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Impact of end-of-century climate change on priority non-timber forest product species across tropical Africa

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Abstract

Plant species providing Non-Timber Forest Products (NTFP) are economically important across Africa. How this heterogeneous and understudied resource will respond to ongoing climate change remains understudied. Here, we modelled the impact of end-of-the-century climate change on the distribution of 40 NTFP plant species distributed across tropical Africa. Occurrence data were extracted from a taxonomically verified database and three different ecological niche modelling algorithms were used. Species distributions were modelled under two end-of-century (2085) climate change models (RCP4.5 and RCP8.5) and two dispersal scenarios (limited and expanded). We show that for the 40 NTFP plant species studied here, different responses are modelled with some species gaining in suitable habitats (47.5%–65% under RCP4.5), whereas others will lose in suitable habitats (35%–52.5% under RCP4.5). Nevertheless, we also show that our results vary between the different methods used, such as modelling algorithms, dispersal scenarios and general circulation models. Overall, our results suggest that the response of NTFP species to climate change depends on their distribution, ecology and dispersal ability.

KEYWORDS

dispersal, NTFP, representative concentration pathways, species distribution modelling

Résumé

Les espèces végétales fournissant des produits forestiers non ligneux (PFNL) représentent une importante ressource économique dans l'ensemble de l'Afrique. La manière dont cette ressource hétérogène et peu étudiée réagira au changement climatique en cours a fait jusqu'à présent l'objet d'un nombre limité d'études. Dans cette étude, nous avons modélisé l'impact du changement climatique de la fin du siècle sur la répartition de 40 espèces végétales de PFNL réparties dans l'ensemble de l'Afrique tropicale. Les données sur les événements ont été extraites d'une base de données basée sur la taxinomie et trois différents algorithmes de modélisation de niche écologique ont également été utilisés. La distribution des espèces a été modélisée selon deux modèles de projection de changement climatique (RCP4.5 et

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RCP8.5) à la fin du siècle (2085) et deux scénarios de dispersion (limité et étendu). Diverses réactions sont ici modélisées pour les 40 espèces végétales de PFNL. Certaines espèces obtiendront des habitats adaptés supplémentaires (47,5 % à 65 % dans le cadre du modèle RCP4.5), tandis que d'autres en perdront (35 % à 52,5 % dans le cadre du modèle RCP4.5). Toutefois, nos résultats varient selon les différentes méthodes utilisées, telles que les algorithmes de modélisation, les scénarios de dispersion et les modèles de circulation générale. Dans l'ensemble, nos résultats suggèrent que la réaction des espèces de PFNL au changement climatique dépend de leur répartition, de leur écologie et de leur capacité de dispersion.

1 | INTRODUCTION

Global change will lead to important biodiversity loss (Bellard et al., 2012; Thomas et al., 2004; Urban, 2015) which is considered a major threat to the safe operating space needed for humanity (Rockström et al., 2009). This is particularly true for Africa (Ittersum et al., 2016; Serdeczny et al., 2017) as the continent will face negative consequences of climate change on food security and malnutrition (IPCC, 2007) coupled with significant continued population growth (Gerland et al., 2014). Studies have demonstrated that climate change across Africa will impact the distribution and abundance of species (Heubes et al., 2012; Ramirez-Villegas et al., 2014; Zhang et al., 2016) and forest ecosystems (Réjou-Méchain et al., 2021). McClean et al. (2005) estimated that between 81% and 97% of sub-Saharan African plant species could face a displacement or a decrease in their suitable habitat by 2085. In addition, between 20% and 35% of the tropical African flora are already estimated to be potentially threatened by extinction (Brummitt et al., 2015; Stévant et al., 2019). Other studies have also underlined the vulnerability to future climate change of specific plant clades in Africa (Blach-Overgaard et al., 2015; Davis et al., 2012; Sanchez et al., 2011).

The consequences of these changes will be considered, especially in Africa (Millennium Ecosystem Assessment, 2005), where 60%–70% of the population live in rural areas (Güneralp et al., 2017) and are directly dependent on plant resources for their subsistence (Cavendish, 2000). Thus, one important question is how will tropical African plant species providing important resources be affected by climate change? To date, most studies have focused on the faith of a few macroeconomically important crops such as maize or pearl millet (Adhikari et al., 2015; Burke et al., 2009; Pironon et al., 2019). In forested regions, the economic value associated with plant species has generally been based on a financial appraisal of its timber stock (Mahapatra & Tewari, 2005). There is, however, little consideration for species that do not produce timber, even though they are a considerable part of the population economic and well-being environment.

Non-Timber Forest Products (NTFP) are defined as natural resources other than wood extracted from wild species (animal or plant) derived from natural, modified or managed forested landscapes and other wooded lands (Ingram, 2014; Ros-Tonen, 2000). Their products are used for food, forage, medicines, aromatic products, fuelwood, construction materials and other cultural uses. NTFP

