Report

Current Biology

Historical baselines reveal suitable conservation landscapes for Javan and Sumatran rhinoceros

Highlights

- Southeast Asian rhino conservation is guided by the ecology of remnant populations
- Past records show they are ecological generalists that existed in diverse habitats
- Rhino habitat still exists across Southeast Asia, including in many protected areas
- Re-establishing populations across their past range may be ecologically feasible

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In brief

Modern baselines suggest that limited habitat exists for Javan and Sumatran rhinos, two of the rarest mammals. Granger et al. use historical, archaeological, and fossil archives to reveal that suitable landscapes exist for these ecological generalists across Southeast Asia, with current-day distributions representing a small fraction of their environmental niches.

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Report

Historical baselines reveal suitable conservation landscapes for Javan and Sumatran rhinoceros

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SUMMARY

Ecological baselines are challenging to establish for tiny surviving populations of threatened species, and historical archives can contain conservation-relevant information about past species distributions and environmental requirements that are unavailable from modern data.[1–4] The Javan rhinoceros (*Rhinoceros sondaicus*) and Sumatran rhinoceros (*Dicerorhinus sumatrensis*) have both experienced catastrophic range collapses due to hunting and habitat loss and are among the world's rarest mammals,[5] with current conservation planning based upon inferences about ecological conditions in landscapes still supporting remnant populations.[6–9] We investigated a large-scale dataset of multi-century historical occurrence records of both species within a species distribution modeling framework to define rhinoceros environmental niches, evaluate habitat suitability within landscapes that contain surviving populations, and assess how realized rhinoceros niche space has changed over time. Historical records demonstrate that Southeast Asian rhinos are ecological generalists that formerly occurred across diverse habitats and a broad elevational range. Substantial suitable habitat still exists across Southeast Asia, including within many protected areas that currently lack rhinos, and both species are able to co-occur within many landscapes. Sites that retain remnant rhinoceros populations vary in suitability and may decrease in suitability under future climate change, and our results highlight the importance and ecological feasibility of re-establishing populations across areas of their former range. Older records demonstrate that both species occupied even broader environmental niches during the Holocene, which were reduced through protracted declines pre-dating the recent historical period. These findings demonstrate the need to integrate past and present evidence into conservation planning for the world's rarest species.

RESULTS

Javan rhinoceros are restricted today to Ujung Kulon National Park in western Java.[10,11] Sumatran rhinoceros recently occurred in three Sumatran national parks (Bukit Barisan Selatan, Gunung Leuser, and Way Kambas) and are only confirmed to survive in Gunung Leuser, with a few individuals in non-protected landscapes in Sumatra and Borneo.[12,13] However, both species formerly had much broader distributions and are widely recorded in historical archives (traveler accounts, hunting records, and museum metadata) made by European visitors and colonists to Southeast Asia during recent centuries.[14–19] We compiled a large-scale dataset of rhinoceros records comprising 48 modern (post-2015) records (Javan, $n = 13$; Sumatran, $n = 35$) and 598 historical records where species identification was possible (Javan, $n = 353$, from 1630–2010 and 10 countries; Sumatran, $n = 245$, from 1835–2015 and 8 countries) (Figure 1; Data S1A and S1B).

Rhinoceros habitat suitability

Species distribution models (SDMs) based upon the statistical relationship between occurrence records and environmental

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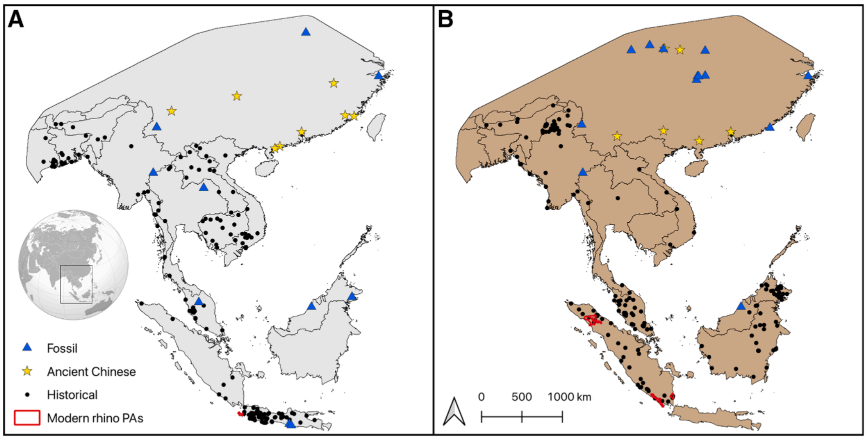

Figure 1. Past occurrence records for Southeast Asian rhinoceros species and Indonesian protected areas that contained populations into the twenty-first century
(A) Javan rhinoceros.
(B) Sumatran rhinoceros.
See also Figure S4 and Data S1.

variables can predict other areas of suitable habitat.[20] SDMs that combined historical and modern records were used to predict habitat suitability across each species' former range and identify which variables primarily influence their distributions. Following data-thinning, the Javan rhinoceros model contained 168 records and the Sumatran rhinoceros model contained 188 records. Models showed high Boyce index scores (strong agreement between predicted suitability and test data) and high test AUCs (strong discriminatory power independent of threshold choice), but omission rates of >10, indicating they potentially overlook suitable habitat with fewer records (Table 1).

