Uso del Pasado para Contextualizar los Impactos Antropogénicos en la Distribución Presente y Futura de un Mamífero Endémico del Caribe
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Palabras clave: áreas protegidas, biogeografía, cambio climático, distribución, especie amenazada, isla, MaxEnt, museos

Resumen. Las especies insulares son difíciles de conservar ya que enfrentan la sinergia del cambio climático, las especies invasoras, la deforestación y la densidad creciente de la población humana en áreas en donde la masa de tierra se está encogiendo. La isla caribeña de La Española representa un reto particular debido a las complejidades geopolíticas que abarcan a dos países y obstaculizan el manejo coordinado de las especies en toda la isla. Empleamos el modelado de distribución de especies para evaluar los impactos del cambio climático y las actividades antropogénicas sobre la distribución de un mamífero endémico de importancia para la conservación: el solenodonte de La Española (*Solenodon paradoxus*). Agregamos puntos de presencia para esta especie muy poco conocida durante el Último Máximo Glacial (LGM, en inglés) y durante el presente (1975 – 2016) con base en colecciones de museos, bases de datos de biodiversidad en línea y nuevos censos de campo. A través de este lente de paleobiología de la conservación encontramos que con el tiempo los humanos tuvieron un papel cada vez mayor en la distribución de *S. paradoxus*, proporcionando así los cimientos para el desarrollo de estrategias de conservación a escalas espacio-temporales adecuadas. La densidad de la población humana fue el pronosticador más importante de la presencia de *S. paradoxus*. Las densidades mayores a 166 personas/km^2 correspondieron con una probabilidad cercana a cero de la presencia de este mamífero. Los modelos que consideraron al cambio climático pero no a las variables antropogénicas identificaron falsamente hábitats aptos en Haití, en donde los censos de campo confirman que no hay hábitat disponible. Los modelos que sólo consideraron el clima también sobreestimaron significativamente el potencial para la conectividad de hábitat entre poblaciones aisladas. Nuestro trabajo resalta que existen destinos alternativos para *S. paradoxus* en el Antropoceno, que además traspasan la frontera política entre Haití y la República Dominicana causada por las realidades económica y política fundamentalmente diferentes de cada país. Las relaciones en el registro fósil confirman que la frontera socio-política de La Española no es significativa biológicamente, sino que representa una frontera impuesta sobre la fauna de la isla durante los últimos 500 años por la actividad colonial. Nuestra estrategia revela cómo la perspectiva paleontológica puede contribuir para concretar la percepción del manejo.

Conservation Focus Contributed Paper

Using the past to contextualize anthropogenic impacts on the present and future distribution of an endemic Caribbean mammal

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Running head: Distribution change

Keywords: island, distribution, climate change, MaxEnt, threatened species, protected areas, museums, biogeography

Article Impact statement: Museum collections and the fossil record can provide past baselines for disentangling the causes of present species declines.

Abstract

Island species are difficult to conserve because they face the synergy of climate change, invasive species, deforestation, and increasing human population densities in areas where land mass is shrinking. The Caribbean island of Hispaniola presents particular challenges because of geopolitical complexities that span 2 countries and hinder coordinated

management of species across the island. We employed species distribution modeling to evaluate the impacts of climatic change and anthropogenic activities on the distribution of an endemic mammal of conservation concern, the Hispaniolan solenodon (*Solenodon paradoxus*). We aggregated occurrence points for this poorly known species for the Last Glacial Maximum (LGM) and the present (1975-2016) based on museum collections, online biodiversity databases, and new field surveys. We quantified degree of overlap between periods and scenarios with Schoener's *D*. Through a conservation paleobiology lens, we found that over time humans played an increasing role in shaping the distribution of *S. paradoxus*, thus providing a foundation for developing conservation strategies on appropriate spatiotemporal scales. Human population density was the single most important predictor of *S. paradoxus* occurrence. Densities >166 people/km^2 corresponded to a near-zero probability of occurrence. Models that accounted for climate but not anthropogenic variables falsely identified suitable habitatin Haiti, where on-the-ground surveys confirm habitat is unavailable. Climate-only models also significantly overestimated the potential for habitat connectivity between isolated populations. Our work highlights that alternative fates for *S. paradoxus* in the Anthropocene exist across the political border between the Dominican Republic and Haiti due to the fundamentally different economic and political realities of each country. Relationships in the fossil record confirm that Hispaniola's sociopolitical boundary is not biologically significant but instead represents one imposed on the island's fauna in the past 500 years by colonial activity. Our approach reveals how a paleontological perspective can contribute to concrete management insights.

Introduction

The unique evolutionary history of island systems places them at the intersection of heightened species diversity and magnified extinction risk. Island fauna today are remnants of a broader community shaped by climatic fluctuations of the latest Quaternary and human-

induced extinctions. Some islands have lost 100% of their native mammals and birds within the past 5,000 years (Wood et al. 2017). In the past 5 centuries, the one-two punch of colonial agriculture and invasive species further decimated the remaining fauna; 80% of global extinctions since AD 1500 occurring on islands (Ricketts et al. 2005). Today, island species are responding to global change in more extreme ways than their continental counterparts (Brooks et al. 2002), particularly because fixed physical boundaries restrict their ability to move to suitable environments or escape novel predators. Incorporating a narrative of past climatic change and extinction on islands can provide critical context in which to assess the conservation status of populations today and forecast their responses to the Anthropocene (Lentini et al. 2018; Barnosky et al. 2017).

