# Global assessment of primate vulnerability to extreme climatic events

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## Abstract

Climate change driven alterations in the extent and intensity of extreme weather events may have catastrophic consequences on primate populations. Using a trait-based approach, we assessed the vulnerability of the world's 607 primate taxa to impacts of cyclones and droughts – two types of extreme climatic events that are expected to increase and/or intensify in the coming decades. We identified 16% of primate taxa that are vulnerable to cyclones particularly those in Madagascar; 22% of primate taxa were vulnerable to droughts which are mainly found in Malaysia Peninsula, North Borneo, Sumatra, and tropical moist forests of West Africa. These findings will help facilitate the prioritization of primate conservation efforts and call for increased efforts to investigate the context-specific mechanisms underpinning primates' vulnerability to extreme climatic events.

## Introduction

Nonhuman primates are iconic elements of tropical ecosystems delivering key ecological processes and supporting the delivery of a variety of benefits to people[1-3]. However, ~60% of the world's primate species are threatened with extinction largely as a result of deforestation, habitat fragmentation, large scale agriculture and cattle-ranching, overexploitation, and urbanisation[4,5]. Along with rapid land use change, long-term variation in human-induced climate change is an emergent and accelerating threat to primate survival. Observed changes in the distribution and intensity of extreme climatic events (e.g., cold waves, droughts, cyclones, tornadoes, wildfires), in particular, may have catastrophic consequences on wildlife populations[6,7], including primates.

A recent analysis showed that, ~6% of the worlds' terrestrial mammals are "significantly" exposed to cyclones and ~23% to droughts[8]; this assessment also revealed that compared to other mammalian orders, primates represent the proportion with the highest degree of exposure to cyclones and droughts in the recent past. Potential vulnerability to extreme climatic events is not currently considered when assessing extinction risk, indicating that the proportion of primates at the brink of extinction could be higher than currently estimated ~60%, should a number of them be particularly vulnerable to extreme climatic events. Impacts of cyclones and droughts have been found on sifakas, lemurs, langurs and Neotropical primate species[9-15]. Therefore, it is urgent to pinpoint which species or subspecies require particular conservation attention.

With the viability of species and ecosystems being increasingly threatened by climate change[16,17], vulnerability assessments have become a key tool for identifying those species that are likely to be most vulnerable, thereby informing adaption planning and management under uncertainty[18]. Species vulnerability to climate change is broadly defined as a function of three main elements: exposure, sensitivity and adaptive capacity, and various frameworks with different levels of complexity have been proposed based on this rationale[19]. In the case of species, vulnerability to extreme climatic events has been related to the nature of the event, including its extent, frequency, and intensity[6]. Vulnerability is also expected to be mediated by the intrinsic biological traits (e.g. dispersal capacity, diet breadth, habitat preferences) that mould species' ability to withstand (sensitivity) or adjust to extreme climatic events (adaptive capacity)[20,21]. Admittedly, other extrinsic threats, particularly from anthropogenic origin, may increase overall vulnerability[22], and so attention has increasingly been placed on these factors in Climate Change Vulnerability Assessments (CCVAs).

Following the IUCN-SSC Guidelines for Assessing Species Vulnerability to Climate Change[18], we conducted a vulnerability assessment to impacts of cyclones and droughts for the world's primates. The assessment incorporated primates' sensitivities and adaptive capacities associated with their intrinsic biological traits — referred collectively as "intrinsic susceptibility" — in relation to their exposure to cyclones and droughts. Primates' conservation status was considered as a proxy of extrinsic pressure level apart from extreme climatic events in the assessment. Our study was designed to identify the primates requiring urgent conservation attention, and the hotspot areas where they are concentrated, highlighting those vulnerable to cyclones and/or droughts and having a high extinction risk.

**Vulnerability of primate taxa to cyclones and droughts**

Of the 607 assessed primate taxa (referring to primate species and sub-species), 100 were found vulnerable to cyclone impacts, 134 were vulnerable to drought impacts, and 19 were vulnerable to both cyclone and drought impacts. In this study, we defined a primate taxon was "susceptible" if it was prone to cyclone/drought impacts for its intrinsic sensitivity/low-adaptive capacity. We identified that 457 taxa (75.3%) were susceptible but non-exposed to cyclone impacts; 382 taxa (62.9%) were susceptible but non-exposed to drought impacts (Supplementary Table S1).

We plotted the global distribution of assessed taxa exposed to and susceptible to cyclone impacts (Fig. 1a) and drought impacts (Fig. 1b). Bivariate maps were used to highlight areas with high richness of taxa that are (i) susceptible only, (ii) significantly exposed only, and (iii) both susceptible and exposed, hence, indicating hotspots of primate vulnerability.

Over the past 4 decades, cyclones of Category 4 and 5 impacted on terrestrial regions including the Caribbean Islands, coastal areas of the Gulf of Mexico, the North Madagascar, the main islands of Philippines, Japan, and coastal areas of the Bay of Bengal (Supplementary Fig. S1). Madagascar is the region with the highest richness of taxa vulnerable to cyclone impacts (Fig. 1a), where 6%, 30% and 40% of the total 103 taxa were assessed as extremely high, highly and moderately vulnerable (Fig. 1c). Comparatively, percentages of cyclone-vulnerable taxa were greatly lower in the other three regions where primates occur: Mainland Africa (0 species), Asia (10%, 17 taxa) and Neotropics (3%, 5 taxa) (Fig. 1c). In these regions, the vulnerable taxa were mainly distributed in tropical forests across Mexico's Yucatan Peninsula, tropical forests of Central America, and the lowland forests lying in eastern Mainland Southeast Asia. We found 161 taxa that were extremely high susceptible but not significantly exposed to cyclone impacts in western Amazon rainforest, and in tropical moist forests of Central Africa, Sri Lanka and Borneo (Fig. 1a).