In contrast to their restricted modern distributions, model projection predicts suitable habitat across continental and insular Southeast Asia for both Javan rhinoceros (total, 2,602,700 km^2; with species-specific Global Human Footprint [GHF] cutoff, 1,214,060 km^2) and Sumatran rhinoceros (total, 1,779,260 km^2; with species-specific GHF cutoff, 1,330,960 km^2) (Figures 2 and S1; Data S1D). Extensive suitable landscapes are predicted for both species in northeast India, Bangladesh, western Myanmar, peninsular Malaysia, Sumatra, and Java (total: 1,296,480 km^2). Landscapes more suitable for Javan rhinoceros are distributed across Indochina and eastern peninsular Southeast Asia, with highly suitable habitat across much of Java and within many Javan protected areas (Figure 3). Landscapes more suitable for Sumatran rhinoceros are distributed across Borneo and northern Myanmar and neighboring regions. Numerous large protected areas across this region (above the minimum size of protected areas containing surviving rhinoceros populations) have high predicted suitability for one or both species, with sites highly environmentally suitable for both species in Myanmar, Thailand, Borneo, and Sumatra (Data S1E).

The most influential model variable for both species was temperature seasonality (average model contribution: 63.52% for Javan rhinoceros, 66.77% for Sumatran rhinoceros), with occurrence probability higher at low seasonal variation. For Javan rhinoceros, mean annual precipitation and precipitation seasonality also made substantial (>10%) model contributions (occurrence probability highest at mid-to-high annual and seasonal precipitation). For Sumatran rhinoceros, mean annual precipitation also made a substantial contribution (occurrence probability highest at mid-annual precipitation) (Figure S2; Data S1F). Elevation was excluded from models due to correlation with other variables, but Pearson's correlation tests to investigate its influence on habitat suitability indicated significant but weak negative correlations with average pixel suitability for both species (Javan rhinoceros, correlation = -0.262, $p = 2.2 \times 10^{-16}$; Sumatran rhinoceros, correlation = -0.143, $p = 2.2 \times 10^{-16}$).

Habitat quality within rhinoceros landscapes

Historical records were also modeled without modern records to independently evaluate habitat quality within protected areas containing surviving populations (i.e., without the circularity of including modern records for these landscapes). Following data-thinning, the Javan rhinoceros model contained 162 records and the Sumatran rhinoceros model contained 170 records, with models showing similar test statistics to the combined models (Table 1). The Javan rhinoceros model predicts that Ujung Kulon represents generally good-quality habitat, with a mean suitability of 0.942 (SD = 0.015) for the peninsular part of the park (the part inhabited by rhinoceros). The Sumatran rhinoceros model predicts that Sumatran national parks all contain areas of suitable habitat. Gunung Leuser contains the highest predicted suitability averaged across the park (mean suitability = 0.927, SD = 0.102), and Bukit Barisan Selatan is also predicted to contain substantial suitable habitat (mean suitability = 0.724, SD = 0.151). Conversely, Way Kambas is only predicted as moderately suitable (mean suitability = 0.447, SD = 0.015), with much lower mean values for mean annual temperature, precipitation seasonality, and ruggedness, and with suitability decreasing in the east (Figure 3).

Combined models were projected using future climate projections to understand the changing suitability of current rhinoceros landscapes. Bioclimatically suitable habitat is predicted to increase progressively across Southeast Asia for Javan rhinoceros under all future scenarios, although trends vary for Sumatran rhinoceros, and the pessimistic higher-impact scenario predicts a future decrease in suitable habitat (Figure S3; Data S1D). Comparisons between current and future combined models predict varying future suitability across Indonesian protected areas: species-specific models predict mean suitability for peninsular Ujung Kulon remains stable under optimistic scenarios but decreases under pessimistic scenarios, Gunung Leuser decreases slightly under all scenarios, Bukit Barisan Selatan increases under optimistic scenarios but decreases under pessimistic

Table 1. Data and parameters for rhinoceros SDMs

Model	Modern records	Historical records	Beta multiplier	Feature types	Variables	Boyce's index	Test AUC	Omission rate
Javan rhinoceros								
Combined	7	161	4	LQPH	BIO1, BIO2, BIO4, BIO12, BIO15	0.76 ± 0.11	0.87 ± 0.02	11.27 ± 7.19
Historicalonly	0	162	1	LQP	BIO1, BIO2, BIO4, BIO12, BIO15, ruggedness	0.81 ± 0.10	0.86 ± 0.02	20.04 ± 10.05
Sumatran rhinoceros								
Combined	21	167	0.25	LQP	BIO1, BIO2, BIO4, BIO12, BIO15, ruggedness	0.80 ± 0.11	0.88 ± 0.02	13.46 ± 5.92
Historicalonly	0	170	0.5	LQP	BIO1, BIO2, BIO4, BIO12, ruggedness	0.74 ± 0.15	0.86 ± 0.02	10.91 ± 6.31

Number of occurrence records, optimal parameters, and evaluation statistics for final models using combined modern and historical records and historical-only records, respectively. Feature types: LQP, linear-quadratic-product; LQPH, linear-quadratic-product-hinge. Details of bioclimatic variables (BIO1–BIO15) are provided in the STAR Methods.
See also Data S1.

scenarios, and Way Kambas decreases under all scenarios (Data S1D).

