

RESEARCH ARTICLE

Drought-tolerant succulent plants as an alternative crop under future global warming scenarios in sub-Saharan Africa

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Abstract

Globally, we are facing an emerging climate crisis, with impacts to be notably felt in semiarid regions across the world. Cultivation of drought-adapted succulent plants has been suggested as a nature-based solution that could: (i) reduce land degradation, (ii) increase agricultural diversification and provide both economic and environmentally sustainable income through derived bioproducts and bioenergy, (iii) help mitigate atmospheric CO₂ emissions and (iv) increase soil sequestration of CO₂. Identifying where succulents can grow and thrive is an important prerequisite for the advent of a sustainable alternative ‘bioeconomy’. Here, we first explore the viability of succulent cultivation in Africa under future climate projections to 2100 using species distribution modelling to identify climatic parameters of greatest importance and regions of environmental suitability. Minimum temperatures and temperature variability are shown to be key controls in defining the theoretical distribution of three succulent species explored, and under both current and future SSP5 8.5 projections, the conditions required for the growth of at least one of the species are met in most parts of sub-Saharan Africa. These results are supplemented with an analysis of potentially available land for alternative succulent crop cultivation. In total, up to 1.5 billion ha could be considered ecophysiologicaly suitable and available for succulent cultivation due to projected declines in rangeland biomass and yields of traditional crops. These findings may serve to highlight new opportunities for farmers, governments and key stakeholders in the agriculture and energy sectors to invest in sustainable bioeconomic alternatives that deliver on environmental, social and economic goals.

KEYWORDS

agriculture, aridity, bioenergy, climate change, crassulacean acid metabolism, drought, *Euphorbia*, *Opuntia*, *Portulacaria*, species distribution modelling

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1 | INTRODUCTION

Dryland communities in sub-Saharan Africa (SSA) are facing a series of emerging challenges in the decades ahead. These include a continued reliance on solid fuels for daily energy requirements (Cerutti et al., 2015; IEA, 2019), increased precipitation variability caused by human-induced climatic changes (Marthews et al., 2019; Ofori et al., 2021; Otto et al., 2018) and increasingly unsustainable pastoral-based activities with a diminishing resource required to support a growing population across SSA communities (Scanes, 2018) resulting in widespread land degradation. Rangelands in particular are under increasing pressure to support sustainable livestock production; and whilst being central to the economies, social traditions and resilience of many communities (Bollig & Vehrs, 2020; Coppock et al., 2017; Godde et al., 2020; Hoffmann et al., 2014), their vegetation dynamics are highly vulnerable to climate change (trends and variability) in terms of both forage availability (Godde et al., 2020, 2021; Louhaichi et al., 2019; McCollum et al., 2017; Ouled Belgacem & Louhaichi, 2013) and feed yields (Jägermeyr et al., 2021; Rosenzweig et al., 2014).

Sustainable strategies that can tackle these challenges and provide solutions to socio-economic requirements and anticipated global warming impacts are needed. One such option is to explore the potential for alternative crops resilient to the impacts of global warming whilst simultaneously offering socio-economic gains, such as nongridded energy supplies and sustainable agricultural practices. Cultivation for bioenergy (Dahunsi et al., 2020; IRENA, 2017) and agricultural diversification (Njarui et al., 2020) have been previously explored as means by which plant-based solutions could be used to deliver benefits across the social, environmental and economic spheres. There are, however, widely differing water-usage requirements and levels of drought resilience among traditional bioenergy crops (Gasparatos et al., 2015; Gerbens-Leenes, 2018; Gerbens-Leenes et al., 2009).

Succulent plants, which typically use the mode of photosynthesis known as crassulacean acid metabolism (CAM), show high water-use efficiency, tolerance of high temperatures and an ability to grow on marginal or degraded land (Borland et al., 2009; Cushman et al., 2015; Yang et al., 2015). The cultivation of such species could be used as a solution to: (i) reduce land degradation as a cover crop in semiarid regions (Honorato-Salazar et al., 2021; Nefzaoui et al., 2014; Nefzaoui & el Mourid, 2009; Neupane et al., 2021), (ii) increase agricultural diversification (e.g. fodder for livestock, biomass for energy and bioproducts) and thereby provide sustainable incomes (Acharya et al., 2019; Buckland & Thomas, 2021; Davis

et al., 2015; Grace, 2019; Holtum et al., 2011; Honorato-Salazar et al., 2021; Mason et al., 2015; Owen et al., 2015; Yang et al., 2015) and (iii) draw down atmospheric CO₂ through photosynthetic carbon assimilation and soil sequestration of CO₂ (Borland et al., 2009; Grace, 2019).

However, the opportunity for CAM plants to be grown on a commercial scale, such as *Opuntia ficus-indica* (prickly pear cactus), has not fully been explored, in terms of either viable species and range or regarding potential growth rates and productivity. Currently, only a handful of CAM species are cultivated at commercial scale for either food or fibre production (e.g. pineapple and several species of *Agave*; Davis et al., 2015, 2019), but the opportunity for expansion into new regions and alternate species is considerable given that rangelands cover 54% of the terrestrial land surface (ILRI et al., 2021), including 20 million km² of semiarid regions.

Whilst *O. ficus-indica* has been grown historically for food and fodder (Inglese et al., 2017; Makumbe, 2010), the opportunity to cultivate it on a larger scale as a crop has only been explored in specific regions (e.g. Brazil and Mexico; FAO, 2013; Guevara et al., 2009; Honorato-Salazar et al., 2021; Reyes-Agüero et al., 2005; Suassuna, 2008) and primarily for the production of bioenergy (Beshir Belay et al., 2018; Espinosa-Solares et al., 2022; Krümpel et al., 2020; Neupane et al., 2021) rather than more broadly as a semiarid crop which can be used as a feedstock for the generation of a variety of end-products. Recent studies have, however, confirmed the potential for these plants (*Opuntia* spp.) to thrive in the harsh conditions of arid environments (Borland et al., 2009; Cushman et al., 2015; Neupane et al., 2021; Yang et al., 2015) and to be used in a range of higher value end-product industries (e.g. food, feed, cosmetics, pharmaceuticals, bioplastics and volatile fatty acids production; Gheribi et al., 2019; Ramadan et al., 2021; Scognamiglio et al., 2020). Likewise, isolated studies have considered the potential distribution of species such as *O. ficus-indica* in certain regions, either to map potential distribution in a specific country (e.g. India and Jordan; Acharya et al., 2019; Louhaichi et al., 2015) or from the perspective of identifying biodiversity regions under threat from advancing invasives (e.g. Hussein & Estifanos, 2023; Masocha & Dube, 2018). But a view on the opportunity at a continent scale across Africa, both under current and end-century climatic conditions, is lacking.

This study aims to identify the regions of SSA where succulent cultivation presents a potential alternative agricultural opportunity in the face of climate change projections. We first explore the future environmental sustainability of succulent distribution under the Coupled Model Intercomparison Project Phase 6 (CMIP6) climate

projections until 2100, using species distribution modelling to map regions predicted to be suitable for growth. We then combine outcomes with an analysis of potentially *available* lands, identified through analysis of projected rangeland suitability, surplus land and crop yields under future anticipated climate changes. Finally, we integrate our assessment of land *suitability* with potential land *availability* in order to: (i) identify regions not suitable for alternative cultivation due to existing socio-economic uses and/or conservation reasons (e.g. food production, urban areas and prime ecosystem) and (ii) highlight regions in which current agricultural systems will become increasingly unviable due to climate change. In doing so, this study addresses the intersection between the areas of potential growth and need, highlighting areas where consideration of succulents as alternative crops could be further developed.

2 | MATERIALS AND METHODS

2.1 | Site and species selection

As noted above, SSA is facing a plethora of emerging challenges, with many individual countries ranking low on the adaptive capacity to the impacts of climate change (Godde et al., 2021) or experiencing increased levels of land degradation. Added to this, much of the sub-Saharan population remains dependent on solid fuels for cooking energy (IEA, 2019) and smallholder pastoral farming, which is exposed to shifts in future climate projections. Given the cultivation and bioeconomic potential as demonstrated in central and southern America, where *Agave* and *Opuntia* spp. are native, this study has focussed on the capability of extending the success found in these existing regions to the African context where combined benefit alternatives can address environmental and socio-economic challenges.

For the initial exploration of CAM plant cultivation, three exemplar species were selected from the wider global pool of CAM plants: *O. ficus-indica* (L.) Mill. (prickly pear cactus, nopal), *Euphorbia tirucalli* L. (milkbush, rubber-hedge euphorbia) and *Portulacaria afra* Jacq. (spekboom, elephant bush). This study focusses on species with relatively high growth rates and biomass potential, together with other favourable properties such as palatability to animals, and potential for ecosystem restoration, which together would make them candidates for potential cultivation as crops. *O. ficus-indica* and *E. tirucalli* are both invasive species (CABI, 2019) that can grow on marginal land and have expanded worldwide well beyond their native ranges (Palgrave, 1977; Webb et al., 1984). *O. ficus-indica* has long been cultivated for food and fodder (see

Section 1), but is also attracting interest as a biomass crop for the generation of energy and higher value bioproducts (Acharya et al., 2019; Inglese et al., 2017; Lueangwattanapong et al., 2020; Mason et al., 2015; Neupane et al., 2021; Ramadan et al., 2021). Similarly, *E. tirucalli* is known to be palatable to animals (Kagunyu & Wanjohi, 2015; Paley & Kerley, 1998; Van Jaarsveld & Le Roux, 2021) and may be suitable in certain situations for sustainable bioenergy production (Hastilestari et al., 2013; Krümpel et al., 2020). *P. afra*, in contrast, is restricted in its distribution to southern and south-eastern Africa, but is fast-growing and consumed by megaherbivores, has been widely found on existing farmland and has been proposed as a suitable species for restoration of degraded semiarid scrubland (Mills & Cowling, 2006, 2014; van der Vyver et al., 2021; Van Jaarsveld & Le Roux, 2021).