Since the 1970s, aridity has been frequently detected over Africa, southern Europe, Arabian Peninsula, South and Southeast Asia, the Caribbean region and central South America (Supplementary Fig. S2). Asia is the region with the highest richness of taxa vulnerable to drought impacts (Fig. 1b), where 1%, 15% and 17% of the total 171 taxa were assessed as extremely high, highly and moderately vulnerable (Fig. 1d). These taxa concentrate in the tropical moist forests on Malaysia Peninsula, Sumatra, North Borneo and Sri Lanka. Following Asia, 8% and 16% of the total 150 taxa in Mainland Africa were assessed as highly and moderately vulnerable to drought impacts, respectively (Fig. 1d). These taxa are distributed in the tropical moist forests of

Guinea, Sierra Leone, Liberia and Central Africa (Fig. 1b). The percentages of primate taxa vulnerable to drought impacts are comparatively low in forests and xeric shrublands covering Madagascar's coastal areas (17%, 17 species), as well as in the tropical forests of Neotropics (14%, 26 species) (Fig. 1d). Thirty-three taxa were found extremely high susceptible but not significantly exposed to drought impacts in central-western Amazon rainforest, tropical moist forests in Gabon, Congo and West Africa, moist forests of eastern side of Madagascar,  and dry forests of the lower reaches of the Mekong in Southeast Asia (Fig. 1b).

## Vulnerable and threatened primate taxa

We examined vulnerability categories of 607 taxa to cyclone and drought impacts and their conservation status in the IUCN Red List of Threatened Species[23], to highlight the vulnerable taxa at risk of extinction. We identified 89 threatened taxa that were vulnerable to cyclone impacts, 72 of which are distributed in Madagascar; 89 threatened taxa that were vulnerable to drought impacts, concentrating in lowland moist forests of Sierra Leone and Liberia in Africa, and Sumatra, Borneo in Southeast Asia (Fig. 2a). The hotspot of threatened taxa overlaps the hotspot of cyclone-vulnerable taxa in the moist forests lying on the eastern side of Madagascar, and overlaps the hotspot of drought-vulnerable taxa in lowland forests of North Borneo and Northern Sumatra (Fig. 2a). Over 90% of the taxa vulnerable to cyclones impacts and 65% of the taxa vulnerable to drought impacts are threatened to become extinct, among which 23 and 26 taxa are "Critically Endangered", respectively (Fig. 2b). Four "Critically Endangered" taxa (*Trachypithecus poliocephalus leucocephalus*, *T. poliocephalus poliocephalus, Varecia rubra* and *Propithecus diadema*) are extremely high vulnerable to cyclone impacts. Two "Endangered" taxa (*Macaca sinica aurifrons* and *M. sinica opisthomelas*) are extremely high vulnerable to drought impacts.

## Conclusions

Under the framework of CCVAs, we identified 16% of the world's primates as vulnerable to impacts of cyclones and 22% vulnerable to impacts of droughts. Our study also highlighted the hotspots of the taxa exposed and susceptible to cyclones and droughts, to facilitate the prioritization of sites for effective risk mitigation. As extreme climatic events are expected to increase in frequency and/or intensity[24], identifying taxa at risk under their impacts would help to improve conservation planning to cope with relevant threats. Primate taxa are anticipated to have relatively lower vulnerability if they are not significantly exposed to cyclones or droughts, but they may have latent risk of being vulnerable due to possible variations of the pattern, frequency and/or intensity of extreme climatic events[25]. The exposed taxa with relatively lower susceptibility were assumed to have greater capability to cope with impacts of cyclones and droughts, and hence to represent a lower priority for risk mitigation actions in the near future[25]. However, it is uncertain whether these primates' attributes would enable them to survive with more severe impacts if exposure increases, and so monitoring will continue to be necessary.

Global predictions based on different dynamic models indicate that global warming may trigger an increase in the averaged intensity of cyclones, while the globally averaged frequency of cyclones is predicted to decrease[26]. As a result, we could not assume that exposed primates would be at higher pressure from cyclones in the future relative to the past, but some predicted variations are cautionary for primate conservation in certain areas. For example, higher resolution modelling projected substantial increases in the frequency of the most intense cyclones, namely cyclones of Category 4 and 5 in Saffir-Simpson Scale, despite of a decrease in the globally averaged frequency of cyclones[26,27]. Empirical evidence of cyclones' negative effects on wild primate populations is accumulating[28,29]. Likewise, theoretical approaches predict a substantial increase in the risk of local extirpations under cyclone impacts, particularly for populations in isolation and experiencing human-driven habitat loss[30]. Should the frequency of the most intense cyclones increase, vulnerability of primates may be compromised directly and/or indirectly due to the more recurrent exposure to cyclone-driven environmental disturbance.

Arid conditions are moreover projected to remain stable or increase in the 21st century over most of Africa, southern Europe and the Middle East, most of the Americas, Australia, and Southeast Asia[31]. These predictions indicate that conservation efforts are especially needed for the Indo-Malay region where we identified the highest richness of taxa vulnerable to drought impacts. Such a tendency is also alarming for the regions inhabited by a high number of taxa highly susceptible to drought impacts, as the intensification or expansion of arid conditions may cause more taxa to be exposed to more severe impacts. The influence of human-induced global warming on droughts is still controversial due to different metrics being adopted for quantifying droughts[32,33]. Despite of this, much of the extra heat added into the climate system by recent warming is expected to increase the rate of drying on land, establishing droughts more quickly with greater intensity and longer duration[34]. The potential changes would threaten survival of primates through impacts on their primary living resource — forest trees by increasing tree defoliation and mortality, or triggering sudden disruptive effects on insect-fungal defoliation dynamics[35]. These conditions may challenge the thresholds of sensitivity and/or adaptive capacity of primates.

