diversity on islands (colonization, speciation and extinction) and the possible influence of diversity on each process (diversity-dependent diversification).

We examine whether equilibrium dynamics govern the noctilionoid bat fauna of the Greater Antilles (GA) by combining molecular phylogenetic and palaeontological data from all known Quaternary species[15]. We focus on the GA (including Cuba, Hispaniola, Jamaica, Puerto Rico and surrounding islands) because their record of Quaternary extinction events is detailed enough to enable quantification of the effects of extinct species on island biogeography[14]. We infer rates of species accumulation in the archipelago by applying DAISIE (dynamic assembly of island biota through speciation, immigration and extinction), a recently developed dynamic stochastic model to estimate rates of accumulation for insular communities resulting from multiple colonization events[20]. We use these estimates to make predictions on the nature of the dynamics (equilibrium versus non-equilibrium).

Results

We extracted colonization and branching times from dated phylogenies for all known species of noctilionoid bats from the GA (Fig. 1). The extant fauna consists of 11 colonist lineages, together comprising 24 species. Our survey of the fossil and subfossil data

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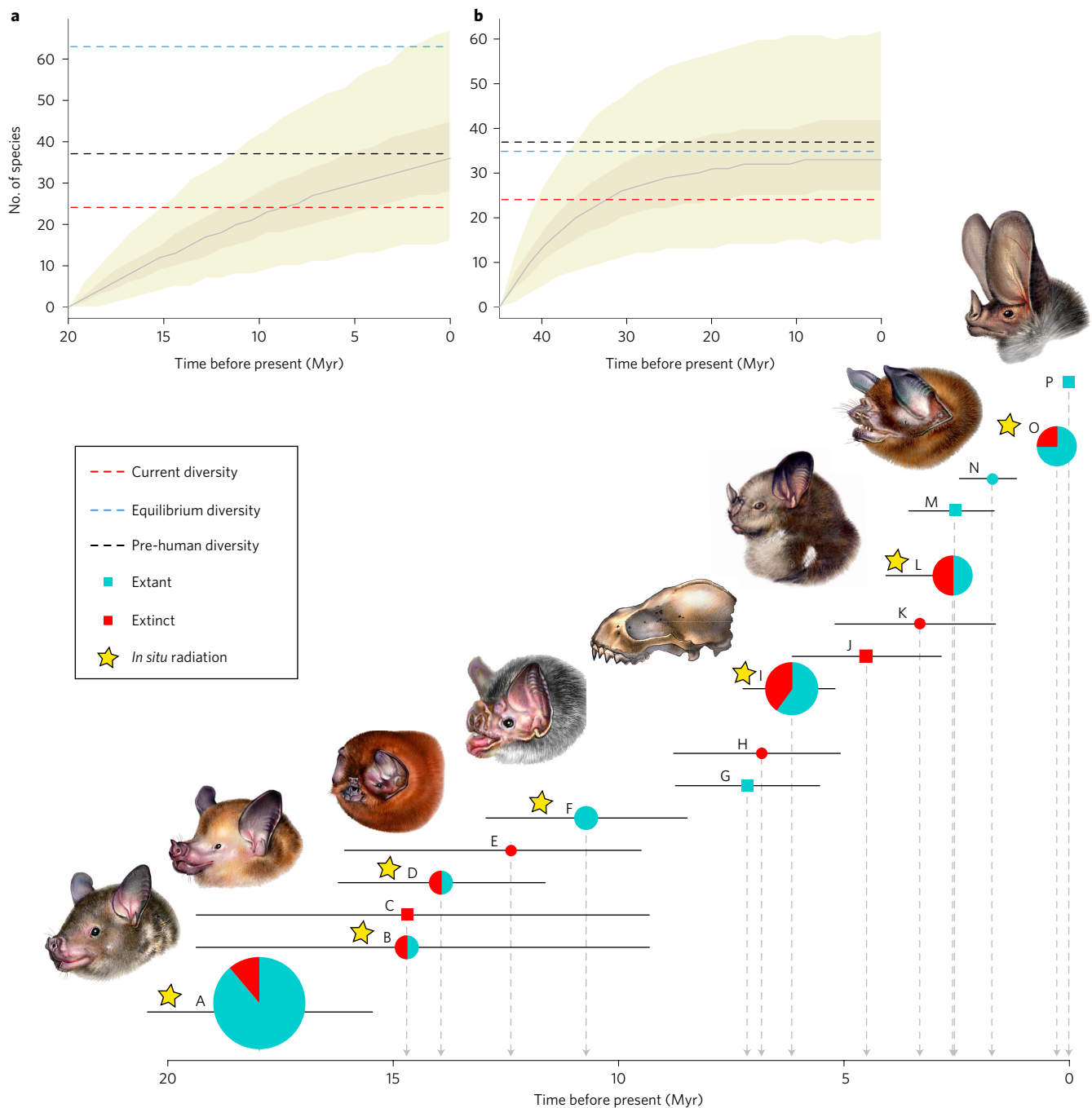
Figure 1 | Quaternary diversity of noctilionoid bats in the GA. Main panel: estimated times of colonization of each independent colonist lineage, in millions of years (Myr) before present (black horizontal lines show 95% CI). Squares, non-endemic; circles, endemic. Sizes of pie charts are proportional to diversity. Letters next to pie charts correspond to codes in Supplementary Table 2. Illustrations show, from left to right (clade in brackets): *Brachyphylla nana* (A), *Erophylla bombifrons* (A), *Mormoops blainvillei* (B), *Desmodus sp.* (E), *Cubanycteris silvai* (H), *Phyllops falcatus* (I), *Pteronotus parnellii* (N), *Macrotus waterhousii* (O). Illustrations by Adrian Tejedor. **a,b,** Diversity-through-time of noctilionoids based on data sets simulated with the DI model. **a,** For $T = 20$ Myr. **b,** For $T = 45$ Myr. Light and dark shaded areas show, respectively, the 2.5–97.5 and the 25–75 percentiles.