2.2 | 'Suitable' land analyses

2.2.1 | Species distribution models

Previous studies have explored the use of analytical hierarchical process modelling, climatic envelope modelling and environmental productivity indices to consider the relationship between climatic conditions and the occurrence of *O. ficus-indica* in drylands (Acharya et al., 2019; Buckland & Thomas, 2021; Louhaichi et al., 2015; Owen et al., 2015). An alternative approach is to use species distribution models (SDMs), which are based on the correlative relationships between a set of environmental predictor variables and known occurrences of individual species (Dormann et al., 2012; Guisan et al., 2017). SDMs capture complex relationships between environmental conditions and the species known occurrences, allowing for interactions between the parameters. Once the relationship has been identified between an observed coupling of data, the model can be used to forecast distributions over new geographies and timeframes—allowing forward projections of sustainability under different climatic futures.

Using the 'biomod2' package in R Studio (Georges & Thuiller, 2013; Thuiller et al., 2014, 2023), ensemble SDMs were used to project both current and future distributions for the three exemplar species: *O. ficus-indica*, *E. tirucalli* and *P. afra* based on a selection of current bioclimatic predictor variables (Fick & Hijmans, 2017) and known occurrences (GBIF, 2023). Model parameterisation and data preparation followed the methods in Buckland et al. (2022) and are detailed in [Supporting Information](#).

Following the predictor dataset analysis for *O. ficus-indica* and *E. tirucalli* SDMs in Buckland et al. (2022), four bioclimatic variables were used in model building for these two species, and three bioclimatic variables

were used to explain the distribution of *P. afra* (Table 1). Whilst the inclusion of more complex climatic indices may characterise environmental conditions that are more directly physiologically relevant to species (Title & Bemmels, 2018), previous research (Buckland et al., 2022; Bucklin et al., 2015) has suggested that the addition of environmental predictors with low levels of variable importance for species' distributions (e.g. aridity index and cloud cover) does not significantly improve overall model performance, but may increase the likelihood of model overfitting (Buckland et al., 2022; Wenger & Olden, 2012).

Paired occurrence-bioclim datasets were split 60% for training and validation of the SDMs and 40% for testing purposes, with individual SDMs then ensembled using the weighted means according to the individual model true skill statistic and relative operating characteristic scores (see Supporting Information). The importance of each environmental predictor variable was calculated using internal biomod2 functions which shuffle the original variable and recompute the model prediction according to the shuffled variable. An importance score of 0 suggests the variable has no influence on the model; the higher the value, the greater the influence of the individual variable on the model. Individual response curves were produced to demonstrate the direction and sensitivity of the model to each environmental variable, with each presenting the probability of occurrence of the species relative to the selected environmental variables. Single and multidimensional response curves were calculated to account for interactions between variables.

2.2.2 | Future climate–society projections

Regions suitable for potential future growth of *O. ficus-indica*, *E. tirucalli* and *P. afra* were projected according to conditions modelled under four different scenarios of future projected climate from the CMIP6 Shared Socioeconomic Pathways (SSPs) scenarios (Table 2). To minimise the effects of individual model biases, bioclimatic datasets across the climatic variables are based on an ensemble-averaged mean projection from nine global climate models contributing to the CMIP6 projections (Fick & Hijmans, 2017). Future climate projections were based on downscaling and bias-correction using the WorldClim v2.1 to provide baseline climates (Fick & Hijmans, 2017).

2.3 | 'Available' land analyses

Defining the regions potentially available for cultivating alternative crops and most in need of adjustments

TABLE 1 Bioclimatic variables used as environmental predictor datasets (Fick & Hijmans, 2017).

Bioclim code	Variable
Bio2	Mean diurnal temperature range (mean of monthly [max temp – min temp]) (°C) Represents the mean of the weekly diurnal temperature ranges (difference between each week's maximum and minimum temperature) and is useful in determining importance of temperature fluctuation for species
Bio4	Temperature seasonality (standard deviation × 100) (°C) A measure of temperature change over the course of the year, the temperature seasonality value is based on the standard deviation of monthly average temperature and thus informs about levels of variability in temperature across an annual period
Bio6	Minimum temperature of coldest month (°C) The minimum monthly temperature occurrence over the baseline period used, informing about species distributions affected by cold temperature anomalies
Bio11	Mean temperature of coldest quarter (°C) A measure of mean temperatures during the coldest quarter, indicating the impact of such factors on species seasonal distributions
Bio12	Annual precipitation (mm) The sum of all monthly precipitation values and useful for determining the importance of water availability on an individual species distribution in the absence of other moisture sources
Bio13	Precipitation of wettest month (mm) A measure of precipitation that occurs during the wettest month and a useful indicator if specifically different precipitation conditions during the year affect a species distribution
Bio15	Precipitation seasonality (coefficient of variation) (mm) A measure of the variation in monthly precipitation over an annual period, calculated as the ratio of the standard deviation of the monthly total precipitation to the mean monthly total precipitation

Note: Bioclimatic variables 2, 6, 12 and 15 were used for *Opuntia ficus-indica* and *Euphorbia tirucalli*; variables 4, 11 and 13 were used in the *Portulacaria afra* SDMs. See Buckland et al. (2022) for details of covariance analysis and predictor dataset selection for *O. ficus-indica* and *E. tirucalli*; details for *P. afra* are provided in Supporting Information.

TABLE 2 Table of CMIP6-SSP scenarios used in the future species distribution projection maps.

Scenario name (comparative RCP)	Forcing category	Radiative forcing in 2100 (W/m ²)	Warming from preindustrial levels by 2100	SSP description
SSP1 2.6 (RCP 2.6)	Low	2.6	1–3–2.9°C	<i>Sustainability</i> : A world with low challenges to adaptation and mitigation with a commitment to achieving development goals, increasing environmental awareness and a gradual move towards less resource-intensive lifestyles
SSP2 4.5 (RCP 4.5)	Medium	4.5	2.1–4.3°C	<i>Middle of the Road</i> : A world in which social, economic and technological trends do not shift markedly from historical patterns. Significant advances in sustainable development are constrained resulting in moderate challenges to mitigation and adaptation
SSP3 7.0	High	7.0	3.0–6.2°C	<i>Regional Rivalry</i> : Countries focus on national and regional energy and food security goals at the expense of broader-based development. Growing resource intensity and fossil fuel dependency along with difficulty in achieving international cooperation and slow technological change imply high challenges to mitigation and adaptation
SSP5 8.5 (RCP 8.5)	High	8.5	3.8–7.4°C	<i>Fossil-fuelled Development</i> : A world with high economic growth enabling many development goals to be achieved. Energy demands grow and rely heavily on fossil fuels leading to high challenges to mitigation. But robust economic growth and highly engineered infrastructure results in relatively low challenges to adaptation to future climate change

Note: SSP scenarios selected to encompass a range of forcing levels and climate/socio-economic futures. See O'Neill et al. (2016, 2017) for detailed descriptions of the individual SSP scenarios. The nine GCMs selected for averaging CMIP6 forecasts were: BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, GFDL-ESM4, IPSL-CM6A-LR, MIROC-ES2L, MIROC6 and MRI-ESM2-0 (Fick & Hijmans, 2017).

Abbreviations: CMIP6, Coupled Model Intercomparison Project Phase 6; GCM, global climate model; SSP, Shared Socioeconomic Pathway.

to current agricultural production requires a multifaceted approach. For example, alternate crop production (e.g. for bioenergy) should be focussed preferentially in regions that avoid potential land competition with food crops (Muscat, 2022; Muscat et al., 2020) whilst also not encroaching on pristine habitats. Thus, the concept of *marginal lands* has been suggested as providing suitable regions for the expansion of these crops (Borland et al., 2009; Dauber et al., 2012; Shortall, 2013). We note, however, that the definition of marginal lands is arbitrary, differing between contexts (Allen et al., 2016; Arshad et al., 2021; Edrisi & Abhilash, 2016; Lewis & Kelly, 2014; Muscat, 2022). Land may be considered economically marginal where cost-effective production is not possible and

outweighs the returns achieved. Alternatively, marginality of land is defined in terms of poor agricultural quality, which is equally crop-specific, or in terms of degradation (Lal, 2009). Others argue for a focus more on total carbon land-use efficiency (e.g. Searchinger et al., 2018) rather than marginality in terms of prioritising land use, production and global carbon stores.

This study examines a series of potential ways in which 'available' lands could be defined based on changing landscapes and land uses under different socio-economic futures and/or different anticipated climate trajectories. Using previously published datasets, we mapped: (1) 'surplus land', as defined by Daioglou et al. (2019), available for bioenergy crops; (2) rangelands under threat from

TABLE 3 Datasets used to identify potential 'available' areas that could be used for alternative succulent biomass cultivation.

