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RESEARCH ARTICLE

Exposure of African ape sites to climate change impacts

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Abstract

Large gaps remain in our understanding of the vulnerability of specific animal taxa and regions to climate change, especially regarding extreme climate impact events. Here, we assess African apes, flagship and highly important umbrella species for sympatric biodiversity. We estimated past (1981–2010) and future exposure to climate change impacts across 363 sites in Africa for RCP2.6 and RCP6.0 for near term (2021–2050) and long term (2071–2099). We used fully harmonized climate data and data on extreme climate impact events from the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP). Historic data show that 171 sites had positive temperature anomalies for at least nine of the past ten years with the strongest anomalies (up to 0.56˚C) estimated for eastern chimpanzees. Climate projections suggest that temperatures will increase across all sites, while precipitation changes are more heterogeneous. We estimated a future increase in heavy precipitation events for 288 sites, and an increase in the number of consecutive dry days by up to 20 days per year (maximum increase estimated for eastern gorillas). All sites will be frequently exposed to wildfires and crop failures in the future, and the latter could impact apes indirectly through increased deforestation. 84% of sites are projected to be exposed to heatwaves and 78% of sites to river floods. Tropical cyclones and droughts were only projected for individual sites in western and central Africa. We further compiled available evidence on how climate change impacts could affect apes, for example, through heat stress and dehydration, a reduction in water sources and fruit trees, and reduced physiological performance, body condition, fertility, and survival. To support necessary research on the sensitivity and adaptability of African apes to climate change impacts, and the planning and implementation of conservation measures, we provide detailed results for each ape site on the open-access platform A.P.E.S. Wiki.

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Introduction

Around one million species are threatened with extinction [1]. Even though climate change is not yet the main driver of biodiversity decline [2], it is projected to increasingly threaten biodiversity [3]. Species have already responded to climate change, for example, by changes in phenology [4], and latitudinal and elevational range shifts [5,6]. Though large uncertainties remain, it has been estimated that between 10 and 30% of terrestrial species could become locally extinct due to climate change [3].

Large taxonomic and geographic gaps remain in our understanding of the impact of climate change on species, and one of these understudied taxa are primates [7,8]. In addition, there are large gaps for Sub-Saharan Africa, even though the region has a high diversity in species and ecosystems, and large remaining forests essential for the global climate system [9]. Primates play an important role within their ecosystems; they contribute to forest community structure by aiding seed dispersal and plant pollination, ecosystem services that could be threatened by climate change impacts [10]. They are also one of the most prominent conservation flagship species [11], and African apes are a major focus of research and conservation activities, and an umbrella species for sympatric biodiversity. For example, the protection of African apes motivates the creation of new conservation areas, benefitting co-occurring species [12].

African apes occur in 21 countries across tropical Africa. There are four species and nine taxa (Table 1). Most African apes have experienced population decline (except mountain gorillas) and all are either listed as Endangered or Critically endangered by the IUCN Red List of Threatened Species [13].

Climate projections show that across Africa, 61% of primate habitat is likely to be exposed to increases in maximum temperatures of more than 3˚C by 2050 and to changes in precipitation patterns [14]. Carvalho et al. [15] estimated that the combination of climate, land-use, and population changes could lead to decreases of up to 85% of African ape ranges. As studies often investigate species exposure to average changes in climate, the impact of extreme events remains understudied [16]. Zhang et al. [17] conducted the first global assessment of primate vulnerability to droughts and tropical cyclones, and found that 16% of primate taxa are vulnerable to cyclones and 22% to droughts. Extreme events can affect apes, for example, by reducing food resources and sources of drinking water, or by the destruction of ape habitat (Table 2).

African apes' behavioral adaptability could allow them to adapt to a certain extent. For example, chimpanzees seem to cope with high temperatures by sitting in water pools or resting in caves [18], and being more active during the night [19]. Mountain gorillas drink more

Table 1. Overview of the nine African ape taxa.

Species	Subspecies	Population size [1]	IUCN Status [2]	Number of sites
Bonobo (*Pan paniscus*)		> 15,000–20,000	EN	39
Chimpanzee (*Pan troglodytes*)	Central chimpanzee (*P. t. troglodytes*)	114,000–317,000	EN	114
	Eastern chimpanzee (*P. t. schweinfurthii*)	170,000–250,000	EN	59
	Nigeria-Cameroon chimpanzee (*P. t. ellioti*)	< 9,000	EN	29
	Western chimpanzee (*P. t. verus*)	17,600–96,700	CR	77
Eastern gorilla (*Gorilla beringei*)	Grauer's gorilla (*G. b. graueri*)	~3,800	CR	15
	Mountain gorilla (*G. b. beringei*)	> 1,000	EN	4
Western gorilla (*Gorilla gorilla*)	Cross River gorilla (*G. g. diehli*)	250–300	CR	8
	Western lowland gorilla (*G. g. gorilla*)	~ 360,000	CR	113

[1] Sop et al., 2021

[2] IUCN, 2022; CR–critically endangered, EN–endangered.

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Table 2. Evidence of impact of changes in climatic variables and extreme events on apes.

Climatic variable / extreme event	Evidence of impact on apes and other taxa	Expected impact on apes
Temperature	chimpanzees at a site with high temperatures experience heat stress and sit in caves and pools, likely a thermoregulatory behaviour [18]; they also show increased nocturnal behaviour [19], gorillas drink more frequently [20] and capuchins rest more and travel less during hottest hours of the day [21]; more energy allocated to thermoregulation can lead to physiological trade-offs (e.g., reduced function of immune system observed for birds [22]); high temperatures can lead to reduced performance (e.g., reduced cognitive performance found for humans [23])	high temperatures lead to reduced physiological performance; energy and time allocated to thermoregulation lead to physiological and behavioural trade-offs which can put constraints on the time budget [24] and reduce survival and fertility; extremely high temperatures can lead to direct mortality
Precipitation	chimpanzees at a site with low annual precipitation experience dehydration stress [18]	lower precipitation leads to lower availability of standing water sources and as a consequence dehydration
Consecutive dry days	higher mortality in capuchin infants and reduced offspring production in spider monkeys during long periods of water shortage [25]; long periods without rainfall lead to unavailability of water sources and high levels of stress hormones in vervet monkeys [26]	direct: longer periods without rainfall lead to reduced offspring production and survival; indirect: reduced food availability [27] and increased uncertainty in food availability, changes in phenology of fruiting trees [28], contamination of water sources [29]
Heavy precipitation	heavy rainfall can lead to the destruction of ape nests [30] causing stress and accidents, heavy rainfall leads to higher prevalence of infectious disease [31] which can lead to higher mortality [32]	direct: higher number of incidences of nest destruction leading to higher stress levels and injuries, higher mortality caused by increased prevalence of infectious diseases; indirect: sudden rise in water level of rivers leading to flooding and causing temporary splitting of social groups or inaccessibility of areas
Crop failure	increased deforestation in years with crop failure [33]	indirect: increased destruction of ape habitat, increased resource use in ape habitat (wildlife hunting, wood collection) to compensate for loss of harvest leading to disturbance of apes
Drought (based on soil moisture)	reduction in food availability with a negative impact on body condition, fertility and survival [8,17,27], 22% of primate taxa are vulnerable to droughts [17]	reduction of food resources leading to increased competition between neighbouring social groups [34] and lower fertility and survival
Heatwave (hot and humid)	heatwave can lead to direct mortality (e.g., in humans [35] or flying foxes [36]) and a cross-taxa review found evidence for decline in body condition and fecundity [16]	direct: mortality, decline in body condition and fecundity, indirect: increased risk of forest fires
River flood	flooding can increase prevalence of water-borne diseases [31]; restrict movement leading to longer travel times; for humans floods are the most prevalent climatic hazard leading to high mortality and economic damages [37]	increased disease prevalence, restriction of ape movement, displacement of people resulting in increased pressure on ape habitat (e.g., extraction of wood as building material or charcoal production)
Tropical cyclone	destruction of food resources for lemurs [38], lower fertility among rhesus macaques [39], 16% of primate taxa are vulnerable to tropical cyclones [17]	direct mortality, reduction in food resources
Wildfire	restricting movement leading to longer travel times, destruction of feeding and nesting trees [40]	restricting ape movement, causing longer travel times to avoid fire, and destruction of nesting and feeding trees