are important resources central to fighting hunger and in reducing poverty (Angelsen & Wunder, 2003). Globally, the reported value of NTFP withdrawals amounted to nearly USD 8 billion in 2015 (FAO and UNEP, 2020). Even though plant species providing NTFP (hereafter NTFP plant species) play a fundamental role in the survival and the well-being of people across tropical Africa, their access is not officially controlled and data on their socioeconomic importance are lacking (Ingram et al., 2010). A recent study suggested that 29 major crop species occurring in sub-Saharan Africa could be resilient to climate changes. This comes from their relationships with crop wild relatives which could be used for their improvement or adaptation (Pironon et al., 2019). In contrast, NTFP plant species do not seem to have this human-assisted advantage. A study focusing on palms, a major NTFP plant family across the tropics and a key plant resource in Africa, showed that over 70% of palm diversity will experience a decline in climatic suitability by the end of the century (Blach-Overgaard et al., 2015). In addition, they showed that this result was independent of the species' habitat, namely rain forest or open ecosystems. This suggests that important wild plant resources might be vulnerable to range contraction and extirpation over the next 80 years. In contrast, useful plants, including NTFP species, tend to have wider geographical distributions (van Zonneveld et al., 2018) which could lead to wider ecological breadth allowing them to cope with future climatic conditions. In this case, we would expect most NTFP species to be able to cope favourably with future climate change. Finally, climate change might have a species-specific impact on the future distribution of NTFP plant species linked to different ecologies such as forest (wetter adapted species) or savannah (drier-adapted species) dwelling NTFP species (van Proosdij et al., 2017). For example, in mountain ecosystems, it was shown that warm-adapted species increased geographic ranges, whereas cold-adapted species decreased in distribution (Gottfried et al., 2012).

Here, we assess the impact of end-of-century climate change models on the potential distribution of 40 top priority NTFP plant species in tropical Africa. How will selected NTFP plant species react to the end of the century climate change in terms of their geographical ranges? Which species are expected to gain or lose climatically suitable areas under different climate change scenarios? Does the response of NTFP species depend on the extent of their distribution or their presence in forested regions versus more open woodlands? To this end, we use Species Distribution Modelling (SDM) to project the present and future

potential distribution of species under two climate change scenarios (RCP4.5 and RCP8.5) for the period 2070–2090 using 10 general circulation models.

2 | MATERIAL AND METHODS

2.1 | Study area

Our study focused on sub-Saharan Africa known as the Afrotropical region (Dauby et al., 2016). The area is broadly delimited by the ecoregions south of Sahel and north of South Africa (–15° and 47° of East longitude and –15° and 30° North latitude). It covers the tropical forest regions; the Guineo-Congolian centre of endemism is divided into three sub-centres: Upper Guinea, Lower Guinea and Congolian (White, 1983). Three climatic regions encompass the studied region: the equatorial, tropical humid and tropical dry climates.

2.2 | Non-timber forest products plant species distribution data

A total of 40 NTFP species considered as 'priority' were selected relying on the classification of Ingram (2014) based on a database of around 500 species from Cameroon. This database provides a ranking of the species importance, or 'priority', based on five criteria: species (1) with products that have a high economic trade value or are important for autoconsumption; (2) with products that are overexploited (this is a function of in situ conservation priority status and domestication); (3) with products that have multiple uses (including conflicting); (4) with uses; (5) that are classified as threatened (e.g., on the IUCN Red List, CITES listed and/or protected by national laws). In this study, we selected the top priority NTFP species for which we could retrieve sufficient data about their distribution (see below). Occurrence data for each species were extracted from the RAINBIO database (Dauby et al., 2016). RAINBIO is a synthesis of several databases from GBIF and several major herbaria of vascular plant occurrence data. It has the advantage of being curated and taxonomically and geographically verified. For each species, we estimated the percentage of their occurrence within (referred to as Forest Fraction) or outside forested regions using polygons representing the map of different ecoregions found in Africa based on (Olson et al., 2001).

2.3 | Climatic data

Climatic data were extracted from AFRICLIM ver. 3 (www.africlim.org), a data set of high-resolution ensemble climate projections for Africa (Platts et al., 2015). This database comprises monthly data on temperature and rainfall together with derived bioclimatic summary variables such as moisture indices and dry season length. Ten variables related to temperature and 11 related to precipitation were downloaded (see Platts et al., 2015 for more details) which are mainly derived from the WorldClim-Global Climate

Database. Finally, all climatic layers were downloaded at 10' of spatial resolution.

2.4 | Climatic variable selection

Following Blach-Overgaard et al. (2015), six climatic predictors suggested to be relevant for building performant distribution models in Tropical Africa were selected. Three variables were associated with temperature: mean annual temperature, temperature seasonality and minimum temperature of the coolest month; three variables were associated with humidity: annual water balance, water-balance seasonality and rainfall deficit. Water-balance variables were built by using monthly precipitation and temperature (Blach-Overgaard et al., 2015). Water-balance seasonality represents the standard deviation of the monthly water balance, whereas annual water balance is the sum of the monthly water balance. Monthly water balance is defined as the difference between monthly precipitation and monthly potential evapotranspiration (PET). PET was computed following the method of Hargreaves and Samani (1985) derived from monthly minimum and maximum temperature. We computed the rainfall deficit *rd* as follows:

$$rd = \sum_{i=1}^{12} \max(0, PET_i - PR_i) \quad (1)$$

where *PR* is the monthly precipitation, and *i* is the month. This is the sum of the positive difference between monthly potential evapotranspiration and precipitation. When the precipitation is higher than the evapotranspiration, the difference is set to 0. High *rd* thus indicates a high rainfall deficit.

2.5 | Species distribution modelling

For each selected NTFP plant species, distribution modelling was undertaken using three different algorithms: Maximum Entropy (MaxEnt; Phillips et al., 2006), Generalised Boosting Model (GBM; Ridgeway, 1999) and Generalised Linear Models (GLM; Hastie & Tibshirani, 1990) which were shown to be amongst the best performing SDM algorithms (Elith et al., 2006; Elith & Graham, 2009). Models were run using the package Biomod2 ver 3.5.1 (Thuiller et al., 2020) in the R environment (R Core Team, 2021).