Mapped datasets	Scenarios and years modelled	Rationale and usage
Surplus land for future biomass production	2100: SSP 1, SSP 2, SSP 3	Daioglou et al. (2019) use the IMAGE 3.0 model (Doelman et al., 2018; Stehfest et al., 2014; Van Vuuren et al., 2017) to examine long-term global interactions between land-use, agricultural, energy and climate systems. Daioglou et al. (2019) map the land available for future energy crop production based on areas classified as abandoned agricultural (due to increases in agricultural efficiency) or other natural lands (restricted to varying degrees due to shifting environmental constraints) according to SSP1, 2 and 3 after food production and other land-use constraints have been accounted for. In this study, we use the data from Daioglou et al. (2019) to overlay the regions classified as 'available for biomass production' with the regions identified in the SDM suitability analysis for three succulent species of interest
Rangeland future herbaceous biomass	2050: RCP 8.5 (with CO ₂ effect)	Godde et al. (2020) use a global rangeland model, G-range (Boone et al., 2018), in combination with livestock and socio-economic data to model the vulnerability of rangelands to climate change. Areas that may be at future climatic risk for rangeland suitability are those where herbaceous biomass is anticipated to decline. In this study, we used the data from Godde et al. (2020) to overlay the regions which show a decrease in herbaceous biomass over the period 2000–2050 under RCP 8.5
Yield projections for major crops	2081–2100: RCP 8.5 (with CO ₂ effect)	Jägermeyr et al. (2021) produce harmonised ensemble projections for global future crop yields based on process-based crop model simulations as part of the Agricultural Model Intercomparison and Improvement Project (AgMIP; Rosenzweig et al., 2013) and the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP, 2021). This work allows us to track changes in anticipated global yields of four major crops according to different radiative climate pathways. In places where farming traditional C ₃ and C ₄ crops such as wheat and maize, respectively, may no longer produce biomass yields akin to current baseline levels, cultivation of succulents may be of potential value without competing with future food production. In this study, we have produced ensemble maps of the change in yield (from baseline yields 1983–2013) for the four major crops (rice, wheat, maize, soybean) according to RCP 8.5 for the period 2081–2100 and have focussed on identifying regions anticipated to experience century-end yield declines in crop yields in excess of 10% relative to 1983–2013. See Jägermeyr et al. (2021) for further details

Abbreviations: SDM, species distribution model; SSP, Shared Socioeconomic Pathway.

future climatic change (Godde et al., 2020); and (3) major C3 and C4 crop yields under pressure due to shifting climates (Jägermeyr et al., 2021; Table 3).

3 | RESULTS

3.1 | Model performance and distribution projections

A total of 100 individual models were run for each species and ensembled to produce a weighted mean projection

with coefficient of variation measurement, based on current (near historical) climatic conditions and known occurrences of the three exemplar plants. Once trained, ensemble models predicted current and future potentially suitable regions for the species according to projected datasets of the environmental predictors for SSP1 2.6, SSP2 4.5, SSP3 7.0 and SSP5 8.5 for the period 2081–2100 (Figure 1). Projected outputs are presented along a scale of 0–100, with 0 referring to low/no suitability for the species to grow in that area, and 100 demonstrating high suitability. All individual models showed high levels of evaluative performance and were included in the overall ensemble modelling (Table 4).

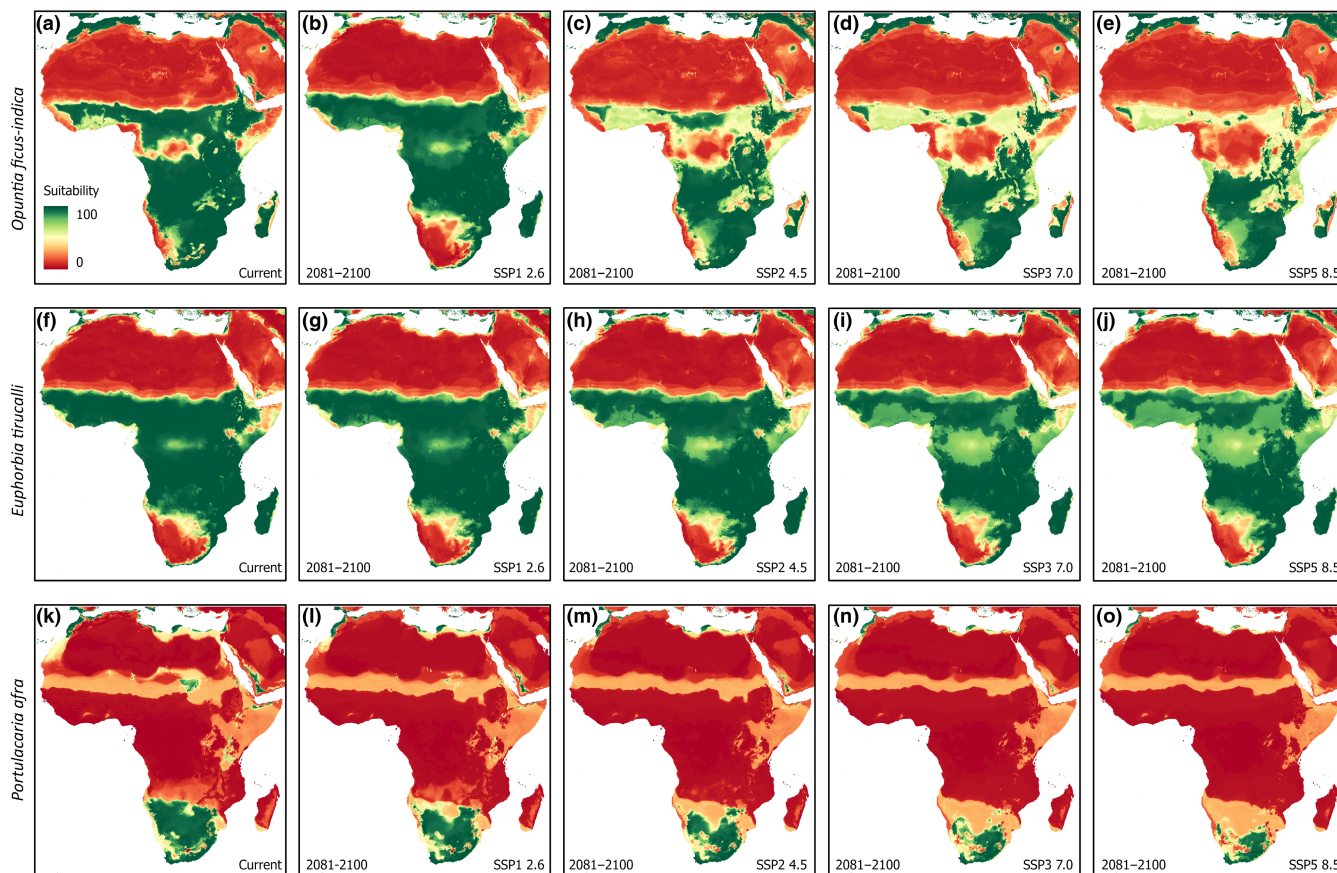


FIGURE 1 *Opuntia ficus-indica* (a–e), *Euphorbia tirucalli* (f–j) and *Portulacaria afra* (k–o) ensemble suitability projections based on current (near historical) conditions and for the period 2081–2100 AD according to different radiative forcing trajectories: SSP1 2.6, SSP2 4.5, SSP3 7.0, SSP5 8.5.

TABLE 4 SDM ensemble evaluation metrics by species.

	Ensemble model evaluation metrics				
	ROC	TSS	Cut-off	Sensitivity	Specificity
<i>Opuntia ficus-indica</i>	0.99	0.93	54.9	96.3	96.7
<i>Euphorbia tirucalli</i>	0.99	0.95	60.0	97.7	97.6
<i>Portulacaria afra</i>	0.99	0.97	53.7	98.6	98.3

Note: The relative operating characteristic (ROC) score is a measure of potential usefulness of a model and is graded between 0 and 1, with 1 indicating a perfect model. The true skill statistic (TSS) measures the accuracy of the model by calculating the difference between sensitivity and specificity of the model, with scores closer to 1 suggesting that the model is better at discriminating between presence and absence points given the cut-off value. Cut-off values allow us to split the results into a binary response of either 'suitable' or 'unsuitable' and correspond with the level at which the model has determined for maximum specificity and sensitivity to be achieved. *Specificity* is a measure of correctly predicted absences, and *sensitivity* represents a measure of correctly predicted presences.

Abbreviation: SDM, species distribution model.

SSP1 2.6 corresponds to low radiative forcing conditions, mitigated to 2.6 W/m^2 by 2100. Whilst suitable growth conditions decline from the present-day in southern Africa for *O. ficus-indica* (Figure 1), suitable land area continent-wide is projected to increase by 13% to 1.74 billion ha (Table 5). In contrast, the SSP2 4.5 'middle

of the road' scenario sees a marked reduction in suitable land area for *O. ficus-indica* by 19% to 1.24 billion ha. Finally, with higher radiative forcing profiles under extensive fossil fuel use, SSP3 7.0 and SSP5 8.5 show the greatest reduction in suitable land area—up to 40% less than present-day for *O. ficus-indica* under the most

	Suitable land area (billion ha)				
	Current	2081–2100			
		SSP1 2.6	SSP2 4.5	SSP3 7.0	SSP5 8.5
<i>Opuntia ficus-indica</i> (55)	1.54	1.74	1.24	1.09	0.93
<i>Euphorbia tirucalli</i> (60)	1.74	1.77	1.80	1.83	1.85
<i>Portulacaria afra</i> (54)	0.33	0.24	0.18	0.13	0.09

Abbreviation: SSP, Shared Socioeconomic Pathway.

TABLE 6 Normalised variable importance scores for the three species.