Our findings revealed that a large percentage of primates vulnerable to impacts of cyclones and droughts are currently listed as “Threatened” in the IUCN Red List. So far, few studies have revealed the interactions between impacts of extreme climatic events and other stressors on primate populations. Nevertheless, we anticipated that the species of higher threatened categories might be less capable of maintaining long-term population persistence, as other extrinsic stressors that reduce species’ resilience and/or resistance to population decline may further increase vulnerability to extreme climatic events[15,30]. Great risk brought by potential ecological synergisms may lead to a bleak future, where a major extinction of primates may be coming sooner than previously anticipated.

Globally, the hotspots of primates vulnerable to cyclone and drought impacts are under severe threats of habitat loss and population decline caused by anthropogenic threats. For instance, in Madagascar, only 10~20% of the original habitats of primates remain, which are highly fragmented and inadequately protected[36,37]. Much of those habitats are exposed to illegal logging, mining and slash-and-burn agriculture, while people experience profound poverty and turmoil of politics[38]. Southeast Asia was identified as another hotspot of primate species vulnerable to drought impacts, where the biota has been continuously threatened by the destruction of forest and human population growth[39]. Expansion of palm agriculture has destructed at least 45% of the forest area in Southeast Asia along with fast human population growth[40]. The latter consequently drove severe population declines in Sumatran orangutan (*Pongo abelii*) and Bornean orangutan (*Pongo pygmaeus*)[41], which were both vulnerable to severe droughts. Population loss caused by hunting is the secondary threat for primate populations in Southeast Asia[5]. In Borneo, hunting was estimated causing an annual loss of 1,950 to 3,100 individuals to orangutans[42], posing a serious threat to the sustainable existence of these drought-vulnerable primates.

As the pressures exerted by extreme climatic events on primates are unpreventable and uncontrollable, it is critical to maintain their resilience to catastrophic mortality and habitat loss caused by these events. These include efforts to minimize impacts, including maintaining spatial and temporal resources by well-connected protected area networks[43], improving human living conditions to reduce illegal hunting, and developing sustainable land-use initiatives to mitigate primate-human conflicts[5,44]. To facilitate effective conservation responses, it is also important to increase the accuracy of risk assessment by revealing the synergisms between extreme climate events and ongoing non-climatic stressors.

Because the occurrence of extreme climatic events is difficult to predict accurately[45,46], our study identified the areas that are most likely to be currently affected by cyclones and droughts by capturing variations of their occurrences in the recent 46 years. However, a bias could be introduced by overlapping recent extreme climatic events with current species geographic range when we calculated exposure, as many species ranges may have changed over the time. Therefore, if a species range has declined/increased over the past 46 years, we may underestimate/overestimate the exposure to cyclones/drought occurred during this period. The data we extracted for assessing intrinsic susceptibility are mostly based on observations from field studies, representing realized niches of the taxa. It may or may not be closely related to their fundamental niche. If some taxon has a broader fundamental niche, the extreme climatic conditions may not have such a significant impact. As with trait-based CCVAs, our analysis is subject to uncertainty in several elements of the framework: (i) equal weight were assigned to each attribute without reflecting the fact that attributes contribute to different extent to species' vulnerability; (ii) arbitrary thresholds were chosen for scoring the two dimensions of vulnerability, which consequently generated relative results instead of the precise measures accounting for actual vulnerability of species[19]; (iii) the assessment did not address the possibility that sensitivity and/or adaptive capacity of species might change over time as a result of increased exposure. Despite of this, we believe the analysis facilitates prioritizing conservation efforts by enabling a comparison of relative vulnerability among taxa.

To reduce uncertainty, it is critical to build an evidence base for weighting characteristics, by clarifying mechanisms of how they influence primates' vulnerability to different extreme climatic events[47,48]. This will also help develop less data-intensive methods that may yield broadly similar results for the purpose of conservation planning and decision making[49]. Solid efforts are required for gathering relevant data from long-term monitored primate populations that periodically experience extreme climate events, to improve the parameterization of thresholds associated with vulnerability. Demographic and behavioral responses to past extreme climatic events should receive more attention, as they carry information on resistant or adaptive mechanisms that might change species sensitivity or adaptive capacity. Quantification of these responses is suggested to be incorporated into future assessments to enhance ecological robustness of the framework[50].

This study identified primate species facing a relatively high vulnerability to impacts of cyclones and droughts as well as the regions where they are expected to be at greatest risk from increased exposure. As anthropogenic pressures on these species and places prevail, we contribute to a more comprehensive yet worrying portray of primates' struggle for survival. Our findings are expected to encourage researchers to reduce data uncertainties through targeted data collection by conducting context-specific assessments of vulnerable species' populations, and so determine immediate action plans and minimize potentially irreversible losses in the long term.

## Methods (online-only)

### Species distribution data

We obtained the geographic distribution maps of 607 primate taxa, referring to primate species and sub-species, from IUCN Red List assessment[23] which uses the 3rd edition of Mammal Species of the World as its mammal taxonomy[51]. These maps were generated using bounding polygons associated with different certainty of a taxon's presence in an area coded as "extant", "possible extant", "possibly extinct", "extinct", and "presence uncertain"[52]. To focus on areas where individuals are most likely to occur, we selected polygons with presence category coded as "extant", as they indicate that individuals are known or thought very likely to occur presently in the area[52]. In doing so we omitted three taxa (*Hylobates lar yunnanesis*, *Mandrillus leucopaheus ssp, Piliocolobus waldronae,* and *Saguinus nigricollis ssp*) since presence polygons with this level of certainty were lacking. Four species on the IUCN Red List (*Cebus brunneus, Piliocolobus pennantii, Pithecia milleri, Pithecia vanzolinii*) which lack distribution data were discarded. We also excluded three species (*Cebus capucinus, Cercopithecus wolfi, Chiropotes sagulatus*) that have not been assessed by the IUCN Red List but are listed in the Catalogue of Life[53], and one newly described species (*Hoolock tianxing*)[54].

