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RESEARCH ARTICLE OPEN ACCESS

Vulnerability to Climate Changes of Tropical Forests Across Africa

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Received: 11 February 2025 | **Revised:** 29 September 2025 | **Accepted:** 30 September 2025

Editor: Rob Cooke

Funding: This work was supported by the Fonds De La Recherche Scientifique-FNRS (O.0026.22).

Keywords: climate change | exposure | risk assessment | safety margin | tropical moist forest | vulnerability

ABSTRACT

Aim: Global climate projections identify tropical regions as hotspots of climate change during the 21st century. The few ground data in tropical Africa confirm significant warming and drying over the last decades, but how plant communities will tolerate these new climate conditions remains vastly uncertain. In this study, we assess the climatic vulnerability of tropical moist forests across Africa.

Location: Tropical Africa.

Methods: We mapped climate change exposure across the tropical moist forest biome, focusing on mean annual temperature (MAT), mean annual precipitation (MAP) and climatological water deficit (CWD) using climate projections for 2085 from five regional models under RCP4.5 and RCP8.5. Using occurrence records for 3,536 tree and shrub species, we estimated species' climatic limits and safety margins, then averaged these margins at the community level. Finally, we combined exposure and safety margins to assess species- and community-level risk by 2085.

Results: Under RCP4.5, corresponding to an average warming of 2.4°C by 2085, 92% of species (3,256) could be at risk in at least one community where they occur. This rate increases to 96% (3,405 species) under RCP8.5, with an average warming of 4.3°C. In all scenarios, the most at-risk communities are concentrated in low-elevation regions, where species have few opportunities to migrate if their climatic limits are exceeded. The high risk across the forest biome results from the combination of significant and widespread temperature increases and the relatively narrow safety margins of the species. Specifically, 50% of species have an average safety margin below 1.6°C above baseline temperatures, suggesting they are already near their observed climatic limits.

Main Conclusions: Beyond refining our understanding of the vulnerability of tropical moist forests across Africa, our results have far-reaching implications for conservation, allowing us to target species and communities of interest for further monitoring and conservation efforts.

1 | Introduction

Tropical forests store more than 200 Pg C in aboveground live biomass (Baccini et al. 2012; Li et al. 2022), contribute over 32% of global primary productivity and exert a significant influence on the hydrological cycle (Beer et al. 2010). Furthermore, they harbour more than half of the described species (Pillay et al. 2022), and provide essential resources to around 1.5 billion

people who depend on these forests for food, medicine, potable water, shelter and energy (Vira et al. 2015).

Global climate projections identify tropical regions as persistent hotspots of climate change during the 21st century (IPCC 2023), meaning that they will experience more intense or rapid climate changes compared with other regions. The situation of tropical forests in Africa is particularly concerning, as they are already found under drier and more seasonal climates than the other tropical regions (Parmentier et al. 2007; Guan et al. 2015). Furthermore, the expected future climate conditions in much of Africa have no current analogues, creating so-called 'novel climates' (Greve et al. 2013). In central Africa, depending on the climate scenarios, temperatures are projected to increase by 2°C–4°C by 2099 compared with the mid-20th century baseline (Aloysius et al. 2016), a trend confirmed by rare ground data, which report warming rates of +0.21 and 0.25°C per decade, respectively, at Yangambi in the Democratic Republic of Congo for the period 1960–2020 (Kasongo Yakusu et al. 2023) and at Lopé in Gabon for the period 1984–2018 (Bush et al. 2020). Unlike temperature, precipitation projections lack consensus due to inter- and intramodel variability (Dosio et al. 2019, 2022), with predicted changes ranging from −9% to +27% (Aloysius et al. 2016), which complicates risk projections for biodiversity (Greve et al. 2013). However, inland regions in tropical Africa are likely to be exposed to an intensification of the dry seasons (Zhou et al. 2014), a trend confirmed by ground data in the two localities of central Africa previously mentioned (Bush et al. 2020; Kasongo Yakusu et al. 2023).

In the Amazon, it has been demonstrated that forests exposed to a 100 mm increase in water deficit lost 5.3 Mg of aboveground carbon per hectare (Phillips et al. 2009) due to widespread mortality of large trees, which are less tolerant to drought-induced water stress than smaller ones (Bennett et al. 2015; Phillips et al. 2010). A significant and widespread decline in carbon sinks has been observed across the Amazon Basin, a pattern that has not been observed for tropical moist forests of Africa (Hubau et al. 2020). However, subregional studies have reported shifts in the taxonomic, functional and phylogenetic composition of forest communities (Aguirre-Gutiérrez et al. 2020). In Ghana, tree functional changes have been identified, with an increase in the abundance of deciduous and canopy species with intermediate light demand, and a decrease in evergreen, subcanopy and shade-tolerant species, and these changes have been associated with two decades of prolonged drought (Fauset et al. 2012; Aguirre-Gutiérrez et al. 2019). In the semideciduous forests of central Africa, a combined analysis of plot data (1982–2008) and models revealed that tree growth declines as drought intensifies, but understory shade-tolerant species are less affected, suggesting that increased drought intensity could shift forest composition (Ouédraogo et al. 2013). Meanwhile, in Afromontane forests, plot data (monitored between 2010 and 2022) highlighted an increase in the abundance of thermophilic species from warmer climates (Cuni-Sanchez et al. 2024). These compositional shifts highlight how African tree species may respond differently to climatic changes, driven by their unique combinations of functional and physiological traits that shape their environmental tolerance ranges and limits. The latter remain largely misunderstood for tropical tree species, despite being crucial for quantifying mortality risks at specific sites under different climate change scenarios.

To quantify the mortality risk in a specific site, species' hydraulic and thermal tolerance are widely employed to identify critical thresholds of water availability or temperature (Tavares et al. 2023). The hydraulic safety margin is calculated as the difference between the minimum water potential experienced by a tree in a given site and the limit of hydraulic tolerance of the species, i.e., the water potential at which the xylem undergoes hydraulic failure due to embolism (Meinzer et al. 2009). Similarly, the thermal safety margin is calculated as the difference between maximum leaf surface temperature in the field and the critical temperature at which metabolic processes, such as photosynthesis, are disrupted (Marchin et al. 2022). Measuring tree physiological safety margins can yield detailed information about species' performance and tolerance under climatic stress. However, the lack of such data for thousands of species in the tropical moist forests of Africa hinders our ability to understand how tree species will respond to rapid climate change and to forecast which forest communities are most at risk from climate-related stress. Functional traits of species (including ecophysiological traits), together with biotic interactions and macroclimate, act as key filters shaping their spatial distribution (Kirschbaum 2000; Pennington et al. 2004). Consequently, information derived from species distributions and realised climatic niche limits can serve as a useful proxy in the absence of direct ecophysiological data (Esperon-Rodriguez, Ordoñez, et al. 2022). Climatic tolerance limits inferred from the observed niche of species are routinely used in ecological and biogeographical studies to estimate species' climatic safety margins and assess the vulnerability of communities and ecosystems to climate change (Gallagher et al. 2019; Esperon-Rodriguez, Tjoelker, et al. 2022; Esperon-Rodriguez, Ordoñez, et al. 2022). In this context, the climatic safety margin is defined as the difference between the observed climatic niche limits of a given species and the climate conditions at the locations where the species currently occurs (Gallagher et al. 2019).

