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Deforestation impacts on Haitian biodiversity

Sexual imprinting in finches

Hierarchy in quantum mechanics

Income inequality and life expectancy

Cesarean sections and brain development

Haiti's biodiversity threatened by nearly complete loss of primary forest

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Tropical forests hold most of Earth's biodiversity. Their continued loss through deforestation and agriculture is the main threat to species globally, more than disease, invasive species, and climate change. However, not all tropical forests have the same ability to sustain biodiversity. Those that have been disturbed by humans, including forests previously cleared and regrown (secondary growth), have lower levels of species richness compared with undisturbed (primary) forests. The difference is even greater considering extinctions that will later emanate from the disturbance (extinction debt). Here, we find that Haiti has less than 1% of its original primary forest and is therefore among the most deforested countries. Primary forest has declined over three decades inside national parks, and 42 of the 50 highest and largest mountains have lost all primary forest. Our surveys of vertebrate diversity (especially amphibians and reptiles) on mountaintops indicates that endemic species have been lost along with the loss of forest. At the current rate, Haiti will lose essentially all of its primary forest during the next two decades and is already undergoing a mass extinction of its biodiversity because of deforestation. These findings point to the need, in general, for better reporting of forest cover data of relevance to biodiversity, instead of "total forest" as defined by the United Nation's Food and Agricultural Organization. Expanded detection and monitoring of primary forest globally will improve the efficiency of conservation measures, inside and outside of protected areas.

conservation | deforestation | mass extinction | remote sensing | species

Primary forest is critical for maintaining much of the world's biodiversity (1, 2), and its loss is the greatest threat to species survival (3), even if primary forest is later replaced by secondary growth (4–7). Nonetheless, most reports of forest cover and deforestation in tropical countries omit the distinction between primary forest and disturbed forest. The latter can include secondary growth (regrowth after complete clearance) and degraded primary forest where selective removal of trees has occurred through logging. Instead, "forest" is typically measured using the United Nation's Food and Agricultural Organization's (FAO) definition of "total forest," which is "land spanning more than 0.5 hectares with trees higher than 5 meters and a canopy cover of more than 10%, or trees able to reach these thresholds in situ" (ref. 8, p. 3). The FAO defines primary forest as "naturally regenerated forest of native species, where there are no clearly visible indications of human activities and the ecological processes are not significantly disturbed" (ref. 8, p. 7).

Knowledge of the extent of the world's primary forests remains poor because its value is not yet widely recognized and the methods used to detect it vary greatly. For example, Brazil, one of the most important countries for biodiversity, reports its primary forest data to the FAO based on indirect (rough) estimates rather than remote sensing or field surveys (9). Reported estimates (10) of primary forest, as a percentage of total forest, vary from 99% (Ecuador) to below 1% (Nigeria), but it is unclear how much of this variation is based on the methods used.

Estimates of Haiti's forest cover using aerial photo analysis in the 1980s (11) and later by satellite imagery analysis (10, 12, 13) have varied greatly, from 1 to 32% of total land area. However, none of those studies explicitly estimated primary forest, which is of importance for biodiversity, and therefore we undertook a time-series satellite image analysis to quantify the loss of primary forest in Haiti from 1988 to 2016. We also surveyed the two dominant vertebrate groups with endemics in Haiti, amphibians and reptiles, to assess species richness on mountains with and without primary forest.

Results

Primary forest in Haiti declined from 4.4% of total land area in 1988 to 0.32% in 2016 (Fig. 1). We also found that using different levels of tree canopy coverage as the threshold value for forest greatly affects the final proportion of forest cover in Haiti. For example, using a threshold of 10% tree canopy (FAO standard) will estimate that forests cover 50% of Haiti whereas a 70% threshold will estimate that forest covers only 7.5% of Haiti (Fig. 1*C*). The time-series approach (*SI Appendix*, Table S1) starts with the stringent 70% threshold and then eliminates cases of major regrowth (secondary growth) by following 30-m pixels back in time to make sure they always represented forested areas. These results explain why a recent study (13) obtained a 100-fold higher estimate (32%) for forest cover in Haiti. That study used a low threshold of 10% canopy per pixel without performing a time-series analysis, and therefore their estimate included many disturbed habitats that would not support the original biodiversity.