### Quantification of exposure

Cyclone data and quantification of cyclone exposure score

We extracted cyclone data from the joint database UNEP/GRID-Geneva[55] available in the Global Risk Data Platform (http://preview.grid.unep.ch/) that allows visualising and extracting data of different extreme weather and earth-system events. The UNEP/GRID-Geneva database uses satellite remote sensing to detect hurricane tracks and estimates areas affected using wind speed buffers available as GIS vector data for the period 1970 to 2015[55]. Each cyclone in the dataset is classified into discrete categories based on the Saffir-Simpson wind scale which measures the intensity of cyclones in terms of their highest sustained wind speed. Those having a maximum speed between 63-119 km/h are considered the least intense (cyclones not reaching category 1), and those equal or greater than 252 km/h are the most intense (cyclones category 5)[56]. We classified cyclone events based on their wind speed intensity ($w$) on a scale from 1 to 6, and integrated these scores into a cyclone exposure metric (See below). A higher weight was thus assigned to cyclones with a higher category in the Saffir-Simpson scale.

To quantify the percentage of each primate taxon's range exposed to cyclones ($E$), we overlaid the extant range of each primate taxon (using the ArcGIS software, version 10.0) one at a time with the path of each cyclone event for the 46-year time window. The taxa with a "significant" cyclone exposure were defined as those in which at least 25% of their extant range overlapped with one or more cyclone events[8]. For the taxa that met this criterion, we further identified those that were exposed on average to at least one cyclone event within the duration of one generation length[23,57]. Generation length is defined as the average age of parents of the current cohort, reflecting the turnover rate of breeding individuals in a population[57]. One hundred and twenty-two taxa met these two exposure criteria and were kept for further analysis.

We then scaled exposure to one generation length of the assessed taxon because different population turnover rates of taxa may influence risk of population decline [58]. Based on the weighted mean of exposure to individual cyclones and average number of cyclones within a primate taxon's generation length, the cyclone exposure score (hereafter, $C_{ES}$) for each taxon was calculated as:

$$\frac{(Ea \times wa + Eb \times wb + \cdots En \times wn)}{wa + wb + \cdots wn} \times \frac{Nc}{46} \times Tgl$$

where $E_a, E_b \ldots E_n$ is the exposure of a primate taxon, expressed as percentage overlap between each cyclone's polygon and the taxon's range, to individual cyclones $a$, $b$ to $n$ between 1970 and 2015 weighted by intensity $w_a$, $w_b \ldots w_n$, respectively. $N_c$ is number of cyclones that occurred in the taxon's range during 1970-2015, and $T_{gl}$ (years) is one generation length of the taxon (Working examples see Supplementary Appendix 1).

Drought data and quantification of drought exposure score

We used global monthly average Standardized Precipitation Index (SPI) data obtained from the Full Data Reanalysis Product of Global Precipitation Climatology Center[59]. The dataset contains SPI values from 1970 to 2017 on a 1° × 1° equally spaced longitude/latitude grid. SPI data of 12-month timescale was chosen to assess the effects of droughts[60]. We targeted grids with SPI-12 values $\leqslant$ -1.5 which indicates the occurrence of severe dry conditions[61]. Drought polygons with these SPI-12 values were delimited by grouping grids of same dryness frequency ($f_a$, $f_b \ldots$and $f_n$) in the past 567 months (from 1971 to 2017). We then calculated the percentage of a taxon's extant range overlapping with each of these drought polygons ($E_a$, $E_{b\ldots}$ $E_n$). We identified drought exposed taxa following the same approach that was used for identifying cyclone exposed taxa (25% range exposure, and occurrence of droughts within one generation). One hundred and fifty-six taxa met the two drought exposure criteria, and hence were kept for the calculation of a drought exposure score ($D_{ES}$) based on the exposure to drought events ($E$) and polygons of each drought frequency ($f$) using the formula:

$$(Ea \times fa + Eb \times fb + \cdots En \times fn) \times Tgl$$

where $E_a, E_b \ldots E_n$ is the exposure of a primate taxon, expressed as percentage overlap between drought polygon and the taxon's range, to drought with a certain frequency $fa, fb, \ldots f_n$ from 1970 to 2017; and $T_{gl}$ (years) is the generation length of the assessed primate taxon. In our study, SPI-12 ⩽ -1.5 was considered as a single drought intensity scale, and weighted mean was not applied for calculating $D_{ES}$ (Working examples see Supplementary Appendix 1).

## Quantification of intrinsic susceptibility

Indicators of sensitivity and adaptive capacity

Based on ecological and extinction risk theory, we conducted a literature review to identify biological intrinsic traits that are likely to influence primates' sensitivity and adaptive capacity to cyclones and droughts, which resulted in 11 traits (Table 1). Extinction risk associated with island endemism was not included, as the effect of geographic isolation is usually beyond the time scale this study focused on (one generation length time). Trait data were extracted from the peer-reviewed literature and general accounts of the natural history and ecology of the taxa available in the online databases IUCN Red List[23], Encyclopedia of Life[62], PanTHERIA[63] and Animal

Diversity Web[64]. The traits were evaluated on their mechanisms of affecting intrinsic susceptibility – heightening sensitivity and/or lowering adaptive capacity (Table 1). Impacts of extreme climatic events can have a direct effect on the state of individuals, and/or indirectly by changing the biophysical environment where these individuals occur[6]. In this regard, cyclone impacts on taxa are expected to derive from high winds and intense rainfall leading to mortality of individuals and loss of vegetation cover with higher defoliation of the canopy compared with the understory[65,66,67]. Drought impacts on primates (e.g., population decline and/or recruitment failure) derive from high temperatures and lack of precipitation which can trigger fires[68]. These factors can affect individual survival by influencing vegetation (e.g., used as food or shelter) and water availability[15,69,70].

### Scoring intrinsic susceptibility

We used a scoring system (from 1 to 6) to quantify the biological traits associated with intrinsic susceptibility to cyclones and droughts for each primate taxon. Score 3 in the system is a neutral value, above/below which cyclones and droughts are expected to be harmful/beneficial to the taxon. Because we assumed cyclones or droughts would generally have negative impacts on the primates, all traits were assigned scores above 3. For the traits described by categorical variables, we scored them according to the clear categorical thresholds. For the traits described by continuous variables, we set scoring thresholds by equally dividing their value range into 3 sub-ranges (Fig. 3).