In this study, we aimed to assess the climatic vulnerability of tropical moist forests across Africa. We applied the approach proposed by Gallagher et al. (2019), which quantifies (1) the exposure to climate change, (2) the climatic safety margin based on the observed species' climatic limits and (3) the climate risk which combines the exposure and the safety margin. Exposure is the extent of climate change that a specific site is likely to experience. The climatic safety margin is the extent of climate change that a species can tolerate in a specific site before exceeding its climatic limit. Climatic risk for a species in a specific site arises when the exposure in that site exceeds the safety margin of the species, and the risk for a community depends on the safety margin of the constituent species. We specifically addressed the following questions:

1. What is the exposure to climate change that will be experienced by tropical moist forests in Africa according to two main scenarios of future climate changes (RCP4.5 and RCP8.5)? We focused on mean annual temperature (MAT), mean annual precipitation (MAP) and

climatological water deficit (CWD). Given the intermodel variability for the prediction of precipitation (Dosio and Panitz 2016), we explore a large ensemble of regional climate model (RCM) simulations, to assess the robustness of the climate change signal and to identify areas of high climate uncertainty.

2. What are the safety margins of tropical moist forest communities and of their constituent species? We will specifically examine how the climatic niche breadth and spatial extent of the species influence their climatic tolerance as demonstrated elsewhere (Lörz et al. 2022; Thuiller et al. 2005), but never tested for tropical forest species in Africa.

3. What is the climate risk encompassed by tropical moist forests across Africa and which forest communities are expected to be more resilient or at greater risks?

2 | Methods

2.1 | Climatic Data

The climate data were extracted from AFRICLIM version 3.0 (https://webfiles.york.ac.uk/KITE/AfriClim/), a high-resolution climate projection designed for ecological applications in Africa (Platts et al. 2015). By applying dynamical downscaling of global circulation models (GCMs) through regional climate models (RCMs), AFRICLIM captures fine-scale climatic gradients—such as orographic and coastal effects—and corrects GCM-related biases, thereby producing internally consistent projections. Although RCM-based products like AFRICLIM add value by resolving fine-scale climatic processes, this advantage is not universal (Feser et al. 2011), and statistically downscaled GCMs can sometimes provide comparable improvements.

To align modelled outputs with observed climatologies, AFRICLIM applied change-factor methods (Tabor and Williams 2010), superimposing modelled anomalies onto observational data sets (CHIRPS for precipitation and WorldClim for temperature). These observational products were therefore not used independently but integrated into the AFRICLIM downscaling process (Platts et al. 2015).

Climate projections were derived from the five RCMs available in AFRICLIM v3.0, each driven by one or more CMIP5 GCMs: CCCma-CanRCM4 (CanESM2), CLMcom-CCLM4-8-17, DMI-HIRHAM5, KNMI-RACMO22T and SMHI-RCA4 (driven by eight GCMs in total). Future climates were simulated under two IPCC AR5 representative concentration pathways (RCP4.5 and RCP8.5), corresponding to global temperature anomalies of +2.4°C and +4.9°C by 2100, respectively (Rogelj et al. 2012). These scenarios were selected because AFRICLIM v3.0 does not yet include CMIP6-based AR6 scenarios (SSPs). Including both provides a relevant range of potential futures for conservation planning, helping identify areas at risk under both moderate and extreme climate change conditions.

For this study, we used climate data at a 10 arc-minute (~18.5 km) resolution, consistent with the spatial accuracy of the occurrence records. The baseline climate corresponds to the period 1961–1990, and future projections to 2071–2100, centred on 2085. Our analyses relied on the multimodel median across the five GCM–RCM combinations provided in AFRICLIM v3.0. To account for projection uncertainty, we also considered the full range of outputs from the individual models in addition to the median values (Almazroui et al. 2020).

We focused on three bioclimatic variables known to influence the distribution and composition of tropical tree species in Africa: mean annual temperature (MAT), mean annual precipitation (MAP) and climatological water deficit (CWD) (Fayolle et al. 2014; Gorel et al. 2022). CWD was calculated as the sum of monthly differences where potential evapotranspiration (PET), estimated from minimum and maximum temperatures (Droogers and Allen 2002), exceeds precipitation:

$$\mathrm{CWD} = \sum_{i}^{12} \max\left(0, \mathrm{PET}_i - P_i\right) \quad (1)$$

2.2 | Floristic Data

We extracted species occurrences from the RAINBIO database (https://gdauby.github.io/rainbio/download_page.html), which includes 673,372 georeferenced records across tropical and subtropical Africa. These data come from herbarium collections, personal databases and floristic inventories carried out between 1785 and 2022. The RAINBIO database contains 25,956 species of vascular plants native to Africa and representing around 89% of the known flora of the African continent (Dauby et al. 2016). The database has been updated since the original publication, including, among others, the occurrences from species lists compiled for tropical forests (Fayolle et al. 2014) and savannas (Fayolle et al. 2019) across Africa, and that contains 44,485 occurrences. For this study, we focused on tree and shrub species, resulting in a total of 360,065 records for 8,582 species. Next, we removed occurrences with poor georeferencing accuracy and species with fewer than 10 occurrences. This preprocessing resulted in 321,727 valid georeferenced occurrence records for 4,808 tree and shrub species across the African continent.

2.3 | Delimiting African Tropical Moist Forests and Defining Forest Communities

To define the spatial extent of tropical moist forests across Africa, we used the biome index map developed by Aleman et al. (2020), which quantifies the relative dominance of forest- versus savanna-specialist species in each 0.5° pixel across tropical and subtropical Africa. The index ranges from −1 (pure savanna) to +1 (pure forest). We applied a threshold of +0.2 (a conservative threshold), which corresponds to a minimum of 20% dominance by forest-specialist species in the floristic composition of each pixel. This threshold effectively excludes savanna-dominated and transitional mosaic areas (i.e., pixels with a biome index near 0), ensuring that only areas with a sufficiently strong forest signal according to the floristics are retained to represent meaningful tropical forest communities. We intersected the cleaned species occurrence data set (321,727 valid georeferenced occurrence records for 4,808 tree and shrub