Significance

The loss of forest from human activities is a global threat to biodiversity, continually diminishing populations of forest-dwelling species. However, species extinction usually is delayed until the last habitats disappear. Nonetheless, mass extinction may be imminent in a small number of tropical countries with low forest cover. Here, we find that Haiti has less than 1% of its original primary forest and is therefore among the most deforested countries in the world. Forty-two of the 50 highest and largest mountains have lost all primary forest. Our surveys of vertebrates on these mountaintops suggest that endemic species have been lost along with the loss of forest. This indicates that Haiti is already undergoing a mass extinction of its biodiversity because of deforestation.

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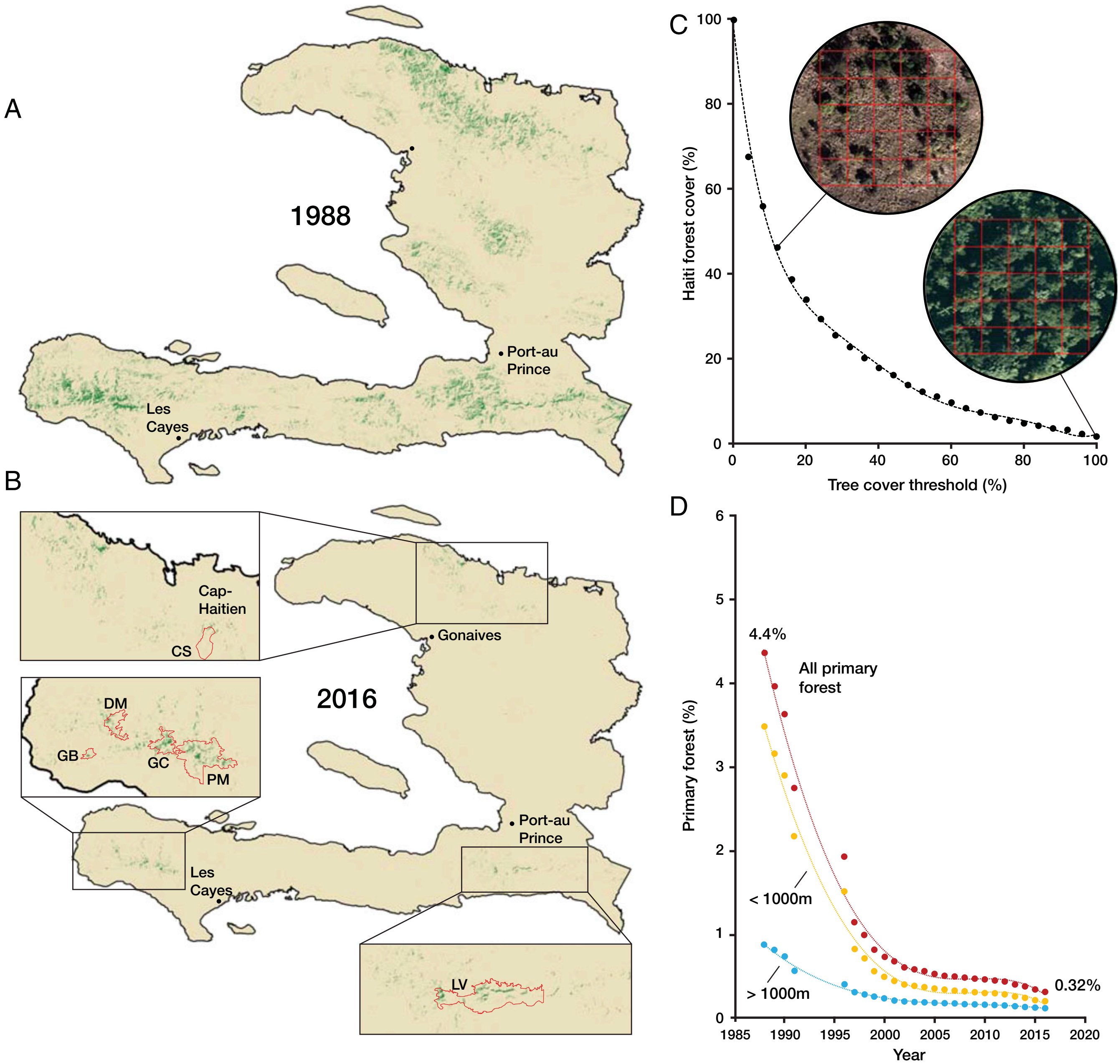

Fig. 1. Recent loss of forests in Haiti. Distribution of primary forest in (*A*) 1988 (4.4% of Haiti) and (*B*) 2016 (0.32%) as estimated by the time-series model. *Insets* in *B* show enlarged views of the three major regions of surviving primary forest. National parks, bordered in red, are Citadelle Sans-Souci (CS), Deux Mamelles (DM), Grand Bois (GB), Grande Colline (GC), La Visite (LV), and Pic Macaya (PM). (*C*) Proportion of Haiti considered forested based on a minimum tree cover threshold but without using the time-series model. *Inset* circles show examples of 0.5-ha plots interpreted for tree cover using a 5 × 5 grid (12% tree cover, plot 280; and 100% tree cover, plot 274). (*D*) Decline in the proportion of primary forest (of all land area) through time at all elevations (red), below 1,000 m (yellow), and above 1,000 m (blue).