	Variable importance metrics			
	Mean diurnal temperature range (%)	Minimum temperature of coldest month (%)	Annual precipitation (%)	Precipitation seasonality (%)
<i>Opuntia ficus-indica</i>	1	72	22	5
<i>Euphorbia tirucalli</i>	2	74	23	1
	Temperature seasonality (%)	Mean temperature of coldest quarter (%)	Precipitation of wettest month (%)	
<i>Portulacaria afra</i>	50	32	18	

extreme projections. Projections of suitable area for *E. tirucalli* vary comparatively little across the different SSP trajectories: distributions show slight increases in land suitability estimates with higher radiative forcing, up to 1.85 billion ha under the SSP5 8.5 scenario, or a 6% increase relative to current projections (Figure 1). Projected distributions of *P. afra* are much more restricted than for both *O. ficus-indica* and *E. tirucalli*, being largely confined to southern Africa, with small areas of suitability suggested around the coastline of the Mediterranean basin, and decreasing significantly from 0.33 to 0.09 billion ha (a decline of 73%) under the most extreme scenario by end of century (Figure 1).

3.2 | Variable importance and species-climate relationships

The variable of greatest importance in explaining differences in the potential distribution of *O. ficus-indica* and *E. tirucalli* is the minimum temperature of the coldest month (Bio6), followed by annual precipitation (Bio12), precipitation seasonality (Bio15) and mean diurnal temperature range (Bio2). By contrast, temperature seasonality (Bio4) is identified as the most important variable in determining the potential distribution of *P. afra*,

TABLE 5 Land suitability estimates by species across Africa for current projections and each of the four SSPs according to binary cut-off statistics (indicated in parentheses for each species) and ecophysiological requirements as suggested by the restricted bioclimatic parameters.

followed by mean temperature of the coldest quarter (Bio11) and precipitation of the wettest month (Bio13; Table 6).

3.2.1 | Two-dimension response curve results

Response curves show the probability of species occurrence relative to the value of the individual environmental predictors (Figures 2 and 3) and illustrate the underlying relationships that contribute to the results shown in Table 6. The response curves give insight into the relationship between the individual species and the climatic parameters, suggesting threshold values of significance and windows of opportunity where species are found.

Both *O. ficus-indica* and *E. tirucalli* (Figure 2) demonstrate strong positive relationships between the probability of occurrence and minimum temperature of coldest month. However, the response curves show that this sharp change in probability occurs at slightly different temperature thresholds for the two species, with an increase in *O. ficus-indica* growth noted above -1°C , whilst *E. tirucalli* is limited to minimum temperatures above 0°C . On an individual parameter basis, a muted response (<0.1) between species occurrence and

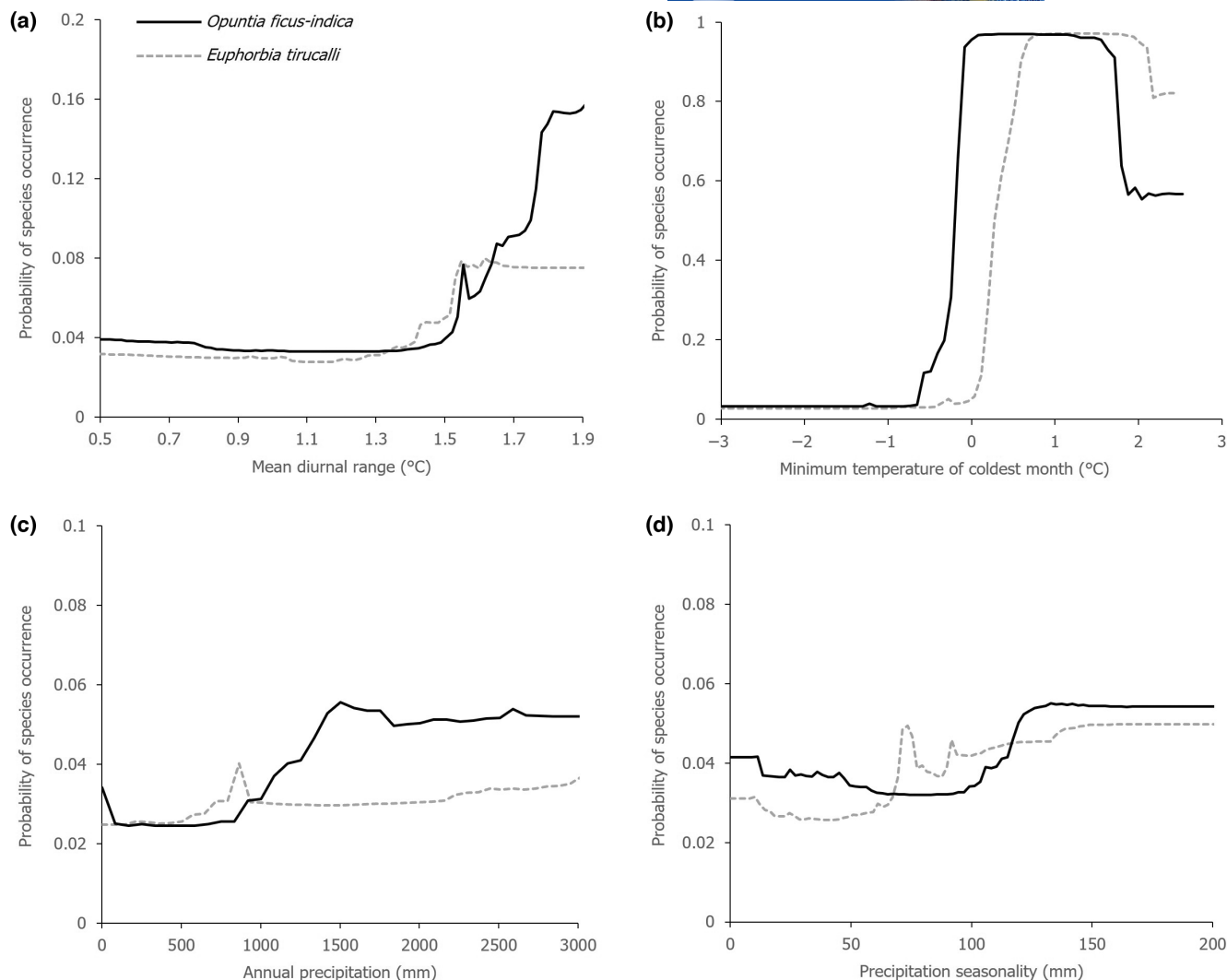


FIGURE 2 Response curves for individual climatic variables for *Opuntia ficus-indica* (black) and *Euphorbia tirucalli* (grey dashed). Each graph plots the probability of species occurrence relative to values for the four bioclimatic variables modelled: (a) mean diurnal range (°C), (b) minimum temperature of coldest month (°C), (c) annual precipitation (mm) and (d) precipitation seasonality (mm).

different values for the other three climatic conditions is seen for these two species, albeit a positive relationship between mean diurnal temperature range and *O. ficus-indica* occurrence is observed.

The response curves for *P. afra* (Figure 3) relative to the environmental variables are complex, suggesting that: (i) the number of occurrences on which the model was trained is relatively small and the relationship is not well defined; (ii) the relationship with these variables is complex and multidimensional; or (iii) a degree of overfitting is seen in the model and algorithms used (Wenger & Olden, 2012). When the probability of *P. afra* occurrence is modelled against temperature seasonality, there is a sharp decline in the likelihood of occurrence of the species with increasing temperature variability. The relationship with mean temperature of the coldest quarter is similar to the relationship found for the other two CAM species with regards

to low temperature, with a clear threshold below which the species cannot exist (approximately 1°C). Finally, the relationship with precipitation of wettest month, which according to the initial variable importance analysis was the third most important in describing the distribution of *P. afra*, shows a muted response and influence on the likelihood of the species occurring. A gradual increase in the probability of species occurrence is seen with increase in precipitation of wettest month, but the influence of this variable is low.

3.2.2 | Three-dimension response curve results

Multidimensional response curves demonstrate the occurrence probability of each species when two