For each species, models were built following four steps:

1. We defined a calibration area by defining the Minimum Convex Polygon or convex hull (Kremen et al., 2008) around the occurrence points of each species. A buffer zone of 5° degrees was created around the convex hull defining the calibration area;
2. We generated pseudo-absence data using the 'Target group sampling' method (Ponder et al., 2011). The number of pseudo-absence cells (or background cells for MaxEnt) was variable amongst species depending on the species-specific calibration

area. The sampling of a species was weighted by the density of all occurrences contained in the RAINBIO database and used as a proxy for botanical sampling effort across the region.

3. Model evaluation was achieved through a cross-validation procedure by partitioning the presence and pseudo-absence data into calibration and validation data. We used a checkerboard approach for partitioning which has the advantage of maintaining the spatial structure of the data (Muscarella et al., 2014). The performance of models was estimated using two statistics calculated for each pair of presence and pseudo-absence data: the area under the receiver operating characteristics curve (AUC, Fielding & Bell, 1997) and the true skill statistic (TSS, Allouche et al., 2006). The AUC and TSS were averaged for all validation–calibration data sets to have a unique AUC and TSS for each algorithm and for each species. We excluded the models with an AUC value <0.7; models with an AUC value ≥0.7 were considered reliable (Elith, 2000). TSS values range from −1 to +1, where +1 is an indication of a perfect model fit and values ≤0 are an indication of models which are no better than random (Allouche et al., 2006).
4. We constructed the potential present-day distribution of each species by projecting in the calibration area and the niche models built were evaluated as robust. Binary maps were produced to predict the presence or absence of each species. This conversion was done using the optimised ROC threshold of Biomod2 (Thuiller et al., 2020), which minimises the absolute difference between sensitivity and specificity and is ranked amongst the most reliable thresholds (Liu et al., 2005).

2.6 | Future climate data and distribution modelling

Future climate variables were also derived from the AFRICLIM data set for the period 2070–2100 (averaged at 2085). The models were built using coupled Atmosphere–Ocean global circulation models (GCM) produced by Swedish Meteorological and Hydrological Institute (SMHI). However, there is a variability in global circulation models (IPCC, 2007) linked to a different set of parameters to represent land-use scenarios and key ecosystem processes (Doherty et al., 2010). Thus, 10 different GCMs were used. In addition, for each GCM, we used two greenhouse gas emission scenarios named representative concentration pathways (RCP 4.5 and RCP 8.5). RCP 4.5 is a gas emission scenario that limits the increase in mean temperature to 1.8°C for 2085s, whereas RCP 8.5 limits this increase to 3.7°C (IPCC, 2014). RCP 4.5 is considered an intermediate emission scenario and RCP 8.5 is a scenario with high greenhouse gas emissions (IPCC, 2014).

For the potential future distribution of NTFP plant species, we projected ecological niche models built from the three algorithms into 2085 (see above). The projections provided for the 40 species were a continuous suitability prediction per algorithm, GCM and RCP. This continuous prediction was converted into binary presence/absence pixels using the same threshold as detailed above (ROC threshold) to determine the suitable habitat in the future for each species.

2.7 | Potential distribution of the species under dispersal limitations

By projecting future projections of model outputs into the whole calibration area, we assume the species will be able to disperse across that area (Bateman et al., 2013). However, as for most species, there is little information on the dispersal capacity of NTFP plant species in Africa. Here, we take an intermediate approach between the commonly applied 'no dispersal' (i.e. dispersal only allowed within the present distribution) and 'full dispersal' (dispersal non-constrained) scenarios (Bateman et al., 2013) as to more realistically infer how species could respond to climate change in a short time frame. As most of NTFP plant species are harvested generally in the wild and are not managed or assisted by humans, a full dispersal scenario, where the entire area is projected as suitable by the model, appears unrealistic. Thus, none of the above dispersal scenarios (i.e. 'no dispersal' and 'full dispersal') appears to be suitable for our study. Here, we use two different scenarios that can be considered as two extremes within our context: (1) 'limited' dispersal scenario where suitability dynamics is within 100km around the convex hull of the present distribution: (2) and 'expanded' dispersal scenario where suitability dynamics is estimated within 500km around the convex hull of each species. The choice of 500km as a maximum upper dispersal limit is realistic for African plants based on the study of past (last 8500years) plant shifts within our study area (Watrin et al., 2009).

2.8 | Impact of climate change on the distribution of the species

The processing of projections was based on the suitability score of each pixel within the study area for present and future climate projections. For the 40 species, we considered all projection combinations (120 projections per species: 3 SDMs × 10 GCMs × 2 RCPs × 2 dispersal scenarios). Since the suitability score for each pixel is continuous, we used a binomial draw (*rbinom* function in R) to determine whether a pixel is suitable with the probability being the output of each model. This procedure gives the number of suitable pixels for each species for each combination in its study area.

The impact of future climate change for each species was assessed by calculating the change in climatic suitability, calculated as the difference between the number of pixels identified as suitable in the study area between the present and the future projections. This was calculated using Change Suitable Habitat (CSH) Thuiller et al. (2011) of the total area, as follows:

$$\text{CSH} = \frac{(\text{Area}_{\text{future}} - \text{Area}_{\text{present}})}{\text{Area}_{\text{present}}} \times 100 \quad (2)$$

The CSH represents the percentage of the climatically suitable area lost or gained in the future by each species. Using this metric, we first classified all modelling combinations of the 40 species into two

different categories as follows: 'climate winners' defined as species which have a positive change in climatic suitability between the present and future models; 'climate losers' defined as species with a negative change. Then, for each combination, we estimated the proportion of 'climate winners' and 'climate losers' species in our data set as previously reported, following previous (Blach-Overgaard et al., 2015; Zhang et al., 2016).