Truncation of realized niche

Both species have broad historical elevational distributions (Javan rhinoceros, mean = 369 m, range = 2–2,135 m; Sumatran rhinoceros, mean = 471 m, range = 1–2,574 m). The elevational distribution of recent Sumatran rhinoceros populations is statistically similar to their historical distribution (mean = 672 m, range = 15–1,829 m; p = 0.101), but Javan rhinoceros now occupy a significantly lower-elevation fraction of their historical distribution (mean = 40 m, range = 8–91 m; $p < 0.00001$) (Figure S4).

Rhinos are also recorded in Chinese historical archives (*difangzhi* gazetteers containing local environmental data together with economic and demographic information) from the first millennium BCE to the twentieth century[21] and in Holocene zooarchaeological and fossil contexts across China and Southeast Asia.[22–25] We compared our historical dataset against 14 Chinese archival records (Javan, n = 8; Sumatran, n = 6) (Data S1G) and 24 Holocene records (Javan, n = 11; Sumatran, n = 13) (Data S1H). Compared with historical records, Chinese and Holocene records show similar elevational distributions for Javan rhinoceros (mean = 530 m, range = 11–2,575 m; p = 0.337), but a significantly higher elevational distribution for Sumatran rhinoceros (mean = 868 m, range = 19–2,414 m; p = 0.028) (Figure S4). Principal component analyses (PCAs) show that many Chinese and Holocene records fall outside the historical niche space of each species, representing substantial additional niche extent along PC1 (Javan rhinoceros, 38.6% greater extent; Sumatran rhinoceros, 39.7% greater extent) and further separation along PC2 for Javan rhinoceros (Figure S4; Data S1I and S1J).

DISCUSSION

Robust conservation evidence is often challenging to obtain for tiny remnant populations that require urgent management.[26,27] Environmental archives are a potentially important source of conservation information, and our study synthesizes historical baselines to reconstruct the former distribution and ecology of two Critically Endangered species, the Javan rhinoceros and Sumatran rhinoceros. Fewer than 100 individuals of each species survive, and they remain vulnerable to poaching, stochastic demographic risks, and additional threats (e.g., habitat degradation, livestock diseases, and tsunami risk).[13,28–31] Without concerted and evidence-based interventions, they may soon become extinct.[5,32] We demonstrate how past data are essential for understanding the environmental drivers of Southeast Asian rhinoceros distributions, assessing habitat quality at sites where they persist, and identifying suitable landscapes for future management. Our results provide new insights into rhinoceros ecology that are unavailable from modern data, with wider implications for integrating environmental archives into conservation planning.

Expanding the ecological niche for Southeast Asian rhinos

Southeast Asian rhinoceros environmental modeling has previously employed past records only to infer continental-scale demographic change across Quaternary climatic shifts,[33] with investigation of habitat suitability only conducted using small datasets from modern rhinoceros landscapes.[9,34–36] Sites where remnant populations persist typically exhibit only a subset of the environmental conditions under which they formerly occurred, with survival often associated with reduced threats rather than habitat suitability.[3,4] SDMs based upon such uneven sampling can produce prediction artifacts (e.g., predicting greater suitability close to modern localities),[37] and using current-day data alone to guide conservation of such populations risks misinterpreting their ecology and setting restrictive or inappropriate intervention targets.[3,4,38]

Conversely, multi-century historical data reveal that both species have broad ecological tolerances, with seasonal temperature variation the most important environmental predictor. Although elevation and average pixel suitability show a weak negative correlation, both species historically occurred across a wide elevational range, and ruggedness made no substantial contribution to models, indicating landscape topography has little effect on broad-scale distribution. Southeast Asian rhinos can