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frequently with increasing temperatures [20]. However, African apes are likely to be vulnerable to climate change impacts due to their slow reproduction [41], limited dispersal ability [42], and the restricted range of some ape taxa (e.g., Cross River gorilla and Nigeria-Cameroon chimpanzee [43]). Climate change has rarely been considered in conservation planning, and adaptation measures have not been included in recent conservation action plans for African apes (e.g., western chimpanzees [44], or western lowland gorillas and eastern chimpanzees [45]). Heinicke et al. [46] reported that climate change was listed as a threat only in 3 out of 59 western chimpanzee sites, and only one site (Moyen Bafing NP, Guinea) has implemented climate change-focused measures. In Senegal additional water holes were created recently for farmers to water their livestock in Senegal, so that natural water holes would be available for chimpanzees in this arid region (Kühl pers. com.).

One reason why climate change adaptation measures are not yet planned for or being implemented, is the prevalence of other threats, such as land-use change [14], while climate change is perceived as having a more long-term impact. However, this underestimates the more immediate impact from extreme events [16].

We used state-of-the-art climate data to calculate climatic variables for 363 ape sites across Africa for the past and future, including average temperature and precipitation, consecutive dry days, and heavy precipitation days. We also used a comprehensive data set on projected extreme climate impact events to estimate future exposure to six types of extreme events: crop failure, drought, heatwave, river flood, tropical cyclone, and wildfire. We estimated exposure at the scale of sites, because this is where decisions on funding allocation and the implementation of specific conservation measures are made. Importantly, there is a need to make this type of information publicly available to conservation decision-makers, which is why results on all sites are made available via the A.P.E.S. Wiki (wiki.iucnapesportal.org).

Materials and methods

Ape data

We included all sites across Africa with known current or historical presence of great apes according to the IUCN SSC A.P.E.S. database [47]. In total, there were 363 sites covering 21 countries (Fig 1) including 333 sites with apes' presence and 30 sites where apes are likely extirpated. Spatial outlines of these sites were compiled from the IUCN SSC A.P.E.S. database, the World Database on Protected Areas [48], and Carvalho et al. [15]. For eight sites, spatial outlines were not available and we used the midpoint of the sites. Analyses were implemented for each of the 363 sites and made available on the open-access A.P.E.S. Wiki. Since apes have been extirpated at some of these sites for several decades, results described below are restricted

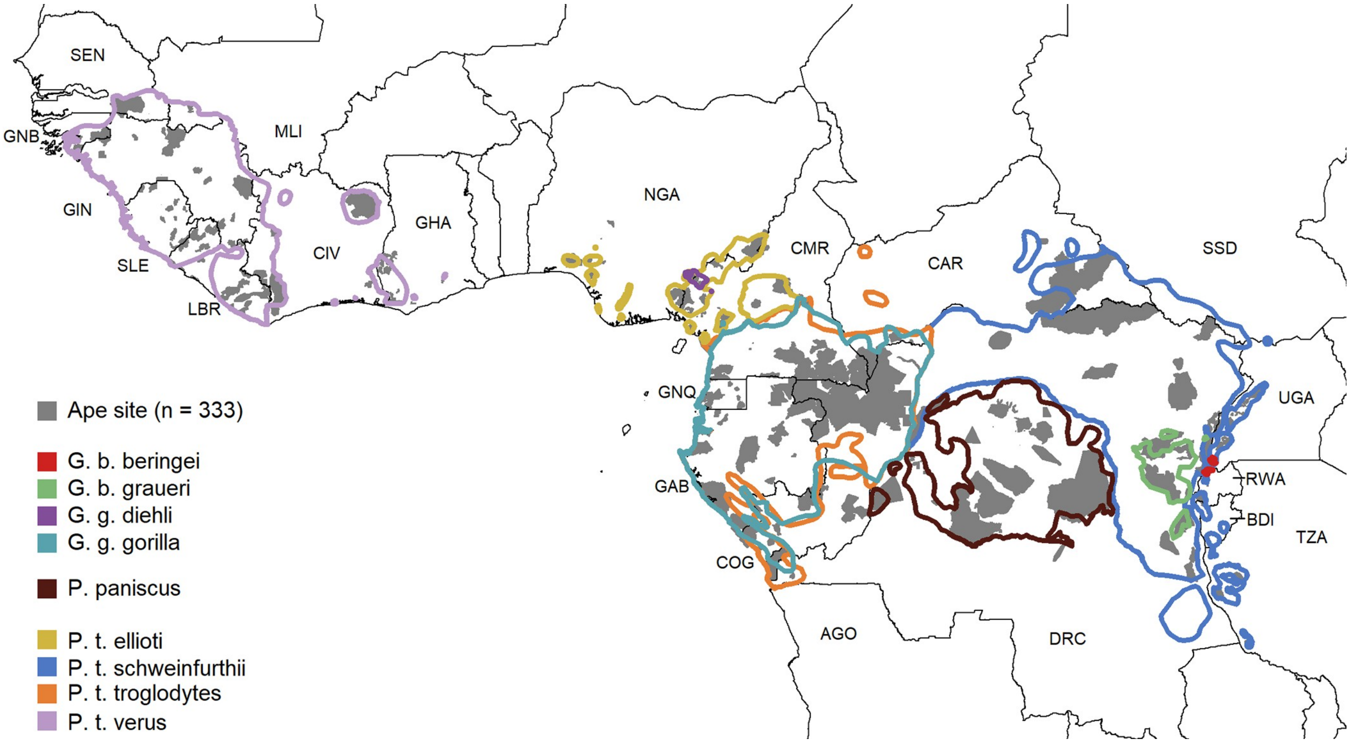

Fig 1. Geographic range for the nine ape taxa for bonobo (*Pan paniscus*), chimpanzee (*Pan troglodytes*), eastern gorilla (*Gorilla beringei*) and western gorilla (*Gorilla gorilla*). Country outline data was obtained from the R package 'mapdata' (cran.r-project.org/package=mapdata).