While primary forest shows decline at all elevations, the greatest rate of decline was in the lowest elevations (Fig. 1*D*). Likewise, the average elevation and slope of primary forest increased from 1988 to 2016: from 700 to 900 m and from 22 to 27% grade, respectively (*SI Appendix*, Fig. S1). This general pattern has been found in other studies of deforestation in tropical areas (14) and is interpreted as related to accessibility: steeper slopes and higher elevations are more difficult to reach by tree cutters. This probably explains the decrease in rate of deforestation with time (0.32%/y in 1988–1998 and 0.0188%/y in 2002–2016; Fig. 1*D*) as the last and steepest areas were reached.

Areas of endemism—places where species occur nowhere else—can be at any elevation, but for most groups in Haiti they are on isolated mountains (15). For this reason, we tracked the history of primary forest on all of the largest mountains in Haiti ($n = 50$; Fig. 2; *SI Appendix*, Tables S2 and S3) using the criteria of elevation (>1,000 m) and area (>1 km^2). In 1988, 43 of the 50 mountains still had primary forest, but by 2016 only 8 had primary forest (Fig. 2 *B* and *C*). Mountains that lack primary forest, such as the large Chaîne des Matheux (Fig. 2*D*), typically lose their soil soon after deforestation and are largely barren. Most (95%) of the remaining montane primary forest in Haiti (as of 2016) is on two mountains, Macaya-Grande Colline in the Massif de la Hotte (1451 ha or 6.5% if its area) and the Massif de la Selle (1,582 ha or 1.5% of its area). The third largest amount of primary forest is on Deux Mamelles in the Massif de la Hotte