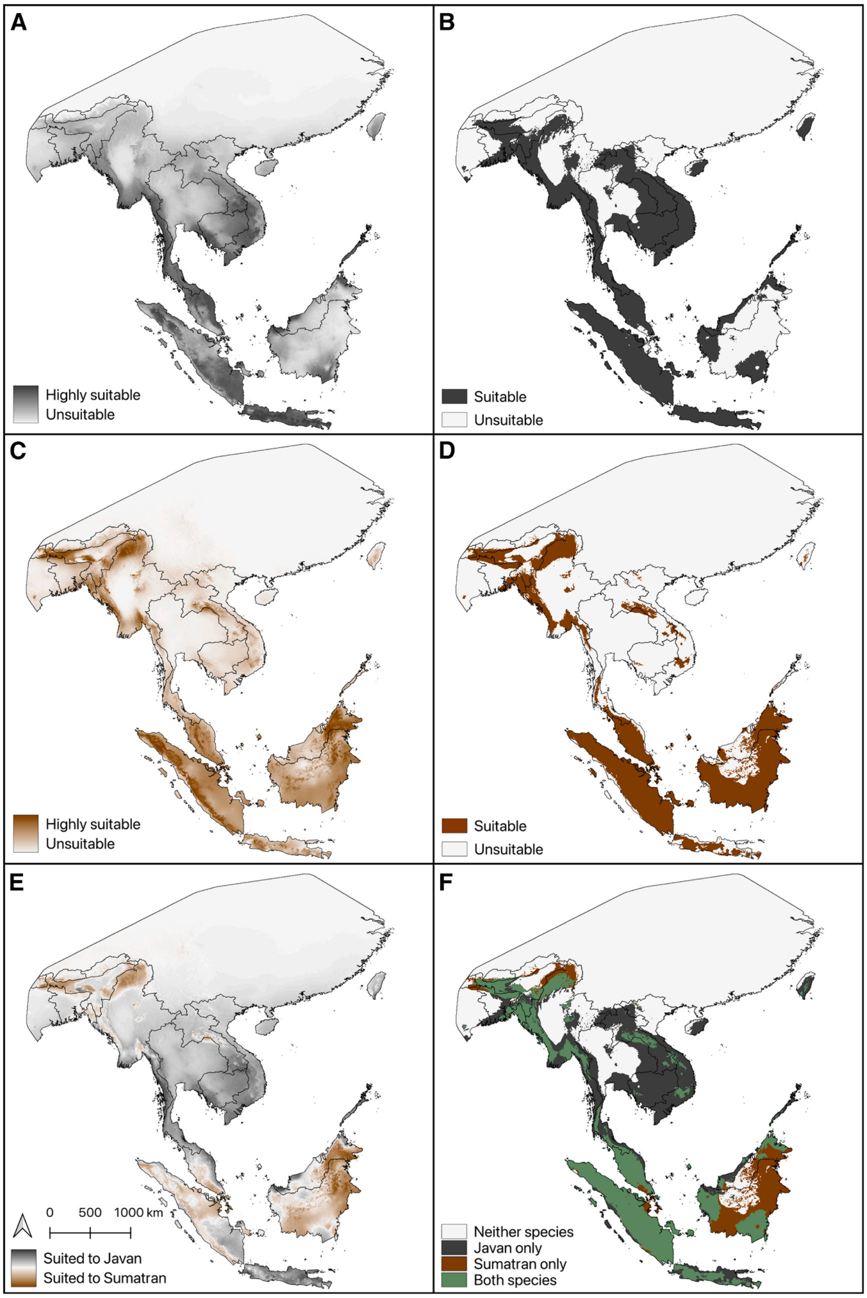

Figure 2. Predicted rhinoceros habitat suitability across Southeast Asia

(A–D) Geographic habitat suitability projections modeled using historical and modern data.
(A) Javan rhinoceros continuous projection.
(B) Javan rhinoceros binary projection.
(C) Sumatran rhinoceros continuous projection.
(D) Sumatran rhinoceros binary projection.
(E and F) Comparative standardized habitat suitability for both species: (E) continuous projection and (F) binary projection.
See also Figures S1–S3 and Data S1.

therefore be interpreted as ecological generalists, with historical data substantially expanding our understanding of niche requirements. Historical accounts also report each species from diverse habitats (Data S1K), and recent studies interpret both as generalist herbivores.[9,39] Whereas recent authors have inferred elevational niche differentiation between the species,[40–42] former co-occurrence was widely reported by contemporary observers (Data S1K), and they co-occur at several Holocene sites,[22,43–45] with their modeled distributions determined by similar bioclimatic parameters and showing considerable overlap. Many landscapes thus formerly supported two rhinoceros species, and sympatric Asian megafaunal assemblages were more diverse than often realized.[46] These broad niches are predicted to remain resilient to climate change, providing a note of hope if immediate threats can be mitigated. However, the wide historical distributions and generalist ecologies of Southeast Asian rhinos highlight the widescale loss of ecosystem processes (e.g., seed mutualisms) regulated by these keystone species,[47] which have been disrupted across the region rather than only lost from specific habitats.

Management implications of historical baselines

Our historically informed baselines can inform real-world decision-making for surviving rhinoceros populations and suggest new directions for conservation. The last two Indonesian protected areas that support rhinos, Ujung Kulon and Gunung Leuser, are predicted to represent good-quality habitat for each species and thus constitute ecologically suitable landscapes for conservation investment. However, suitability at both sites is predicted to decrease slightly under most future scenarios. Survival of Javan rhinoceros near sea level at Ujung Kulon has led to perceptions that it is a lowland forest specialist,[6,8,9,40] with few other landscapes considered suitable due to extensive lowland deforestation across Indonesia.[48] However, historical data reveal this species can occupy a broad elevational range, with past observers regularly remarking upon its occurrence at high elevations across Java and other regions (Data S1K). Translocation of Javan rhinoceros to a second Indonesian landscape has been suggested to enable population growth and mitigate against site-specific risks,[10,31,49] and we highlight the ecological feasibility of this potential strategy.