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to the 333 sites with apes' presence, covering around 42% of the current distribution of African apes. Ape abundance estimates were compiled from the A.P.E.S. database and A.P.E.S. Wiki.

Climate and extreme event data

We used climate and extreme event data provided by the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP, www.isimip.org), the largest platform of the global climate impact modelling community. ISIMIP provides bias-adjusted and downscaled forcing data for the historical and future period, and modelling protocols fully harmonized across climate impact sectors. ISIMIP data has been extensively evaluated and used in cross-sectoral analyses (e.g., [49]).

For the historical period, we used temperature (mean and maximum daily temperature) and precipitation from the bias-corrected daily observational EWEMBI dataset from ISIMIP2a [50] described in [51]. For the future period, we used climate projections for four global climate models (GCMs; IPSL-CM5A-LR, HadGEM2-ES, MIROC5, GFDL-ESM2M) and two Representative Concentration Pathways (RCP2.6 and RCP6.0) from ISIMIP2b [52] described in [53], to be in line with the extreme event data (see below). RCP2.6 is a scenario with strong mitigation measures in which global temperatures would likely rise below 2˚C by 2100, and RCP6.0 is a scenario with medium emissions where the lack of additional mitigation efforts would lead global temperatures to likely rise up to 3˚C by 2100 [54]. The spatial resolution of the climate data is 0.5 degrees (approximately 50 km at the equator).

We used a previously published dataset of extreme climate impact events provided by Lange et al. [55]. This dataset includes six types of extreme events: crop failure, drought, heatwave, river flood, tropical cyclone, and wildfire. Data is based on climate impact simulations from ISIMIP2b [53] and provides extreme event data for the future period for the same four GCMs and two RCPs described above (spatial resolution 0.5 degrees). For each year and grid cell, the proportion of area exposed to an extreme event is provided. Lange et al. [55] based exposure to crop failure on three crop models, drought and river flood on eight hydrological models, wildfire on five vegetation models, and tropical cyclones on one model. Exposure to heatwaves was derived from temperature directly. Details are described in the original publication [55].

For each ape site, we first determined which grid cell midpoints from the climate and extreme event datasets fell within the spatial outline of the site. For the eight sites where we did not have a spatial outline, we identified the grid cell midpoint closest to the site. We then extracted data for each grid cell, and in cases where several grid cell midpoints were within one site, we calculated the average per site.

Climatic variables

To comprehensively describe climatic conditions at each site, we derived four climatic variables based on published evidence of how temperature and precipitation can influence great apes (Table 2). For each year from 1979 to 2016, we calculated:

- temperature (annual mean of mean daily and maximum daily temperature in ˚C)
- precipitation (total annual precipitation in mm/day)
- consecutive dry days (maximum number of consecutive dry days per year, with a dry day defined as precipitation <1mm/day)
- heavy precipitation (number of days with heavy precipitation per year, for the reference period 1979–2013 we calculated the 98th percentile of all precipitation days (>1mm/day) as

a site-specific threshold for a heavy precipitation event, and then derived for each year the number of days above that threshold)

To quantify changes in temperature and precipitation, we calculated temperature and precipitation anomalies. For this, we first calculated the mean temperature for the reference period 1979–2013 (as also used in ISIMIP2b) and then for each year the difference between temperature and the reference value. Thus, a positive anomaly implies that the temperature in that year was higher than the reference period, and a negative anomaly that temperatures were lower. We implemented this approach for mean and maximum temperature and for precipitation.

To be able to compare future climate with past climate, we also calculated the average for each climatic variable across three 30-year periods. We calculated the past average from 1981 to 2010, and future averages from 2021 to 2050 (referred to as 'near term') and from 2071 to 2099 ('long term'). We derived calculations separately for each GCM and then calculated the median across all four GCMs [49,55].

Extreme climate impact events

We analysed the exposure of African apes to six types of extreme events for which there is evidence that they can negatively impact African apes (Table 2) and that were available from the dataset by Lange et al. [55]. For each year of the 'near term' and 'long term' period described above, we extracted the proportion of area affected within each site. For crop failure, we extracted data for the site with a buffer of 50 km to account for the effect that crop failure in areas surrounding an ape site can lead to increased destruction of ape habitat (Table 2). Lange at al. [55] defined droughts based on soil moisture and thus differ from the climatic variables described above which are based on precipitation. Heatwaves were defined by Lange et al. [55] as hot and humid conditions. Thus, climatic variables and extreme events describe different aspects of climate change impacts on apes. For each time period and site, we calculated the number of years with an extreme event and the average proportion of area exposed to events. As above, we first implemented analyses separately for each GCM and then calculated the median across all four GCMs. Maps of projected exposure for the scenarios RCP2.6 near term and RCP6.0 long term typically reflect the range of projected exposure and are shown in the main text (maps for all four scenarios are shown in Fig E-J in S1 Text).

Data processing and analysis was implemented in QGIS version 3.20 [56] and R version 3.6 [57] with the following R packages: 'geosphere' [58], 'maps' [59], 'mapdata' [60], 'ncdf4' [61], 'raster' [62], 'shapefiles' [63] and 'splancs' [64].

Results

Climatic variables

Across the 333 sites analysed, the average annual temperature for the past period (1981–2010) was 24.70˚C. Temperatures were lowest for sites where mountain gorillas occur and highest for western chimpanzees (Fig 2). Sites with eastern chimpanzees covered the widest range of temperatures (9.29˚C, Table A in S1 Text, Fig 2) while sites with bonobos covered the narrowest temperature range (1.29˚C). At the majority of sites temperatures have increased since 1979 (Fig 3). 36 sites with 13,986 apes had positive temperature anomalies for each of the past ten years (2007–2016), and for an additional 135 sites with 106,623 apes, nine of the past ten years had positive temperature anomalies. Average temperature anomalies across the past ten years ranged from 0.01 to 0.56˚C (relative to the reference period 1979–2013) across all sites, with a mean of 0.23˚C (Fig 3). Of the 30 sites with the highest average temperature anomalies,