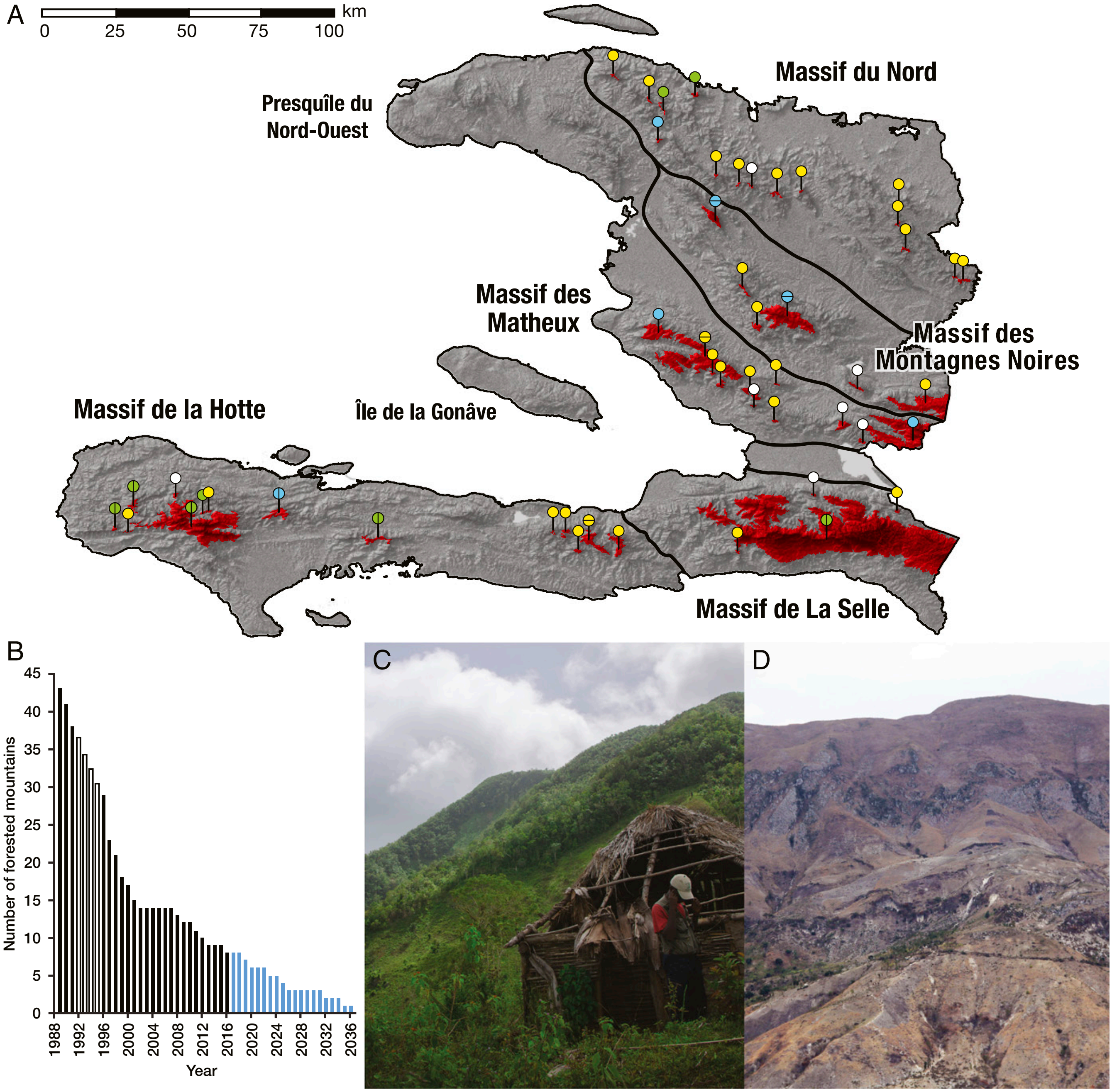

Fig. 2. Loss of areas of endemism in Haiti. (*A*) Terrain map showing elevation (dark gray), geographic features (labeled), and distribution (red) of the 50 largest mountains in Haiti, >1 km^2 above 1,000-m elevation. Green pins are mountains with primary forest in 2016 (>0.5% of total area for the mountain), blue pins are mountains where primary forest was negligible (0.5–0.1%) in 2016, and yellow pins are those that had completely lost primary forest by 2016 and are bald. Mountains with white pins became bald before the earliest measurement (1988), probably during 1986–1988. Mountains surveyed for biodiversity (2009–2015) are indicated by lines in pins based on the status of primary forest at time of collection (vertical line, present; horizontal line, absent). (*B*) Number of mountains by year with primary forest, with future years (blue) projected based on current, mountain-specific rates of deforestation. Years missing data (1992–1995, hollow bars) are interpolated. Grand Bois [*C*; image courtesy of Sarah Hanson (Temple University, Philadelphia), taken in June 2013] is a mountain with existing primary forest, and Chaîne des Matheux (*D*; image courtesy of S.B.H., taken in April 2011) is a range with no primary forest.

(51.3 ha or 7.1% of its area), with all other mountains each having less than 20 ha of primary forest above 1,000 m. We project that primary forest of the remaining eight mountains will disappear by 2036 at the current mountain-specific rates of deforestation (Fig. 2*B* and *SI Appendix*, Table S3).

To determine if some mountains lost their primary forest (i.e., are "balded") before others in a predictable way, we regressed the date of mountain balding with two other factors related to accessibility: distance from the capital city (Port-au-Prince) and height of the mountain. The former is important because much of the charcoal harvested throughout Haiti is transported to Port-au-Prince. Both showed weak but significant correlations (*SI Appendix*, Fig. S2).

Data on species richness before and after deforestation are not available for Haiti, and therefore we surveyed and compared mountains with and without primary forest. Our team of biologists visited 10 of the 50 highest mountains in Haiti (Fig. 2*A*) between 2009 and 2015, mostly with the use of a helicopter to access remote areas (*Materials and Methods* and *SI Appendix*). Primary forest was present on six mountains and absent on four mountains. The presence or absence of primary forest was determined by remote sensing (our temporal analysis of forest cover) and confirmed by ground observation. Additionally, the four mountains lacking primary forest were heavily disturbed, as is typical in Haiti, exhibiting mostly open areas with few trees. To control for any biogeographic effect, such as amphibian and reptile species being more numerous in one part of the island than in another, we include species presence data from the three mountains with primary forest in the Dominican Republic that border Haiti: the Cordillera Central, Sierra de Neiba, and Sierra de Baoruco. Significantly more species were encountered on mountains with primary forest than on those without primary forest (Fig. 3*A*; $P = 0.001$, $t = 5.56$, df = 10). The same relationship was obtained with endemic species, those known only from a single mountain (Fig. 3*B*; $P = 0.009$, $t = 3.44$, df = 8). Controlling for size of mountain (46.8 km^2, average size of the four mountains lacking primary forest), the drop in species richness with loss of primary forest was 83% in total species and 95% in endemic species.