Our models predict that extensive rhinoceros habitat exists across Southeast Asia and identify areas lacking rhinos but containing optimal habitat with high ecological potential to re-establish populations, including within many large protected areas. Although translocation to sites outside Indonesia is currently

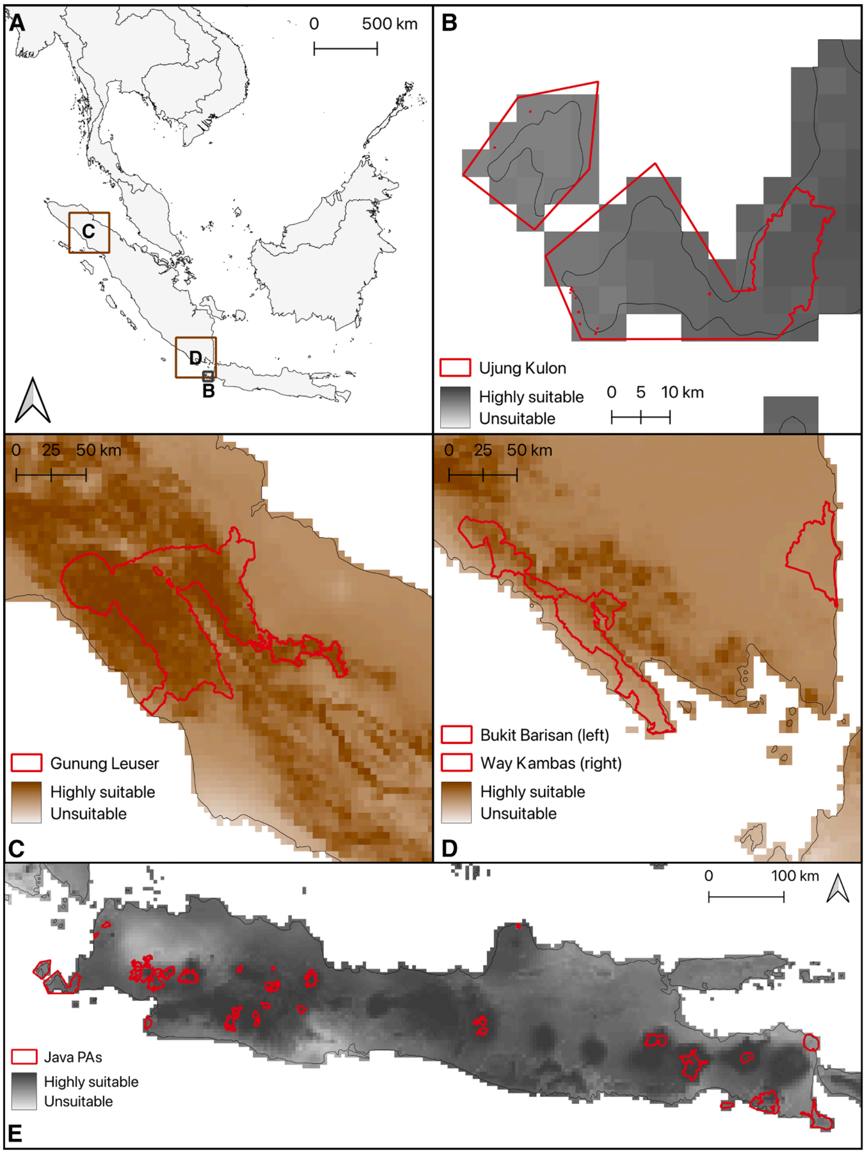

Figure 3. Predicted habitat suitability within current Southeast Asian rhinoceros landscapes and neighboring regions

(A) Distribution of Indonesian protected landscapes where rhinos still occurred in the twenty-first century.

(B) Continuous projection of Javan rhinoceros model (historical data) onto Ujung Kulon National Park (Javan rhinoceros occur only on the Ujung Kulon peninsula, not Panaitan Island).

(C) Continuous projection of Sumatran rhinoceros model (historical data) onto Gunung Leuser.

(D) Continuous projection of Sumatran rhinoceros model (historical data) onto Bukit Barisan Selatan and Way Kambas.

(E) Continuous projection of Javan rhinoceros model (historical and modern data) across Java, showing predicted habitat suitability of protected areas outside Ujung Kulon National Park.

See also Figures S2 and S3 and Data S1.

unlikely, considerable habitat exists for Javan rhinoceros across Java, including higher-elevation areas previously considered unsuitable, with several Javanese protected areas representing possible translocation sites. Suitable landscapes are also predicted in eastern Java, a region with few historical records and where several observers considered rhinos to be rare or absent in recent centuries (Data S1K). Java has an east-west precipitation gradient with drier eastern habitats and distinct vegetation communities,[50] but Quaternary Javan rhinoceros fossils are known from this region, supporting its likely suitability.[51,52] Conversely, Sumatran rhinoceros reintroduction to Way Kambas is not ecologically appropriate, as this landscape is predicted to be marginal habitat that will decrease further in suitability.