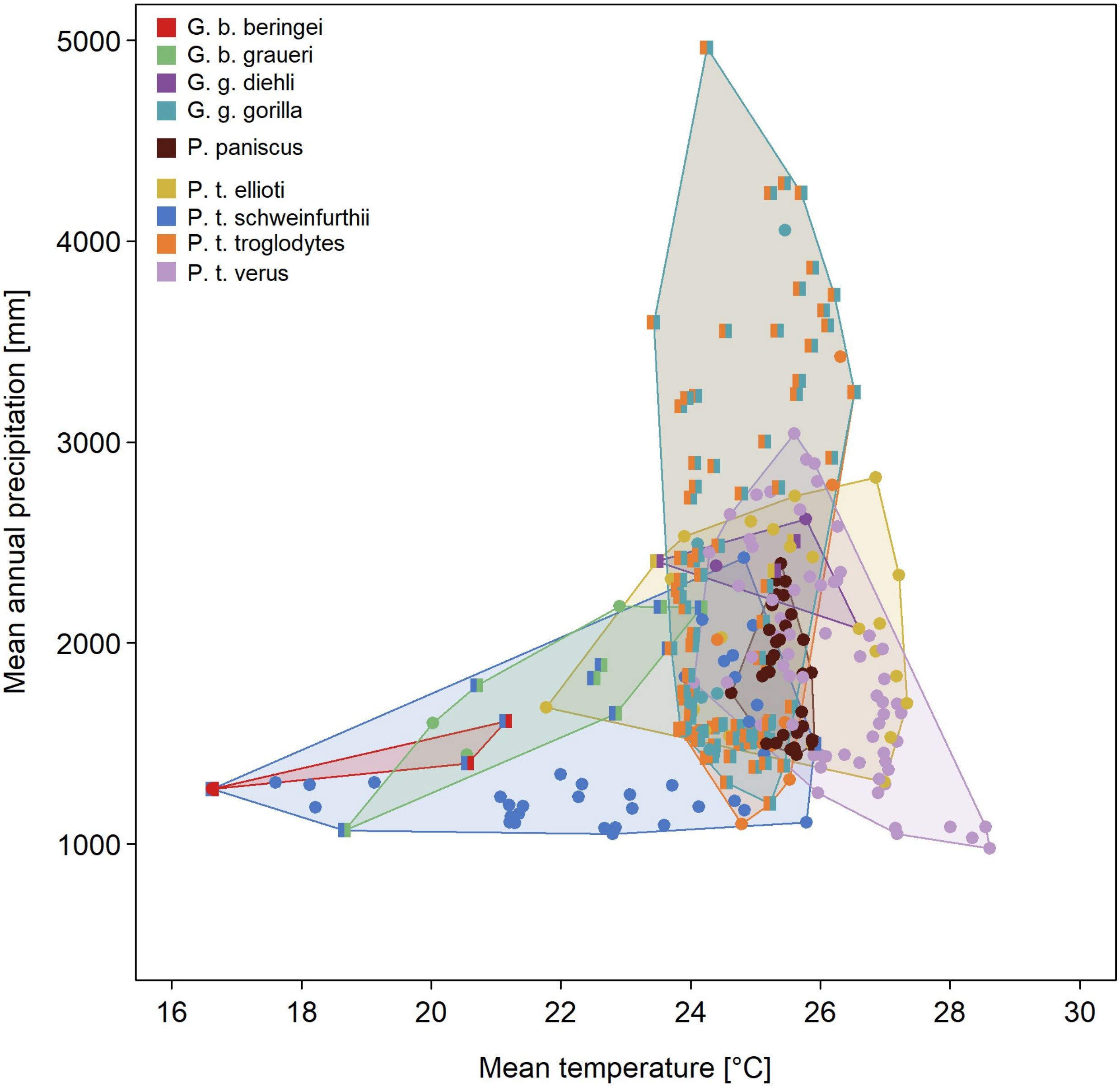

Fig 2. Mean temperature and annual precipitation for the past period (1981–2010) across 333 ape sites. Sites where chimpanzees and gorillas occur are drawn as squares with two colours.

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all but one were within the range of eastern chimpanzees exposing 13,469 apes. For RCP2.6, an increase in annual temperatures of around 1˚C (relative to the past period, 1981–2010) was projected for the near and the long term across all ape taxa. For RCP6.0, the projected increase in the near term was also around 1˚C, and an increase of more than 2˚C was projected for the long term, with a cross-site average of 2.43˚C increase (Supporting information).

The maximum daily temperature averaged across all sites, was 30.53˚C for the past period (Table B in S1 Text), and was highest for sites with western chimpanzees reaching an annual average of 35.42˚C for Niokolo Koba National Park in Senegal. General patterns regarding temperature anomaly and magnitude of projected increases were very similar compared to the patterns described above for daily mean temperature (Table B in S1 Text, Fig A in S1 Text).

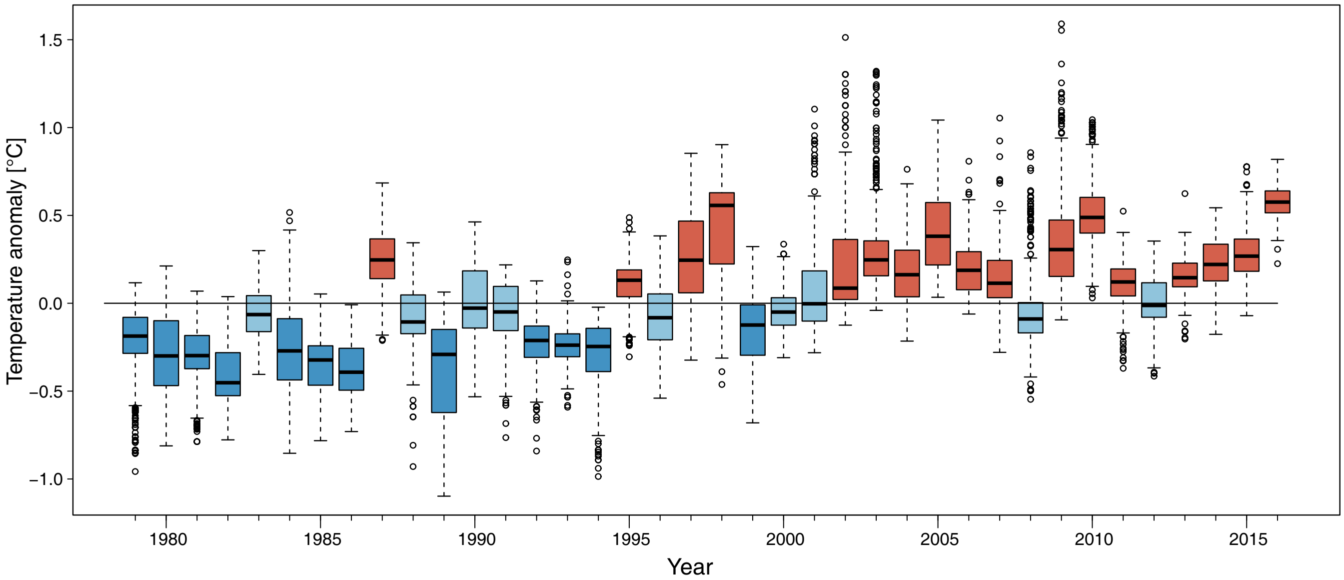

Fig 3. Temperature anomaly across all ape sites. Temperature anomaly is the difference to the average annual temperature of the reference period 1979–2013. Thick lines in the boxplots show the median, bottom end of the box the first quartile and top end of the box the third quartile. Dark blue: Third quartile below zero, light blue: Median below zero and third quartile above zero, light red: Median above zero and first quartile below zero, dark red: Median and first quartile above zero.