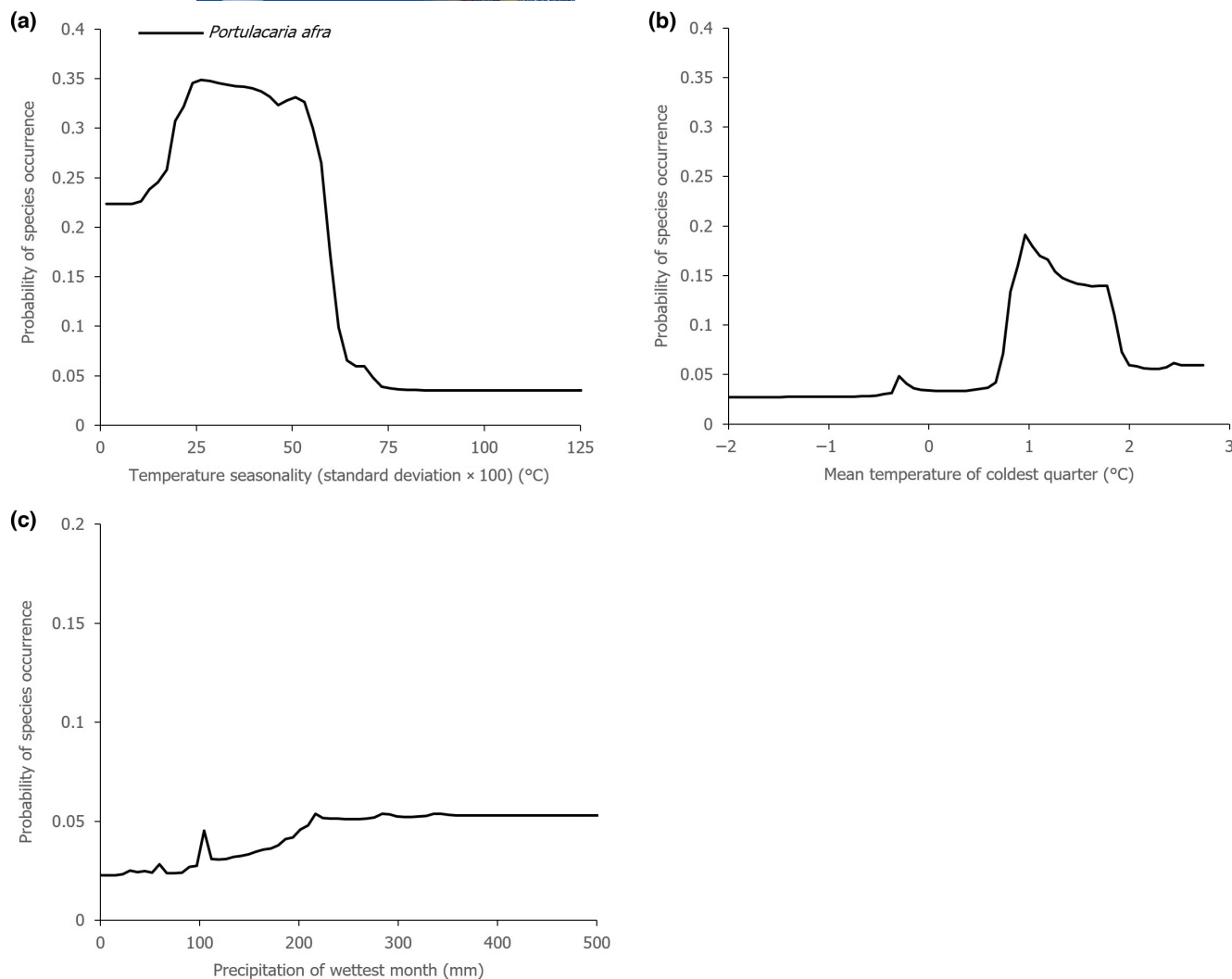


FIGURE 3 Response curves for individual climatic variables for *Portulacaria afra*. Each graph plots the probability of species occurrence relative to different levels of the three bioclimatic variables modelled: (a) temperature seasonality (°C), (b) mean temperature of coldest quarter (°C) and (c) precipitation of wettest month (mm).

environmental factors vary, highlighting the range of niche spaces suitable for growth (see [Supporting Information](#)). When plotted against mean diurnal temperature range, the region of high *O. ficus-indica* occurrence likelihood occurs across a wide range of mean diurnal temperature environments but remains constrained by the minimum cold temperature threshold ([Figure S1](#)). When viewed against annual precipitation levels, we see a threshold level of minimum precipitation (approximately 200 mm), and again the likelihood of occurrence is constrained within the bounds of the minimum coldest temperature ([Figure S1](#)). Finally, a slightly more complex relationship emerges between the combined effects of minimum coldest temperature and precipitation seasonality. A region of highest probability of occurrence is found between 0 and 18°C minimum temperature and with relatively low-to-moderate

degrees of precipitation seasonality. With increased precipitation seasonality, we see a narrowing of the feasible band of minimum cold temperatures within which *O. ficus-indica* could grow—that is, in regions where the precipitation seasonality is higher, in order to retain a level of suitability for *O. ficus-indica* growth, the minimum cold temperature value is more restricted to between 0 and 10°C. The results show that regions of likely suitability are also found when an increase in the minimum cold temperatures (i.e. in regions that are marginally warmer) is combined with a reduction in precipitation seasonality, that is less variable rainfall patterns.

The multidimensional response curves for *E. tirucalli* show similar patterns to those noted for *O. ficus-indica*, but subtle differences and variations in threshold values in the climatic variables explain the difference in

projected distributions seen between the two species (Figure S1). Whilst variable importance scores (Table 6) present similar relative importance of the bioclimatic variables for *E. tirucalli* and *O. ficus-indica*, the projected distributions of their potential niches are different (Figure 1). The detailed results from the response curve analysis demonstrate that whilst the individual variables may have comparable importance on the distribution of these two species, the biological relationship is slightly different with individual thresholds within the variables affecting the likelihood of occurrence for these two species. Across the three multidimensional response curves for *P. afra*, the region of greatest likelihood of species

occurrence occurs where the mean temperature of the coldest quarter is between 6 and 20°C and the overall variability in temperature (temperature seasonality) is low to moderate.

3.3 | Available land

Results from the combined potential future *available* and *suitable* land analysis are shown in Figures 4–7, identifying regions where SDM projections for the three species coincide with each of the different available land metrics across the African continent (Table 7).

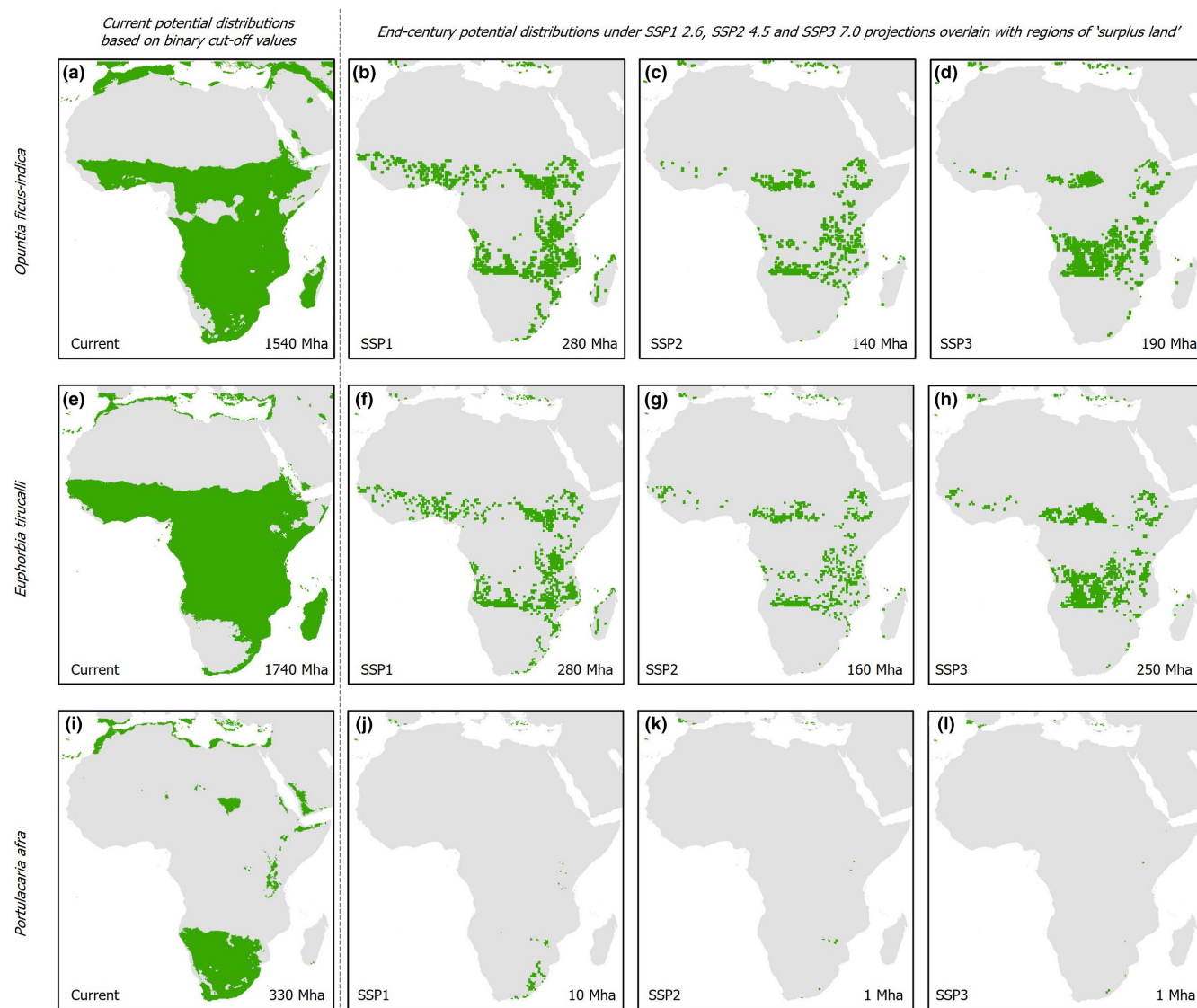


FIGURE 4 Potential current and future distribution maps per species according to binary output and 'available' regions defined by 2100 projections shown in Daioglou et al. (2019). Total areas are shown in Mha in the bottom right-hand corner of each panel. Panels in the first column (a, e, i) show the binary output of ecophysiologically suitable regions for each of the respective species under current conditions, prior to overlay with the 'available' land projections for each of the SSP1 (b, f, j), SSP2 (c, g, k) and SSP3 (d, h, l) scenarios by 2100.