We recommend that large contiguous protected areas of high-suitability habitat should be evaluated as potential reintroduction sites through assessment of factors including community support,[53] habitat area required for viable populations,[28] and presence of habitat features associated with local-scale rhinoceros site selection (e.g., wallows browse quality[54–57]). Both species can occur sympatrically and thus could potentially be managed within the same landscapes, with many protected areas containing suitable habitat for both species, although relative benefits (e.g., shared investment of conservation resources) and risks (e.g., potential interspecific competition for ecological resources) would require careful consideration.

Can historical archives determine rhinoceros ecology?

The usefulness of environmental archives can be impeded by data incompleteness. Although we cropped projections by species-specific GHF, historical records cannot be correlated directly with indices of recent forest change or other modern human activities, which are key factors regulating mammal distributions.[58] Habitat integrity and associated pressures must therefore be evaluated across all candidate translocation sites, with future predictions representing 'best-case' scenarios that do not accommodate ongoing forest clearance across Southeast Asia.[59]

Although incorporating historical distributions into SDMs is recognized as essential for predicting species' environmental requirements and responses to future change,[60] global temperatures have risen by 1.1°C since 1850–1900,[61] raising methodological concerns with modeling older records using recent bioclimatic data. This issue affects all historical data in SDMs of current and future distributions, potentially leading to underprediction or overprediction.[62] Most rhinoceros records predate 1970–2000, the temporal limit of available bioclimatic data,[63] but no temporally well-resolved bioclimatic layers are available across the multi-century period of our records.[64] Current and future predictions should therefore be interpreted as guidelines, with the suitability of candidate translocation sites requiring verification. However, this issue is more likely to bias models for range-restricted species with limited records instead of ecological generalists with broad historical distributions,[65] and the largest source of uncertainty in predicting climate change responses is typically variation in estimated future scenarios.[66] Our models provide broadly consistent predictions across optimistic and pessimistic future scenarios, supporting their likely validity.

Data quantity does not reflect data quality, and large datasets may contain sampling biases that affect SDM accuracy.[67] Our models show high omission rates, indicating they potentially overlook suitable habitats with lower representation of existing records. Models therefore represent minimum estimates of suitable niche space, and rhinoceros environmental tolerances and historical distributions may have been broader than predicted, with even more habitat still present across Southeast Asia.

Due to spatial imprecision of Chinese records[21] and bioclimatic imprecision of Holocene records,[64] these data types were not included within SDMs, and their environmental characteristics are generalized and potentially imprecise. However, they fall outside the niche space of well-resolved historical records and exhibit wider variation across several environmental factors, with differing elevational distributions between the two rhinoceros species suggestive of a valid ecological signal despite potential imprecision. The strong predictive power of temperature seasonality in our models may therefore be an artifact reflecting rhinoceros extirpation from China, where populations occurred in temperate or subtropical rather than tropical conditions with differing seasonality. Early loss of the northern part of rhinoceros ranges, where Sumatran rhinoceros occurred close to the Tibetan Plateau,[25] thus drove substantial contraction of global realized niche space, although rhinos potentially persisted in southern China until relatively recently.[21,68] Protracted pre-modern declines are also shown by other species due to ancient human pressures,[24,69] posing important considerations for interpreting evidence from different archives and defining historical biodiversity baselines.[70]

Further conservation evidence might be available from Pleistocene rhinoceros records, which are distributed more widely than Holocene records.[71] Unfortunately, many Pleistocene records have poor temporal and taxonomic resolution,[72,73] with limited availability of paleoclimatic reconstructions.[65] Future work could also explore whether geographically and genetically distinct populations (subspecies, discrete conservation units) exhibited local differences in niche flexibility.[74,75] However, substantial environmental variation is shown by extinct populations that occurred close to surviving populations (e.g., across Java), indicating that even subspecies-level datasets would show broad tolerances.

Our study highlights the unique information content and expanded ecological baselines provided by biodiversity archives for conservation decision-making. Historical data exist for many species and systems, and mechanisms to increase their uptake into modern decision-making are a recognized priority.[76] This approach requires careful consideration to ensure research findings represent comprehensive, unbiased insights into key ecological parameters but has crucial potential to shape conservation planning for the world's rarest species.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Samuel Turvey (samuel.turvey@ioz.ac.uk).

Materials availability

This study did not generate any new, unique reagents.