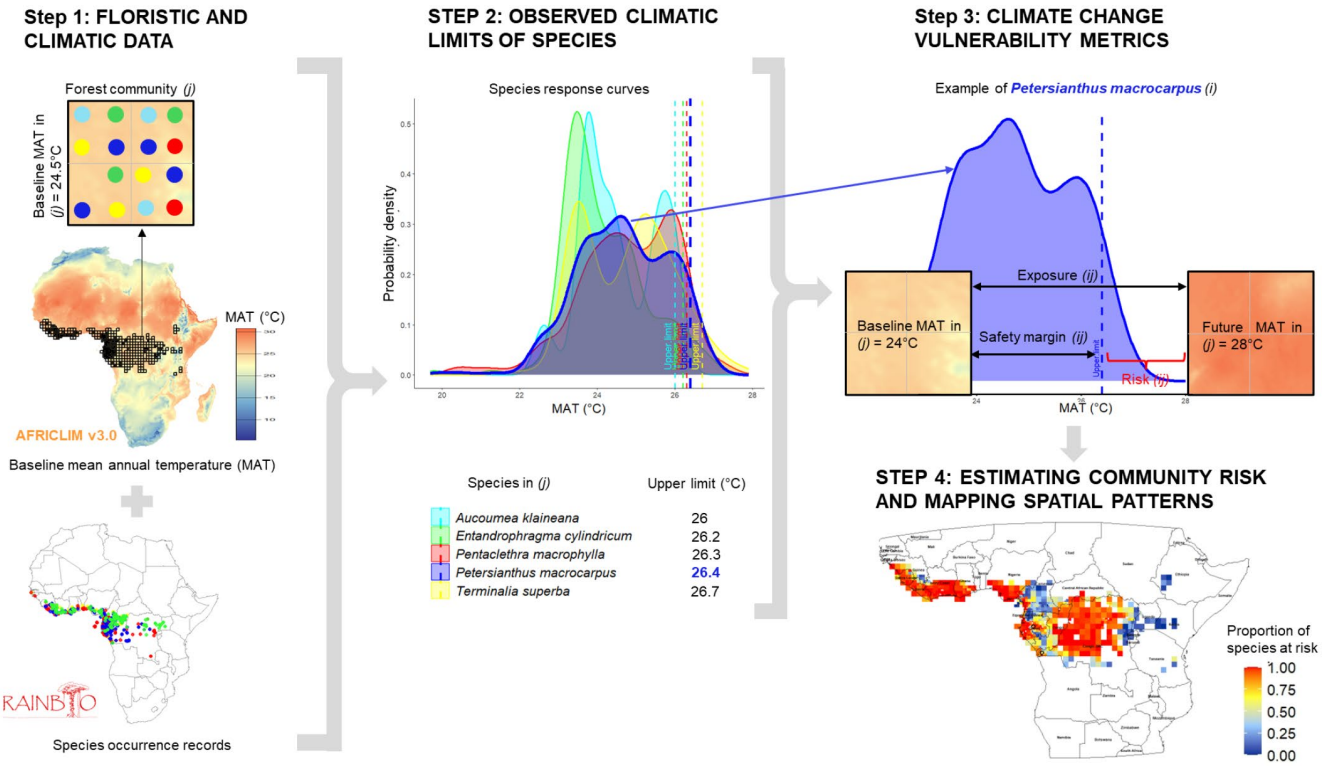

FIGURE 1 | Conceptual example of climate risk assessment for tree and shrub species (adapted from Gallagher et al. 2019). The framework is illustrated using mean annual temperature (MAT) in a virtual forest community (*j*) composed of five species: *Aucoumea klaineana*, *Entandrophragma cylindricum*, *Pentaclethra macrophylla*, *Petersianthus macrocarpus* and *Terminalia superba*. Step 1: Floristic and climatic data. We extracted georeferenced occurrence records for the species of the community at the continental scale from the RAINBIO database and overlaid them with baseline climate data from AFRICLIM v3.0 to retrieve the MAT values associated with each occurrence. Step 2: Observed climatic limits of species. For each species, we quantified thermal upper limits by extracting the 95th percentile of MAT values across their known occurrence records (e.g., 26.4°C for *P. macrocarpus*). Step 3: Climate change vulnerability metrics. For a given species (*i*) within a specific community (*j*), exposure was calculated as the difference between the average projected future (2085) MAT and the baseline MAT (1961–1990), using only the pixels actually occupied by the species (e.g., under RCP8.5, 28°C vs. 24°C, corresponding to an exposure of +4°C). The safety margin was calculated as the difference between the species' upper limit and the average baseline MAT across those same pixels (e.g., 26.4°C vs. 24°C, resulting in a safety margin of +2.4°C). Climate risk was then defined as the difference between exposure and safety margin (e.g., +1.6°C for *P. macrocarpus*). A positive value indicates that future climate conditions are expected to exceed the species' tolerance threshold, suggesting a high risk of thermal stress. Step 4: Estimating community risk and mapping spatial patterns. By repeating this calculation for all species within each community, we quantified the proportion of species at risk. Applying this process across all communities allowed us to map climate risk patterns throughout African tropical moist forests. This approach was similarly applied to mean annual precipitation (MAP) and climatic water deficit (CWD).

species) with this forest mask and retained only species falling within tropical moist forest pixels.

To investigate spatial patterns of species vulnerability, we subdivided the extent of tropical moist forests into distinct forest communities (tree and shrub species coexisting within pixels, Figure 1), which served as analytical units in subsequent assessments. To deal with the heterogeneity of botanical collections across tropical Africa and to balance sampling sizes across communities (Droissart et al. 2018), we used the interactive web application 'Infomap Bioregion' (Edler et al. 2016) to define pixels of varying size according to the density of occurrence records. Forest communities ranged from 0.125° (minimum size) to 1° (maximum size) and contained at least five species occurrences. Communities with more than 500 occurrences were iteratively subdivided into smaller units, down to the minimum permitted size of 0.125°. This procedure yielded 1,009 communities, including 199,787 occurrence records, representing 3,536 tree and shrub species belonging to 145 botanical families (mean = 113, median = 85 species per community; range = 5–712).

Finally, we gathered information on species conservation status from the IUCN Red List and related sources (IUCN 2024). Among the 3,536 tree and shrub species included in this study, 0.4% were classified as critically endangered (CR), 2.5% as endangered (EN), 7.6% as vulnerable (VU), 3.4% as near threatened (NT), 44.0% as least concern (LC), 0.1% as data deficient (DD), and 41.8% as not evaluated (NE).

2.4 | Estimation of the Observed Climatic Limits of Species

Assessing species vulnerability to climate change requires knowledge of their ecophysiological tolerance thresholds. However, such physiological tolerances are unknown for tree

and shrub species in African tropical forests. In this context, realised climatic niche limits, inferred from species' geographic distributions, can serve as useful proxies for estimating climate tolerance (Esperon-Rodriguez, Rymer, et al. 2022).

For the 3,536 species identified as occurring within the extent of African tropical moist forests (as previously defined), we compiled all available cleaned occurrence records at the continental scale—including those from both inside and outside the tropical moist forest biome in Africa—to extract values of key climatic variables under baseline climate conditions (1961–1990).

For each species, we then estimated upper climatic limits for MAT and CWD, and a lower limit for MAP. Specifically, we calculated the 95th percentile of MAT and CWD values and the 5th percentile of MAP values across the occurrence records. These thresholds were interpreted as proxies for each species' climatic tolerance limits, corresponding to the hottest, most water-stressed and driest conditions under which the species currently occurs (Gallagher et al. 2019). An example using MAT is provided in Figure 1.

2.5 | Climate Change Vulnerability Metrics

To assess the climatic vulnerability of tropical moist forests in Africa, we adopted the approach initially proposed for the Australian flora (Gallagher et al. 2019) and then adapted for urban tree species selection in Canada (Esperon-Rodriguez, Tjoelker, et al. 2022). This approach considers three key dimensions of climate impact: (1) exposure, (2) safety margin and (3) risk. These metrics were calculated for three climatic variables (MAT, CWD and MAP) under two emissions scenarios (RCP4.5 and RCP8.5).

Exposure to climate change refers to the extent of climate change likely to be experienced by a species or location. It depends on the rate and magnitude of change in climatic variables (MAT, MAP and CWD) in regions occupied by the species (Dawson et al. 2011; Foden et al. 2013).

For a given species (i) in a specific community (j), exposure was calculated as the difference between the average projected future climate and the baseline climate, calculated only across the pixels actually occupied by the species within that community (Equation 2, see Figure 1 for an example with MAT). This approach accounts for spatial heterogeneity, particularly in mountainous regions where a single community may span contrasted climatic conditions. Averaging across the entire community could overestimate exposure for climate-specialist species by attributing to them environmental conditions they do not experience.

$$\text{Exposure}_{(ij)} = \text{Future Climate}_{(ij)} - \text{Baseline Climate}_{(ij)} \tag{2}$$

where (i) denotes the species and (j) the community under consideration. Positive exposure values for MAT and CWD indicate that the species is expected to experience higher temperatures and increased water stress, respectively. Conversely, negative exposure values for MAP indicate that the species is likely to face reduced precipitation within this community.

2.6 | Climatic Safety Margin

This metric captures a species' intrinsic sensitivity to climate change and provides an indication of its potential tolerance to shifting environmental conditions in natural ecosystems (Esperon-Rodriguez, Ordoñez, et al. 2022). This margin reflects how much warmer (for MAT), drier (for MAP) or more stressful due to water deficit (for CWD) the climate can become before exceeding observed climatic limits (Gallagher et al. 2019; Esperon-Rodriguez, Rymer, et al. 2022).