Increasingly, conservation biologists are using species distribution models (SDMs) to assess the environmental parameters that shape species distributions today and project these species-environment relationships into the future (Elith & Leathwick 2009; Phillips et al. 2006). In island systems, the majority of studies have focused on predicting the spread of invasive species rather than the impacts of climate or landscape change on insular endemics (e.g., Hardman et al. 2012). Many of these species lack comprehensive occurrence data; however, and the abiotic and biotic limits to species distributions are poorly understood (Lomolino & Heaney 2004). This Wallacean shortfall can be addressed using SDMs to develop range and habitat suitability maps, which can be generated with as few as 5-25 occurrence points without knowledge of absence points (Hernandez et al. 2006; Pearson et al. 2006).

We used an SDM approach to investigate the present and future conservation needs of an endemic Caribbean mammal species, the Hispaniolan solenodon (*Solenodon paradoxus*) and combined modern and fossil records of this species as a test case for "conservation paleobiology" (Barnosky et al. 2017). Out of more than 130 native Caribbean mammals alive

during the Late Pleistocene, only 13 nonvolant species and 60 bats remain today (Cooke et al. 2017), including 2 species of an endemic family of Eulipotyphlans, the solenodons (Solenodontidae). The Hispaniolan solenodon is an ideal species for this approach because it is an insular endemic in a biodiversity hotspot that overlaps with many other endemic animals; its range straddles a north-south political border of two countries (the Dominican Republic and Haiti); there is a large gap between basic knowledge of the species and its management; and it has a known Quaternary fossil record.

Solenodons are nocturnal insectivores that weigh up to 1 kg and secrete venom through a modified salivary gland; however, they evolved in the absence of native mammalian carnivores and the venom does not deter predation (Derbridge et al. 2015). They diverged from their closest living relatives— true shrews, hedgehogs, and moles—more than 70 million years ago, making them a priority for the conservation of evolutionary diversity (Springer et al. 2018). Once thought to be extinct, solenodons are found on the islands of Hispaniola and Cuba, where they are poorly understood and inadequately protected. *S. paradoxus* diverged from its only living congener, the Cuban almiqui (*Solenodon cubanus*), ~5.53 million years ago (Springer et al. 2018). *S. cubanus* is restricted to the very eastern edge of Cuba and is considered more vulnerable to predation by invasive carnivores than *S. paradoxus* due to its smaller body size (Borroto-Páez & Mancina 2017). Both species are recognized as endangered by the International Union for Conservation of Nature (IUCN), though their status is currently being reassessed (Turvey et al. 2017).

The decline of *S. paradoxus* has been linked to predation by village dogs and deforestation inside and outside nationally protected landscapes (Turvey et al. 2014; Rupp & Leon 2009). Quaternary fossil records document an island-wide distribution for solenodons (Ottenwalder 2001), yet today's distribution consists of 3 allopatric populations scattered across fragmented habitat; the remnant population in Haiti is entirely isolated and nearly

extinct (Turvey et al. 2016). Although genetic data for this species are limited and lack historic baselines, they suggest *S. paradoxus* may have multiple subspecies facing varying levels of genetic impoverishment (Brandt et al. 2017; Mychajliw 2017; Grigorev et al. 2018).

Given the recent climatic legacy of Last Glacial Maximum (LGM) on continents and many islands in which vegetation regimes and sea levels were substantially altered, it is unclear whether modern range fragmentation is linked to natural and anthropogenic climate change or is instead a product of differential environmental policies and land use. We capitalized on the exemplar study system of Hispaniola, in which land-use practices between 2 countries varied for over 500 years and destroyed 90% of the island's natural vegetation (Anadon-Irizarry et al. 2012). Protected areas within the Dominican Republic have nearly 5 times the species richness as those in Haiti, where there exist immense problems with land degradation, human population density, poverty, and limited ability to cope with the impacts of climate change (Sheller & Leon 2016).

We construct models of three periods—past (LGM), present (1975-2016), and future (2050)—to track changes in distribution and predictor variables (both bioclimatic and anthropogenic) through time. By projecting fossil-record-derived LGM climate relationships into the present, we avoided the assumption of niche conservatism and provided a null hypothesis of present solenodon distribution in the absence of human activity (Davis et al. 2014; McGuire & Davis 2014). Our team included expertise from local conservation practitioners, species experts, modelers, and paleoecologists to appropriately build and interpret the SDM results in the context of immediate conservation application.