Furthermore, we evaluated the relationship between the pattern (narrow ranged or widespread) and the change in suitable areas of all the 40 species. For that, we estimated the EOO (extent of occurrence; that is the area contained within the shortest continuous imaginary boundary of occurrences) for each species using the function *EOO.computing* of the R package ConR (Dauby et al., 2017). Waterbodies were excluded from the EOO calculation. We plotted EOO values against the relative change in habitat suitability (CSH) and calculated the Pearson correlation value. We also estimated the relationship between species belonging or not to forested regions (Forest fractions) and the response of species to future climate change defined as CSH. We plotted the forest fraction for each species in the function of relative change in habitat suitability (CSH) as for the EOO explained above. Forest fraction was estimated by calculating the percentage of occurrences for each species in forested areas in our study area following the tropical rain forest region as described by Dauby et al. (2016) which was derived from Mayaux et al. (2004).

3 | RESULTS

3.1 | Data set

A total of 4380 unique occurrences (occupied cells in the climatic raster used) contained in 7052 herbarium specimens were recorded for the 40 species (Table S1). The mean number of occupied cells per species was 110. *Rauvolfia vomitoria* had the largest number of occurrences (360), whereas *Aframomum citratum* had the smallest number of occurrences (14). Amongst our species, *Senegalia senegal* is the most widespread species (EOO = 17,691,058 km²) and *Guibourtia tessmannii* is the least widespread species (EOO of 260,392 km²). On average, the EOO of all 40 species was of 3,638,315 km².

The species *Morinda lucida*, *Raphia hookeri*, *Raphia vinifera* and *Xylopia aethiopica* had their occurrences falling in forested areas, whereas *S. senegal* and *A. citratum* have 6% and 11% of their occurrence, respectively, belonging to forest areas, thus mainly being savannah species (Table S1).

3.2 | Contribution of variables and model performance

The contribution of the six selected bioclimatic variables to the models differs amongst species (Table S2). The rainfall deficit had the greatest contribution to the prediction models for most of NTFP species and the mean annual temperature has the smallest contribution.

Model evaluations of all species revealed an AUC value well above 0.7 indicating an overall good performance of the models (Table 1). Models developed using MaxEnt showed the highest value of AUC for all species. The values of the TSS index obtained after evaluation of the models vary between 0.29 and 0.61 with an average value of 0.46 (± 0.07). Species with an AUC score below 0.7 also received a TSS score below 0.5 confirming the poor performance of these models (Table 1).

3.3 | Present-day and future distribution models

For more than 50% of species (Figure 1, Table 2), we projected on average an increase by 2085 of climate suitability compared to their present predicted range, referred to as 'climate winners' (Table 2). The proportion of species classified as 'climate winners' or 'climate losers' varied depending on the algorithms or the dispersion scenario used (Table 2). The most important proportion of 'climate losers' (19/40) was observed when using MaxEnt (Table 2), under a limited dispersal scenario and the RCP 8.5 scenario. In contrast, the smallest proportion of 'climate losers' (10/40) is observed when using a full dispersion scenario with a low emission RCP (4.5).

For the algorithm MaxEnt and the climatic scenario RCP 4.5, the highest positive change was predicted for the following 'climate winners': *Garcinia kola*, *Raphia hookeri* and *Carpolobia lutea*. The highest negative changes ('climate losers') were predicted for *Prunus africana*, *Lophira alata* and *Aframomum danielli* (Figure 1).

Our results showed that 'climate losers' will lose on average 37% of their present potential distribution by 2085 under scenario RCP4.5 (i.e. the most conservative in terms of radiating forcing), whereas they lose 56% under scenario RCP 8.5. These percentages vary according to the GCM, the emission scenario RCP and the dispersion scenario (Figures S2-S4).

For almost all species, the magnitude of change in habitat suitability increased for predictions under RCP 4.5 when compared to RCP 8.5 (Figure 1). This difference was observed for all the model algorithms (Figures S2-S4). For example, for the species *Lophira alata*, a 'climate loser', the suitable habitat is reduced by 30% when compared between scenarios RCP 4.5 and RCP 8.5. Similarly, for *Carpolobia alba*, a 'climate winner', its suitable habitat is increased by 30% between scenarios RCP 4.5 and RCP 8.5.

3.4 | Relationship between forest fractions and climate change

There is no correlation between the extent of occurrence of the species (estimated using EOO) and the predicted response to climate change (Pearson's $R^2 = -0.07$, Figure 2). For example, species with small (e.g.: *Poga oleosa*) or wide (e.g. *Raphia hookeri*) distribution ranges can be positively impacted by climate change (Table 1; Figure S1). In the same way, there is no correlation between species occurring mainly in forested regions and their future response to climate change (Pearson's $R^2 = -0.1$, Figure 2).