For a given species (i), within a specific community (j), and for a given climatic variable, the safety margin was calculated as the difference between the species' climatic limit and the average baseline climatic conditions across the set of pixels occupied by the species within that community (Equation 3 and Figure 1).

$$\text{Safety Margin}_{(ij)} = \begin{cases} \text{Species } (i) \text{ upper limit} - \text{Baseline Climate}_{(ij)}; \text{for MAT and CWD} \\ \textit{or} \\ \text{Baseline Climate}_{(ij)} - \text{Species } (i) \text{ lower limit; for MAP} \end{cases} \tag{3}$$

A negative safety margin (<0) indicates that the species has exceeded its tolerance limit in that specific community, suggesting that it is potentially facing stressful climate conditions. For each community and climatic variable, we mapped the average safety margin across all species (hereafter referred to as the *community average safety margin*) as well as the standard deviation within the community.

We then investigated the relationship between the community average safety margin, the climatic niche breadth and spatial extent of the species within the communities. The climatic niche was characterised by the minimum, optimum, maximum and amplitude values for mean annual temperature (MAT), mean annual precipitation (MAP) and climatic water deficit (CWD), extracted from the selected occurrences. The spatial extent was estimated using the extent of occurrence (EOO), calculated with the minimum convex hull method using the R *rgeos* package (Dunnington and Pebesma 2020). We then performed a principal component analysis (PCA) on the matrix containing information on the climatic niche and spatial extent of the species. The community average scores were calculated by averaging the scores on the first two principal components (PC1 and PC2) of all the species in each community. Finally, we analysed the correlations between the community average safety margins and these community average scores using linear regressions.

Climate risk refers to the potential for adverse impacts on biological systems resulting from climate change (Foden et al. 2019). For a given species (i) within a specific community (j), risk was calculated as the difference between the exposure and the safety margin (Equation 4, see Figure 1 for an example with MAT).

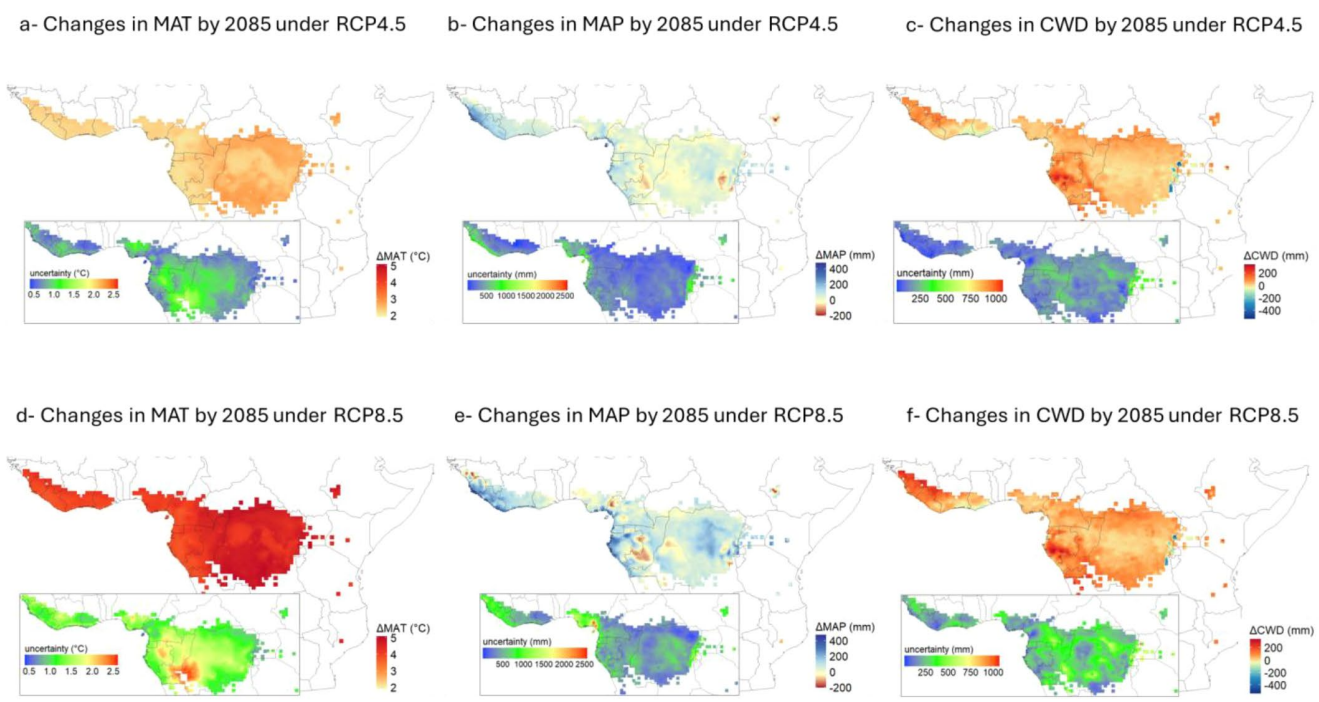

FIGURE 2 | Projected exposure to climate changes across African tropical forests. Exposures (a–f) highlight regions in red where MAT or CWD are projected to increase, and MAP to decrease. Conversely, regions in blue indicate where MAT or CWD are projected to decrease, and MAP to increase. Inset maps illustrate the uncertainty associated with each variable, calculated as the range between the highest and lowest projections across five regional climate models (RCMs).

$$\text{Risk}_{(ij)} = \begin{cases} \text{Exposure}_{(ij)} - \text{Safety Margin}_{(ij)}; \text{for MAT and CWD} \\ \textit{or} \\ \text{Safety Margin}_{(ij)} + \text{Exposure}_{(ij)}; \text{for MAP} \end{cases} \quad (4)$$

If exposure exceeds the safety margin, the resulting risk is positive for MAT and CWD, indicating that the species is likely to experience future climatic conditions (temperature or water stress) beyond its observed tolerance limits. Conversely, for MAP, a negative risk indicates that the species is likely to face drier conditions than it can tolerate. For each climatic variable and emissions scenario, we mapped the proportion of species potentially at risk within communities, that is, those for which projected climatic conditions exceed their observed climatic tolerance limits.

3 | Results

3.1 | Exposure to Climate Change

We first examined the exposure to climate changes, that is, the nature and extent of climate change according to MAT, MAP or CWD, that a species or community is likely to experience. A considerable increase in MAT will be observed for the whole tropical moist forest biome in Africa by the year 2085 (Figure 2a,d). The average exposure to a MAT increase is 2.4°C ± 0.2°C for the RCP4.5 scenario. The magnitude of exposure is relatively uniform (ranging between 1.9°C and 2.9°C), with approximately 74% of the tropical moist forest biome experiencing a MAT increase greater than 2°C. Under the RCP8.5 scenario, the average MAT increase reaches 4.3°C ± 0.4°C (ranging between 3.3°C and 5°C), with 85% of the biome area experiencing a MAT increase greater than 4°C. Importantly, the associated uncertainty for MAT exposure remains relatively low (mostly < 2.5°C; see inset maps in Figure 2a,d), indicating strong agreement across the five regional climate models (RCMs).

The MAP projections show no consistent trends and are characterized by high variability among models (Figure 2b,e). Although each RCM predicts substantial changes in precipitation (exceeding 200 mm) under both RCP4.5 and RCP8.5, the direction of change—whether an increase or decrease—varies considerably across models (Figure S1). This inter-model disagreement results in pronounced spatial uncertainty, particularly under the RCP8.5 scenario.