Methods

Area of study

The island of Hispaniola is divided geopolitically with Haiti in the west and the Dominican Republic in the east. At 76,192 km^2, Hispaniola is the second largest island in the

Caribbean and has an elevation ranging from 3,098 m asl to 46 m bsl. Though lacking in significant seasonal and latitudinal variation (Hijmans et al. 2005), the island's topographical diversity yields many ecosystem types, including moist forest, dry forest, pine forest, grasslands, and savannas. Both countries have approximately the same population size (~10.6 million people each), yet Haiti occupies only one-third of the island's area. Haiti now has an estimated 66% of its land area devoted to agriculture and <4% saved as forest, whereas the Dominican Republic has roughly 50% agricultural land cover and about 40% forest cover (Central Intelligence Agency 2017) (Fig. 1a). In the past and presently, *S. paradoxus* occupies habitats ranging from sea level to approximately 2000 m. Quaternary fossil localities include Massif de La Hotte and Massif de La Selle in Haiti and dry and wet subtropical forest caves in the Dominican Republic, such as Parque Nacional Jaragua and Sierra de Neiba (Ottenwalder 1991, 2001; Mychajliw 2017) (Fig. 1).

Species occurrence data set

We compiled a data set of fossil (*n*=19) and recent (museum records and field surveys; *n*=447) occurrence points of *S. paradoxus* from across Hispaniola for use in past (Last Glacial Maximum, LGM, 22,000 years ago), present (1975-2016), and projected future (2050) models (see Supporting Information for details on occurrence point collection and discussion of the fossil record). To correct for biases in clustered or oversampled locality data, we used a subsampling technique in which we conservatively removed presence points located within a 10-km radius of one another (Fourcade et al. 2014; Elith et al. 2010). Twelve fossil occurrence points and 29 recent occurrence points remained after subsampling (Fig. 1b). Our quality-controlled, subsampled data set of occurrence points exceeded low sample number thresholds suggested by Pearson et al. (2006) and others.

Environmental predictors

Surface geology data for Hispaniola (alluvium, marine strata, metamorphic rock, and volcanic rock) were available from the U.S. Geological Survey (French & Schenk 2004). *S. paradoxus* relies on limestone karst formations for shelter during daylight hours; thus, the distribution of this geologic formation could be a limiting environmental resource. As *S. paradoxus* is an insectivore that searches for prey in certain soils, we also included SoilGrids, a system that uses environmental variables and fitted models to predict most probable World Reference Base soil group (Hengl et al. 2017). We also included elevation data from WorldClim 1.4 (Hijmans et al. 2005).

We incorporated 19 bioclimatic variables from WorldClim 1.4's Community Climate System Model Version 4.0 (CCSM4) for the LGM and present day (Hijmans et al. 2005) and used CCSM4 global climate model projections for 2050 (4 distinct future climate scenarios) (IPCC 2013). Although we ran bioclimate-only models of both the LGM and Mid-Holocene (6,000 years ago), the results exhibited extremely strong spatial overlap (Schoener's D=0.944) and shared the same main predictor variable. We therefore included only the LGM models here to provide an understanding of species responses to climate change in the absence of human activities.

Anthropogenic predictors

Humans did not colonize Hispaniola until approximately 6,000-7,000 years ago (~6,000 calibrated years before present for Vignier II-III and Laurier III marine shell dates [Cooke et al. 2017]); thus, no anthropogenic variables were included in our model for the LGM. In the present, assessments by both the IUCN and local conservation experts recognize predation by free-roaming village dogs and habitat destruction as major threats facing this species across its range (Rupp & Leon 2009; Turvey et al. 2014). Direct hunting for human consumption is also a factor in Haiti (Turvey et al. 2017). To represent these threats in our

model, we incorporated anthropogenic predictor variables including human population density, forest cover, and land use (see Supporting Information).

We created a gridded map of population density with section-level data from the National Statistics Office of the Dominican Republic (2003 national census) and from the U.S. Census Bureau's Demobase map of Haiti, which combines satellite imagery and 2002 national census data (Azar et al. 2010; U. S. Census Bureau 2010; National Statistics Office of the Dominican Republic & Minnesota Population Center 2015). We used forest cover layers derived from Landsat satellite images of tree canopy closure for vegetation >5 m tall in 2000 (Hansen et al. 2013). We also included 22 categories of land cover from the Global Land Cover 2000 (GLC2000) project (Fritz et al. 2003). Because both these data sets were developed in 2000, they present a conservative view of habitat loss on Hispaniola in the present day and reflect the time span of our museum and field-based occurrences.

We developed future anthropogenic predictors for the year 2050 by extrapolating recent trends for human population density (U. S. Census Bureau 2010) and deforestation (Hansen et al. 2013) (Supporting Information).

Species distribution modeling with MaxEnt

We built multiple models for each of the chosen periods in the maximum entropy program, MaxEnt version 3.3.3 (Phillips et al. 2006; Phillips & Dudík 2008). We created 1 model with the fossil occurrence data set and the 19 bioclimatic variables typically used in SDMs for the LGM (Hijmans et al. 2005) (past 1). We created a second past model (past 2) that also included landscape variables (soil type, geology, and elevation) in addition to the bioclimatic variables. For the models of present distribution of 1975-2016, we built a model with the recent occurrence data set and only bioclimatic variables (present 1) and a second model that also incorporated landscape and anthropogenic variables (present 2).

We used the raw output of MaxEnt to yield the relative occurrence rate (ROR) of *S.*

paradoxus across the island because ROR does not require knowledge of the average presence probability of the focal species across the study area (Elith et al. 2010; Merow et al. 2013). Each map was standardized so that the RORs of all cells summed to 1. The maximum number (10,000) of background samples was randomly selected from across the entire island to build the background probability distribution. This allowed MaxEnt to build a basis of comparison for the presence locations that spans the range of environments present in Hispaniola, thus creating a model that accurately captured the island-wide conditions in which this generalist species has been found (Derbridge et al. 2015).