Data and code availability

- All data necessary to interpret and replicate results are available in the main text and Figures S1–S4 and Data S1.
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

S.T.T., B.L., and M.A.H. designed and oversaw the project; M.G., S.T.T., P.A.B., S.M.B., M.G., A.S., R.M., K.O.K., S., R.S., I.-T.T., and H.M. collected data; M.G., M.A.H., and J.P.H. conducted analyses; and S.T.T. and M.G. wrote the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
- METHOD DETAILS
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Species distribution modeling
  - Comparison of record types

SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Georeferenced historical locality data for Javan rhinoceros and Sumatran rhinoceros	This paper	Data S1B
Georeferenced locality data from Chinese historical gazetteers (difangzhi) for Javan rhinoceros and Sumatran rhinoceros	This paper	Data S1G
Georeferenced locality data from Holocene fossil and zooarchaeological records for Javan rhinoceros and Sumatran rhinoceros	This paper	Data S1H
Dataset of historical observations about past ecology, habitat use, and co-occurrence of Javan rhinoceros and Sumatran rhinoceros	This paper	Data S1K
Software and algorithms		
MaxEnt v.3.4.4	American Museum of Natural History, New York, NY	https://biodiversityinformatics.amnh.org/open_source/maxent/
R v.4.4.0	R Foundation for Statistical Computing, Vienna, Austria	https://cran.r-project.org/
QGIS v.3.16	Open Source Geospatial Foundation Project	https://www.qgis.org/

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

To reconstruct the changing distribution and ecology of the Javan rhinoceros and Sumatran rhinoceros over time, we compiled new large-scale datasets of geographic occurrence records for each species, comprising recent, historical, zooarchaeological and fossil data.

Recent rhinoceros locations (Ujung Kulon and three Indonesian protected areas where Sumatran rhinoceros occurred into the twenty-first century) were obtained by extracting coordinate data from available environmental rasters, using the midpoint of each rhinoceros-occupied pixels. Specific locality data for surviving Southeast Asian rhinoceros populations cannot be shared due to concerns over continued poaching risk for these highly vulnerable populations.[77]

Post-1600 CE historical records from outside recent rhinoceros distributions were obtained from a survey of the published literature using the Rhino Resource Centre (http://www.rhinoresourcecenter.com/); museum accession records identified through the literature, online museum databases, the Global Biodiversity Information Facility (https://www.gbif.org/), the Natural Sciences Collections Association (NatSCA), and email requests to curators; and personal communications with field researchers (Data S1B). Most records lacked coordinate data; coordinates were determined through requests to local researchers or by georeferencing locality descriptions using Google Earth (https://earth.google.com/web/) using consistent rules to reduce spatial bias (Data S1A). Records were excluded if their geographic details were too limited to be georeferenced using these rules, or where species identification was ambiguous.

Javan and Sumatran rhinos are the only rhinoceros species known to have occurred in China during the Holocene based upon their presence in archaeological and recent fossil sites,[24] and historical rhinoceros records from China that could be identified to either species based upon accompanying descriptions (Data S1G) were obtained from a compilation of Chinese gazetteers or *difangzhi*.[21]

Postglacial records of rhinoceros material from archaeological or recent fossil contexts (Data S1H) were also collected from the literature, georeferenced, and assigned to one of three *ca.* 4000-year subdivisions of the Holocene for which palaeoclimatic estimates are available.[64]

METHOD DETAILS

We investigated our rhinoceros datasets using species distribution modelling and principal component analyses to gain new insights into historical rhinoceros ecology. Given the limited understanding of environmental factors that might predict habitat suitability and distribution of Javan and Sumatran rhinoceros, a range of variables associated with temperature, precipitation, topology and geology were considered for each species (Data S1C). Bioclimatic data were obtained from WorldClim v.2.1,[63] with all 19 bioclimatic variables initially considered. Elevation data were obtained from the 30m ASTER Global Digital Elevation Model[78] and were also used to calculate separate slope and ruggedness layers, with ruggedness calculated as the standard deviation of the elevation pixels of the 30m raster that fall within each 20km^2 pixel.[79] Geological data were obtained from GLiM v.1.0,[80] which uses vector polygons to define spatial distributions of 15 geology types; these were included within one categorical layer, with pixels assigned the geology type with highest local percentage cover. Modern land-cover or human footprint variables could not be used to generate SDMs, as these metrics have changed across the timespan represented by historical records.

QUANTIFICATION AND STATISTICAL ANALYSIS

Species distribution modeling

SDMs were built using maximum entropy modelling in MaxEnt v.3.4.4,[81] which has higher predictive performance, fewer assumptions, and reduced risk of overfitting compared to other approaches for modelling presence-only data.[82–84] The study area was defined as a minimum convex polygon of 8,025,280 km^2 around all modern, historical, Chinese, zooarchaeological and fossil records before dataset thinning, with a 200 km buffer (following VanDerWal et al.[85]) to provide a background area of pseudoabsence for MaxEnt to contrast against presence areas. Model resolution was based upon rhinoceros home range size. Both species are considered to have similar home ranges, although with considerable within-species disparity in estimates (Javan rhinoceros: 2.6-105.5 km^2, Sumatran rhinoceros: 5-50 km^2), and with further variation between seasons, sexes, breeding status and life stage.[28,31,86,87] A mid-range value of 20 km^2 was selected for both species. This relatively large resolution will reduce the effect of spatial autocorrelation and provide an error buffer for potential small-scale inaccuracy in estimating historical localities. To further control for spatial bias, each species' combined dataset of historical and modern records was thinned using the 'spThin' package in R v.4.4.0,[88] using a 5.8 km radius around each record (matching largest home range estimate of 105.5 km^2). Higher-resolution layers were resampled to match model resolution in QGIS v.3.16[89]; each new pixel assumed the mean value of constituent pixels. Layers were reprojected to Asia South Albers Equal Area Conic. Rasters were cropped to the study area.