For 607 taxa, we scored 0-9 traits (mean = 7, median = 6) associated with susceptibility to cyclone impacts, and 1-9 traits (mean = 7, median = 7) associated with susceptibility to drought impacts (Supplementary dataset 1). To account for the uncertainty in trait data, we assigned a confidence level (0 "data deficient", 1 "moderate confidence" or 2 "good confidence") to each trait. "Data deficient" (0) was assigned to the traits without data available for the assessed taxon or from closely related subspecies, and thus these traits would not be used for susceptibility assessment. "Moderate confidence" (1) was assigned to the traits whose data was not available for the assessed taxon, but can be estimated from the data of closely related subspecies, or congeneric species in the case of estimating "generation length". "Good confidence" (2) refers to the case that trait data are from reliable sources that can be retrieved, such as peer-reviewed papers, books, or online databases. These confidence levels were then used to calculate the reliability of the susceptibility score for each taxon (Supplementary dataset 1).

We obtained susceptibility scores respectively to cyclone and drought impacts for each primate taxon, which were calculated with the trait scores based on the additive rule proposed by Graham et al.[71]:

$$Susceptibility = {}^{(\mathrm{Sa} + \mathrm{Sb} + \cdots \mathrm{Sn})}/_{N}$$

where $S_a$, $S_b$,…$S_n$ are scores assigned to trait *a* to *n*, and *N* is the number of traits used for assessment. The taxa with the lowest 25% of susceptibility scores (≤ 4.5) were assumed to be "non-significantly susceptible" to short-term and long-term impacts of cyclones or droughts whereas those with a score > 4.5 were assessed as "significantly susceptible". The reliability of susceptibility score per taxon was estimated by averaging confidence-level values of all traits, provided that the data was available for more than half of the traits. The reliability was identified as "Good" if the average of confidence level values was > 1.5, and was identified as “Moderate” if not. The susceptibility was classified as “unknown”, when data was available for less than half of traits. For a working example of these calculations, see the Supplementary Information Appendix 1. Overall, we assessed susceptibility of 499 and 506 taxa to impacts of cyclones and droughts, respectively. Among them, “good confidence” was assigned to 281 taxa for the assessment of cyclone susceptibility, and to 272 taxa for the assessment of drought susceptibility (Supplementary dataset 1).

## Assessing species vulnerability

Categorizing vulnerability in exposure and susceptibility dimensions

The vulnerability of primates to cyclones and droughts was assessed in two dimensions, namely, exposure and susceptibility. We first classified exposed and susceptible taxa separately into three levels: “significant”, “high”, and “extreme” based on their exposure and susceptibility scores, respectively. We did so using three classification approaches, namely, equal interval, lower-upper quartile and jenks (Supplementary Appendix 2).

The classification approach that generated the least variation to assessment results (Supplementary Table S4) was chosen to assign species into different categories in two vulnerability dimensions. Thus, the equal interval was chosen to assess primates’ vulnerability to cyclone impacts whereas the lower-upper quartile was chosen to assess vulnerability to drought impacts. In this way, the total 607 taxa were classified into “non-significant”, “moderate”, “high”, “extreme” and “unknown” in exposure and susceptibility dimensions (Supplementary dataset 2).

Relative vulnerability index

We developed a matrix to combine both the exposure and susceptibility dimensions based on a published framework for assessing climate-related decline in recent historical range[72] (Supplementary Table S3). Based on this matrix, vulnerability of a taxon is assessed as "extremely high" when it was categorized as "extreme" in both susceptibility and exposure dimensions. For taxa categorized as "high" and/or "extreme" in both dimensions vulnerability was assessed as "high". Taxa falling in the vulnerability categories "moderate", "high", and "extremely high" were defined as "vulnerable" while those determined "very low" and "low" were grouped together as "non-vulnerable". Finally, if a primate taxon was categorized as "non-assessed/unknown" in either dimension, its vulnerability assessment was categorized as "unknown".

Impacts of the stressors other than extreme climatic events

Conservation status represented by the IUCN Red List categories[23] of primate taxa (using the 2001 IUCN Red List Categories and Criteria version 3.1) was adopted as a proxy for incorporating the impacts of extrinsic stressors other than extreme climatic events into CCVA. The category of a species was applied to its subspecies if the IUCN Red List categories were not available for subspecies. In this regard, we referred taxa grouped in the categories "Critically Endangered", "Endangered", and "Vulnerable" as "Threatened", whereas those classed as "Near Threatened, and Least Concern" are referred to as "Non-Threatened". Seventeen "Data Deficient" taxa with range polygons coded as "extant" were also included in the assessment. We highlighted the taxa that were "Threatened" in the IUCN Red List and "Vulnerable" to cyclones and droughts, since the threats indicated by their conservation status and extreme climatic events could have synergistic impacts on these taxa, and thus make them at higher risk compared with “Non-threatened” taxa.

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## Author contributions

L.Z., and E.I.A., conceived and designed the study; G.M.M., G.C., N.P., and W.F., contributed in the design of the vulnerability framework proposed by L.Z. and E.I.A. L.Z., E.I.A., and G.C., reviewed and collected data. L.Z. analysed data and all authors contributed greatly to the discussion of results; L.Z. wrote the initial draft of this manuscript and all authors contributed on improvements of the manuscript, and agreed the final version to be published.

## Competing interests

The authors declare that they have no competing interests and that no institutional review board or institutional animal and welfare committee approval was needed for this study.

## Data availability

The authors declare that the data supporting the findings of this study are either available through the references provided within the article or the supplemental materials. Additional data related to this paper may be requested from the corresponding author.

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**Table Legends**

Table 1. Traits used for assessing inherent susceptibility (high sensitivity and low adaptive capacity) of primate taxa to impacts of cyclones (C), droughts (D) or both (C, D).