MaxEnt setting selection has been shown to fundamentally impact the model's accuracy and therefore reliability in conservation planning (Phillips & Dudík, 2008; Merow et al. 2013; Morales et al. 2017). We systematically built multiple iterations of each model using all 12 possible combinations of feature classes at varied regularization multiplier values (1, 2, 5, 10, 15, 20) (Morales et al. 2017; Warren & Seifert 2011). This resulted in 72 iterations of each model, each built with a different combination of feature classes and regularization multiplier values and executed using a Windows batch file (Supporting Information).

Model selection, comparison, and projection

We evaluated the 72 iterations of each model with the small sample size corrected Akaike information criterion (AICc), a statistic shown to be robust against sampling bias and to perform well when comparing the relative fit of MaxEnt models built on small sample sizes (Galante et al. 2017; Warren & Seifert 2011). We selected feature classes based on model iterations yielding the lowest AICc score while retaining at least 1 predictor variable. Keeping those feature classes constant, we progressively fine-tuned the regularization multiplier by working in increments of 0.25 until we could not produce a lower AICc. We conducted a Pearson correlation test in ENMTools to ensure that no 2 predictor variables

exceeded a threshold of $r^2 > 0.70$ (Merow et al. 2013; Warren et al. 2010). We employed a jackknife evaluation of variable importance to compare the relative contributions of predictor variables for the finalized models within each period (e.g., past 1 vs. past 2, present 1 vs. present 2). We used model AICc to determine which of the generated models in a given period should be designated the best model based on internal model performance (Table 1).

We generated a null hypothesis of *S. paradoxus* distribution in the absence of human impact by projecting the best-fit past 1 SDM into present day conditions as present 0. We projected present 1 and present 2 into the year 2050 given 4 possible climate scenarios, or representative concentration pathways (RCPs), each based on a different amount of carbon dioxide emitted in the near future (IPCC 2013; Supporting Information; Table 1). With RCP 2.6 humans rapidly mitigate carbon dioxide emissions to avoid planetary warming of 2° C or more (IPCC 2013). The RCP 8.5 scenario represents the most severe global warming in which temperatures could reach 4° C above pre-industrial times (IPCC 2013). Representative concentration pathways 4.5 and 6.0 are intermediate scenarios.

We quantified the spatial overlap of the predicted distributions within and between each period with Schoener's *D* in ENMTools, which outputs a similarity value ranging from 0 (no similarity of distributions) to 1 (identical distributions) (Schoener 1968; Warren et al. 2008; Warren et al. 2010).

Results

Past Distribution

We constructed 2 past SDMs: past 1, with only bioclimatic variables, and, past 2, which incorporated bioclimatic and landscape variables. There was a high degree of overlap between past 1 and past 2 SDMs (Schoener's *D*=0.88). Because past 1 had a lower AICc score than past 2 (ΔAICc=1.22), we discuss only past 1 here (Supporting Information).

Precipitation seasonality and mean diurnal temperature range significantly influenced the predicted spatial distribution (Table 1).

Present Distribution

We constructed 2 present (1975-2016) SDMs: present 1 included only bioclimatic variables and present 2 included bioclimatic, landscape, and anthropogenic variables. The initial present 2 SDM included forest cover as a significant predictor that negatively correlated with *S. paradoxus* presence. However, both field surveys and expert opinion suggest this was a sampling artifact (see Supporting Information for discussion of potential biases). Therefore, we omitted forest cover as a factor for present 2. Present 1 and present 2 showed a high degree of spatial overlap (Schoener's *D*=0.88) (Fig. 2); however, present 2 had an AICc score 2.35 points lower than present 1 (Supporting Information).

Out of the 25 initial input variables, only human population density significantly influenced present 2 (Fig. 2). Relative occurrence of *S. paradoxus* declined precipitously with increasing human population density, showing a stepwise decrease to nearly 0 at values at or above 166 people/km^2 (Table 1). When the fossil distribution of past 1 was projected into the present as present 0, the resulting distribution map demonstrated a high degree of spatial overlap with present 2 (Schoener's *D*=0.88) despite clear qualitative differences linked to national borders (Fig. 2).

Future Distribution

The projection of present 1, future 1, included only bioclimatic variables under 4 alternative RCPs (IPCC 2013)--RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5--in order of increasing warming severity (Supporting Information). Future 2, the projection of present 2, included the full set of available bioclimatic and human variables. These 2 future projections (climate only, climate and humans) (Fig. 3) yielded conflicting distributions that differentially enforce range fragmentation. Projections under the 4 RCPs of future warming

scenarios yielded nearly identical distribution maps (Schoener's D=0.95-0.99) (Supporting Information), indicating that climate alone was not a significant governing factor. These 4 projected distributions were more dissimilar to future 2 (Schoener's D=0.86) than to each other.