revealed 13 species and five whole lineages have gone extinct from the islands (Supplementary Table 1). We identified a total of 16 independent colonist lineages contributing to the Quaternary noctilionoid fauna of the GA, seven of which underwent *in situ* radiations (Supplementary Table 2).

The causes of Quaternary West Indian mammal extinctions are controversial[12]. Although climate change explains shifts in richness[13], radiocarbon dates rejected the climate change hypothesis by showing extirpated Caribbean bat populations persisted after

deglaciation[8,10]. Indeed, analyses of extinct Caribbean bat assemblages revealed the Holocene wave of extinction following human arrival was the most important of several waves of Quaternary extinction on the islands[21]. Together with evidence of landscape transformation following settlement[22], current data strongly point to anthropogenic extinction for the majority of Caribbean taxa. To account for uncertainty in causes of extinction, we considered two alternative scenarios that assumed high (100% of extinction events anthropogenic) and low (3 out of 13 extinction events
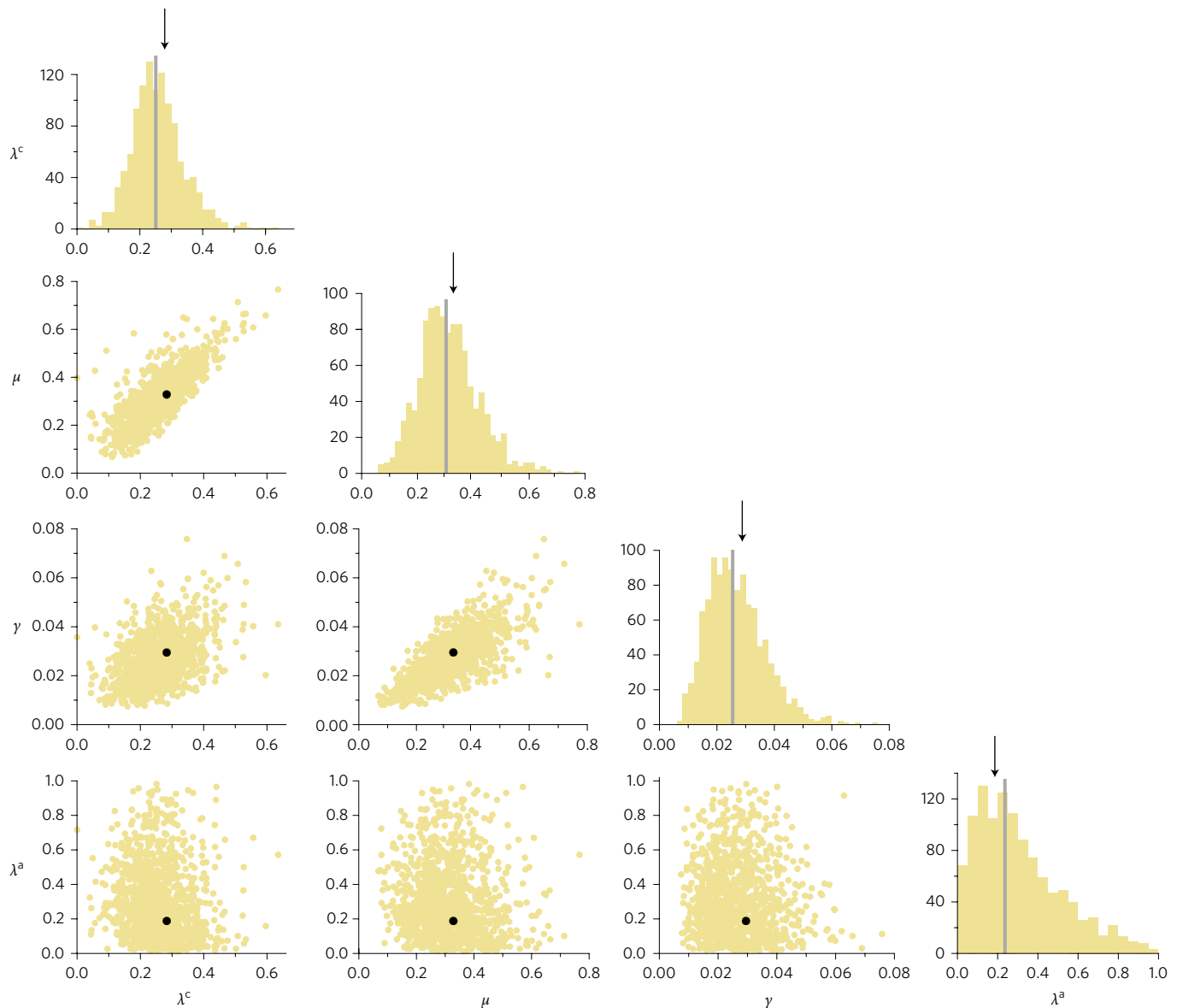
Figure 2 | Bootstrap precision estimates of the parameters of the DI model. Parametric bootstrap analysis fitting the DI model to 2,000 data sets simulated with ML parameters of the DI model. Plots on diagonal are frequency histograms of estimated parameters. Grey lines show the median estimated values across all simulations and the black arrows the simulated values. Scatterplots show relationships between the parameter shown at the start of the row to the parameter below the column. Black dots are the (true) values used in simulations.

(23%) anthropogenic, corresponding to three species that survived into the Holocene[8,21]) human impact. For the high human impact scenario, all 13 extinct species were assumed to be extant. For the low impact scenario, 3 out of 13 extinct species were assumed to be extant. To understand how extinct species affect estimates of speciation, colonization and natural extinction, we analysed a third data set including only extant species (contemporary data set), equivalent to the data typically available to biologists working on groups lacking a preserved or well-described fossil record.