TABLE 1 Summary statistics of predictive performance (AUC and TSS) given for each algorithm and for 40 NTFPs' species

Species	MAXENT-AUC	GM AUC	GBM-AUC	MAXENT-TSS	GLM-TSS	GBM-TSS
<i>Aframomum citratum</i> (Zingiberaceae)	0.51	0.54	0.52	0.45	0.47	0.29
<i>Aframomum daniellii</i> (Zingiberaceae)	0.82	0.81	0.74	0.53	0.53	0.50
<i>Aframomum melegueta</i> (Zingiberaceae)	0.71	0.64	0.64	0.38	0.30	0.31
<i>Baillonella toxisperma</i> (Sapotaceae)	0.81	0.80	0.82	0.56	0.54	0.57
<i>Carpolobia alba</i> (Polygalaceae)	0.82	0.81	0.83	0.54	0.54	0.54
<i>Carpolobia lutea</i> (Polygalaceae)	0.78	0.77	0.79	0.46	0.45	0.48
<i>Cola acuminata</i> (Malvaceae)	0.78	0.77	0.76	0.47	0.45	0.44
<i>Cola nitida</i> (Malvaceae)	0.70	0.69	0.75	0.38	0.38	0.47
<i>Coula edulis</i> (Malvaceae)	0.84	0.83	0.84	0.59	0.57	0.57
<i>Dacryodes edulis</i> (Burseraceae)	0.83	0.82	0.82	0.52	0.50	0.52
<i>Garcinia kola</i> (Clusiaceae)	0.75	0.71	0.73	0.45	0.39	0.43
<i>Garcinia lucida</i> (Clusiaceae)	0.78	0.72	0.77	0.52	0.45	0.52
<i>Garcinia mannii</i> (Clusiaceae)	0.78	0.78	0.77	0.47	0.47	0.47
<i>Gnetum africanum</i> (Gnetaceae)	0.76	0.74	0.74	0.45	0.42	0.40
<i>Gnetum buchholzianum</i> (Gnetaceae)	0.70	0.72	0.67	0.40	0.40	0.36
<i>Guibourtia tessmannii</i> (Fabaceae)	0.68	0.66	0.67	0.34	0.35	0.34
<i>Irvingia gabonensis</i> (Irvingiaceae)	0.76	0.77	0.75	0.45	0.45	0.44
<i>Irvingia wombolu</i> (Irvingiaceae)	0.80	0.77	0.66	0.56	0.54	0.40
<i>Khaya ivorensis</i> (Meliaceae)	0.71	0.69	0.67	0.43	0.39	0.34
<i>Laccosperma robustum</i> (Arecaceae)	0.75	0.74	0.72	0.42	0.42	0.38
<i>Lophira alata</i> (Ochnaceae)	0.76	0.77	0.77	0.42	0.43	0.46
<i>Milicia excelsa</i> (Moraceae)	0.78	0.77	0.78	0.44	0.43	0.46
<i>Monodora myristica</i> (Annonaceae)	0.75	0.75	0.71	0.42	0.42	0.38
<i>Morinda lucida</i> (Rubiaceae)	0.73	0.72	0.73	0.38	0.40	0.39
<i>Pausinystalia johimbe</i> ^a (Rubiaceae)	0.78	0.78	0.76	0.48	0.47	0.46
<i>Piper guineense</i> (Piperaceae)	0.79	0.79	0.78	0.48	0.49	0.47
<i>Poga oleosa</i> (Anisophylleaceae)	0.75	0.73	0.75	0.49	0.49	0.49
<i>Prunus africana</i> (Rosaceae)	0.87	0.86	0.85	0.61	0.62	0.61
<i>Raphia hookeri</i> (Arecaceae)	0.75	0.74	0.72	0.44	0.42	0.40
<i>Raphia mambillensis</i> ^b (Arecaceae)	0.62	0.72	0.64	0.57	0.61	0.57
<i>Raphia regalis</i> (Arecaceae)	0.73	0.69	0.68	0.47	0.39	0.39
<i>Raphia vinifera</i> (Arecaceae)	0.76	0.65	0.72	0.50	0.38	0.45
<i>Rauvolfia vomitoria</i> (Apocynaceae)	0.78	0.79	0.80	0.43	0.45	0.48
<i>Ricinodendron heudelotii</i> (Euphorbiaceae)	0.75	0.74	0.74	0.44	0.43	0.43
<i>Scorodophloeus zenkeri</i> (Fabaceae)	0.78	0.77	0.76	0.46	0.44	0.40
<i>Senegalia senegal</i> (Fabaceae)	0.84	0.84	0.84	0.57	0.57	0.57
<i>Terminalia superba</i> (Combretaceae)	0.69	0.66	0.70	0.36	0.30	0.36
<i>Trichoscypha arborea</i> (Anacardiaceae)	0.82	0.75	0.72	0.57	0.50	0.49
<i>Voacanga africana</i> (Apocynaceae)	0.77	0.76	0.75	0.43	0.43	0.42
<i>Xylopia aethiopica</i> (Annonaceae)	0.85	0.84	0.85	0.58	0.56	0.59

^a*Corynanthe johimbe* K.Schum.^bSee Mogue et al. (2019) for an updated taxonomy of this species.