**Figure Legends**

Fig. 1 Distribution of vulnerable primate taxa and number of taxa in each vulnerability category. Ditribution of cyclone-vulnerable taxa (a): areas with high richness of cyclone-susceptible taxa only are shown in cyan, and those with cyclone-exposed taxa only are shown in pink; areas with high richness of cyclone-vulnerable taxa (the taxa susceptible and exposed to cyclones), are shown in purple. Distribution of drought-vulnerable taxa (b): areas with high richness of drought-susceptible taxa only are shown in orange, those with drought-exposed taxa only are shown in purple; areas with high richness of drought-vulnerable taxa (the taxa susceptible and exposed to droughts), are shown in maroon. Number of taxa in categories of cyclone vulnerability (c) and drought vulnerability (d) in each region. Mainland Africa includes small associated islands.

Fig. 2 Distribution and number of primate taxa that are threatened and vulnerable to cyclones and droughts. The distribution of taxa classified as “Threatened” by the IUCN Red List, taxa that are threatened and cyclone-vulnerable, and taxa that are threatened and drought-vulnerable are shown in (a). The number of cyclone-vulnerable taxa, and drought-vulnerable taxa in each vulnerability category (moderate, high, extremely high) are shown in (b). The IUCN Red List categories (VU, Vulnerable; EN, Endangered; CR, Critically Endangered; NT, Near Threatened; LC, Least Concern) of primate taxa in each vulnerability category are also shown.

Fig. 3 A framework for assessing intrinsic susceptibility of primate taxa under cyclone and drought impacts. Intrinsic susceptibility is composed of sensitivities and adaptive capacities associated with biological traits of assessed taxa. For each trait, we assigned a score indicating its effect (4, least; 6, most) in shaping intrinsic susceptibility to impacts of cyclones (C), droughts (D) or both (C, D). Susceptibility of primates lacking data for more than half of traits was considered as “unknown”. When data was available for over half of the traits and the average of trait scores > 4.5, the primate taxon was considered “significantly susceptible”, otherwise “non-significantly susceptible”. Reliability of susceptibility score of each taxon was estimated by averaging confidence-level values of all traits, if data were available for over half of the traits. Finally, the susceptibility scores of assessed taxa were divided into three ranges from low to high, and the taxon with a score falling within each range was assessed as “significant”, “high” or “extreme” susceptible, accordingly. †A sensitivity analysis was conducted using 3 approaches to classify susceptibility and exposure, and the average number of taxa classified into each vulnerability category was then calculated. The classification approach with the least variation from the average was adopted for vulnerability assessment (Classification approaches are described in Supplementary Appendix 2).

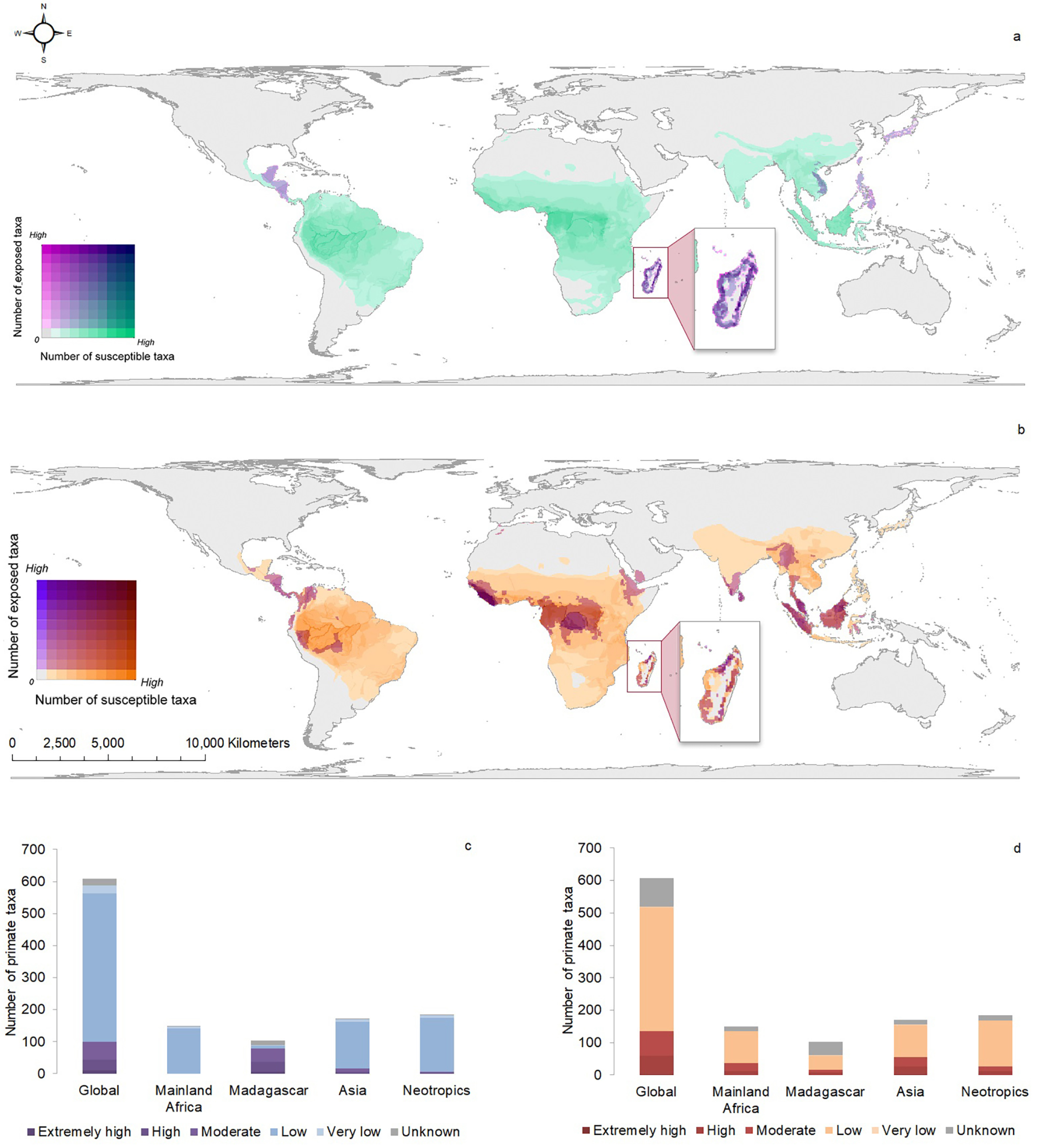
## Tables

Table 1. Traits used for assessing inherent susceptibility (high sensitivity and low adaptive capacity) of primate taxa to impacts of cyclones (C), droughts (D) or both (C, D).