To reduce redundancy and computational load, collinear variables were removed until VIF scores were <5. The final reduced set of non-collinear variables used in all models included: mean annual temperature (BIO1), mean diurnal temperature range (BIO2), temperature seasonality (BIO4), mean annual precipitation (BIO12), precipitation seasonality (BIO15), geology, and ruggedness. All pairwise Pearson correlation coefficients for these variables had values of $\leq$0.7. VIF reduction led to removal of elevation from models because it was correlated with BIO1. Elevation does not influence species distributions directly but is instead correlated with bioclimatic factors that have direct physiological effects (e.g., precipitation, temperature), and this correlation varies with latitude; as our study area ranges from the equator to 35.0°N, the potential predictive relationship of elevation may thus be spatially variable.[90] To investigate whether elevation influences rhinoceros habitat suitability, a Pearson's correlation coefficient test of suitability against elevation was performed, whereby elevation and average suitability scores from the combined model were extracted from 10,000 random pixels across the study area. Pixels containing higher elevations than the highest record for each species were removed, leaving 9,006 pixels for Javan rhinoceros analysis and 8,980 pixels for Sumatran rhinoceros analysis.

Each model used an 80:20 split of training data to test data, and 10,000 random background points. Models were calibrated with the 'kuenm' package,[91] which builds large numbers of candidate models with varying predictor combinations, feature types and beta multipliers. Models were selected if they were statistically significant (assessed using partial ROC), had an omission rate below 5%, and had the lowest Akaike Information Criterion with correction (AICc) score, which is more accurate for small sample sizes. Every combination of two or more variables was tested (excluding geology, as kuenm cannot accommodate categorical variables), with combinations of four feature types (linear, quadratic, product, hinge: l, lq, lqp, lqph) and five beta multipliers (0.25, 0.5, 1, 2, 4), resulting in 2400 candidate models. The candidate model with lowest AICc for each species was run 1000 times with bootstrap sampling, both with and without geology as a variable, to find the best-performing model. Final models were assessed using Boyce's index,[92] test AUC,[93] and omission rate (using maximum sensitivity and specificity thresholds)[94] to test how well they identified areas of suitable habitat that lacked records.

To convert models into binary projections, maximum sensitivity and specificity thresholds averaged across the 1000 replications were used.[95] To identify areas that are suitable for each species and have low human pressure, models were cropped using GHF data for 1995-2004[96] rescaled to 20 km^2, to exclude all pixels above the highest species-specific GHF score for recent locations of each species (i.e., only including areas with comparable human pressures to those rhinos can tolerate today). To compare spatial differences in projected habitat suitability between species, suitability scores were standardized between the two final models, and the

Sumatran rhinoceros suitability projection was subtracted from the Javan rhinoceros suitability projection (scores >0 show areas more suitable for Javan rhinoceros, scores <0 show areas more suitable for Sumatran rhinoceros). Using the binary projections, Javan rhinoceros scores were doubled and Sumatran rhinoceros scores were subtracted to define four suitability categories (2: suitable for Javan but not Sumatran; 1: suitable for both, 0: suitable for neither; -1: suitable for Sumatran but not Javan).

Future climate projections were based upon three General Circulation Models from CMIP-6 data[97]: GFDL-ESM4, IPSL-CM6A-LR and MPI-ESM1-2-LR.[98–100] A mean climate layer was generated from these three models for future projection to four time bins: 2021-2040, 2041-2060, 2061-2080, and 2081-2100. Projections were run for two shared socioeconomic pathways (SSPs[101]): an optimistic scenario of low warming impacts (SSP126) and a more pessimistic scenario of higher warming impacts (SSP370), totaling eight future projections for each species. Future projections were compared against a current-day projection for each protected area also generated from the combined model to evaluate predicted change in suitability for each landscape.

Comparison of record types

Two sets of analyses were conducted to investigate differences in realized niche space shown by records from different periods, and whether rhinoceros niches were already truncated by the period represented by modern and historical records. Differences in elevational range were investigated between modern records and historical records, and between historical and combined older records, using two-tailed heteroscedastic t-tests in R v.4.4.0 (Javan rhinoceros: modern, n=13, historical, n=353, older, n=19; Sumatran rhinoceros, modern, n=35, historical, n=245, older, n=19). PCAs were conducted using all record types for each species, using the same variables retained in our final combined model (Table 1). Because Chinese historical records do not represent precise localities, mean variable values were calculated across administrative regions where rhinos were reported. Holocene bioclimatic data were obtained for corresponding Holocene subdivisions in PaleoClim v.1.0.1.[64] Variables were centered to 0 and scaled to a standard deviation of 1.