Comparisons between SDMs through time

The spatial distribution of past 1 overlapped with the distribution predicted by present 2 (Schoener's D=0.84). There was complete overlap between present 2 and its projection into the year 2050, future 2 (Schoener's D=1), because our projected human population density map for 2050 was based on the assumption of equal population growth across all parts of Hispaniola. However, overlap between past 1 and this future projected distribution was weaker (Schoener's D=0.84) (Supporting Information).

Discussion

Climatic and anthropogenic changes in habitat can reduce the realized niche of a species, shrinking its geographic distribution (Scheele et al. 2017). Comparison of a species' distribution through time can pinpoint geographically variable causes of range contraction and identify opportunities for conservation intervention. Such comparisons are only possible with access to historic and fossil collections (McDonald et al. 2018; Lentini et al. 2018). Our models, which relied on fossil and modern data sets, suggest that humans are directly contributing to the niche reduction of *S. paradoxus*. Sharing this result with conservation partners allowed us to pinpoint locations that may benefit from targeted management approaches.

Our results highlight the utility of the fossil record in disentangling the relative roles and time scales of both the anthropogenic and climatic factors that determine a species' distribution in the present day (Barnosky et al. 2017). Most models of future climate scenarios assume niche conservatism—that is, species climatic envelopes do not change.

However, recent studies reveal mismatches in predicted and true fossil ranges when using SDMs to hindcast distributions from the present (Davis et al. 2014). We suggest the Quaternary fossil record should be used as an additional resource for calibrating niche models in conservation planning (McGuire & Davis 2014), particularly because it is unclear if such deviations from niche conservatism are due to a changing envelope or instead biased by occurrence point collection in anthropogenic habitats. We found no evidence of a climatic niche shift through time based on independent fossil and modern observations for *S. pardoxus*. In both the past and present, precipitation seasonality and temperature predicted occurrence when assessing bioclimatic variables alone (Table 1). This suggests that future projections made based on bioclimatic relationships in the present can be made with confidence for *S. paradoxus*.

Climate change is only one dimension of Anthropocene challenges faced by species, and inclusion of climate variables alone can underestimate true levels of risk (Barnosky et al. 2017). Range contractions in the present may be due to the legacy effects of Pleistocene and Holocene climatic changes on its taxon cycle or instead may represent a recent reaction to human activities. These 2 drivers require 2 different management responses (Garrido-Garcia et al. 2017). We assessed whether the present fragmented distribution of *S. paradoxus* is due to natural decline in its taxon cycle by projecting past 1 (LGM) into the present as present 0. The resulting distribution map demonstrated a high degree of quantitative spatial overlap with present 2 (Schoener's *D*=0.88), and there were clear qualitative differences in fragmentation, suggesting *S. paradoxus* would have a more continuous distribution in the absence of human activities (Fig. 2). Our results are consistent with ecological niche models of Caribbean bat species that display stability from the Last Glacial Maximum to present (Soto-Centeno & Steadman 2015).

The best-fit model of present *S. paradoxus* distribution accounted for bioclimatic, landscape, and anthropogenic variables and was over 3 times more supported than models accounting for bioclimatic variables alone, implying humans are the primary determinant of the solenodon's limited distribution. The cumulative strength of these impacts is perhaps clearest when comparing SDMs of the past's projection into the present (present 0) and present 2 (Fig. 2). Present 0's bioclimatic variables alone would suggest high occurrence in Haiti, yet anthropogenic variables make it virtually impossible for the species to persist. In the absence of human population density, our future climate model suggests many areas of Haiti will be viable as habitat for *S. paradoxus*; however, surveys on the ground (Turvey et al. 2008) confirm that *S. paradoxus* is absent from virtually all of Haiti except the westernmost tip of the Tiburon peninsula, in the Departement du Sud and Departement de l'Ouest in Haiti. These conflicting results across models confirm the pervasive impact of human activities in shaping the distribution of *S. paradoxus*.

Recent genetic studies suggest the 3 allopatric populations of *S. paradoxus* represent 3 subspecies: *S. paradoxus paradoxus* in northeastern Dominican Republic, *S. paradoxus woodi* in southwestern Dominican Republic, and *S. paradoxus haitensis* remaining only on the Tiburon peninsula in Massif de la Hotte (Brandt et al. 2017; Turvey et al. 2016; Grigorev et al. 2018) (Fig. 1). These genetic data reveal extremely low migration rates between putative subspecies in the present day. Our future projection based on climate would reinforce separation of these populations (or putative subspecies) within the Dominican Republic while maintaining a corridor between *S. p. woodi* and *S. p. haitensis* (Fig. 3). Conversely, our projection that includes both climate and human impacts suggests a more realistic scenario given on-the-ground surveys. It maintains the potential for gene flow within populations (or putatitive subspecies) in the Dominican Republic (that is, between *S. p. woodi* and *S. p. paradoxus*) while effectively dooming *S. p. haitensis* to low population sizes,

inbreeding, and extinction. Turvey et al. (2016) report estimates of effective population size as ~3000 for *S. p. paradoxus* in the northern Dominican Republic, yet only ~30 each for the other 2 groups. These genetic data, combined with our SDM results, suggest urgent attention is required to ensure the survival of these 2 populations in the future and contribute to a discussion for the role of corridors.