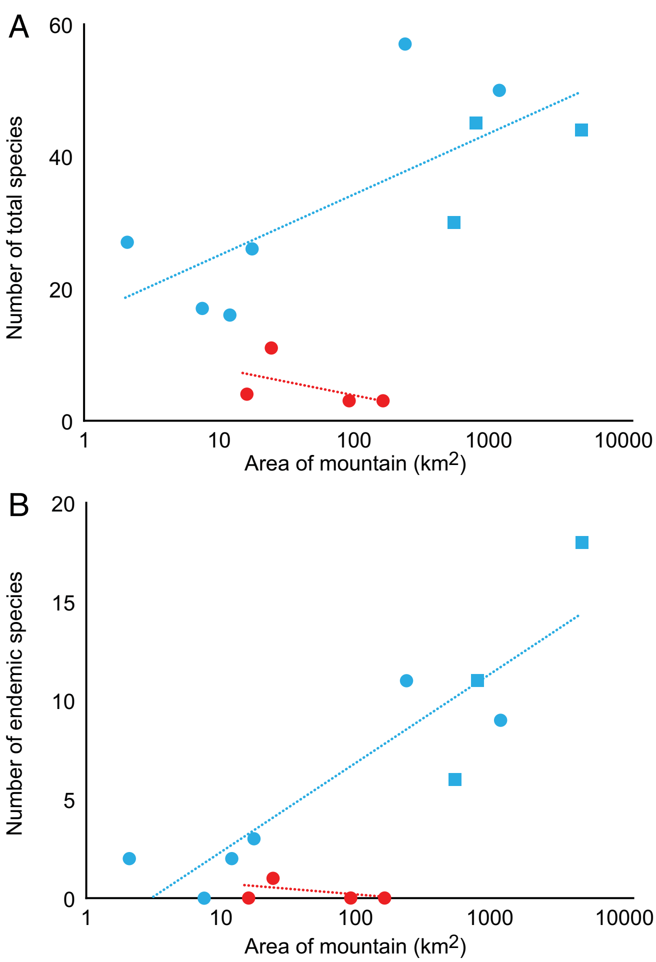

Fig. 3. Effect of forest quality on species diversity and endemism. Graphs show the number of species of amphibians and reptiles occurring on mountains with primary forest (blue, $n = 9$) and with no primary forest (red, $n = 4$). (*A*) Total species: primary forest, $r = 0.744$: $P = 0.022$, two-tailed, $t = 2.95$, df = 7; no primary forest, r = n.s. (*B*) Endemic species: primary forest, $r = 0.909$: $P = 0.001$, two-tailed, $t = 5.77$, df = 7; no primary forest, r = n.s. Symbols indicate mountains in Haiti (circles) and the Dominican Republic (squares).

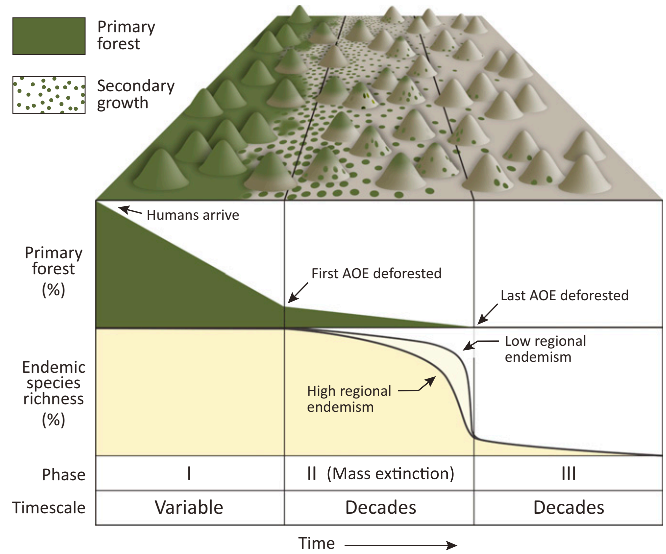

Fig. 4. Dynamics of species loss linked to deforestation. Model shows hypothetical landscape of mountains (areas of endemism, AOEs) with primary forest and secondary growth in a defined region (island, country, etc.). Phase I: primary forest or any original habitat holds the greatest species richness, and this begins to decline after humans arrive, initially causing regional species extirpations but few extinctions. Timescale: hundreds to thousands of years. Phase II (mass extinction): major species extinctions occur, beginning when primary forest is lost from the first AOE, increasing in rate as other AOEs are lost, and decreasing in rate as primary forest in the last AOE is lost. Regional endemism and patterns of deforestation affect shape of decline in richness. Phase III: only secondary growth or other degraded habitat remains, supporting a small fraction of the original biodiversity. Other factors can cause species loss (see *Discussion*).