We investigated whether GA noctilionoid bat diversity is inherently equilibrial, that is, whether the diversity of the system tends towards a constant value as time approaches infinity. There are two different ways in which equilibrium in diversity can be achieved: (a) diversity-dependence in the rates of colonization and cladogenesis causes each colonist lineage to tend to a carrying capacity or (b) the rate of extinction exceeds the rate of cladogenesis (in the absence of diversity-dependence), that is the island forms a macroevolutionary sink and would become unpopulated if colonization

ceased[20]. We compared two DAISIE models: a diversity-independent (DI) model and a model with diversity-dependence (DD) in cladogenesis and colonization rates. On the basis of palaeo-ecological reconstructions[18,23], the GA could be as recent as 20 Ma and as ancient as 45 Ma. We fitted models for each date between and including the two extreme values for archipelago age (T) in Myr (Supplementary Fig. 1). Unless otherwise noted, we report the results from the high human impact scenario. Parametric bootstraps revealed that the method performs well in recovering the correct parameter values with very little bias (Fig. 2).

Using a bootstrap likelihood ratio test, we found the DI model could not be rejected and the power of the method to detect DD for this data set was low (Supplementary Fig. 2). The likelihoods of the two models were very similar for all extinction scenarios and archipelago ages (Table 1 and Supplementary Table 3). Because the DI model had one fewer free parameter than the DD model (K', the carrying capacity), we favoured the DI model (Table 1 and Supplementary Table 3). Under the maximum likelihood (ML)

Table 1 | DAISIE analyses of ML parameters of the DI and DD models, for the two different assumed archipelago ages, with $M = 100$ species.

Data set	Archipelago age (Myr)	Model	λ^c	μ	K'	γ	λ^a	LogLik
High human impact	20	DI	0.28	0.33	-	0.030	0.19	−141.97
		DD	0.34	0.34	32	0.028	0.17	−141.76
	45	DI	0.32	0.41	-	0.036	0.16	−143.69
		DD	0.35	0.42	53	0.035	0.14	−143.58
Low human impact	20	DI	0.30	0.34	-	0.020	0.26	−108.17
		DD	0.37	0.35	30	0.019	0.24	−107.93
	45	DI	0.34	0.43	-	0.024	0.24	−109.53
		DD	0.38	0.44	57	0.023	0.22	−109.43
Contemporary	20	DI	0.22	0.26	-	0.017	0.27	−105.88
		DD	0.27	0.26	28	0.017	0.26	−105.74
	45	DI	0.26	0.35	-	0.021	0.27	−107.37
		DD	0.28	0.35	61	0.021	0.26	−107.33

λ^c, per lineage rate of cladogenesis; μ, per lineage rate of extinction; K', carrying capacity; γ, per lineage rate of immigration; λ^a, per lineage rate of anagenesis; LogLik, Log likelihood.

parameters of the DI model the system was inherently equilibrial because the rate of extinction on the islands exceeded the rate of cladogenesis (Supplementary Fig. 3). Because of the low power of the method, we could not rule out DD as a good candidate model to explain these data, but we concluded that if DD is present, it is not detectable. Under DD, the system would also have been inherently equilibrial. Hence, our analyses strongly support an equilibrium model of biodiversity for noctilionoids in the GA; that is, the total number of species through time behaved asymptotically.

Next, we assessed how far from equilibrium the system was before anthropogenic extinctions. Assuming $T = 20$ Myr, total diversity at equilibrium is 63 species and thus pre-human diversity (37 species) was far from equilibrium. This can be seen in the species-through-time plot for this archipelago age (Fig. 1a), which shows diversity had not yet reached a plateau. Assuming $T = 45$ Myr, total diversity at equilibrium is 35 species and pre-human diversity was at or very near equilibrium, as confirmed by the asymptotic shape of the species-through-time plot (Fig. 1b). Regardless of the assumed archipelago age, contemporary diversity (24 species) is below the theoretical equilibrium (Supplementary Fig. 4).

To measure the effect of recent extinctions on the natural diversification dynamics of the system, we introduce a new metric: the time required for island diversity to recover to pre-human levels. This return time provides an estimate of how the removal of species by humans sets back the clock on the natural path to equilibrium. This is the first quantitative method to estimate return times

to natural diversity conditions from phylogenetic data and can serve as a new metric to assess the long-term effects of human-induced biodiversity loss. To estimate future diversity, we developed a set of equations for diversity given a set of DAISIE parameters (see Methods). Assuming the scenario with greatest human impact, for $T = 20$ Myr it would take approximately 8 Myr to regain pre-human endemic species diversity (Fig. 3) and 13 Myr to regain the same number of lineages (Supplementary Fig. 5). Assuming $T = 45$ Myr, it would take over 30 Myr for the community to return to equilibrium diversity values attained before human colonization (Fig. 3 and Supplementary Fig. 5).