Differences in governance can create artificial environmental gradients across an otherwise homogenous landscape (Dallimer & Strange 2015). Hispaniola's international border is qualitatively visible in all models that account for anthropogenic influences solely based on the predicted suitable habitat for *S. paradoxus*. The geotectonic history of Hispaniola has generated a distribution of endemic species shared between Haiti's Tiburon peninsula and the southwestern Dominican Republic (Turvey et al. 2016). Protecting these species, such as *S. paradoxus*, the Hispaniolan hutia (*Plagiodontia aedium*), and the rhinoceros iguana (*Cyclura cornuta*), across their full transboundary ranges has almost entirely relied on work by nongovernmental organizations. The 2017 inclusion of the Haitian UNESCO biosphere reserve, La Selle, into the La Selle-Jaragua-Bahoruco-Enriquillo Transboundary Biosphere Reserve provides an unprecedented opportunity for the preservation of ecological corridors on Hispaniola. Additional work with local governments and private landowners will be necessary to link La Selle with habitat on the Tiburon peninsula.

The extremely slow reproductive rate of *S. paradoxus* (litter size of 1-3; gestation >80 days [Derbridge et al. 2015]) coupled with its highly fragmented distribution and low genetic diversity presents a clear need for targeted on-the-ground management that protects existing populations from predators and habitat loss and fosters connectivity across habitat fragments. Culling of feral dogs likely promoted the continued survival of *S. paradoxus* (*haitensis*) in Haiti's Massif de la Hotte (Turvey et al. 2008), suggesting that targeted culling in protected

areas may be a viable management option for this island with no native mammalian carnivores. Maintenance of native habitat complexity by minimizing grazing can decrease the impact of invasive carnivores (Doherty et al. 2015), although such grazing activities are already prevalent in many protected areas.

The recent and rapid transformation of land in the past 500 years necessitates a conservation paleobiology approach for Caribbean islands. Based on bioclimatic needs alone, we have demonstrated that there are many potential places for reintroduction of *S. paradoxus* to its former island-wide range; however, our inclusion of the human variables shows there is much work to be done by NGOs before these landscapes are viable. Because captive breeding efforts have failed and solenodons have >90% mortality in their first year in captivity when taken from the wild (Ottenwalder 1991), targeted support for corridors, decreased predation by invasive carnivores, and enhanced support for transboundary conservation are vital to preserving the full evolutionary diversity of this species in the Anthropocene.

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Table 1. MaxEnt models created to predict *S. paradoxus* distribution.

Model	Variable types	Feature classes	Regularization multiplier	AICc[a]	Significant predictor variables	Relative contribution of variables (%)	ROR[b]
Past 1[c]	bioclimatic	linear quadratic product	0.75	198.50	precipitation seasonality	50	decreases linearly with increasing seasonality
					mean diurnal temperature range	50	decreases linearly with increasing range
Past 2[c]	bioclimatic landscape	linear	1.50	199.72	surface geology	59.2	equally high for alluvium, marine

							strata, and metamorphic rocks
					soil type	40.8	high, associated with ferralsols
Present 1[d]	bioclimatic	linear quadratic product threshold	2.25	661.43	maximum temperature of warmest month	58.0	higher at lower temperatures; threshold drop off at approximately 34 ℃
					precipitation of warmest quarter	20.6	declines linearly with increasing precipitation

					precipitation seasonality	20.6	declines linearly with increasing seasonality
Present 2[b]	bioclimatic landscape anthropogenic	hinge	9.50	659.08	human population density	100	steep, immediate quadratic decline with increasing population density

[c]Built with n=11 fossil localities, pruned from 29 localities total.

[d]Built with n=29 modern localities, pruned from 447 localities total.