Because several of the larger mountains contained species counts from multiple sites, which could bias results, we also analyzed site-specific, rather than mountain-specific, project data ($n = 16$ sites) obtained with the same methods (*Materials and Methods* and *SI Appendix*). Again, the drop in total species richness (per site), comparing sites with primary forest to those lacking primary forest, was significant: a 66% drop in total species (15.4 vs. 5.25 species, average; $P = 0.005$, $t = 3.83$, df = 8) and a 88% drop in endemic species (2.17 vs. 0.25 species, average; $P = 0.003$, $t = 3.58$, df = 13). While species numbers on any mountain are expected to increase with repeated visits, these analyses show that loss of primary forest is associated with a large drop in species richness.

Discussion

Taken together, these primary forest and vertebrate species data suggest a general model of biodiversity loss from deforestation applicable to other areas (Fig. 4). This model of biodiversity loss pertains to any geographic region, such as a country or island, which contains primary forest and endemic species. The first of three phases begins with the arrival of humans and onset of deforestation and ends with loss of primary forest in the first area of endemism, leading to extinction of endemic species. Until that point, considerable loss of forest occurs along with extirpation of populations, and possibly extinctions from other factors (see below), but with relatively few extinctions directly linked to deforestation. The second phase corresponds to a mass extinction, starting at that point and continuing until all primary forest is lost from all areas of endemism. The shape of the mass extinction curve is influenced by the amount of regional endemism and any correlation between areas of endemism and accessibility of forest. During the third and final phase, additional extinctions are expected to occur as the environment declines in quality, although some physiologically tolerant species will likely survive and expand in poor-quality habitats (16).

Our data for Haiti provide some parameters for this model. The first humans were in Hispaniola 6,000 y ago, possibly numbering more than one million by the time the Spanish arrived in 1492 (17). They utilized trees and apparently caused extinctions of birds and large mammals (18, 19). However, the greatest deforestation occurred subsequent to European colonization, where we estimate (Fig. 2*B*, extrapolation of pre-2000 rate of mountain balding) that primary forest was completely lost on the first of the 50 mountains by 1986 (CI, 1985.6–1986.7), defining the end of phase I. At that point, primary forest was already down to 4.8%, by reverse extrapolation of the loss rate in the 1980s and 1990s (Fig. 1*D*). It is likely that some extinctions occurred in Haiti before 1986, especially in lowland areas of endemism. However, the montane cloud forests probably harbor the majority of Haiti's endemic biodiversity and provide refuges for some species that once had a greater distribution in lowland areas.

While our model (Fig. 4) concerns only species loss linked to deforestation—the primary threat to species survival (3)—other factors such as disease, invasive species, hunting, and climate change may cause additional extinctions. Forest fragments and lightly disturbed habitats, such as degraded primary forest, are transitional because they contain high species richness in the short term (7) but lower richness in the long term (20). In Haiti, we observed that degraded primary forest is short-lived, converting quickly to unforested areas. However, lightly disturbed habitats could provide lifelines for some species if protected and allowed to recover.

We project that all primary forest in Haiti will disappear by ~2035 (CI, 2033.5–2035.4) at the current rate, defining phase II as a 49-y period from 1986 to 2035 during which the final 4.8% of primary forest in the country will be lost. Assuming that our estimated loss of vertebrates is representative of the biodiversity in general, then 66–83% of species will be lost in Haiti during 1986–2035 because of deforestation. Thus, Haiti is well into a mass extinction, with only 8 of 50 mountains still holding primary forest. Unfortunately, Haiti's neighbor, the Dominican Republic, is not a major refuge for Haitian species because more than half of the species surveyed (51%, average) on mountains with primary forest are endemic to Haiti and 12% are endemic to an individual mountain in Haiti (*SI Appendix*). In addition, forest loss in the Dominican Republic is a threat to that country's biodiversity (21).