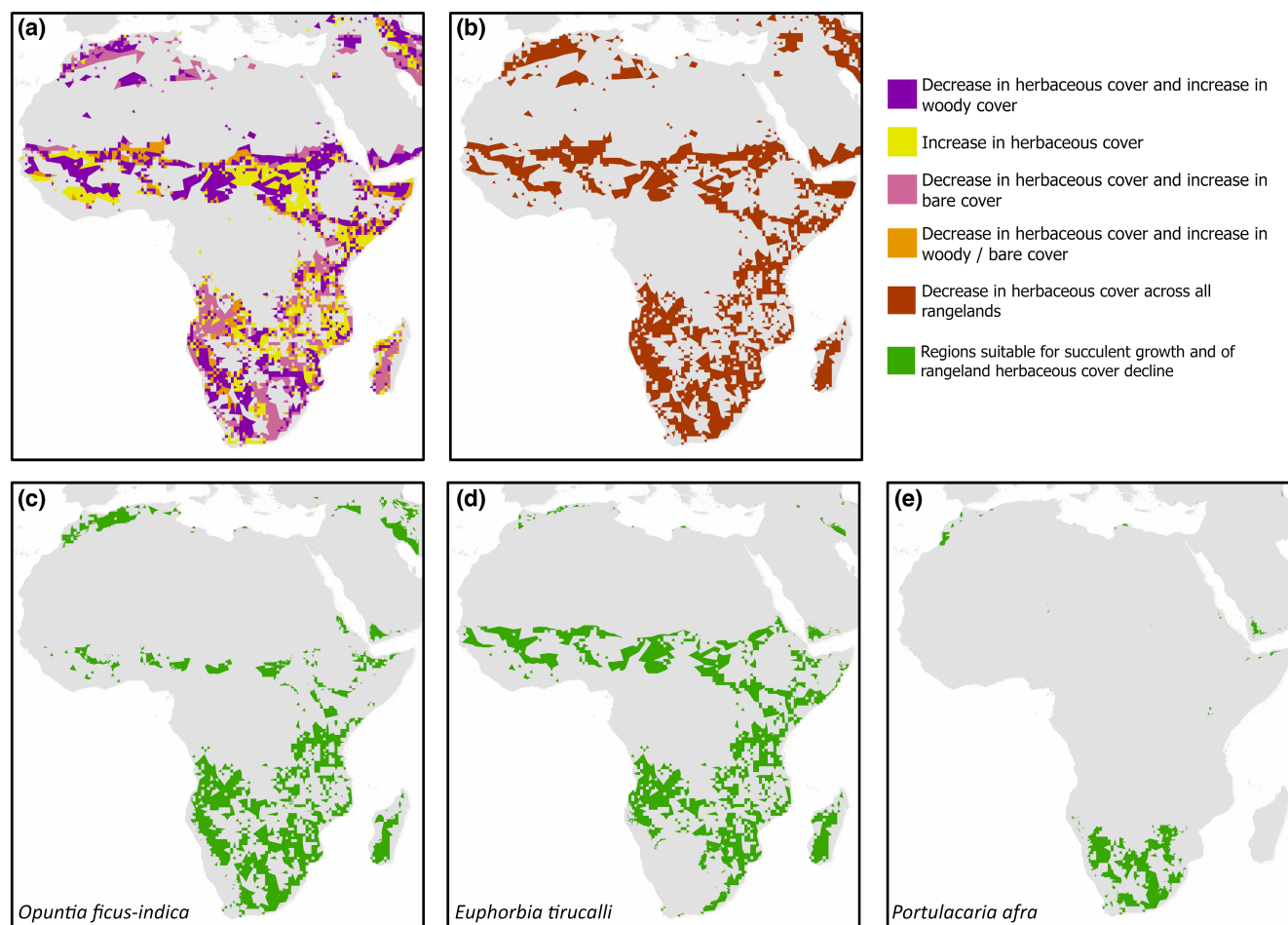


FIGURE 5 Upper: Projections adapted from Godde et al. (2020) showing trends in herbaceous cover between 2000 and 2050 as projected by G-range: (a) under four classifications in relation to changes in herbaceous biomass cover, woody encroachment and bare ground and presented in relation to changes in woody and bare ground cover; and (b) all regions projected to experience a decline in herbaceous biomass cover by 2050 under SSP5 8.5. Lower: Areas projected to be suitable for (c) *Opuntia ficus-indica*, (d) *Euphorbia tirucalli* or (e) *Portulacaria afra* production taken from Figure 1 and overlapping with rangelands projected to decrease in herbaceous biomass as noted above.

3.4 | Surplus land for biomass production

Using the IMAGE 3.0 model, Daioglou et al. (2019) identified surplus lands available for biomass production by 2050 and 2100 under three different SSP scenarios (Doelman et al., 2018), with surplus lands being defined as those that are either abandoned agricultural lands or other natural habitats (e.g. grasslands, savanna) considered noneconomically active. The three scenarios follow separate socio-economic development pathways (SSP1, SSP2 and SSP3), capturing varying land and energy use globally. Once land has been allocated for agricultural production, biodiversity protection and alternative land uses (i.e. urban, forests, projected agricultural lands and protected reserves), the remaining lands available were assessed for biomass production. Some regions were removed for biophysical reasons (steep slopes, permafrost and wetlands) and nature conservation, with Daioglou

et al. (2019) summarising that the potential land for biomass could amount to 0.987, 0.480 and 0.435 billion ha globally for the three SSPs, respectively, by 2100.

Using these mapped estimates, we separately combined each of the projected binary outputs (i.e. as determined by the cut-off values) of *O. ficus-indica*, *E. tirucalli* and *P. afra* for SSP1 2.6, SSP2 4.5 and SSP3 7.0 in the period 2081–2100 to identify zones of congruence across Africa (Figure 4) and project revised suitable and potentially available land area estimates (Table 7). Whilst estimates demonstrated a general decrease in land suitability from SSP1 2.6 to SSP2 4.5 to SSP3 7.0 (Table 5), when combined in Figure 4 we see a decrease between SSP1 2.6 and SSP2 4.5, but an increase in the SSP3 7.0 scenario projections of potentially available land for *O. ficus-indica* and *E. tirucalli* (Table 7). Although climatic conditions reduced the suitable land area available, the estimates across Africa are greater under SSP3 which anticipates larger areas of available natural lands in

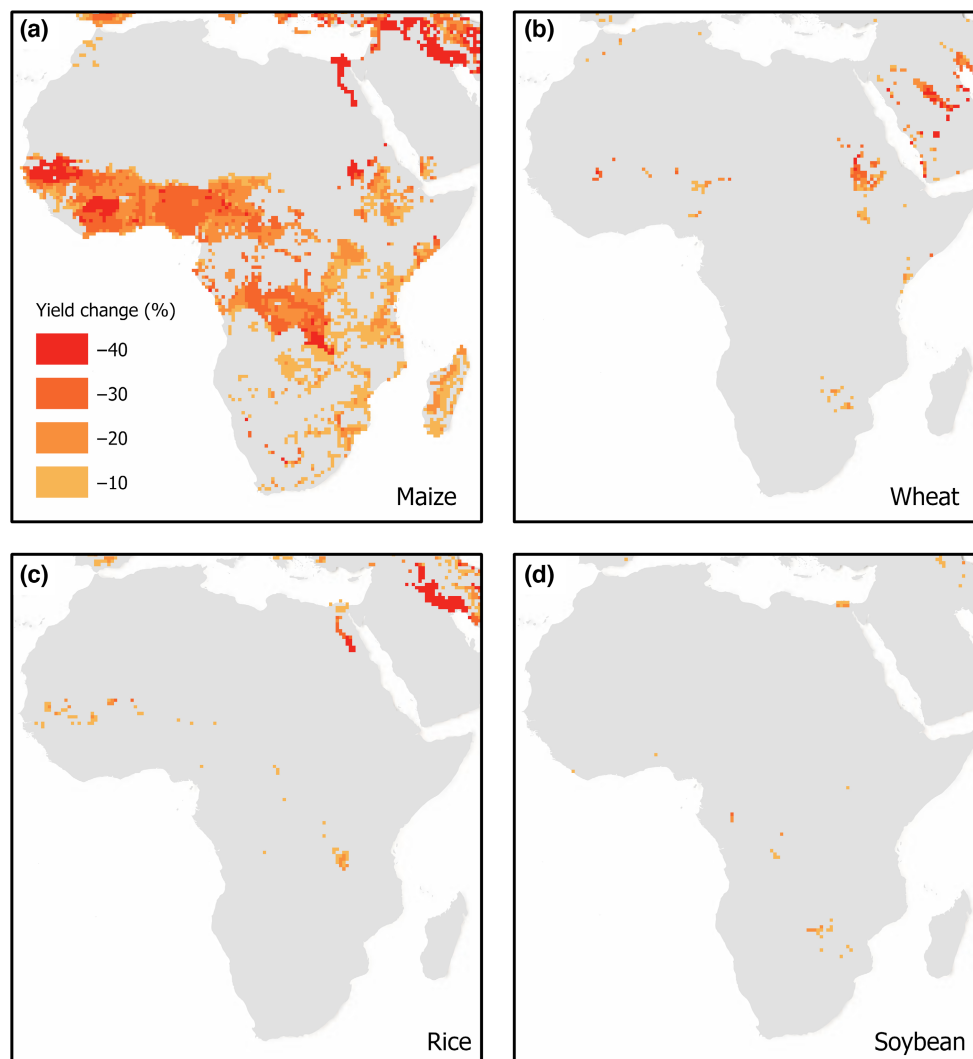


FIGURE 6 Mean yield changes by 2081–2099 for (a) maize, (b) wheat, (c) rice and (d) soybean for regions anticipated to experience a greater than 10% decrease in yield in current growing regions (>10 ha) relative to 1983–2013. Data sourced from Jägermeyr et al. (2021).

Tanzania, Angola and Zambia—the three countries combined accounting for 33%–57% of the *O. ficus-indica* available land estimates across the three SSPs (see [Supporting Information](#)). South Africa, Kenya and Zimbabwe overall accounted for the greatest suitable and available areas for *P. afra* cultivation under the three SSPs.