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Maximum daily temperatures have increased at the majority of sites (Fig A in S1 Text) and temperature anomalies were highest for sites with western and eastern chimpanzees (e.g., average temperature anomaly of 0.58˚C for Semuliki National Park in Uganda). For RCP2.6 near and long-term and RCP6.0 near term, an increase in average maximum daily temperatures by around 1˚C was projected, and for RCP6.0 long term an increase by 2.41˚C was estimated (Table B in S1 Text).

Annual precipitation differed strongly across ape sites and ranged from 978.14 to 4962.42 mm, with an average of 1940.02 mm across all sites for the past period (Fig 2, Table C in S1 Text). Western chimpanzees occur at sites with the lowest annual precipitation, and western gorillas and central chimpanzees at sites with the highest annual precipitation. For 79 sites with 145,203 apes, seven of the past ten years (2007–2016) were wetter than the reference period (mean precipitation anomaly: 135.40 mm, max: 1056.11 mm). For 54 sites with 51,987 apes, seven of the past ten years were drier than the reference period (mean: -168.48 mm, min: -453.63 mm). Increased precipitation occurred at ape sites in coastal areas of central Africa, and at some savanna sites in western Africa, with drier conditions found in coastal areas at the border between Côte d'Ivoire and Ghana, and around the tri-border area of the Central African Republic, the Democratic Republic of the Congo (DRC) and Gabon (Fig B in S1 Text). Regarding future projections of annual precipitation, there was no clear trend with drying and wetting projected across both RCPs and time periods (Fig B in S1 Text). Decreases in precipitation were consistently projected for chimpanzee sites in western Guinea, Guinea-Bissau, and Senegal. Increases in precipitation were consistently projected for chimpanzee sites at the tri-border area of Guinea, Liberia and Côte d'Ivoire, and north-eastern Côte d'Ivoire and Guinea. Similarly, increases in precipitation were also consistently projected for most sites in central Africa, and the northern range of eastern chimpanzees.

For the number of consecutive dry days, the average across all sites for the past period was 35 days per year (Table D in S1 Text), with lowest values for eastern gorillas (mean: 12 days) and bonobos (mean: 15 days), and longest dry period for western chimpanzees (mean: 47 days). An increase in the number of dry days was consistently projected for all eastern gorilla sites (exposing 4,161 apes) with an increase by more than 20 days in, for example, Kahuzi-Biega and Luama-Kivu in eastern DRC. A strong decrease by more than 30 days was projected for sites in coastal Gabon which was in line with the projected increase in precipitation.

For the number of days with heavy precipitation events, the average for the past period was six days (average across all sites) and similar across all taxa (Table E in S1 Text). For future periods, an increase in heavy precipitation events was consistently projected across 288 sites with 429,924 apes, while only for two sites a decrease in heavy precipitation was consistently projected.

Extreme events

In terms of number of sites affected, wildfires (Fig 4) and crop failures (Fig 5) were the most prevalent extreme events, as across all scenarios 100% of sites were exposed (exception: two sites not exposed to wildfires for RCP6.0 near term). For wildfires, the frequency of events was very high, with almost every year experiencing an event (Table K in S1 Text). For crop failures, frequency was the second highest across event types, with around 15 years (out of a 30-year period) exposed to crop failures for RCP2.6 near and long term (Table F in S1 Text). However, for both crop failure and wildfires, the proportion of area affected was low, with less than 5% exposed under all scenarios.

River floods (Fig 6) and heatwaves (Fig 7) were also very prevalent in terms of number of sites affected. Most sites were exposed to floods under RCP2.6 near term (78%) and long term (92%, Table I in S1 Text). But the frequency was low with around one year with an event for RCP2.6 long term and three years with an event for RCP6.0 long term. River floods had low spatial extent with an average of 1–2% of area affected across all scenarios. However, the range

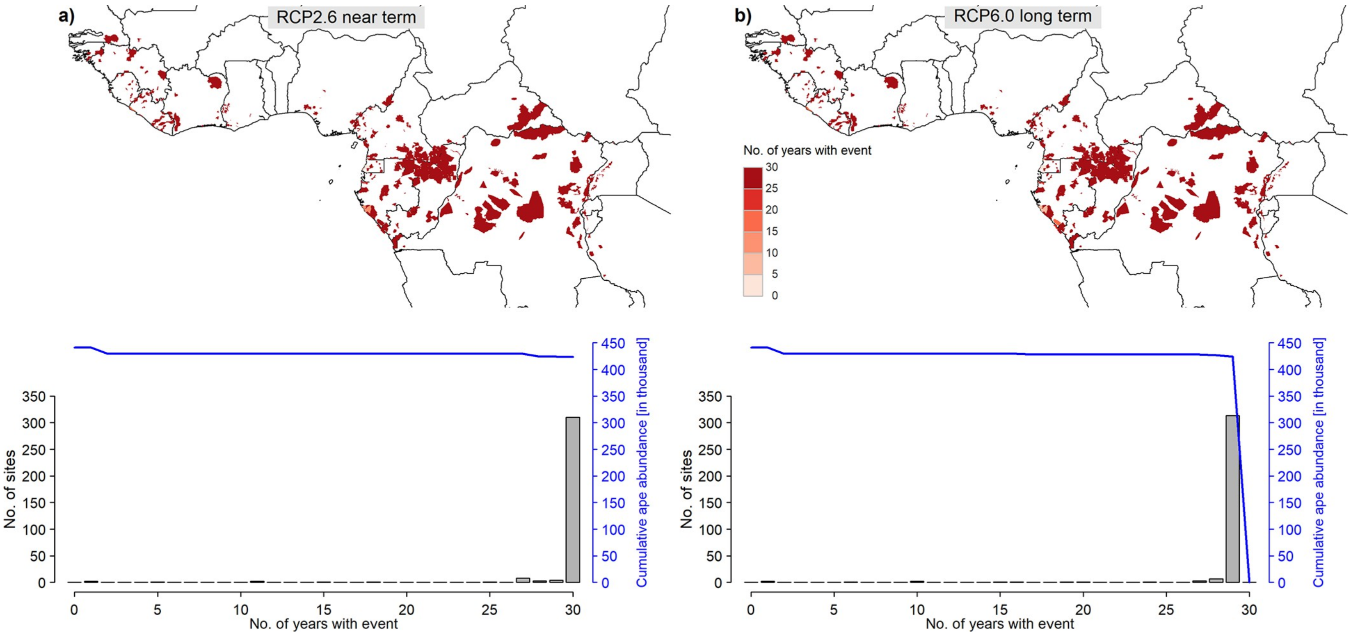

Fig 4. Projected exposure of African ape sites (n = 333) to wildfires for two scenarios. (a) RCP2.6 near term (2021–2050) and (b) RCP6.0 long term (2071–2099). Top row: Number of years with an event within the time period. Bottom row: Number of sites and number of apes projected to be exposed to the respective number of years with an event. Maps for all four scenarios in Fig J in S1 Text. Country outline data was obtained from the R package 'mapdata' (cran.r-project.org/package=mapdata).