It is common for deforestation to occur within protected areas of tropical countries (22), and, during the course of our surveys in Haiti, we observed ongoing destruction of primary forest inside all of the national parks. We also estimate that 60–75% of primary forest in the two original national parks, Pic Macaya and La Visite (Fig. 1*D*), has disappeared since they were declared as protected areas 35 y ago (*SI Appendix*, Fig. S3). In both cases, the rates of primary forest loss (pre-2000 and post-2000) were greater than the overall rates for all of Haiti, indicating that protection was minimal or nonexistent. This indicates that the mass extinction of biodiversity in Haiti will continue unabated unless greater protective measures are taken. More generally, this suggests that the phrase "protected area" be reserved only for areas where protection has been confirmed.

Scientific data often drive important conservation policy decisions. Here, we show that distinguishing a small subset of forest most relevant to biodiversity can raise awareness of an ongoing mass extinction that was not evident previously. Globally, time-series analysis of such primary forest can effectively test and monitor the quality of areas designed for biodiversity protection. This will provide the data needed to address the greatest threat to terrestrial biodiversity.

Materials and Methods

Analyses of Primary Forest Cover. We used Landsat time series from 1984 to 2016 to characterize primary forest cover in Haiti. Because our analysis was based on remote sensing, primary forest cover was defined by what we could observe from imagery during those 33 y. For 2016, if there had been continual closed forest cover (≥70% tree cover) of an area since 1984, i.e., no deforestation or significant degradation of cover percentage during that period, we assumed that area was covered by primary forest in 2016. This conceptual logic holds, walking back in time, annually to the beginning of the time series. Our approach used a 5-y window to allow for a single-year classification error in labeling of closed forest, yielding a trajectory of primary forest cover from 1988 to 2016.

All available L1T Landsat TM, ETM+, and OLI data during 1984–2016 for Haiti were used in this analysis and converted to surface reflectance (23, 24). From this full collection, medoid annual composites were created (25), except for 1992–1995, for which no data were available. Some composite image pixels in certain years other than 1992–1995 had missing data because there were no cloud-free data available for the composites for those other years. All composite images contained the six reflectance bands commonly associated with Landsat data, but with slightly varying waveband widths across sensors. Due to significant differences in radiometric properties of OLI and ETM+ data, OLI reflectance data were radiometrically normalized to ETM+ reflectance using coefficients from ref. 24. Negligible differences between TM and ETM+ data were ignored (26).

Reference data from Google Earth (GE) were used to classify closed forest for each annual medoid composite image. With visual interpretation of high spatial resolution images available in GE, we collected 360 polygon samples for three basic land cover classes: 132 nonforest (0–9% tree cover in agricultural, urban, and other nonforest environments), 168 open forest (10–69% tree cover in natural environments), and 60 closed forest (70–100% tree cover in natural environments). Samples were distributed around the whole country to capture geographic variability for each class, and varied in size from 1 to 22 ha (median 2 ha). Interpretations were made of imagery from the most recent available clear data (most from 2007–2011 and lesser amounts from 2002–2006 and 2012–2013). A Random Forest prediction model (with 500 trees) was constructed to relate the three interpreted reference data cover classes to the six band medoid composite data (*SI Appendix*, Table S1). The composite year most contemporaneous with the GE interpretation date for each polygon was used. The model was applied to all pixels in each medoid composite, and the most probable class was chosen as label for each pixel in each year.

A simple time-series logic was used to label primary forest, starting with 1988. Cover model prediction error was low, but significant; thus, to allow for classification error, a given pixel was labeled primary forest in 1988 if four of the five annual cover labels (1984–1988) were closed forest (an 80% threshold). If this 80% threshold was not achieved, the pixel was masked from the 1988 primary forest map and the primary forest maps for all subsequent years. For pixels labeled as primary forest in 1988, cover labels for 1985–1989 were queried, and the same 80% threshold rule was applied to derive the primary forest map for 1989. For 1990 and later, the same masking, 5-y moving window and threshold rules were applied such that only maintenance of primary forest was allowed, with no additions possible. When missing pixel-level reflectance data were encountered within the 5-y window (due to cloud/shadow in years other than 1992–1995), we used an all-but-one rule to determine whether the primary forest label should be maintained for the relevant year. Three of 4, 2/3, or 1/2 of the cover labels (depending on how many years were missing data) had to be classified as closed forest for the primary forest label to be maintained. In extremely rare cases, where only one or zero cover labels existed in a 5-y window, the primary forest label was maintained. For the period from 1992 to 1995, for which there were no data, we ignored those dates and examined consecutive years; i.e., we used same 80% threshold and all-but-one rules across the date window containing 1990–1991 and 1996–1998 data.

The individual primary forest maps were spatially filtered to remove all primary forest patches <0.5 ha in size to accommodate the definition of forest used by the FAO. The maps were then summarized at the national level to derive a temporal trajectory of Haiti's primary forest during 1988–2016. Trajectories were also created for land below and above 1,000 m.