Discussion

This study presents the first demonstration of colonization–speciation–extinction equilibrium dynamics for an insular community comprising multiple radiations. Our results provide evidence for the ecological, deterministic regulation of the bat assemblage of the GA. Past evidence for speciation–extinction equilibrium has only emerged from single lineages[4,20] and previous studies have found no evidence for community-wide diversity regulation[20]. Equilibrium models remain controversial[1,2] and the main argument against them on islands is the ever-changing nature of island area and connectivity between landmasses[24,25]. Increasingly, it has become clear that diversity carrying capacities and equilibrium conditions themselves may shift through time[26–28]. Notwithstanding a long history of major geological changes in the region[18,23], the robust fit of the equilibrium model to the noctilionoid data indicates a tendency of this bat community towards a diversity steady state.

The integration of palaeontological and phylogenetic data highlights the extreme extent to which Quaternary extinctions have shaped this Caribbean biota[8,13]. Over a third of species and nearly a third of lineages went extinct from the islands, probably as a consequence of human colonization[8,10,21]. Including extinct taxa in the analysis led to higher speciation, natural extinction and colonization rates than in the absence of this information (Table 1). Models of diversity relying exclusively on extant taxa often lack the data to estimate extinction rates[29]. Our analyses show that underestimating the rate of colonization is another artefact from neglecting the fossil record. This has important implications for island biogeography studies. For instance, previously estimated low turnover dynamics[4] might instead reflect unobserved instances of colonization followed by extinction.

Island diversity increasingly reflects human influence instead of natural biogeographical and macroevolutionary processes[30], but
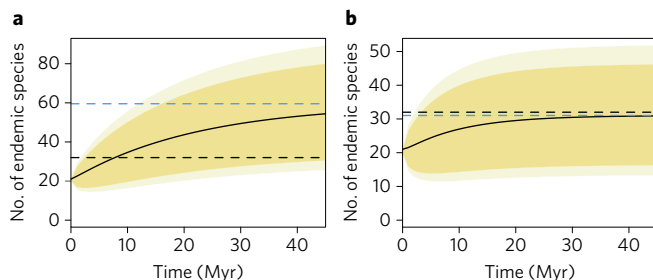

Figure 3 | Expected future noctilionoid bat endemic diversity in the GA for the high human impact scenario. Data shown from the DI model, starting from current extant diversity. **a**, For $T = 20$ Myr. **b**, For $T = 45$ Myr. Black dotted line, pre-human diversity levels; blue dotted line, expected number of endemic species at equilibrium. Light and dark shaded areas show the 2.5–97.5 and the 25–75 percentiles, respectively.

the effect of anthropogenic extinctions on the diversity dynamics of islands had not been quantified[10]. Our results indicate recent extinctions have clearly depressed West Indian bat diversity to values below equilibrium. The remarkably long time required to re-establish pre-human levels of diversity reveals the staggering consequences of extinctions, many of them anthropogenic, on long-term, natural evolutionary dynamics in this system. Measuring biodiversity loss in the time required to regain natural diversity provides a crucial perspective; at least 8 Myr are needed to recover the diversity lost over the last few thousand years in the Caribbean. Our new approach combining phylogenetic data, fossils and modelling serves as a template for future studies examining how human activities on islands interact with biogeographical dynamics to change the path of biological communities to equilibrium.

Methods

Data. We obtained phylogenetic and biogeographic data on Greater Antillean noctilionoids from recent phylogenetic analyses (Supplementary Table 1). These analyses account for 85% of noctilionoid bat species, including 100% of the 24 extant GA island species. Additionally, we conducted a literature survey to identify noctilionoid taxa recorded as extinct in the GA and identified 13 such species (Supplementary Table 1): ten of these are known only from Quaternary fossils or subfossils and the remaining three species are still extant, but have been extirpated from the GA. Phylogenetic data of the three extirpated taxa were obtained from a study on extant non-GA populations of the species[15].