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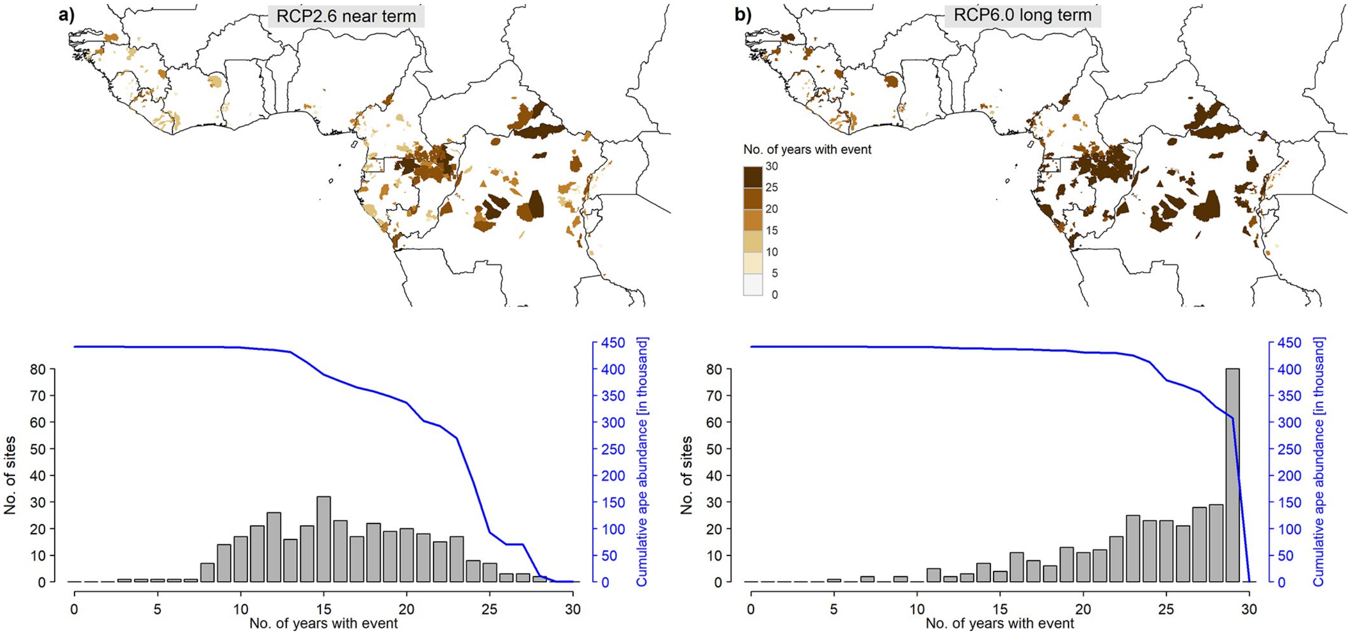

Fig 5. Projected exposure of African ape sites (n = 333) to crop failure for two scenarios. (a) RCP2.6 near term (2021–2050) and (b) RCP6.0 long term (2071–2099). Top row: Number of years with an event within the time period. Bottom row: Number of sites and number of apes projected to be exposed to the respective number of years with an event. Maps for all four scenarios in Fig E in S1 Text. Country outline data was obtained from the R package 'mapdata' (cran.r-project.org/package=mapdata).

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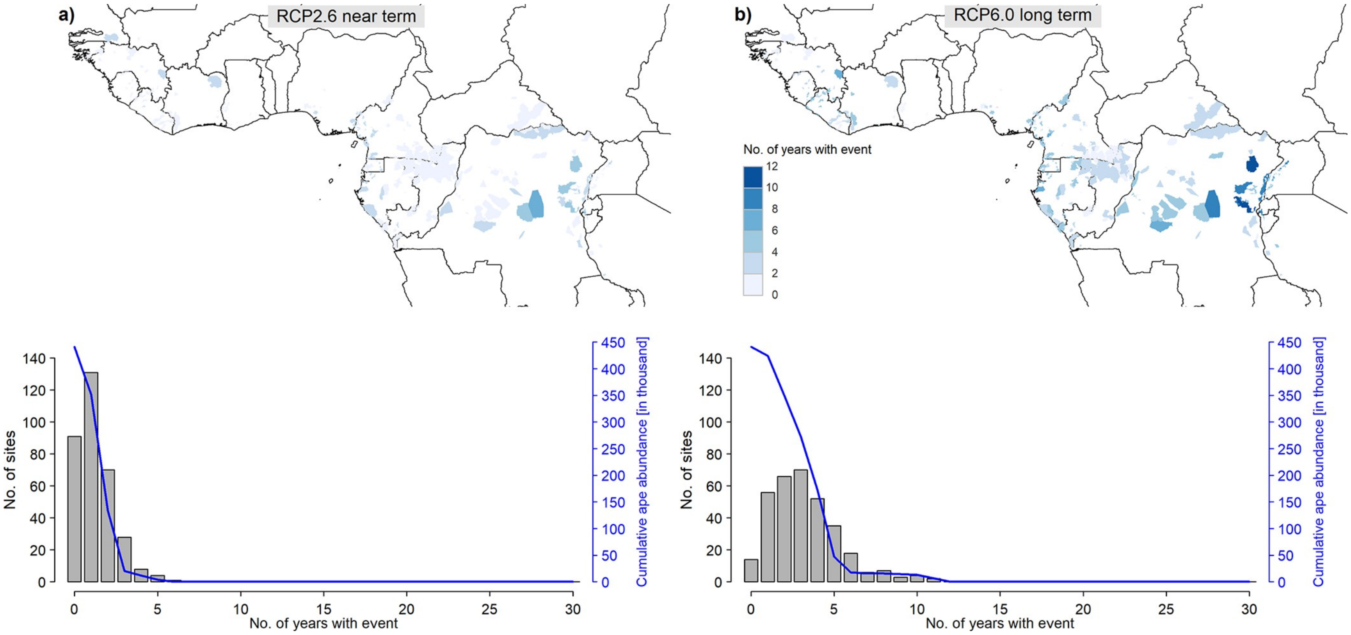

Fig 6. Projected exposure of African ape sites (n = 333) to river floods for two scenarios. (a) RCP2.6 near term (2021–2050) and (b) RCP6.0 long term (2071–2099). Top row: Number of years with an event within the time period. Bottom row: Number of sites and number of apes projected to be exposed to the respective number of years with an event. Maps for all four scenarios in Fig H in S1 Text. Country outline data was obtained from the R package 'mapdata' (cran.r-project.org/package=mapdata).