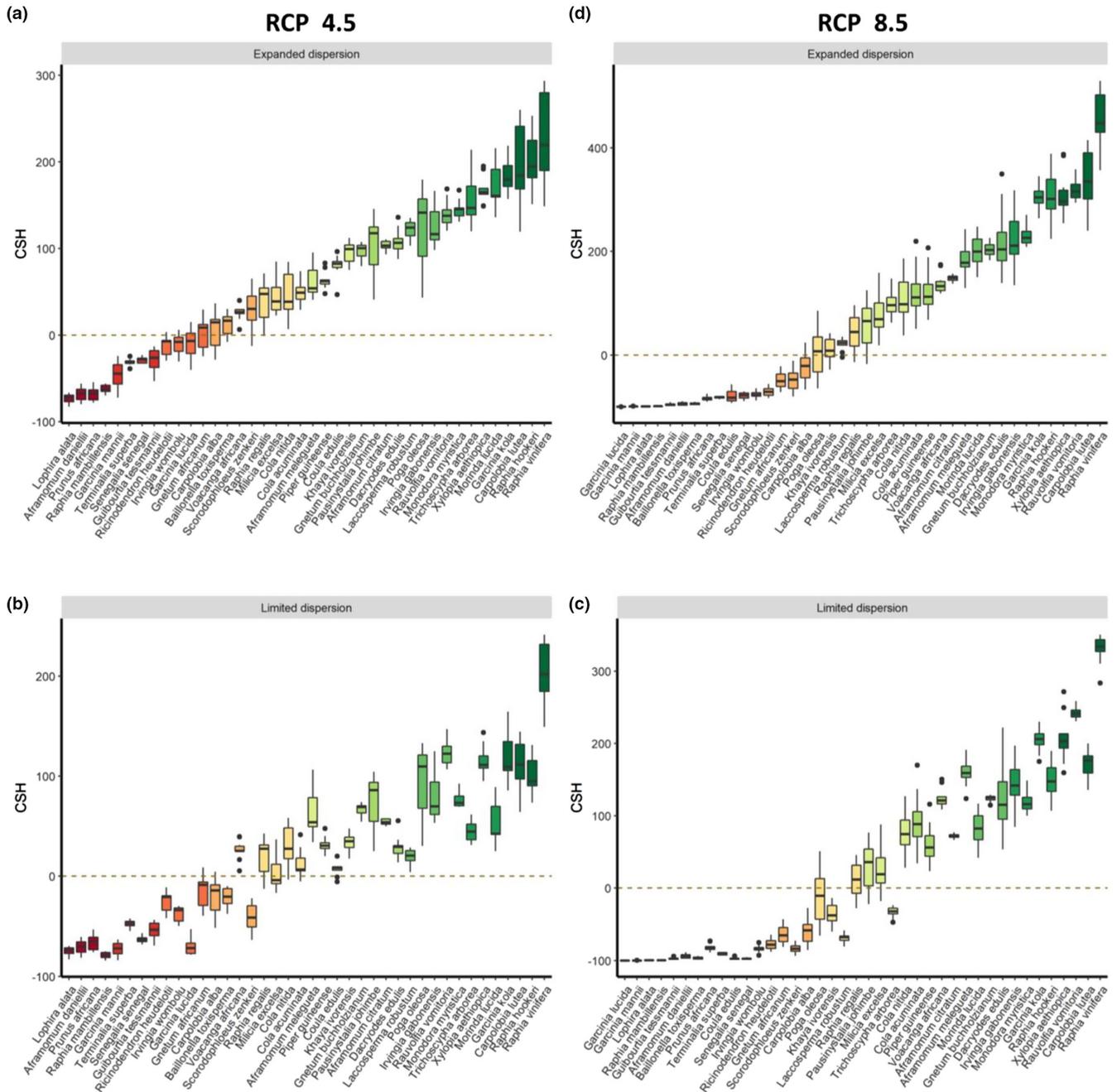


FIGURE 1 Relative change in suitable habitat (CSH) using MaxEnt for: (a) considering RCP 4.5 and expanded dispersion scenario; (b) considering RCP 4.5 and limited dispersion scenario considering RCP 4.5; (c) considering RCP 8.5 and expanded dispersion scenario and (d) considering RCP 8.5 and limited dispersion scenario. Values represent arithmetic means of all model combinations from 10 general circulation models. The box indicates the interquartile range. Colour gradients of boxes show a range of species from 'loser species' (CSH < 0) in red to 'winner species' (CSH > 0) in green

4 | DISCUSSION

4.1 | Effect of climate change on NTFP plant species

Our study focused on 40 NTFP plant species described as 'priority' resources in Cameroon by Ingram (2014). These 40 species were, on average, a geographic range of 3.6 million km² (Table S1). When compared to the geographic ranges of all tropical African

plant taxa (from Sosef et al., 2017, Figure S5), these species are at the high end of the spread, being amongst the most widespread species. This is consistent with the idea that useful plant species generally have large geographic areas across the region they are used in and under the influence of human-induced factors (van Zonneveld et al., 2018). In addition, 27 species had most of their occurrence records (more than half) within a forested region underlining the importance of forests to supply NTFP products in tropical Africa (Table S1).

TABLE 2 Number and proportion of NTFPs providing species projected to be 'climate winners' (W) or 'climate losers' (L) for three algorithms (MaxEnt, general linear models (GLM) and generalised boosting models (GBM), two RCPs (4.5 and 8.5) and two dispersal scenarios (limited and expanded)

	MaxEnt		General linear models (GLM)				Generalised boosting models (GBM)					
	Limited		Expanded		Limited		Expanded		Limited		Expanded	
	W	L	W	L	W	L	W	L	W	L	W	L
RCP 4.5	22 (55%)	18 (45%)	25 (62.5%)	15 (37.5)	19 (47.5%)	21 (52.5%)	26 (65%)	14 (35%)	22 (55%)	18 (45%)	26 (65%)	14 (35%)
RCP 8.5	17 (42.5%)	23 (57.5%)	20 (50%)	20 (50%)	15 (37.5%)	25 (62.5%)	18 (45%)	22 (55%)	15 (37.5%)	25 (62.5)	23 (57.5)	17 (42.5%)