[a]Akaike information criterion, corrected for small sample sizes; lower values indicate stronger model performance.
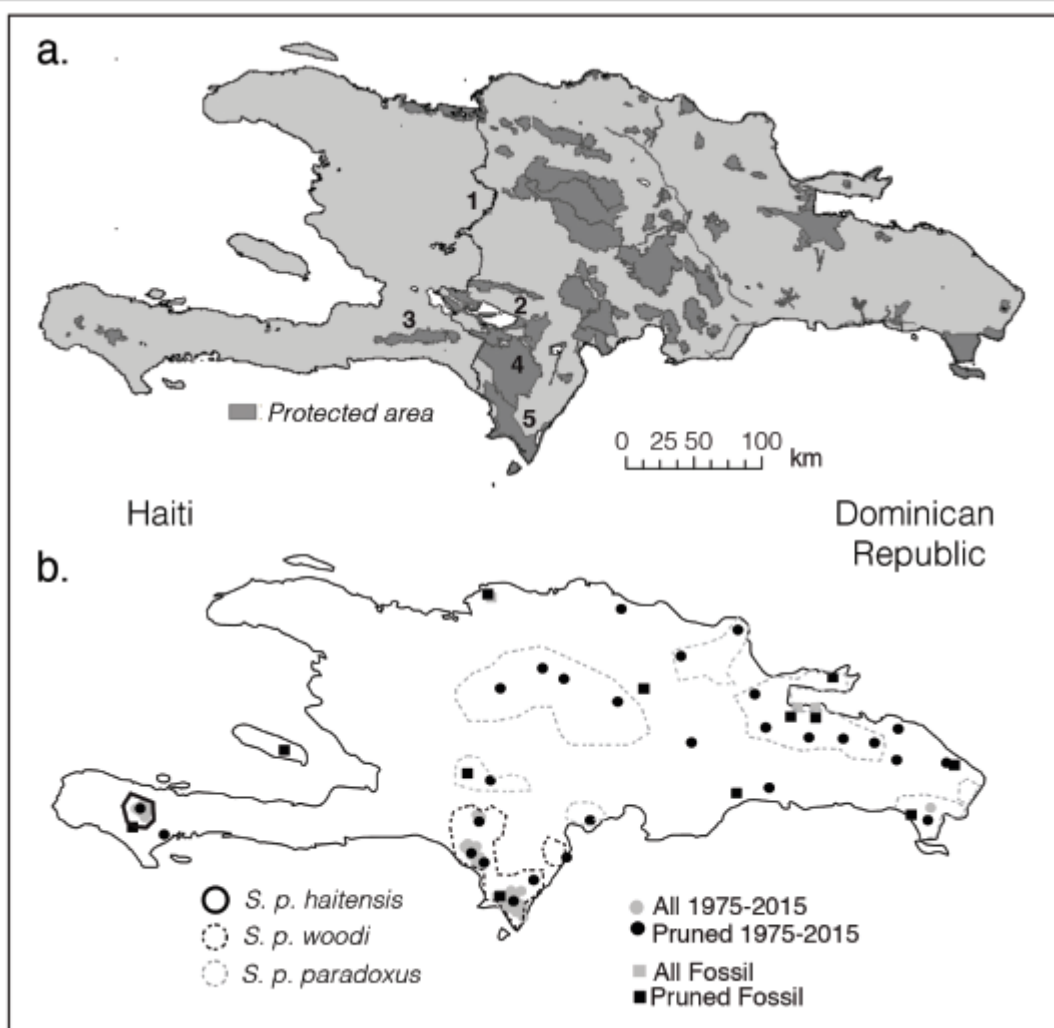
[b]Relative occurrence rate of *S. paradoxus*.

Figure 1. (a) Protected areas of Hispaniola (Haiti and Dominican Republic) and (b)

Solenodon paradoxus occurrence data (full and pruned occurrence data sets) (1, Dominican-

Haitian border; 2, Enriquillo; 3, La Selle; 4, Bahoruco; 5, Jaragua; 2-5, the La Selle-

Bahoruco-Jaragua-Enriquillo UNESCO Biosphere Reserve). Range of *Solenodon paradoxus*

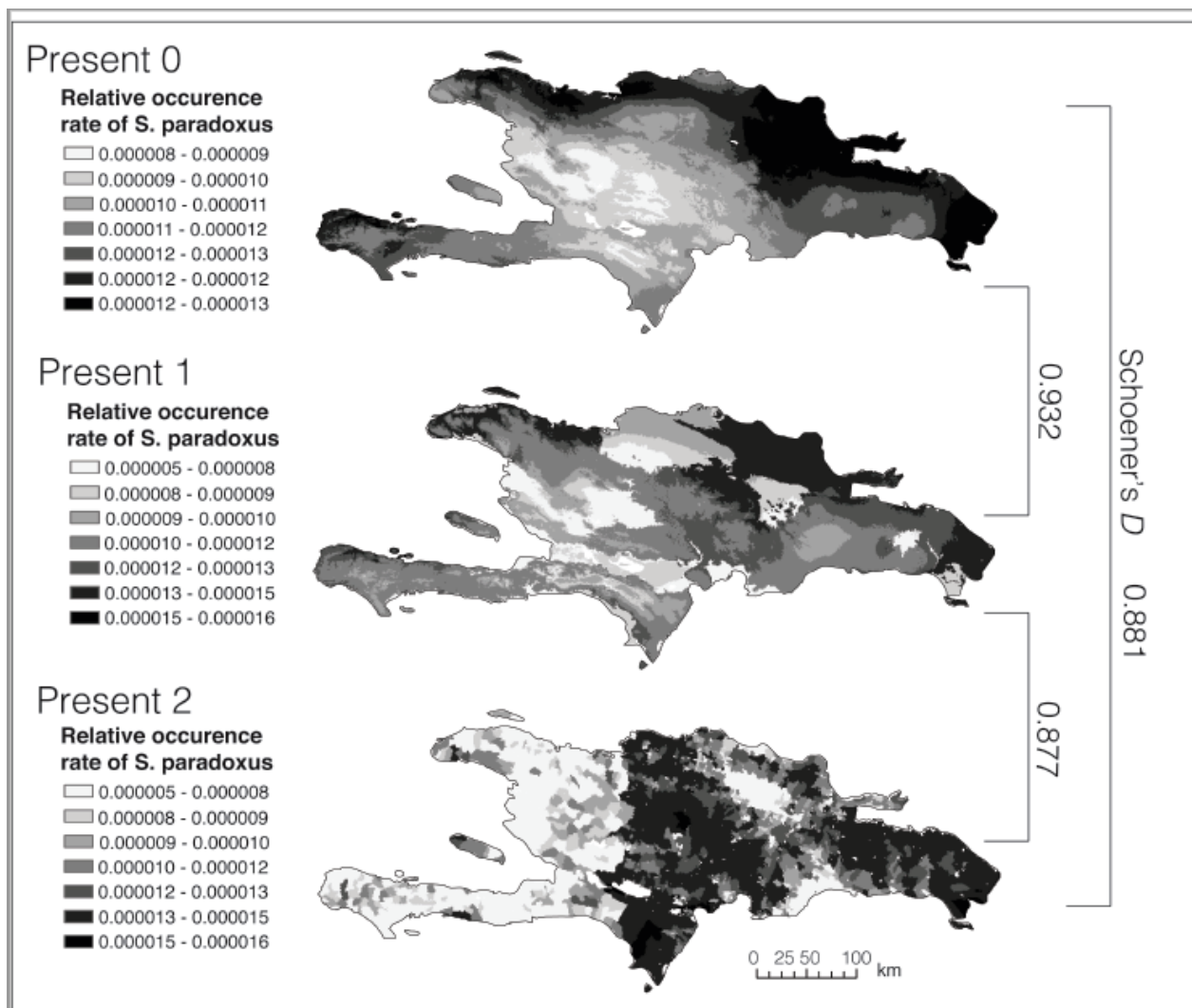as of 2017 and putative subspecies names are from Turvey et al. (2017).