3.5 | Succulent production versus rangeland use

Godde et al. (2020) have characterised projected vegetation trends to identify the extent and magnitude of climate change impacts on global rangelands, focussing specifically on herbaceous biomass because of its importance for forage supply in livestock farming. Whilst inter- and intra-annual variability on herbaceous biomass cover is

projected to increase, the overall mean herbaceous biomass is predicted to decrease by 4.7% under the SSP5 8.5 climate projection, with 74% of global rangelands expected to experience some level of herbaceous biomass decline and an increase in woody cover or bare ground (Godde et al., 2020). Overlaying areas across Africa that are expected to experience some level of herbaceous biomass decline, with the projections for the three species suitability under RCP 8.5 projections by 2050, [Figure 5](#) identifies regions where each of the three succulents could be cultivated in place of declining herbaceous biomass and thus livestock systems.

Overall, declines in herbaceous biomass on existing rangelands across Africa represent a greater area than available areas identified according to the ‘surplus land’ projections of [Figure 4](#). This highlights the impending vulnerability of pastoral livelihoods with anticipated

climate change across the continent. Given the wide-ranging suitability of conditions for the three species, areas where succulent cultivation could successfully

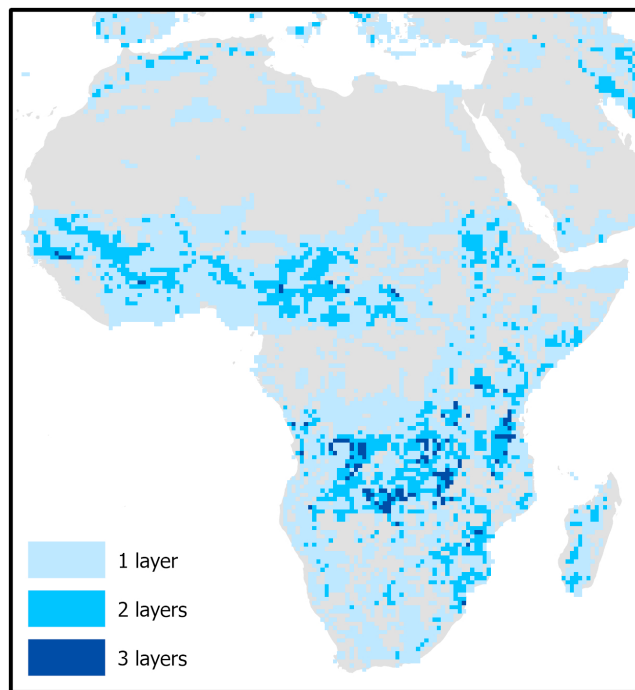


FIGURE 7 Map showing areas available for cultivation of succulents, graded by zones of overlap between the three layers of land availability: (i) areas with surplus land according to SSP3 2100 projections from Daioglou et al. (2019); (ii) areas anticipated to experience decrease in herbaceous biomass by 2050 according to Godde et al. (2020); and (iii) areas with more than 10% decline in yields of four major crop species by 2081–2099. Areas are colour-coded according to one layer (light blue), two layers (mid-blue) and three layers (dark blue) of land availability with darker colours representing hotspots of opportunity where multiple land availability metrics suggest potential suitability for land-use repurposing for succulent cultivation.

TABLE 7 Projected future available and ecophysiologicaly suitable land estimates according to three different lenses of ‘available land’ or land that could be considered for alternate crop cultivation.

	Suitable land area (billion ha)				
	‘Surplus land’ ^a			Rangelands ^b	Reduced yield maize ^c
	SSP 1 (2100)	SSP 2 (2100)	SSP 3 (2100)	SSP5 8.5 (2050)	SSP5 8.5 (2081–2099)
<i>Opuntia ficus-indica</i>	0.28	0.14	0.19	0.47	0.35
<i>Euphorbia tirucalli</i>	0.28	0.16	0.25	0.56	0.84
<i>Portulacaria afra</i>	0.01	0.001	0.001	0.10	0.01

Note: Estimates are reported in billion hectares and refer only to the African continent.

^aBased on the definition of ‘lands available for biomass production’ as calculated in Daioglou et al. (2019).

^bBased on rangelands considered under climatic risk and likely to experience declines in herbaceous biomass according to Godde et al. (2020).

^cRefers to the regions calculated from AgMIP projections (Jägermeyr et al., 2021) as anticipated to have >10% reduction in maize yields and which could be considered suitable candidate regions for trialling alternate succulent crops.

Abbreviation: SSP, Shared Socioeconomic Pathway.

replace pastoralism are found throughout Africa, except for central and Saharan regions. Approximately 0.47 and 0.56 billion ha of overlapping zones are identified for *O. ficus-indica* and *E. tirucalli*, respectively, with a considerably smaller estimate for *P. afra* of ca. 0.1 billion ha restricted to southern Africa, where it is currently found. Key countries with potentially large regions of anticipated herbaceous declines include Angola, Tanzania, Mozambique and South Africa, together equating to 0.21 billion ha of rangeland.

3.6 | Succulents in place of declining major crop yields

Projections from the AgMIP Global Gridded Crop Model Intercomparison (GGCMI) project Phase 3 of likely climate-related impacts on four major future crop yields indicate that major food-producing regions face substantial anthropogenic climatic risks within the near future (10–20 years; Jägermeyr et al., 2021). Not least are these results of major societal concern regarding global food supplies, but they will also directly impact sustainable agricultural livelihoods and economies in these regions.

We focus specifically on potential regions under the highest emission scenario (SSP5 8.5) that are anticipated to experience century-end yield declines in crop yields in excess of 10% relative to 1983–2013. Results show the vast majority of yield declines will be in the maize-producing zones of central, eastern and south-eastern Africa (Figure 6). Individual pockets of significant decline are anticipated for the other major crops (soy, rice and wheat), but relative to the impact on maize, are smaller and more fragmented. In comparison with previous projections from GGCMI-CMIP5 (Rosenzweig et al., 2014), projected

maize losses are higher in the updated GGCM-IP6 projections (Jägermeyr et al., 2021), explained by a higher warming sensitivity of the crop models, a lower compensating effect from CO₂ fertilisation and higher degree of warming projected in CMIP6. Comprising approximately 0.89 billion ha (Figure 6—maize), the areas of greatest yield decline could be considered for alternative crop cultivation by the end of the century.

3.7 | Hotspots of opportunity

Aside from the widescale opportunities highlighted for succulent cultivation and biomass production, our results identify a number of regions that could be considered ‘hotspots of opportunity’, where succulents could succeed in broad regions where multiple metrics of land availability or repurposing coincide with ecophysiological suitability (Figure 7). Angola, Malawi, Mozambique, Tanzania and Zambia in particular, all have large rangeland areas that by 2100 could be experiencing significant land-use pressures due to climate change effects, where succulent cultivation could present a future-proof desirable alternative.

4 | DISCUSSION

Whilst strategies for combating the impacts of global warming are widely discussed in the literature, comparatively little consideration is given to the most *efficient* use of land and the need for adaptation to future climate change through repurposing and alternative land uses. The main results from our study show that potentially large regions of SSA are anticipated to experience significant challenges under future climates whilst continuing with current agricultural practices, and an exploration of alternative crops is warranted. Rangeland biomass projections suggest areas with a decrease in herbaceous cover are anticipated to be greater than areas with herbaceous cover increase under SSP5 8.5 by 2050—suggesting future pressures on livestock supply without significant changes in practices and technologies under the most extreme climate scenarios. Likewise, declines in the yields of major crops, such as maize, are anticipated to follow future climate and agricultural projections, with ramifications for feed and food supply chains.

Results from correlative species distribution modelling demonstrate the relationship between specific bioclimatic variables and known occurrences of the species, allowing us to predict the current and future theoretical regions of ecophysiological suitability. *O. ficus-indica* estimates are

larger than those produced using climatic envelope methods (e.g. Louhaichi et al., 2015), capturing the range of conditions that the model identifies as suitable based on the current distribution of the species. *E. tirucalli* and *P. afra* distributions have not been widely projected in the literature, despite existing studies commenting on their biofuel potential (Borland et al., 2009, 2014; Hastilestari et al., 2013), and the results from this study concur with existing occurrences and noted in the literature, suggesting a wider region where potentially these species could grow in the absence of nonclimatic limitations.

Our findings show the potential regions supporting the ecophysiological requirements of these perennial species are wide-ranging and fluctuate in response to future climates, but are largely resilient and potentially thus sustainable. Demonstrating both the long-term and wide-ranging capacity for these plants to grow is essential in considering their viability as alternatives to traditional crops, either replacing stressed agricultural practices or capitalising on abandoned land. Whilst our results suggest that maize yield and current herbaceous biomass levels will decline over the coming century, the SDM results for *O. ficus-indica* and *E. tirucalli* in particular—which are primarily limited in their distribution by their susceptibility to minimum cold temperatures—show little variation in theoretically suitable regions over the coming decades. Despite the models being trained relative to the same bioclimatic variables, differences in the distribution of *O. ficus-indica* and *E. tirucalli* are driven by specie-specific sensitivities to the individual variables, as shown in Figure 2. For example, whilst minimum temperature is the strongest limiting factor on both species' distribution, the two species have slightly different temperature thresholds, and *O. ficus-indica* also demonstrates marginally greater sensitivity to increasing mean diurnal temperature ranges and levels of annual precipitation. These subtle variations in the sensitivity to individual parameters explain the difference in current projected potential distribution and how future zones of ecophysiological suitability will change by the end of the century (Figure 1). On the contrary, the results suggested a relatively limited potential zone of ecophysiological suitability for *P. afra*—restricted to southern Africa, and declining sharply with climatic changes by 2100. This limited distribution could be a reflection of the genuinely restricted spatial potential of *P. afra* because of ecophysiological requirements, or it could be an artefact of a relatively small and less geographically distributed training dataset. Unlike the wide distribution of the *O. ficus-indica* and *E. tirucalli* occurrence datasets, the *P. afra* training data are more

limited, preventing the model from identifying the full range of potential bioclimatic zones in which the plant could grow successfully in the absence of nonclimatically limiting factors (i.e. distributional limitations).