Phylogenetic relationships and divergence dates for fossils representing four of the ten globally extinct species were obtained from Bayesian analyses[31] of morphological characters and DNA sequences of the subfamily Stenodermatinae (Tavares, V. D. C. *et al.*, manuscript in preparation; trees available from Dryad). Briefly, Bayes factors were used to select the best-fit relaxed character clock and this model was applied in combined analyses with node-based calibration dates, based on posterior dates for the subfamily[15], and tip-based dates, based on fossil stratigraphy. The remaining six globally extinct species were assigned to their putative clades on the basis of taxonomic information.

The distribution of species was obtained from ref. [15], which was based on the IUCN review of land mammals[32]. Several GA noctilionoids range into the Bahaman archipelago, including the Turks and Caicos (for example, *Macrotus waterhousii minor*, *Brachyphylla nana pumila*), or into the Lesser Antilles (for example, *Brachyphylla cavernarum*). These were assumed to originate in the GA and not the Bahamas or the Lesser Antilles, on the basis of lower mean genetic diversity in the Bahamas relative to the GA[33] and biogeographic optimizations placing ancestral populations for the clades in the GA (for example, *Brachyphylla*, *Erophylla*, *Phyllonycteris*)[34].

Colonization and branching times. We assumed the time of colonization of the GA corresponded to the time of divergence of a GA lineage from its most closely related non-GA lineage. For endemic GA species or clades, this age was the stem age of the GA species/clade. For non-endemic species, this was the stem age of the GA populations of the species. For four non-endemic species, only a maximum age of colonization was known: for *Glossophaga soricina*, DNA sequences indicate the Antillean population is undifferentiated[35]; for *Tonatia saurophila* and *Mormoops megalophylla* GA populations are only known from subfossil deposits[36,37] and no sequence data are available; and only individuals from non-GA populations of *Noctilio leporinus* have so far been sequenced. For these four cases we used the divergence time of the continental species from its sister lineage as the upper bound limit of colonization time.

Extinction scenarios. To account for uncertainty in causes of extinction, we considered two scenarios: (a) high human impact, that is, we assumed 100% of the extinction events were anthropogenic; and (b) low human impact, that is, we assumed only three extinction events to be anthropogenic, corresponding to three species that have unequivocally been shown to have persisted through the Holocene until 2,000–3,000 years before present and most probably became extinct because of humans (*Phyllonycteris major*[21], *Pteronotus parnellii* species complex[8] and *Macrotus waterhousii* in Puerto Rico[38]).

As anthropogenic extinctions do not count towards the natural background rate of extinction, for both scenarios we treated the species that went extinct because of humans as though they had survived until the present. This was accomplished by extending the phylogenetic branch leading to the extinct species to the present. For the high human impact scenario, all 13 extinct species were assumed to be extant (data set included 24 extant + 13 extinct species = 37 species). For the low human impact scenario three out of 13 extinct species were assumed to be extant (data set included 24 extant + 3 extinct species = 27 species). The low human impact scenario has been ruled out by most recent studies[8,21] and we thus discuss the high impact scenario in the main text.

In addition, to understand how extinct species affect estimates of speciation, colonization and natural extinction in island biogeography, we analysed a third data set including only extant species (contemporary data set; 24 species), which was equivalent to the types of data typically available for island biologists working on groups lacking a preserved or well described fossil record (note that this data set also corresponds to an extreme case in which none of the extinction events were caused by humans, but this scenario has been rejected by radiocarbon dating). The data sets for the three scenarios are available in the Supplementary Information.

DAISIE model fitting and selection. DAISIE is a ML method used to estimate parameters of a dynamic stochastic island biogeography model on the basis of phylogenetic information[20]. DAISIE analyses an entire insular community resulting from multiple colonization events, estimating diversification and biogeographical rates for the archipelago as a whole and not for specific colonist clades. We used the DAISIE R package to estimate archipelago-wide rates of colonization (γ), extinction (μ), speciation via cladogenesis (λ^c), speciation via anagenesis (λ^a) and diversity-limits (K') for GA noctilionoid bats. Model parameters were estimated via ML by fitting models to the times of colonization and speciation of GA noctilionoids.