We used a curated and verified tropical African occurrence database (Dauby et al., 2016) combined with three SDM algorithms, and 10 different Global Climate Models (GCMs) under two different future predictions (RCP 4.5 and 8.5) to estimate how these valuable plant species will be impacted by end of the century (2085) climate change (Figure 1). Based on these models, species were categorised into two different groups: 'climate winners' and 'climate losers' (Table 2). Our results suggest that, independent of the models or dispersal scenarios used, NTFP species across tropical Africa will not respond in a similar manner to end-of-century climate change (Figure 1; Table 2; Figures S1-S4). Interestingly, under the RCP 4.5 scenario, there is a higher percentage of climate winners than losers for NTFP species (Figure 1, Table 2). Indeed, between 55% and 65% of NTFP species will be climate winners within their present range distribution, whereas between 35% and 45% of species will be climate losers (Table 2). Thus, more NTFP species will gain or remain stable in the future than lose suitable habitat. However, the trend is inverted when considering the RCP 8.5 scenario where more species will lose climate suitability in the future than win (between 42.5% and 62.5%, Table 2; Figure 1). The RCP 8.5 scenario depicts a future on intensive fossil-fuel usage, excludes any kind of climate mitigation policy and is generally not considered a realistic scenario (Hausfather & Peters, 2020; Moss et al., 2010). Considering the two dispersal scenarios used in this study, we found that for some species (12/40), the location of future suitable habitat is not within their present range distribution but rather inside the buffer zone of 500-km area around the present distribution. Thus, we decided to mainly interpret the results from the RCP 4.5 scenario from here on, unless otherwise explicitly stated.

Overall, our results contrast with several studies generally showing a decrease in future climate suitability for single useful species (e.g. *Senegalia senegal* (Lyam et al., 2018); *Adansonia digitata* L. (Sanchez et al., 2011), *Hyphaene petersiana* Klotzsch ex Mart. (Blach-Overgaard et al., 2009) or for a keystone plant family in general like palms (Blach-Overgaard et al., 2015). Our results suggest that a common global climate change response of a heterogeneous group of plant species is probably not valid as suggested for some floras of Africa (van Proosdij et al., 2017). This is certainly linked to the fact that different environmental variables selected here explain the distribution of different species (Figure S6). Interestingly, individual species-dependent responses to past climate change (e.g. Last Glacial Maximum, ca. 20k years ago) have also been demonstrated in Africa based on pollen (Watrin et al., 2009) or genomic data (Helmstetter et al., 2020).

Neither geographical range nor ecology (via 'forest fraction') appears to be driving factors in understanding how these species will respond. Indeed, there is no correlation between EOO or forest fraction with change in habitat suitability (Figure 2). The most widespread species in our data set, *Senegalia senegal* (gum acacia), is a tree of the dry Sahel region occurring throughout tropical Africa and parts of southern Africa. Our models show that this species will be amongst the most affected of the group, losing around 80% of suitable habitat

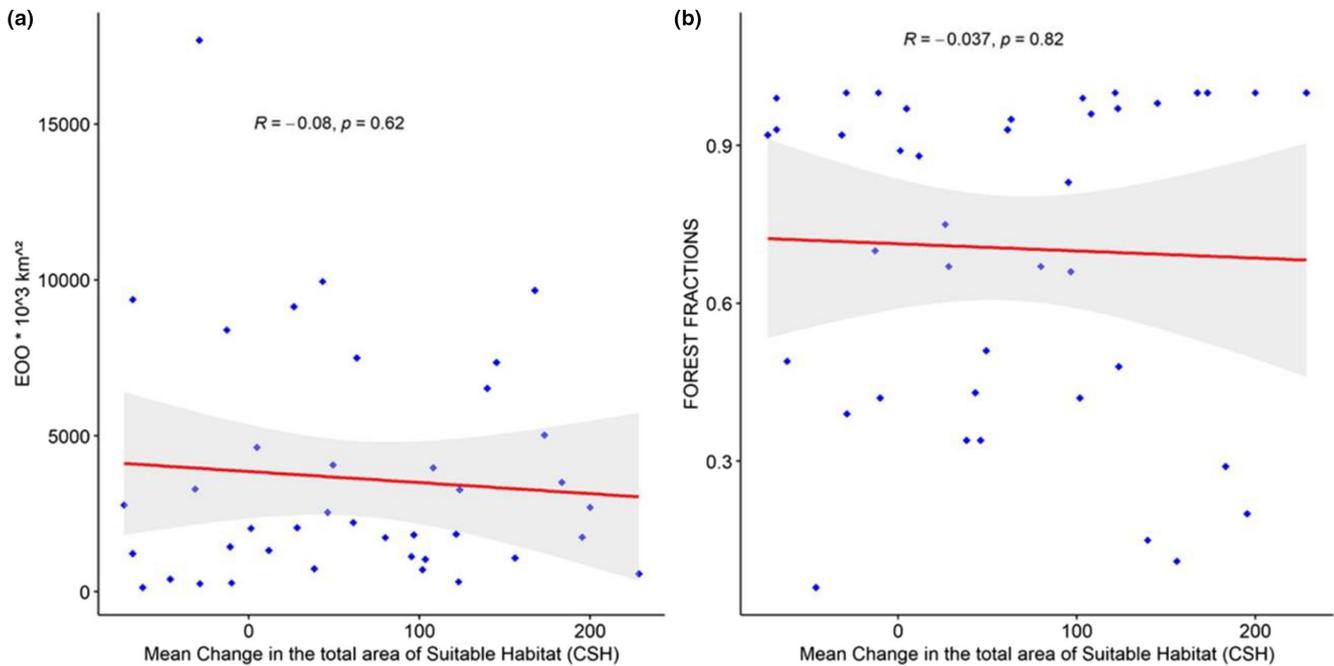


FIGURE 2 Relation between the sensitivity of NTFP species to climate change and (a) the range of the species and (b) the belonging of the species to forested regions. (a) correlation between the mean change in suitable habitat (CSH) and extent of occurrence (EOO). (b) correlation between the mean change in the total area of suitable habitat (CSH) and Forest fractions mean CSH are calculated here for 'RCP 4.5' and 'limited dispersion'