In total however, across the three species, land suitability estimates suggest that >1.8 billion ha across Africa could be suitable for the growth of succulent plants, revised downward to approximately 1.5 billion ha when considered under different 'available' land measures. This estimate is greater than those in the earlier literature (Buckland & Thomas, 2021; Gibbs & Salmon, 2015) which were premised on various definitions of degraded and abandoned land only, as opposed to considering the potential for repurposing land which may become less efficient under current land uses. However, given the spatial resolution of the datasets used, it is unlikely that entire grid cells will be suitable for repurposing, so 1.5 billion ha should be considered the upper estimate of potentially available land accessible to succulent plants.

Likewise, whilst this study has identified hotspots of opportunity based on overlapping regions of either future available land and/or regions with unsustainable agriculture, the relatively low resolution of the underlying datasets means that some areas are perhaps overlapping due to duplication of grid cells that are only partially covered with either land use. Regional- and local-scale analyses with higher resolution datasets of areal estimates per land use would better approximate at the local scale the specific regions of focus for succulent-based alternatives.

Combined with the indicative results for both current and future distribution maps for these species, our findings suggest there is unexplored potential for succulent plants to be cultivated as an alternative crop, capitalising on their high water-use efficiency and an ability to withstand harsh climatic conditions. Regional hotspots of opportunity at the continent scale where multiple available land metrics overlap have served to identify specific countries of interest for which a CAM-based future could be considered valuable in the face of changing climates and increased energy demands, particularly in parts of southern and eastern Africa.

4.1 | Implications

Our findings present opportunities to diversify agricultural livelihoods across Africa, in addition to tackling global climate, localised land degradation and socio-economic challenges. Aside from the potential benefits of cleaner bioenergy production from plant biomass, succulent plantations in arid and semiarid regions could provide much needed income diversification in agriculturally

marginalised areas and those dominated by smallholder pastoralism (Nefzaoui et al., 2014). Integrating the results from the SDM analysis with the challenges faced by livestock farming provides a view on the potential benefits that a new succulent-based bioeconomy could deliver. In particular, Angola, Tanzania and Mozambique, which showed large areas of theoretically suitable land for succulent cultivation and projected levels of rangeland under threat from biomass decline, have all scored highly as regards livestock-related vulnerability factors (Godde et al., 2021).

Local and regional land restoration can also be advanced through stabilising exposed soils that have been degraded and depleted of natural vegetation in recent years. Existing studies have highlighted the capacity of succulents, such as *O. ficus-indica*, to grow in harsh and challenging environments, with their roots improving and rehabilitating wind- and rain-eroded soils (Louhaichi et al., 2017; Nefzaoui et al., 2011, 2014; Nefzaoui & el Mourid, 2009). Thus, the potential for establishing succulent-based cultivation could diversify and stabilise both environments and local economies that are precariously exposed to the shocks of livestock farming, as well as contributing to bio-based industries such as nongridded energy (biogas) supplies in rural communities (Buckland & Thomas, 2021).

Nevertheless, there is a need to develop markets for the range of end-products that can be derived from such bio-based industries, as well as individual economic feasibility studies for individual regions. For example, the projections of growth suitability shown in our results do not necessarily map onto the same distribution of anticipated yield and productivity for each species. For example, Neupane et al. (2021) showed that there are large variations in the productivity potential of *Opuntia* spp. depending on whether cultivation takes place under rain-fed circumstances (3–15 dry matter tonnes [DMT] ha⁻¹; Mason et al., 2015; Sánchez et al., 2012; Santos et al., 2016) or under irrigated conditions (40–50 DMT ha⁻¹; Dubeux et al., 2006; Flores-Hernández et al., 2004; Guevara et al., 2009; Mason et al., 2015; Nobel, 1991, 1996; Nobel et al., 1992; Nobel & García de Cortázar, 1991; Reis et al., 2018) and even higher yields of >65 DMT have been observed with additional fertiliser treatments in eastern Brazil (Suassuna, 2008). Thus, an assessment of localised productivity potential and the impact of varying conditions and precipitation levels on leaf size, cladode size and weight is essential to determine the viability of succulent plantations, especially if seeking to replace other crops that are declining in yields. Equally, whilst declines in traditional crop types *may* lead to current croplands becoming available for alternate succulent cultivation, it is also likely that a series of agronomic interventions (e.g. Krishna

et al., 2021) would be explored and implemented under current crop types prior to replacing existing agricultural systems with an entirely new succulent-based alternative. The crop yield projections reported in Jägermeyr et al. (2021) do not currently include adaptation measures, so real-world declines in yields may be smaller than those used above.

Equally, we need to be cognisant of potential conflicts in suggesting that regions with declining yields in major food crops could be repurposed and cultivated for new crops, which may or may not be used for food production. Whilst results suggest that some major maize-producing regions are likely to experience drastic declines in yields in the coming decades, replacing them with an alternate crop may alleviate land degradation and provide sustainable energy, but would not address the impending food crisis if it is not a viable alternative for human consumption, with the same calorific and nutritional benefits. Globally, the FAO note that only 13% of maize production is used for human food consumption (FAOSTAT, 2022), but this is not replicated in SSA where almost two-thirds of produced maize is grown for human consumption (Erenstein et al., 2022; Santpoort, 2020). Maize-dependent smallholders in SSA are typically highly vulnerable to multiple environmental changes (Bedeke et al., 2019), as the majority rely on rain-fed systems and are located on degraded lands with poor soil fertility (Adimassu et al., 2014; Grote et al., 2021). Aside from the climate-induced impacts on future maize production, other factors such as disease, infestations and high fertiliser prices are also projected to result in lower maize productions in the coming years (Mtaki & Snyder, 2022). Although it is known that some succulent species are palatable to livestock and could be used as a replacement for feed, determining the calorific equivalent with current food streams for either livestock or humans is yet to be fully investigated.

On the contrary, with improvements in appropriate technologies and agricultural intensification, any land released from traditional cropping practices could result in *more* opportunities for combined harvesting of major traditional crop and succulent species. In sum, whilst this study has suggested opportunities, regions and the future potential of alternative production systems, detailed region-specific analyses will be needed to determine their viability alongside addressing local food, feed and fuel requirements.

Lastly, the cultivation of succulents could aid with global climate mitigation targets in both direct and indirect capacities, through: (i) carbon sequestration and the drawdown of CO₂ (Inglese et al., 2017) and (ii) diversion away from carbon-intensive fossil fuel energy sources and increased efficiency in the way in which land is used

(Searchinger et al., 2018). The greater water-use efficiency of succulents relative to C₃ or C₄ plants is primarily due to the CAM photosynthetic pathway, which is more efficient in converting available water and CO₂ to plant dry matter (Han & Felker, 1997; Nobel, 1991, 1994, 2009), with biomass generation per unit of water approximately 5–10 times higher than in C₃ and C₄ species (Alary et al., 2007; Borland et al., 2009). Given their adaptations to arid and semiarid conditions, CAM cultivations could operate as carbon sinks, especially in locations where precipitation is low and unable to support other crops (Osmond et al., 2008). This being said, due to the invasive nature of some CAM species, cultivation would need to be combined with appropriate management practices (e.g. bio-control agents, adoption of sterile lines and spineless varieties) in order for their usage to be widely considered without impacting on local biodiversity.

5 | CONCLUSION

For at least one, if not two, succulent species of interest, SDMs have shown continent scale (other than Sahara/Sahel regions) viability of growth under both current and CMIP6 end-century climate projections. Whilst the widespread species *O. ficus-indica* and *E. tirucalli* show greatest land suitability estimates, the native *P. afra* also shows potential to be grown in regions predicted to be less suitable for the others in southern Africa. Scrutiny of current land-use and agricultural practices highlight potentially high levels of unsustainability in both livestock farming and traditional crop cultivation under mid- and end-century climate projections. Future climate projections indicate a complex matrix whereby future climates may lead to the potential distribution of a succulent species to increase, yet also limit the land available due to land-use changes and food demands.

Coarse-scale land suitability estimates suggest potentially >1.8 billion ha of land to be suitable for the growth of succulent plants across the continent, revised downwards to approximately 1.5 billion ha when considered in terms of different assessments of *available* land. Hotspots of coarse-scale opportunity identify specific countries of interest for which a succulent-based future could be considered viable in the face of changing climates, challenged agricultural systems and greater levels of land degradation. These findings present opportunities for economic and agricultural diversification and the potential capacity to generate scalable bioenergy resources for off-grid rural communities lacking access to electricity (IEA, 2019). Future research should also look to explore the potential yields of understudied native species of

succulent plants, which may find greater acceptance at regional level compared with non-native species, as well as considering other productive synergies in tackling Sustainable Development Goals in the most vulnerable dryland communities.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the [Supporting Information](#) of this article and can be downloaded from the DRYAD data repository: <https://doi.org/10.5061/dryad.8sf7m0cv8>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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