The CWD projections indicate an exposure to more stressful conditions (Figure 2c,f) that are driven by MAT increase, but with high uncertainty, especially in the centre of the Congo Basin (Figure 1c,f) due to the huge uncertainty on MAP changes.

3.2 | Climatic Safety Margins and Determinants

The climatic safety margin represents the extent of climate change that a species can tolerate within a specific community before exceeding its climatic limit. Given the uncertainties associated with MAP and CWD projections (Figure 2), we focused solely on the MAT safety margin (Figure 3). However, the

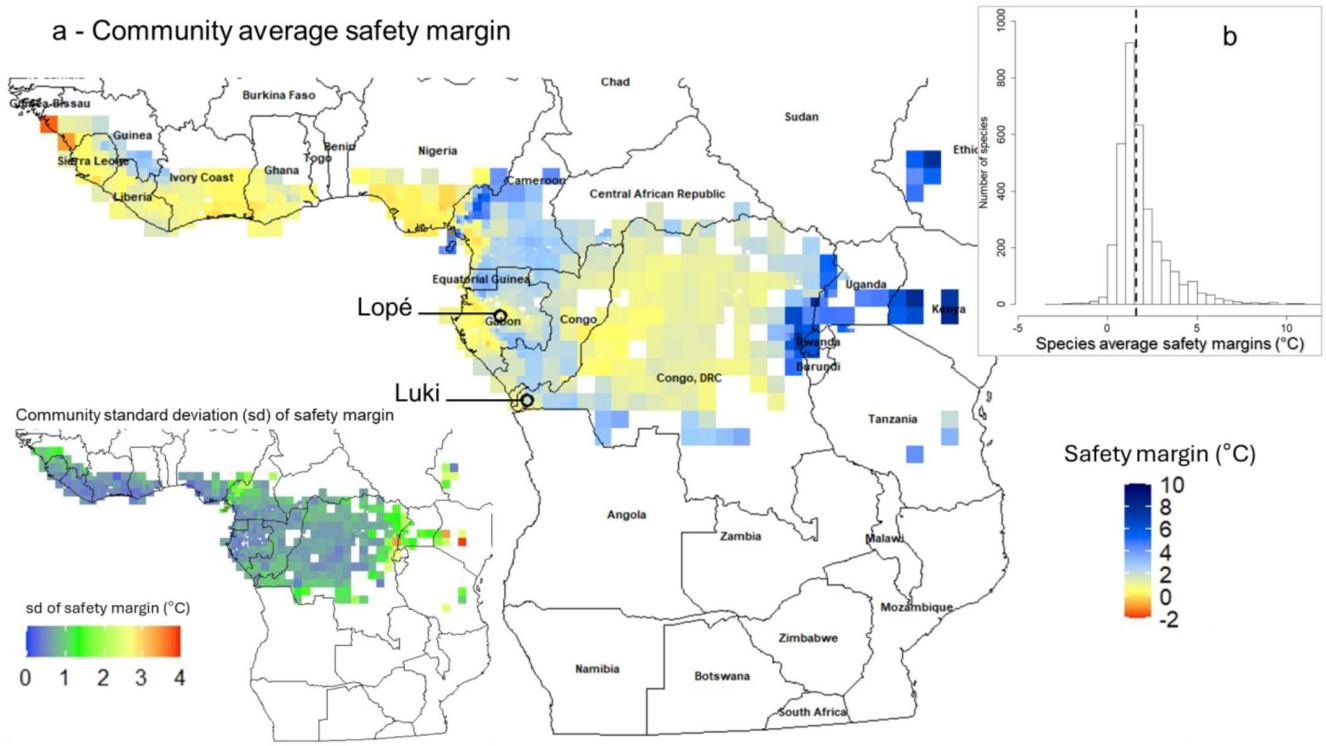

FIGURE 3 | MAT safety margin of tree and shrub species in the forest communities of tropical Africa. (a) Map of community average safety margin (inset maps illustrate the community standard deviation of safety margin), calculated by averaging the safety margins of all species within each community. (b) Distribution of species average safety margins, calculated for each species by averaging the safety margins across all the communities in which it occurs. Negative values indicate species currently exceeding their tolerance limits for MAT in all or most of the communities where they have been observed. The dotted black line represents the median across all species.

same approach was also applied to MAP and CWD (Figures S3 and S4).

The average safety margin per species for MAT (i.e., averaged across all the communities in which the species occurs) ranges from −3.3°C to 15.9°C (Figure 3b). We found that more than half of the study species (2,033 species, 57%) are already experiencing temperatures exceeding their observed climatic limits in at least one of the communities where they occur. Additionally, 29 species (1%) have already surpassed their climatic limits in all communities where they have been observed, indicating that these species are currently highly vulnerable (species with negative safety margins). However, only 10 of these species are listed in the IUCN Red List—five as EN, three as VU, and two as NT (Table S1).

We found that more than 50% of the moist forest communities across tropical Africa had an average safety margin (i.e., averaged across all species within the community) below 2°C, with low variability within communities (less than 1°C, Figure 3a). Spatial analysis revealed that regions with the smallest community average safety margins include most of West Africa, Atlantic central Africa (e.g., Lopé in Gabon), and most of the DRC. In these regions, more than a quarter of species in some communities already exceed their climatic limits for MAT (Figure S2). Notably, the coastal evergreen forests of Gabon, the southwest evergreen forests of the DRC, and forests in southern Nigeria and southeastern Ivory Coast stand out as currently vulnerable.

Communities with the largest average safety margins (>2°C) are primarily located in high-altitude regions (>1000 m a.s.l.), such as the Albertine Rift, Ethiopian highlands, the Cameroon volcanic line and the Adamaoua region of Cameroon, where safety margin variability is also high (>1°C). They are also found in the southeast of Guinea in West Africa, the TRIDOM Dja-Odzala-Minkébé (transboundary forest complex across Cameroon, Congo and Gabon), the Batéké Plateau (the transboundary region between southern Gabon and western Congo), and along the northern and southern margins of the Congo Basin (east of Luki, Figure 3a).

We then investigated the correlates of the community average safety margins, and notably species climatic niche descriptors (optimum, amplitude, minimum and maximum) for MAT, MAP and CWD, as well as the extent of occurrence (EOO) of the species composing the community. We identified two dominant and independent axes of the climatic niche and spatial extent of species (Figure 4a), which together explained 69.1% of the total variance. The first axis of the PCA (PC1, 48.5% of variance) differentiated species living in drier and more seasonal climates—higher water deficit (CWD.max, CWD.opt), tolerating wide variations in temperature (higher MAT.amp)—from those restricted to wetter climates with low water deficit, lower temperature amplitude and limited range (EOO). The second axis (PC2, 20.6% of variance) differentiated species according to maximum (MAT.max) and optimum (MAT.opt) temperatures, both negatively correlated with the altitudinal gradient. Correlation analysis revealed significant relationships ($R^2 = 0.52$, $p < 0.001$) between community