Figure 2. Alternative models (1-3) of the present day distribution of *Solenodon. paradoxus*:
present 0 (null model projected from Last Glacial Maximum distribution), present 1
(bioclimatic variables of the present only), and present 2 (bioclimatic, landscape, and human
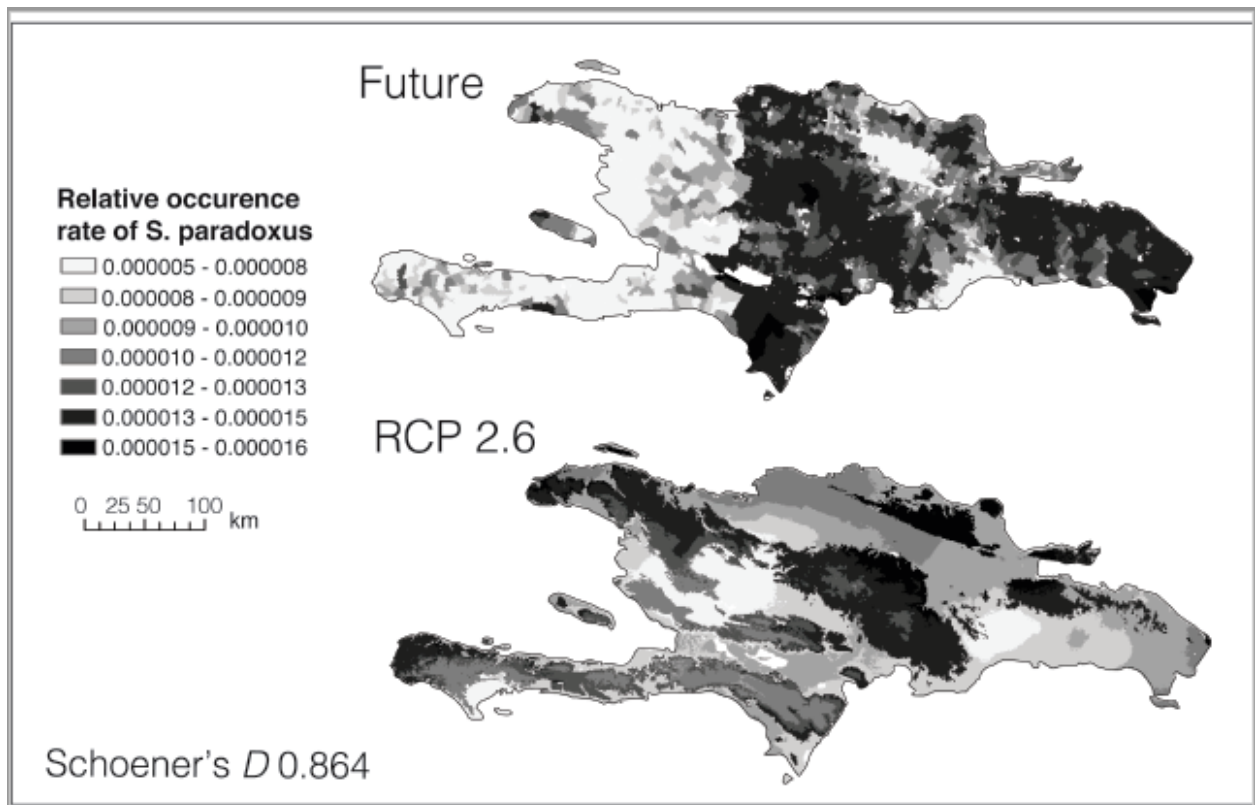variables) (brackets, pairwise Schoener's *D* overlap values).

Figure 3. Projected future distribution of *Solenodon paradoxus* in 2050, including future (projected from the present 2 model that includes bioclimatic, landscape, and anthropogenic variables) and RCP 2.6 (projected into climate change representative concentration pathway 2.6 from the present 1 model that includes only bioclimatic variables) (Schoener's *D*, overlap between the 2 projected distributions).