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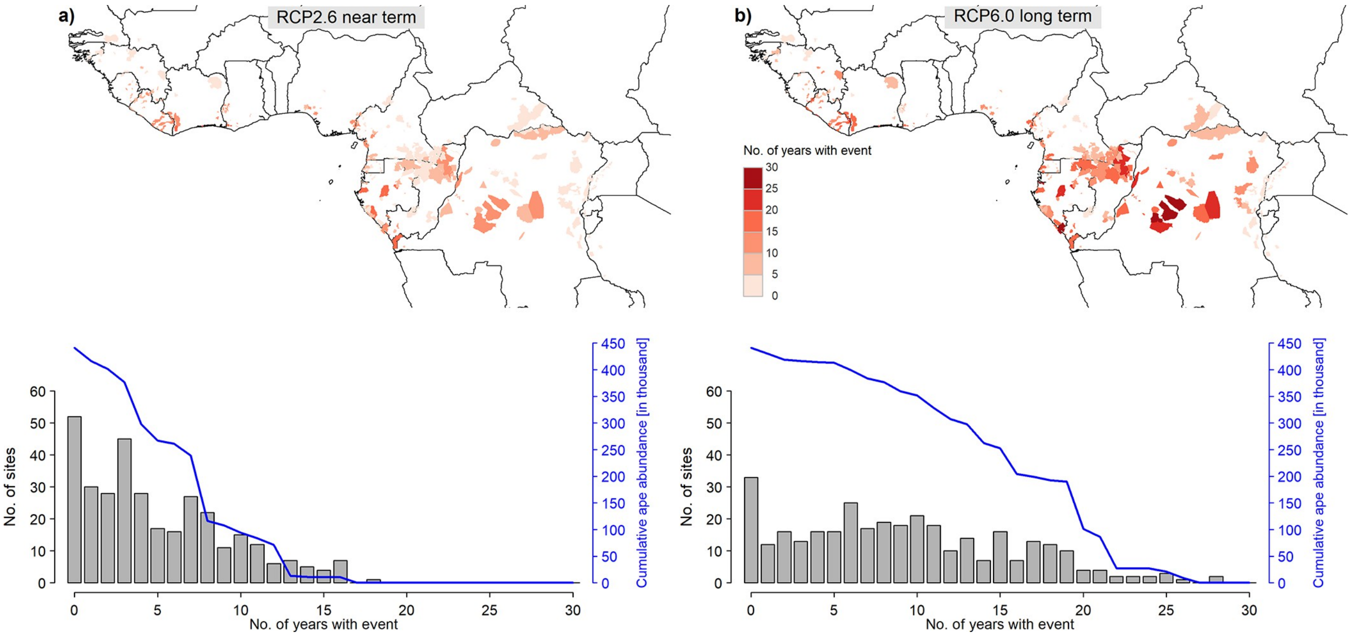

Fig 7. Projected exposure of African ape sites (n = 333) to heatwaves for two scenarios. (a) RCP2.6 near term (2021–2050) and (b) RCP6.0 long term (2071–2099). Top row: Number of years with an event within the time period. Bottom row: Number of sites and number of apes projected to be exposed to the respective number of years with an event. Maps for all four scenarios in Fig G in S1 Text. Country outline data was obtained from the R package 'mapdata' (cran.r-project.org/package=mapdata).

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was relatively large (up to 14%) and for Budongo, Bugoma and Mahale (eastern chimpanzee) more than 10% of area were affected in three out of four scenarios. Most sites were exposed to heatwaves for RCP2.6 near term (84%) and long term (85%, Table H in S1 Text). The frequency of events was on average around five years with events for RCP2.6 near and long term. Frequency was higher for RCP6.0 long term with an average of nine years with events. Sites with high frequency in heatwave events were located in southern Côte d'Ivoire and neighbouring areas, and in central Africa (Fig 7). The extent of spatial exposure was high with more than 80% of the area affected for RCP2.6 near and long term.

For droughts, 8% of sites were exposed under RCP2.6 near and long term (Table G in S1 Text, Fig C in S1 Text, S6). They were located in the tri-border area of Guinea, Guinea-Bissau and Senegal, in Côte d'Ivoire and Ghana, and two sites in central Africa (Canbinda and Tshuapa-Lomami-Lualaba). The event frequency was low (mean across sites for RC2.6 near term 0.14 years), and highest for western chimpanzees with an average of 4.5 years for RCP2.6 near term. However, similar to heatwaves, the spatial extent of exposure was projected to be high with an average of 53.78% for RCP2.6 near term, and lower exposure of 35.75% for RCP2.6 long term.

For tropical cyclones, only few sites were projected to be exposed (Table J in S1 Text, Fig D, I in S1 Text). For RCP2.6 near term only sites within the range of western chimpanzees were exposed, for example, Cantanhez Forest in Guinea-Bissau and Nialama in Guinea. For RCP2.6 long term, sites in Sierra Leone were also projected to be exposed (e.g., Loma Mountains and Western Area Peninsula). Only for RCP6.0 long term, tropical cyclones were also projected for coastal sites in central Africa (e.g., Cabinda and Conkouati-Douli) which could expose western lowland gorillas and central chimpanzees.

In summary, crop failure and wildfires are projected to affect all sites at a high frequency and low spatial extent. A large majority of sites are projected to be affected by heatwaves with a medium frequency but high spatial exposure, and river floods with a low frequency and typically low spatial extent. Droughts and tropical cyclones were projected to only affect specific sites. Numbers were typically higher for RCP6.0 in comparison to RCP2.6, and only for droughts a decrease in average spatial exposure was projected.

Discussion

For the first time, we showed that African ape sites have already experienced changes in climatic conditions and are likely to be exposed to extreme events in the future. We found that temperatures have increased over the past decades at the majority of ape sites, and in line with a previous study [14], we found a consistent increase in future temperatures. Bonobo sites covered the narrowest temperature range, which indicates a potentially lower physiological tolerance that might make bonobos more sensitive to climate change impacts [65]. We also showed that the majority of ape sites will be exposed to a high frequency of heatwaves. It has been shown that chimpanzees occurring in an area with high temperatures experience heat stress [18]. The impact of heatwaves on primates has not yet been studied, but high mortality of humans during heatwaves [35] and mass die-offs for some taxa (e.g., flying foxes [36]) have been observed. Thus, given the projected prevalence of heatwaves across ape sites, there is a need to understand sensitivity of apes to this extreme event. Thermoregulation behaviours have already been observed in apes (e.g., higher drinking frequency, nocturnal behaviour, sitting in caves and pools [18–20]). Though the behavioural flexibility of apes allows them to adapt to higher temperatures to some degree, these behaviours have only been observed for a few study sites, and it is not known how effective these adaptation strategies are, given, for example, that apes compete for access to standing water sources with humans and their livestock in dry habitats. In addition, these adaptive behaviours entail trade-offs, such as less time for feeding, or increased predation pressure at night. When more energy is used for thermoregulation this can reduce other physiological processes such as reduced functionality of the immune system, as observed for birds [22]. Behavioural and physiological trade-offs can result in a decline of body condition, as well as lower survival and fertility (Table 2).