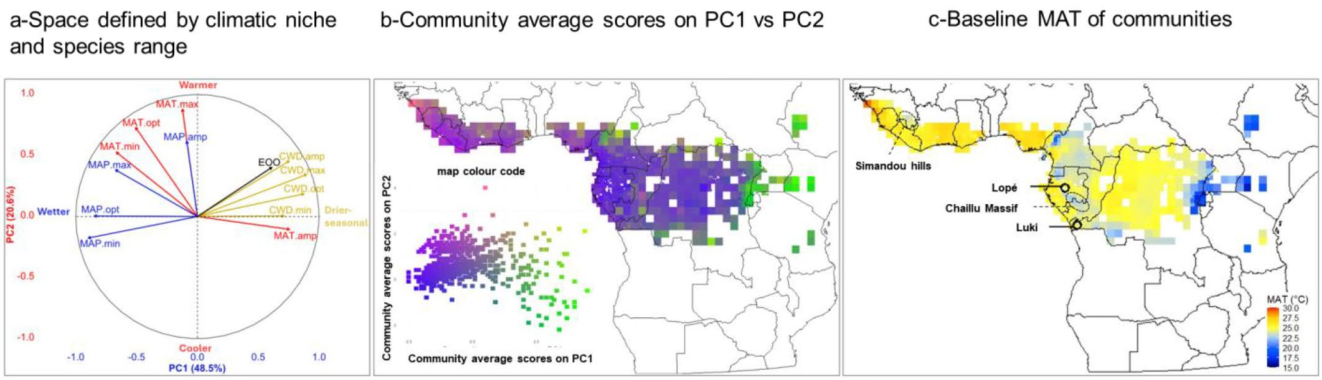

FIGURE 4 | Determinants of community safety margin, that is, averaged across species. (a) Correlation circle (PC1 and PC2) of the principal component analysis (PCA) based on the climatic niche descriptors and spatial extent of the species. This includes the minimum (min), optimum (opt) and maximum (max) values, as well as the amplitudes (amp) for mean annual temperature (MAT, in red), mean annual precipitation (MAP, in blue) and climatic water deficit (CWD, in yellow), along with the species' Extent of Occurrence (EOO, in black). (b) Community average scores on PC1 vs. PC2, representing the average scores per community of species on the first two principal components of the PCA. (c) Baseline MAT for each community. In blue, communities where temperatures are consistently below 25°C, and where the average safety margin exceeds 2°C (Figure 3b).

average safety margins and community average scores on the first two principal components of the PCA (i.e., species average in each community), highlighting the influence of the species climatic niche and spatial extent on the community safety margin. Forest communities in west Africa are characterised by low average safety margins, driven by species that tolerate diverse moisture and seasonality conditions and are associated with warm climates (variable average scores on PC1 and high average scores on PC2, Figure 4b). However, in the Simandou Hills of southeastern Guinea, cooler temperatures (Figure 4c) increase the safety margins of these communities, despite being dominated by species with similar climatic niches. Similarly, in the Congo Basin, where average safety margins are also low, forest communities predominantly consist of species restricted to warm-moist climates (low average scores on PC1 and high average scores on PC2). Yet, in the Batéké Plateau, the Chaillu Massif provides cooler local temperatures (Figure 4c), enhancing the safety margins of these communities, despite their composition being dominated by species with similar climatic niches. Along the northern and southern margins of the Congo Basin, forest communities exhibit relatively high safety margins, supported by species with wide geographic ranges that tolerate broad gradients of moisture and seasonality (high average scores on both PC1 and PC2, Figure 4b). In high-altitude regions, where safety margins are generally higher, communities are composed, on average, of species adapted to drier and more seasonal climates, capable of thriving across a broad altitudinal gradient (high average scores on PC1 and low average scores on PC2).

3.3 | Climate Risk

The climate risk refers to the vulnerability of species to projected future climate change. We calculated the risk as the difference between the exposure and the safety margin of a given species in a given community. We highlighted the risk associated with MAT (Figure 5), but the same approach was applied for MAP and CWD (Figures S5 and S6). Widespread temperature increases predicted for the end of the century will pose a considerable risk to many forest species. Under the RCP4.5 scenario, 3,256 species (92%) are projected to face risk in at least one community where they occur, while 617 species (17%) are expected to be at risk in all communities where they have been observed (inset histogram, Figure 5a). By 2085, approximately 75% of the communities are projected to have 75%–100% of species at risk (Figure 5a). The proportion of species at risk is particularly high in west Africa, Atlantic central Africa (including Lopé), and the DRC. Communities with a moderately low proportion of species at risk (around 50%) are primarily located in the Albertine Rift, the southern margin of the Congo Basin (east of Luki), the Cameroon volcanic line, and the Adamaoua region of Cameroon. They are also found in the Batéké Plateau, the TRIDOM area, the northern margin of the Congo Basin, and the Simandou hills. Under the RCP8.5 scenario, the projected risks are even more severe. The number of species at risk rises to 3,405 (96%) in at least one community and 1,2747 species (49%) in all communities where they occur (inset histogram, Figure 5b). By 2085, only communities in the Albertine Rift, the Ethiopian Highlands and along the Cameroon Volcanic Line are expected to maintain a proportion of species at risk below 50% (Figure 5b).

4 | Discussion

In this study, we aimed to assess the climatic vulnerability of tropical moist forests across Africa by quantifying the exposure to climate change, the climatic safety margins and the climate risks of the species and communities. We focused on changes in three key climate variables—mean annual precipitation (MAP), mean annual temperature (MAT) and the climatological water deficit (CWD)—under two representative concentration pathways, RCP4.5 and RCP8.5, representing intermediate and high emission trajectories, respectively. We found that future climate projections predict a considerable and widespread increase in temperature in tropical moist forests across Africa that will create novel climate conditions (Williams and Jackson 2007). The projected MAT increase in African tropical moist forests is estimated, on average, at 2.4°C ± 0.2°C under RCP4.5 and 4.3°C ± 0.4°C under RCP8.5 by 2085. However, no consistent trend is observed for precipitations, with models sometimes