Analyses of Primary Forest Cover in 2010. Recent analyses based on satellite imagery (13) indicate substantially more forest cover in Haiti than conventional wisdom and existing reports suggest. To provide more reliable data on recent forest cover (combined primary and secondary), we took advantage of a high spatial resolution (0.65 m) true color digital aerial image dataset acquired between 25 and 31 January 2010 just days after the January 12 Haiti earthquake (27). Our approach was to photo-interpret the percentage of tree cover within a random sample of 0.5-ha plots across the entire country. Because we used this FAO minimum patch size for forest, we could readily equate our percentage of tree cover interpretations to percentage of forest cover after choosing a tree cover threshold to define forest and applying an appropriate estimation statistic.

We randomly selected 2,000 point locations from within Haiti and located an aerial image having each location close to its center. We created a 0.5-ha square polygon with the plot at the polygon's center. Each plot polygon was gridded into 25 evenly sized cells (5×5) within which tree cover was interpreted. For each cell, at least 50% had to be covered by tree crowns to be counted as tree cover for that cell; otherwise, the cell was not counted as covered by trees. The number of cells containing at least 50% tree cover was counted, and with 25 cells per plot, plot-level tree cover was calculated from 0 to 100% in 4% increments. Trees included palms, plantations of fruit trees (e.g., mangoes, coconuts), and cacti >5 m, but not *Musa* spp. (bananas, plantains) or bamboo.

Using the plot data, forest cover was estimated using a range of thresholds from 4 to 100% tree cover. Using a variable threshold of tree cover to define forest cover allows for a more flexible definition of forest cover to suit different applications and interpretations based on a host of considerations about ecosystem health, carbon storage, and biodiversity. Because our sample was random, at each tree cover threshold level the proportion of interpreted plots that met the given threshold was equal to the proportion of Haiti covered by forest.

Defining, Measuring, and Projecting Decline of Primary Forest on 50 Mountains. First, we defined a mountain as being greater than 1,000 m in elevation and greater than 1 km^2 in area, resulting in exactly 50 mountains throughout Haiti (Fig. 2 and *SI Appendix*, Fig. S2). The 1,000-m elevation threshold corresponds to the approximate low limit of cloud forest containing high moisture and high species richness and endemism in Haiti (28). The 1-km^2 area size threshold corresponds to the approximate low limit of mountain size for presence of endemic species (Fig. 3). In most cases, mountain names are from 1:50,000 scale topographic maps (29). The large mountain M7 includes Chaîne de la Grande Colline and Chaîne de Macaya, but is less inclusive than Massif de la Hotte, so we use the descriptor "Montagnes" in accordance with usage elsewhere in Haiti, and hence Montagnes Macaya (*SI Appendix*).

We define the complete loss of primary forest using a near-zero threshold of 0.5% rather than a zero threshold. This avoided cases where a few mountains (e.g., M20) effectively reached zero but continued to show nonzero amounts of primary forest over years (*SI Appendix*, Table S3). Using this threshold, 42 of the 50 mountains became bald (i.e., lost their primary forest) before 2016 (*SI Appendix*, Table S2). For the eight mountains with primary forest in 2016, we projected the year when each mountain will become bald, using the same threshold. To do this, we used the rate of decline from the preceding 5 y (*SI Appendix*, Table S3). It was not possible to project forest-loss rates backward for the seven individual mountains that were already bald in the first year (1988). However, we extrapolated backward using the rate of balding (Fig. 2*B*), estimating that the first mountain became bald in 1986, and thus assign the dates of 1986–1988 for those seven mountains.

Biodiversity Surveys and Analyses. Six mountains with primary forest (M1, M3, M6, M7, M8, and M47) and four mountains lacking primary forest (M14, M20, M32, and M46) were surveyed for amphibians and reptiles in Haiti from 2009 to 2015 (Figs. 2*A* and 3 and *SI Appendix*, Table S2). All but two of these mountains were newly surveyed. Because of limited access, we used a helicopter, in most cases, to visit sites near the peaks of mountains. At each site, our team of four to six biologists searched in daylight and at night over 1–2 d for amphibians and reptiles. Data on species encountered at each site are in *SI Appendix*. In the cases of M7 and M47, we include species found in earlier surveys and in the literature (30), which are indicated by "ES" (*SI Appendix*). For three mountains in the Dominican Republic, adjacent to Haiti and with primary forest still present, we used species lists based on existing data (15, 30) (Fig. 3).

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