We compared a DI model (four parameters: γ, μ, λ^c and λ^a) and a DD model, with DD in λ^c and γ (five parameters: γ, μ, λ^c, λ^a and K'). Under the DD model, λ^c and γ declined linearly with increasing diversity. To account for uncertainty in geological age, we re-fitted the models assuming a range of T of between 20 and 45 Myr, derived from palaeoecological reconstructions of the archipelago[18,23]. We ran all analyses for two different static mainland pool sizes (M), 20 and 100. The ML parameters were similar for both M values, with the exception of colonization rate, which, as expected, was lower for $M = 100$ (Table 1) than for $M = 20$ (Supplementary Table 3). We therefore discuss only the results for $M = 100$.

We did not compare models with among-lineage variation in parameters, as we did not identify any lineage as a clear candidate for exhibiting exceptional colonization–speciation–extinction dynamics (for example, as is the case for the radiation of Darwin's finches in the Galápagos Islands[20]). In particular, we believe the assumption of similar dispersal rates was warranted because, relative to other clades, bats have wide distributions and population genetics analyses have shown noctilionoid bats maintain connectivity across oceanic dispersal barriers[33].

We fitted DAISIE models separately to each of the data sets representing the three extinction scenarios (high human impact, low human impact and contemporary). For each scenario, we fitted all models to a consensus data set (Supplementary Information) representing the mean colonization and branching times across all phylogenetic trees. For each combination of T and M in the model, we ran ML with 50 different, random, initial starting conditions to ensure that searches were not trapped on local sub-optima. For the high human impact scenario, we repeated analyses for each of 100 posterior trees representing uncertainty in topology and branch lengths (trees deposited in Dryad). The branching times extracted from the 100 posterior trees are also available in Dryad and the parameter estimates are presented in Supplementary Table 4. For the analysis on the posterior distribution of trees, we used ten initial random starting conditions per tree. Analyses ran in the high-performance ZEIK computer cluster of the University of Potsdam.

Precision and power. We used a parametric bootstrap approach to assess the accuracy of the parameters estimated by DAISIE. We simulated 2,000 *in silico* islands with the parameters of the DI model and assessed bias and precision of the ML inferences, by estimating the ML parameters from each of the simulated data sets and comparing them with the 'true' values estimated from the data.

We used a likelihood ratio test based on bootstrapping to assess model selection reliability following a recommended step-by-step protocol[39]. In brief, this method compares the likelihood ratio of DD and DI for the real data with the distribution of likelihood ratios obtained from simulated data sets (1,000 data sets for each model). Using this method, we found the power to select DI or DD, when either was the underlying model, was low.

Simulations. We simulated islands with the ML parameters of the preferred model (DI). This enabled us to both assess whether the number of GA noctilionoid species tended towards an equilibrium value and model how this number changed over time. For each model, we simulated 5,000 islands from the birth of the archipelago to the present. To assess goodness-of-fit of the models, we produced histograms representing the distribution of various summary statistics for each of the simulated islands: total number of species, number of colonization events, number of endemic clades and number of anagenetic species (endemic species with no close relatives on the island). We then compared the median of these distributions to those of the empirical data set. The simulations indicate the DI model fits the data very well (Supplementary Fig. 6).

To visualize the level of dynamism of the system, we recorded the total number of events of each type (colonization, cladogenesis, anagenesis and extinction) that took place for the entire duration of each simulation; the results for $T = 20$ are plotted in Supplementary Fig. 7, which shows that during the course of 20 Myr the

median total number of events was: 59 colonization events (3 events per Myr), 117 cladogenesis events (6 events per Myr), 12 anagenesis events (0.6 events per Myr) and 138 extinction events (7 events per Myr).