by 2085 regardless of the dispersal scenario (Figure 1). Our result is in agreement with a similar but more focused study showing a likely reduction of *Senegalia senegal* suitable habitat in the future in West Africa (Lyam et al., 2018). The palm *Raphia mambillensis* has the most restricted range in our study (but see Kamga et al., 2019 for an update on its taxonomy). This species is restricted to altitudes above 1500m in the Cameroun Volcanic Line in western Cameroon and eastern Nigeria (Cosiaux & Couvreur, 2020). It is one of the most important plants in the region both economically and socially (Mogue Kamga et al., 2020). As for *Senegalia senegal*, *R. mambillensis* is estimated to lose around 80% of its range independent of the dispersal scenario (Figure 1). Because it is a mainly montane species, dispersal to higher altitudes will be limited resulting in a drastic reduction of its distribution possibly resulting in the extinction of this species in the Cameroon Volcanic Line. The loss of this species could lead to important economic and social impacts for the societies that depend on it (Cosiaux & Couvreur, 2020).

We show that the dispersal capacity will be an important component of the future of NTFP species (Figure 1, Table 1). Even though dispersal is hard to estimate in general and not implicitly taken into account in the modelling process (Bateman et al., 2013), we applied two intermediate scenarios (limited or expanded) allowing species to migrate between 100 and 500km during this short time frame. Consistently, and, independent of both the SDM models and RCP scenarios, the proportion of winner species increased between 10% and 17.5% under the expanded model when compared to the limited one (Figure 1, Table 2). These results confirm the findings of several studies that predicted a higher loss of habitat currently assessed as suitable (Lei et al. 2014) or an important extinction of species under

a no-dispersal hypothesis (Thomas et al., 2004; van Proosdij, 2017). This suggests that given enough geographical space (and time), our selection of NTFP species could migrate to more favourable regions, a common response in plants when faced with rapid climate change (Corlett & Westcott, 2013; Huntley, 1991).

We also showed that closely related species might have alternative responses to future climate change, complicating generalisations. For example, two sister fern species of the Gnetaceae family (Hou et al., 2015), *Gnetum africanum* and *Gnetum buchholzianum*, have similar geographical distributions and both occur in humid tropical rain forests below 1500m (Clark & Sunderland, 2004). However, our models estimated different habitat loss proportions by 2085. According to MaxEnt predictions, *Gnetum africanum* will experience a loss of suitable habitat between 50% and 70%, whereas *Gnetum buchholzianum* will undergo a more moderate loss of about 12%–35% (Figure 1). Thus, other factors depending on each species (physiological traits) interfere in the estimation of a species response to climate change. Indeed, several studies have demonstrated that other variables related to local adaptation and phenotypic plasticity, dispersal capabilities and physiological responses can be involved in the estimation of the future distribution of species in the response to climate change (Gardner et al., 2019; Ruiz-Benito et al., 2020).

4.2 | Climatic variables

In this study, we selected six bioclimatic variables known to be ecologically relevant to determine the distribution of tropical species in

general (Blach-Overgaard et al., 2015). Other alternatives concerning the selection of variables exist. For example, Peterson et al. (2012) suggested an analysis of collinearity to select variables or a transformation of original variables to many combined variables via a PCA. Another method is to use all variables simultaneously and let the algorithm select the most important variables through variable permutation or the use of AIC (Akaike Information Criterion; Braunisch et al., 2013). However, models build from a few number or many variables have lower quality (Warren & Seifert, 2011). Although the method of selection used here appears robust, the question remains; is it judicious to use the same variables for all species included in the study? Leibold (1995) suggests that the number or the type of predictors used to estimate the niche should depend on the ecology of each species. Nevertheless, most of our models have a good predictive potential suggesting that our models are robust (Table S1).

4.3 | Modelling algorithm and evaluation

Modelling algorithms are a major source of uncertainty in predicting the impact of climate changes on species (Beale & Lennon, 2012). Indeed, 29%–51% of uncertainty in future projections are explained by model algorithms (Buisson et al., 2010). Here, we accounted for this uncertainty by using three different algorithms (MaxEnt, GBM and GLM) to model present and future potential distributions. Overall, these different models tended to result in similar predictions (for 34 species out of 40) in terms of winner and loser species. However, this was not always the case. For example, for the species *Cola nitida* and *Garcinia kola*, the MaxEnt and GBM predicted a gain of suitable habitats (winner species), whereas GLM predicted a loss of suitable habitats (loser species; Figures S1–S4). One alternative, not applied here, would be to use ensemble forecasts (Araújo & New, 2007), whereby the different outputs of the models are averaged.

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CONFLICT OF INTEREST

None declared.

DATA AVAILABILITY STATEMENT

Raw distribution data for the 40 species was extracted from the RAINBIO database (Dauby et al., 2016).

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