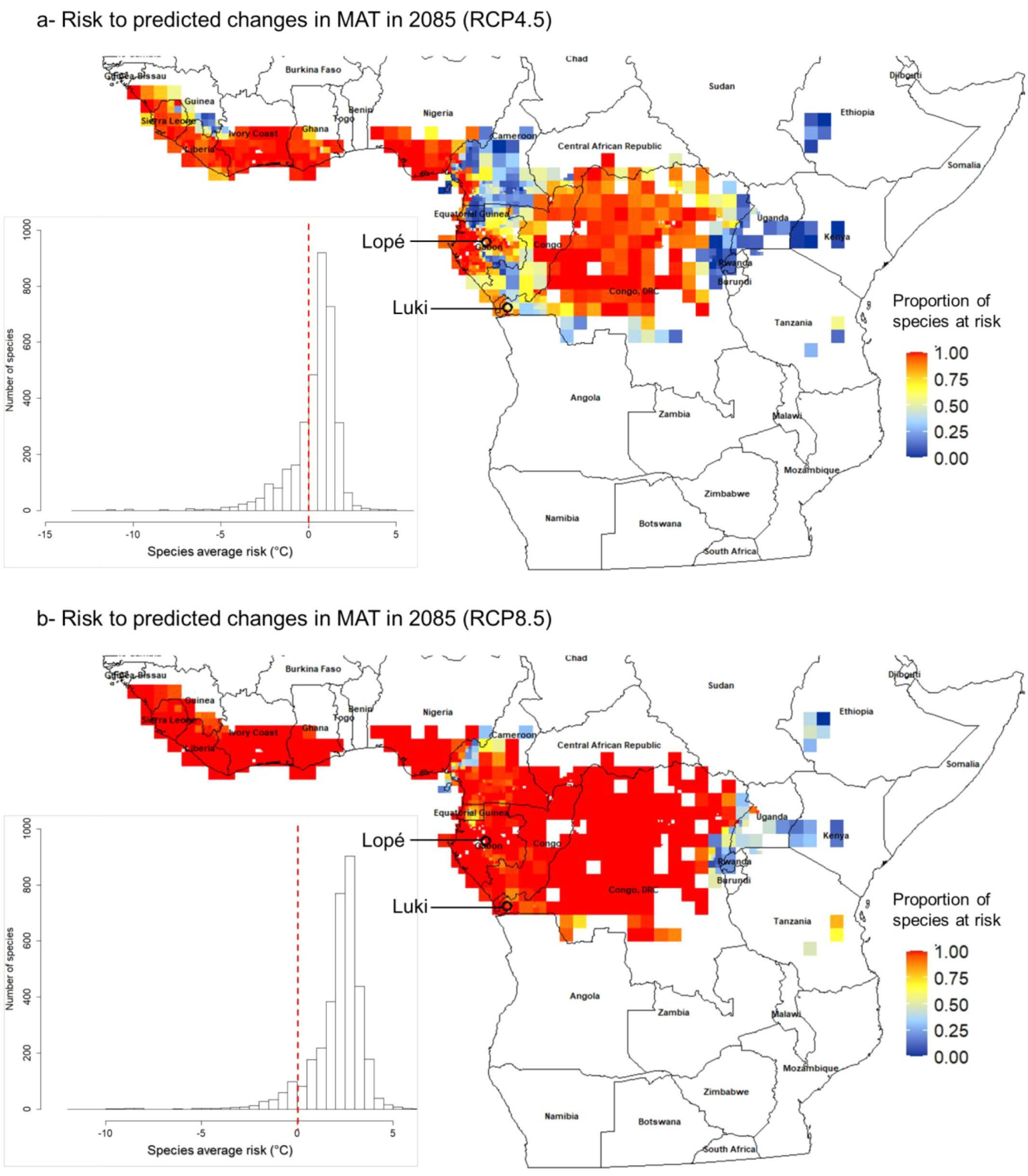

FIGURE 5 | Risk to forest species and communities from the predicted rise in temperatures. (a, b) Proportion of species projected to be at risk in each community by 2085 under the RCP4.5 and RCP8.5 scenarios, respectively. The inset histograms display the distribution of average species-level risk for MAT under RCP4.5 and RCP8.5 scenarios. For each species, the average risk was calculated by averaging the risk values across all communities where the species was observed. The dashed red line represents zero risk. Positive values indicate species likely to exceed their tolerance limits for MAT at all or most of the observed sites by 2085.

showing opposing changes—reflecting uncertainties that have already been highlighted for Africa (Dosio and Panitz 2016; Dosio et al. 2019; Almazroui et al. 2020).

It should be noted that our estimates of exposure to climate change are based on the AR5 scenarios (RCPs) and the CMIP5 simulations. However, the CMIP6 simulations associated

with the AR6 scenarios (SSPs) project more marked temperature rises over a large part of Africa. For example, projected temperatures in the northern hemisphere of Africa are up to 2.5°C higher in CMIP6 than in CMIP5, particularly in the region around Sudan and Niger (outside our study area), while the difference is around 1°C in the southern hemisphere (Almazroui et al. 2020). This suggests that the levels of thermal exposure we report may be underestimated if we consider the CMIP6 projections. In contrast, the precipitation projections between CMIP5 and CMIP6 show more mixed signals (Almazroui et al. 2020).

Our climatic safety margin analyses show that most of the 3,536 tree and shrub species studied have narrow safety margins for MAT (< 1.6°C), indicating high sensitivity—and potentially limited tolerance—to rising temperatures based on their known distributions. Species in lowland forest communities are particularly vulnerable, with narrow safety margins often below predicted exposure levels. This narrow safety margin is likely linked to the relatively stable temperature conditions across lowland tropical forests, which are characterised by minimal spatial and seasonal variations (Jirinec et al. 2022). Under such conditions, species may not be able to cope with temperature fluctuations but may instead thrive near their maximum tolerance thresholds for MAT. Consequently, even modest temperature increases could have potentially damaging effects (Trew and Maclean 2021).

More than 50% of moist forest communities across tropical Africa exhibit relatively narrow thermal safety margins (< 2°C in community average) in response to projected increases in MAT exceeding 2.4°C, even under the RCP4.5 scenario. These community-level safety margins are primarily shaped by local altitudinal gradients (Gallagher et al. 2019) and the climatic niche breadths of the constituent species (García-Robledo et al. 2016; Feeley et al. 2020). More alarming, our analyses identified the coastal evergreen forests of Gabon, the southwestern evergreen forests of the DRC and those in southern Nigeria and southeastern Ivory Coast as currently vulnerable. In these regions, more than a quarter of species are already experiencing temperatures beyond their observed upper limits of MAT. These findings are consistent with those of Réjou-Méchain et al. (2021), who also highlighted the sensitivity of the evergreen coastal forests of Gabon and central DRC to ongoing climate change.

In contrast, some communities show markedly broad thermal safety margins. Forest communities with the largest safety margins are mostly found in high-altitude regions, such as the Albertine Rift, Ethiopian Highlands, Cameroon Volcanic Line and the Adamaoua region of Cameroon. They are also present in the Simandou Hills, the Batéké Plateau, the TRIDOM and along the northern and southern forest margins of the Congo Basin. The large safety margins observed in mountainous regions are consistent with the broad thermal niche breadth (8.8°C) of Afromontane tree species (Cuni-Sanchez et al. 2024). However, such wide distributions may mask a mosaic of genetically distinct populations, each adapted to local climatic conditions (Savolainen et al. 2007). Moreover, the resolution of climate data may artificially inflate safety margins in mountainous areas by grouping lowland and upland species within the same community. Along the northern margin of the Congo Basin, where topographic relief is low, we also observed relatively high safety margins. These are primarily driven by generalist species with wide geographic distributions and broad climatic niches—characterised by wide CWD amplitudes and extensive EOOs—and found in both forest and savanna ecosystems, such as *Erythrophleum suaveolens* (Gorel et al. 2019).

The projected widespread warming, combined with the relatively narrow thermal safety margins of species, is likely to pose a significant risk of temperature-induced stress to most forest communities by the end of the century. By 2085, under RCP4.5, 92% of species are projected to be at risk in at least one location where they currently occur, and 96% under RCP8.5. Across African tropical moist forests, climatic exposure varies little, with projected increases of 2.4°C ± 0.2°C and 4.3°C ± 0.4°C under RCP4.5 and RCP8.5, respectively. Species risk—and thus the proportion of species at risk within communities—is largely driven by species composition and thermal safety margins. Communities dominated by species with narrow margins, such as lowland forests, are more vulnerable, whereas highland forests, hosting species with broader thermal margins, may be more resilient depending on the scenario.

This widespread vulnerability is consistent with growing empirical evidence suggesting that tropical forests worldwide are approaching critical thermal limits. In a pantropical study, Doughty et al. (2023) combined leaf thermocouple measurements, remote sensing (ECOSTRESS) and heating experiments to show that canopy leaves already reach midday peak temperatures close to—or in some cases exceeding—the critical threshold for photosynthetic function ($T_{(crit)} \approx 46.7$°C). The convergence between our projected increase in mean annual temperature under RCP8.5 (+4.3°C ± 0.4°C) and the functional tipping point identified by Doughty et al. (+3.9°C ± 0.5°C above current ambient temperatures) suggests that some African forests may face widespread physiological disruption by the end of the 21st century. Moreover, Trew et al. (2024) show that novel below-canopy thermal regimes are already emerging across large parts of the African tropics (56%), especially in the Congo Basin—highlighting that many forest ecosystems are now operating under climatic conditions with no recent analogue, which may challenge species' adaptive capacity and ecosystem functioning.