Expected future diversity. To estimate future diversity, we used a set of deterministic equations for the expected number of species and lineages given a set of DAISIE parameters. The deterministic counterpart of our stochastic model without diversity-dependence (the model best supported by our data) can be summarized by two ordinary differential equations, one for the number of endemic species (E) and one for the number of non-endemics (I):

$$\frac{dE}{dt} = \lambda^c E + 2\lambda^c I + \lambda^a I - \mu E$$
$$\frac{dI}{dt} = \gamma(M-I) - \lambda^a I - \lambda^c I - \mu I \tag{1}$$

here λ^c is the per lineage rate of cladogenesis, μ the per lineage rate of extinction, γ the per lineage rate of immigration, λ^a the per lineage rate of anagenesis and M the number of species in the mainland pool.

The solution to this system, assuming we start at $E(0)=E_0$ and $I(0)=I_0$ is:

$$E(t) = \frac{C-\gamma}{C}\left(\frac{M\gamma}{A} - \frac{M\gamma}{B} + \left(\frac{C}{C-\gamma}E_0 - \frac{M\gamma}{A} + I_0\right)e^{-At} + \left(\frac{M\gamma}{B} - I_0\right)e^{-Bt}\right)$$
$$I(t) = \frac{M\gamma}{B} - \left(\frac{M\gamma}{B} - I_0\right)e^{-Bt} \tag{2}$$

where we have defined:

$$A = \mu - \lambda^c$$
$$B = \gamma + \mu + \lambda^a + \lambda^c \tag{3}$$
$$C = \gamma + \lambda^a + 2\lambda^c$$

The equilibrium values are:

$$E^* = \frac{M\gamma(C-\gamma)}{AB}$$
$$I^* = \frac{M\gamma}{B} \tag{4}$$

Therefore the total equilibrium number of species on the island, predicted by the deterministic model, is given by:

$$N^* = E^* + I^* = M\gamma\frac{B-\gamma}{AB} \tag{5}$$

These results are identical to the expected values in the stochastic model. The full probability distribution for the number of endemics and non-endemics can be obtained by considering the dynamics of this joint probability:

$$\frac{dP_{E,I}}{dt} = \gamma(M-(I-1))P_{E,I-1} + \mu(I+1)P_{E,I+1} + \mu(E+1)P_{E+1,I}$$
$$+ \lambda^a(I+1)P_{E-1,I+1} + \lambda^c(I+1)P_{E-2,I+1} + \lambda^c(E-1)P_{E-1,I} \tag{6}$$
$$- ((\mu+\lambda^c)E + (\mu+\lambda^a+\lambda^c)I + \gamma(M-1))P_{E,I}$$

for any $E, I > 0$. This set of equations can be solved numerically when assuming a large cut-off value for E and I.

If we choose M to be 1, then we model the probability of having E endemics and I non-endemics for each colonizing lineage. The probability of this colonist establishing is therefore $P_C = 1 - P_{0,0}$. Because the colonists are independent, the distribution of the number of colonizations from a mainland with M' species not already on the island is binomial with parameters M' and P_C. The distribution of the total number of colonizations, including those initially on the island, is the convolution of this binomial distribution with the probability of each colonization still (or again) being present on the island at a future time t. We implemented these probability distributions in a new version of the R package DAISIE (available from CRAN).

We estimated expected future diversity for both high and low human impact scenarios. Assuming the scenario with lowest human impact, the number of pre-human lineages is equal to the number of contemporary lineages (11); therefore, we show only the results for the expected future number of endemic species (Supplementary Fig. 8). According to the low human impact scenario, for $T = 20$ Myr it would take approximately 2.75 Myr to regain pre-human endemic species diversity (Supplementary Fig. 8). Assuming $T = 45$ Myr, it would take over 15 Myr to return to equilibrium diversity values attained before human colonization, even in the low human impact scenario.

Code availability. The DAISIE R package is available at https://CRAN.R-project.org/package=DAISIE.

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Author contributions
L.M.D. and L.V. designed the study and wrote the manuscript. L.V. performed the analyses. R.S.E. provided theoretical input and developed analytic tools. All authors read and commented on the manuscript.

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Competing interests
The authors declare no competing financial interests.