| | Rationale | Reference |
|---|---|---|
| **Traits to assess high sensitivity** | | |
| <u>Body mass</u> (C,D) (62,63,64)<br>Average mass of individual adults (males and females) | Smaller taxa are less physically robust and so more likely to be sensitive to the strong winds and rainfall caused by cyclones; smaller body mass is also associated with relatively lower energy reserves, which increases sensitivity to food scarcity as a result of either cyclone or drought. Weakened individuals may ultimately die as a result of predation, starvation or disease. | (48,73-75) |
| <u>Day journey length</u> (C,D) (103)<br>Daily distance travelled | During and following cyclones and droughts, survival may initially depend on the ability of individuals to range widely and find surviving pockets of resources. Taxa that make shorter day journeys are therefore more likely to experience nutritional stress. | (87,88) |
| <u>Diurnality</u> (D) (63, 64)<br>Behaviour characterized by activity during daytime, with a period of inactivity at night | Diurnal taxa are more exposed to the extreme daytime temperatures associated with droughts, and therefore more vulnerable to hyperthermia. | (76-78) |
| <u>Home range size</u> (C) (63, 64)<br>Size of the area within which daily activities of individuals are restricted | Due to local topography, there are areas comparatively less affected by cyclone disturbances. Taxa are less likely to find these areas within smaller home ranges. | (79,80) |
| <u>Litters per year</u> (C,D) (63, 64)<br>Number of litters per female per year | Within the one generation assessment period, animals that produce a smaller number of litters per generation may be less able to recover quickly from a reduction in population size following droughts or cyclones. This in turn can make the population more vulnerable to extinction from other stochastic events. | (81,82) |
| <u>Mean group size</u> (C,D)* (63, 64)<br>Number of individuals in group | Taxa that live in larger groups (due to higher predation pressure or intergroup competition) may be more vulnerable to food scarcity associated with cyclones and droughts because they require more food resources to maintain their larger groups. | (73, 96-98) |
| <u>Primary diet</u> (C,D) (62, 63, 103)<br>Folivore, frugivore, insectivore, omnivore | During and following cyclones and droughts, fruit abundance decreases sharply while exploitable foliage may still exist. Likewise, plants are likely to regenerate foliage before bearing fruits during the recovery phase. Frugivorous, as opposed to folivores, are therefore more likely to experience nutritional stress. Insectivores may also find it difficult to supplement their diet, as invertebrates are negatively affected by these disturbances. | (83-86) |
| **Traits to assess low adaptive capacity** | | |
| <u>Diet breadth</u> (C,D) (23, 62, 63)<br>Number of different dietary categories** consumed | Taxa with selective, narrow diets are less able to diversify their foraging habits and therefore more likely to be affected by the loss of key resources during periods of food scarcity associated with cyclones and droughts. | (89-92) |
| <u>Habitat breadth</u> (C,D) (23,64,104)<br>Number of different habitat types used | Taxa that specialize in certain habitats may require particular conditions of some microhabitat; once these have been disrupted or lost due to cyclones or droughts, such taxa may be difficult to adapt to disturbed or alternative habitats. | (93-95) |
| <u>Terrestriality</u> (C) (63)<br>Use of habitat strata | Following a cyclone, semi-terrestrial and terrestrial taxa that have the flexibility to exploit both arboreal and terrestrial niches will be better able to adapt to the disturbed habitat than strictly arboreal species due to the disruption of the tree canopy. | (65, 99-100) |
| <u>Dispersal velocity</u> (D) (105)<br>Speed at which a species is able to move beyond its home range, as a function of dispersal distances and dispersal frequencies in a year | Certain areas may become unsuitable due to drought for extended periods of time. Taxa that have the ability to move out of areas within its wider geographic range are most likely to avoid these areas affected by droughts. | (101,102) |

*Some primates (e.g. spider monkeys) are able to cope with negative post-hurricane consequences by reducing their group size[106], and this behavioral flexibility increases their adaptive capacity to cyclone-related disturbance. Such data is lacking for most other primates, and thus we did not consider the degree of fission–fusion dynamics when scoring the mean group size.