For precipitation, the results were heterogenous for the historical as well as future period. For sites that have been and are projected to be exposed to less precipitation or an extended period without any precipitation (e.g., projected for eastern gorillas), this can result in a reduced availability of standing water sources. As chimpanzees at a site with low annual precipitation already experience dehydration [18], and as drinking more water is a strategy gorillas use to cope with high temperatures [20], the combined impact of rising temperatures and reduced precipitation might lead to high levels of stress and result in a decline of body condition and fecundity, and ultimately to population declines [16].

Exposure to droughts was projected only for few sites (mostly in West Africa) and there droughts could lead to a reduction in food sources. For forest elephants in Gabon, drier conditions led to lower encounter rates of ripe fruits and resulted in a decline in elephant body condition [27]. In contrast, some sites in savanna areas are projected to have an increase in precipitation, and thus projections show a lower proportion of area exposed to droughts in the long term, which is in line with updated model projections [66]. While there were extensive droughts in the 1970s and 1980s across the Sahel, rainfall has increased since the 1990s, which has been linked to changes in the West African monsoon [67]. In combination with the CO_2 fertilization effect this could lead to a further greening of the Sahel [67,68] and potentially an increase in suitable habitat for apes.

Our finding of an increase in the number of days with heavy precipitation at a majority of sites is in line with findings that rainfall patterns will become more erratic [69]. Heavy precipitation can destroy ape nests [30]. At the same time, up to 90% of sites are projected to be exposed to river flooding, which can restrict animal movement, lead to splitting of social groups, make affected areas inaccessible to animals and can ultimately lead to higher mortality due to higher disease prevalence [32].

The high spatial exposure of ape sites to crop failures and wildfires can intensify forest fragmentation and deforestation. Especially the combination of several stressors, such as drying, fires and deforestation could lead to a self-reinforcing process that could even lead to a tipping of the Congo rainforest into savanna [70] and thus a loss of ape habitat.

The prevalence of exposure of ape sites to climate change impacts stresses the need to plan, for example, in conservation action plans, and implement conservation measures that will increase ape resilience to climate change. At sites facing water shortages, the creation of additional water sources or the protection of such sources specifically for apes would be an important measure. In addition, measures that protect nesting and feeding trees and ape habitat in general, are needed to improve ape resilience. This can also include measures that prevent the unintentional spread of wildfires, for example, cutting fire breaks, as is implemented in Moyen-Bafing National Park in Guinea [46]. As we found a high projected prevalence of crop failures, interventions that support farmers in years of crop failure or supplementary income sources can contribute to avoiding deforestation. It has not yet been studied to which extent apes are able to track their climatic niche by shifting their range. However, dispersal velocities of primates are lower than for most other taxa [17,42]. Thus, to support adaptation to climate change impacts, the creation of corridors and new protected areas are needed to avoid isolation of ape populations.

Limitations

One limitation of this study pertains to uncertainties inherent in modelled climate data and simulated climate change impacts as discussed by Lange et al. [55]. However, the bias-adjustment implemented by ISIMIP reduces some of these uncertainties. To reduce bias, we implemented analyses separately for each GCM and then calculated the median across all four GCMs [49,55]. The choice of two emission scenarios allowed for estimating a possible corridor of future developments, as recent observations show that global greenhouse gas emissions are already exceeding the low-emission scenario RCP2.6. In addition, the climate data we used has a coarser resolution than other available data sources. We chose ISIMIP climate data because the same data was used to force the climate impact models that provided the input for estimating extreme event exposure [55]. This type of extreme event data, especially the inclusion of different types of impacts, is not available at higher resolution from other sources. Further, other sources of high-resolution climate data that are commonly used in biodiversity research (e.g., CRU [71] or WorldClim [72]) also have shortcomings, including the low and decreasing coverage of weather stations across Africa [73] or limitations in mountainous regions [74]. Similarly, we did not use CMIP6 climate data as the corresponding climate impact simulations are not yet available, and consequently not the respective extreme event data. Future research with climate and extreme event data based on CMIP6 will be useful to corroborate the findings of this study and to better understand modelling uncertainties, for example, regarding the ongoing discussion on whether a subset of CMIP6 models can be considered 'too hot' [75].

With the exception of the study by Zhang et al. [17] on the exposure of primates to past droughts and tropical cyclones, studies on the exposure of great apes to past extreme events are rare. Closing this research gap would be an important contribution to assessing the extent to which apes may be able to adapt to the projected prevalence of extreme events.

Conclusion

Our study shows that African apes are and will be increasingly exposed to climate change impacts. However, the vulnerability of animals to the impacts of climate change, and in particular to extreme events, remains poorly understood. Long-term research sites may be well placed to investigate how sensitive animals are to climatic stressors at physiological and behavioural levels. In addition, systematic data collection across sites with different climate change contexts would be important to better understand the mechanisms underlying climate change impacts on animals. Although large gaps remain, our study highlights the need to integrate climate change adaptation into conservation action planning.

Supporting information

S1 Text. Supporting tables Table A in S1 Text. Annual mean temperature. Table B in S1 Text. Annual maximum temperature. Table C in S1 Text. Annual precipitation. Table D in S1 Text. Maximum number of consecutive dry days. Table E in S1 Text. Number of days with heavy precipitation. Table F in S1 Text. Projected exposure to crop failures. Table G in S1 Text. Projected exposure to droughts. Table H in S1 Text. Projected exposure to heatwaves. Table I in S1 Text. Projected exposure to river floods. Table J in S1 Text. Projected exposure to tropical cyclones. Table K in S1 Text. Projected exposure to wildfires. Supporting figures Fig A in S1 Text. Anomaly of maximum daily temperature. Fig B in S1 Text. Projected exposure of African ape sites to changes in precipitation. Fig C in S1 Text. Projected exposure of African ape sites to droughts. Fig in S1 Text. Projected exposure of African ape sites to tropical cyclones Fig in S1 Text. Maps of projected exposure of African ape sites to crop failure for all four scenarios. Fig in S1 Text. Maps of projected exposure of African ape sites to droughts for all four scenarios. Fig in S1 Text. Maps of projected exposure of African ape sites to heatwaves for all four scenarios. Fig in S1 Text. Maps of projected exposure of African ape sites to river floods for all four scenarios. Fig in S1 Text. Maps of projected exposure of African ape sites to tropical cyclones for all four scenarios. Fig in S1 Text. Maps of projected exposure of African ape sites to wildfires for all four scenarios.
(PDF)

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