Our findings therefore highlight the vulnerability of African tropical forests to future warming. However, given the inherent assumptions and limitations in our approach, our results should be interpreted with caution. We rely on realised climate niches to infer species' climatic limits—a common approach in large-scale vulnerability assessments (Foden et al. 2013; Pacifici et al. 2015; Foden et al. 2019; Gallagher et al. 2019). Yet, these realised niches may underestimate the species' fundamental climatic niche due to historical, geographical or biotic constraints (Guisan et al. 2017; Scherrer et al. 2021), as well as the persistence of marginal populations in microclimates or as climate relicts in otherwise unsuitable areas (Hampe and Petit 2005; Morelli et al. 2016; Esperon-Rodriguez, Tjoelker, et al. 2022). In addition, using coarse-resolution climate data risks overlooking both horizontal (topography-driven) and vertical (vegetation-driven) microclimatic heterogeneities. Microclimates are particularly pronounced in tropical moist forests, where the three-dimensional canopy structure drives shading, air mixing and evapotranspirative cooling (Zellweger et al. 2019). For

instance, understory species may experience cooler and more humid conditions than those captured by standard climate data sets. Accounting for forest microclimate dynamics is therefore essential to better understand the responses of tree species to climate change (Zellweger et al. 2020). The choice of the baseline period (1961–1990) may also introduce bias, as it likely no longer reflects current climatic conditions (Bush et al. 2020; Kasongo Yakusu et al. 2023).

A further methodological assumption concerns the use of a space-for-time substitution approach, inferring temporal responses from spatial patterns (Adler et al. 2020). This introduces additional uncertainty, as the assumption does not always hold (Guisan et al. 2017). Projections become particularly uncertain when species are not in equilibrium with their environment (Guisan et al. 2017), when transient processes dominate or when future climates have no analogues (Veloz et al. 2012; Worth et al. 2014; Perret et al. 2024). Furthermore, several unaccounted-for processes—such as phenotypic plasticity and rapid adaptation through high genetic diversity (Kremer et al. 2012, 2014, 2025)—could help tropical trees endure future climate stress.

In this study, we focused primarily on thermal risk, while risks related to MAP and CWD were more uncertain. The effects of rising temperatures on plants will strongly depend on future precipitation patterns and their interaction with warming (Teskey et al. 2015), as higher temperatures can intensify drought through increased evapotranspiration—even in regions where total rainfall remains relatively stable (Gallagher et al. 2019). Beyond these variables, unmodelled climate extremes—such as maximum temperatures, multimonth water deficits and heatwaves—may trigger abrupt physiological failures that are not captured by long-term climate averages (Choat et al. 2018; Anderegg et al. 2020). As such extremes are projected to intensify across Africa (Dosio 2017; Dosio et al. 2022), their exclusion from our analysis likely resulted in a conservative estimate of climate risk. Integrating them would probably reveal even more pronounced vulnerabilities, but local factors such as soil properties can also modulate species' responses to water availability (Luo et al. 2024).

Finally, the vulnerability of Africa's tropical moist forests cannot be fully understood through the prism of climate variables alone. Climate risks need to be considered in conjunction with other major anthropogenic pressures, such as overexploitation, habitat conversion, overgrazing and fires—all of which are often intensified by rapid population growth (Réjou-Méchain et al. 2021). In central Africa, overexploitation remains the greatest threat to tree species, followed by habitat conversion and climate change, while other disturbances such as overgrazing and fires appear less influential (Ceccarelli et al. 2022). Although not addressed in this study, these pressures may nonetheless exacerbate species' vulnerability (Brice et al. 2019; Zellweger et al. 2020) and must be considered in conservation planning.

Forest conservation programs must now integrate climate considerations into planning, policy development and implementation (Malakoutikhah et al. 2020). This includes prioritising communities already identified as vulnerable—hosting unique assemblages of tree species (Réjou-Méchain et al. 2021) and mammals (Fonteyn et al. 2023)—such as the coastal evergreen forests of Gabon, the evergreen forests of southwestern DRC and those of southern Nigeria and southeastern Ivory Coast. In these regions, conservation efforts should aim to reduce non-climatic pressures, which may otherwise amplify the impacts of climate change. In parallel, the establishment of new protected areas under the 30×30 agenda should focus on ecologically and climatically strategic zones, with their relevance validated through field-based assessments. Ensuring large-scale ecological connectivity—especially across transboundary landscapes (Miles et al. 2004)—remains critical to regional and national strategies (Carr et al. 2017; Lapola et al. 2020; Merenlender et al. 2022). Expanding protected area networks, particularly in regions encompassing both lowland and montane forests, will help maintain ecological corridors and strengthen community resilience (Miles et al. 2004). The TRIDOM region, which combines high climatic safety margins with an existing protected area network, stands out as a conservation priority. In this context, our maps should be viewed as strategic tools—to guide future research, prioritise monitoring and support conservation planning under climate change.

Author Contributions

M.P.N.M., A.-P.G. and A.F. contributed to the conceptualisation of the study. G.D. assembled and provided the data. M.P.N.M. analysed the data with assistance from G.D. M.P.N.M. led the writing of the manuscript and all authors critically reviewed the manuscript and approved the final version.

Acknowledgements

This study is part of the CANOPi project (EOS number O.0026.22), which has received funding from the FWO and F.R.S.-FNRS under the Excellence of Science (EOS) program. We also extend our thanks to the Centre for Biodiversity Synthesis and Analysis (CESAB) for providing access to the occurrence data. We are specifically grateful to Yves Brostaux, Éric Marcon and to the entire CANOPi team for stimulating discussions.

Disclosure

Permission to reproduce material from other sources: Occurrence data were extracted from the RAINBIO database available at https://gdauby.github.io/rainbio/download_page.html. The database has been updated since the original publication, including, among others, the occurrences from the species lists assembled by Fayolle et al. (2014) for forest sites and by Fayolle et al. (2019) for savanna sites across Africa. The distribution of the moist forest biome across Africa was derived from the biome index of Aleman et al. (2020) and the conservation status of tree and shrub species was extracted from the IUCN Red List. Baseline and future climatic data were obtained from the Africlim database (Platts et al. 2015).

Ethics Statement

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All the data used in this study, including species occurrence records and climate projections, are available on the Dryad repository: https://doi.org/10.5061/dryad.7h44j105d.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Projected changes in mean annual precipitation (MAP, mm) according to regional climate models (RCM) for the RCP4.5 and RCP8.5 scenarios: reduction zones in red. **Figure S2:** Proportion of species within communities exceeding their climatic limits for mean annual temperature (MAT). **Figure S3:** Mean annual precipitation (MAP) safety margin of tree and shrub species in the forest communities of tropical Africa. (a) Community average safety margin (and community standard deviation of safety margin in a), calculated by averaging the safety margins of all species within each community. (b) Species average safety margins, calculated for each species by averaging the safety margins across all the communities in which it occurs. Negative values indicate species currently exceeding their climatic limits for MAP in all or most of the communities where they have been observed. The dotted black line represents the median. (c) Proportion of species within communities exceeding their tolerance limits for MAP. **Figure S4:** Climatological water-deficit (CWD) safety margin of tree and shrub species in the forest communities of tropical Africa. (a) Community average safety margin (and community standard deviation of safety margin in a), calculated by averaging the safety margins of all species within each community. (b) Species average safety margins, calculated for each species by averaging the safety margins

across all the communities in which it occurs. Negative values indicate species currently exceeding their climatic limits for CWD in all or most of the communities where they have been observed. The dotted black line represents the median. (c) Proportion of species within communities exceeding their tolerance limits for CWD. **Figure S5:** Risk to forest communities from the predicted decrease in mean annual precipitation (MAP). (a, b) Proportion of species projected to be at risk in each community by 2085 under the RCP4.5 and RCP8.5 scenarios, respectively. **Figure S6:** Risk to forest communities from the predicted increase in climatological water deficit (CWD). (a, b) Proportion of species projected to be at risk in each community by 2085 under the RCP4.5 and RCP8.5 scenarios, respectively.

Biographies

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