**Dietary categories were defined as vertebrate, invertebrate, fruit, flowers/nectar/pollen, leaves/branches/bark, seeds, grass and roots/tubers[63].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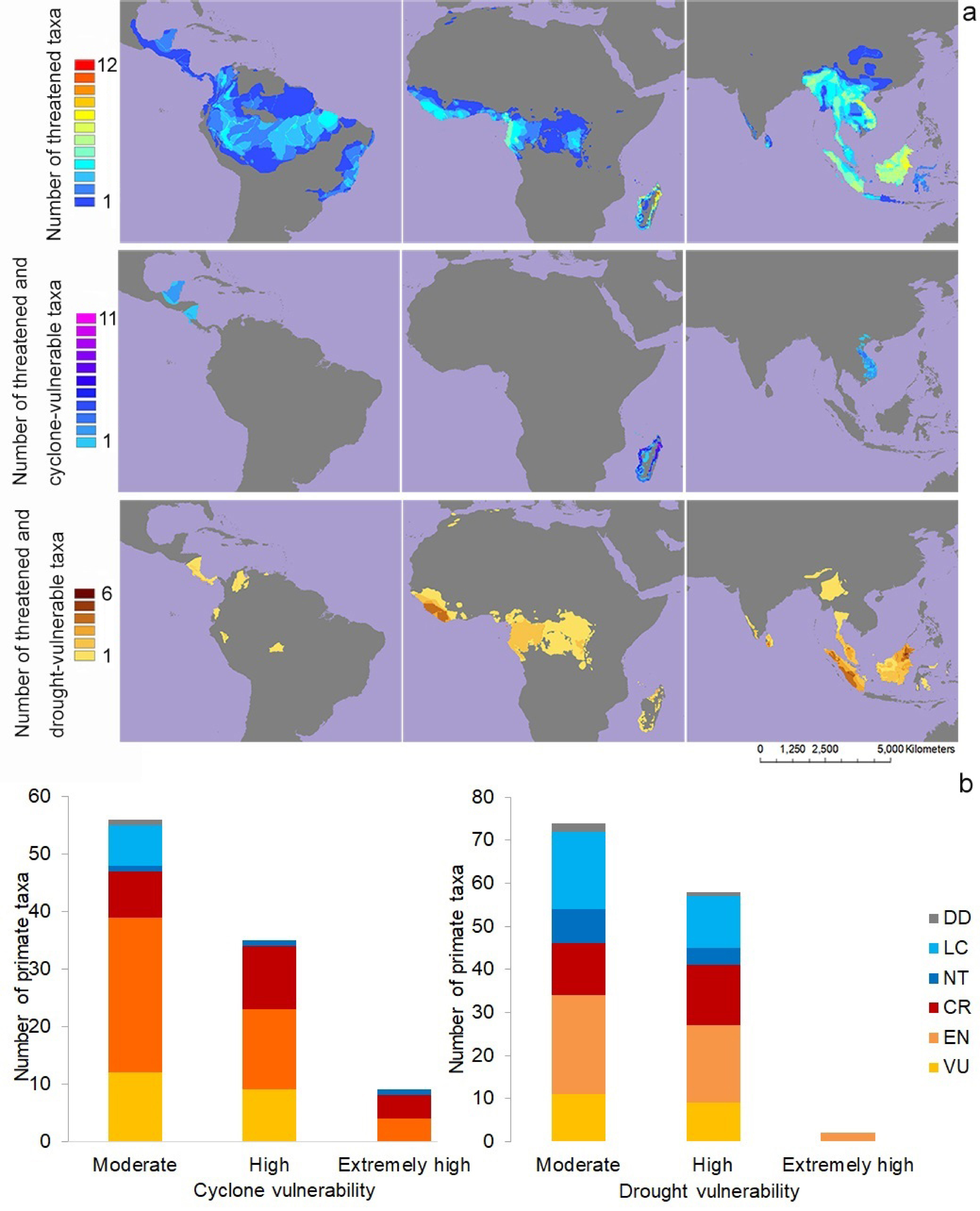
a
High
Number of exposed taxa
0
High
Number of susceptible taxa
b
High
Number of exposed taxa
0
High
Number of susceptible taxa
0 2,500 5,000 10,000 Kilometers
c
700
600
500
400
300
200
100
0
Number of primate taxa
Global
Mainland Africa
Madagascar
Asia
Neotropics
Extremely high
High
Moderate
Low
Very low
Unknown
d
700
600
500
400
300
200
100
0
Number of primate taxa
Global
Mainland Africa
Madagascar
Asia
Neotropics
Extremely high
High
Moderate
Low
Very low
Unknown



a
Number of threatened taxa
12
1
Number of threatened and cyclone-vulnerable taxa
11
1
Number of threatened and drought-vulnerable taxa
6
1
0 1,250 2,500 5,000 Kilometers
b
Number of primate taxa
60
50
40
30
20
10
0
Moderate
High
Extremely high
Cyclone vulnerability
80
70
Drought vulnerability
DD
LC
NT
CR
EN
VU


Traits used to assess high sensitivity
Traits used to assess low adaptive capacity
Body mass (C,D)
12 < x ≤ 18kg Score 4
6 < x ≤ 12kg Score 5
0 < x ≤ 6kg Score 6
Day journey length (C,D)
x ≥2500 m Score 4
1250 m ≤ x < 2500 m Score 5
250 m ≤ x < 1250 m Score 6
Diurnality (D)
Mostly nocturnal Score 4
Mostly diurnal Score 6
Home range size (C)
5.8 <x ≤ 8.7 km² Score 4
2.9<x ≤ 5.8 km² Score 5
0<x ≤ 2.9 km² Score 6
Litters per year (C,D)
2.7 < x ≤ 4 Score 4
1.4 < x ≤ 2.7 Score 5
x ≤ 1.4 Score 6
Mean group size (C,D)
Solitary or 2 ≤ x <20 Score 4
20 ≤ x <40 Score 5
> 40 Score 6
Primary diet (C,D)
Omnivorous Score 4
Folivore Score 5
Frugivore or insectivore Score 6
Diet breadth (C,D)
5 or more food classes Score 4
3 to 4 food classes Score 5
1 to 2 food classes Score 6
Dispersal velocity (D)
x > 2 km/yr Score 4
1 km/yr ≤ x < 2 km/yr Score 5
0<x ≤ 1 km/yr Score 6
Habitat breadth (C,D)
5 or more habitat categories Score 4
2 to 4 habitat categories Score 5
1 habitat category Score 6
Terrestriality (C)
Semi-terrestrial/terrestrial Score 4
Arboreal Score 6
Is data available for more than half of the traits?
Yes
No
Susceptibility = (Sa+Sb+···Sn)/N
Is susceptibility score > 4.5?
Yes
No
Significantly susceptible
Non-significantly susceptible
Unknown susceptibility
Which value range does the primate taxon's susceptibility score fall into?
Upper quartile
Medium quartile
Lower quartile
Extremely high
High
Significant