

CONTRIBUTED PAPERS

Combined impacts of future climate-driven vegetation changes and socioeconomic pressures on protected areas in Africa

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Abstract

Africa's protected areas (PAs) are the last stronghold of the continent's unique biodiversity, but they appear increasingly threatened by climate change, substantial human population growth, and land-use change. Conservation planning is challenged by uncertainty about how strongly and where these drivers will interact over the next few decades. We investigated the combined future impacts of climate-driven vegetation changes inside African PAs and human population densities and land use in their surroundings for 2 scenarios until the end of the 21st century. We used the following 2 combinations of the shared socioeconomic pathways (SSPs) and representative greenhouse gas concentration pathways (RCPs): the “middle-of-the-road” scenario SSP2–RCP4.5 and the resource-intensive “fossil-fueled development” scenario SSP5–RCP8.5. Climate change impacts on tree cover and biome type (i.e., desert, grassland, savanna, and forest) were simulated with the adaptive dynamic global vegetation model (aDGVM). Under both scenarios, most PAs were adversely affected by at least 1 of the drivers, but the co-occurrence of drivers was largely region and scenario specific. The aDGVM projections suggest considerable climate-driven tree cover increases in PAs in today's grasslands and savannas. For PAs in West Africa, the analyses revealed climate-driven vegetation changes combined with hotspots of high future population and land-use pressure. Except for many PAs in North Africa, future decreases in population and land-use pressures were rare. At the continental scale, SSP5–RCP8.5 led to higher climate-driven changes in tree cover and higher land-use pressure, whereas SSP2–RCP4.5 was characterized by higher future population pressure. Both SSP–RCP scenarios implied increasing challenges for conserving Africa's biodiversity in PAs. Our findings underline the importance of developing and implementing region-specific conservation responses. Strong mitigation of future climate change and equitable development scenarios would reduce ecosystem impacts and sustain the effectiveness of conservation in Africa.

KEYWORDS

aDGVM, global change, grassland, human population, land use, RCP, savanna, SSP

Resumen

Las áreas protegidas (AP) de África son el último bastión de la biodiversidad distintiva del continente, pero cada vez están más amenazadas por el cambio climático, crecimiento sustancial de la población humana y cambio de uso de suelo. La planificación de la conservación enfrenta el reto de la incertidumbre de cuan fuerte y donde interactuarán estos factores a lo largo de las siguientes décadas. Investigamos los impactos futuros combinados de los cambios en la vegetación impulsados por el clima dentro de AP africanas y

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las densidades de población humana y el uso de suelo en sus alrededores en 2 escenarios hasta el final del siglo 21. Utilizamos las siguientes 2 combinaciones de las trayectorias socioeconómicas compartidas (SSP) y las trayectorias representativas de concentración de gases de invernadero (RCP): el escenario de “mitad del camino” SSP2-RCP4.5 y el escenario recurso intensivo “desarrollo impulsado por combustibles fósiles” SSP5-RCP8.5. Los impactos del cambio climático sobre la cobertura de árboles y el tipo de bioma (i. e., desierto, pastizal, sabana y bosque) fueron simulados con el modelo vegetación global dinámica adaptativo (aDGVM). En ambos escenarios, la mayoría de las AP fueron afectadas adversamente por lo menos por 1 de los factores, pero la coocurrencia de los factores fue mayoritariamente específica por región y escenario. Las proyecciones de MVGDa sugieren incrementos considerables en la cobertura de árboles impulsados por el clima en las AP en pastizales y sabanas actuales. Para AP en África Occidental, los análisis revelaron cambios en la vegetación impulsados por el clima combinados con sitios clave con numerosa población y gran presión de uso de suelo en el futuro. Excepto en muchos PA de África del Norte, los decrementos en la población y presiones de uso de suelo en el futuro fueron raros. A escala continental, SSP5-RCP8.5 condujo a mayores cambios impulsados por el clima en la cobertura arbórea y en la presión de cambio de uso de suelo, mientras que SSP5-RCP8.5 se caracterizó por una mayor presión demográfica en el futuro. Ambos escenarios SSP-RCP implicaron mayores retos para la conservación de la biodiversidad en AP africanas. Nuestros hallazgos subrayan la importancia de desarrollar e implementar respuestas de conservación específicas para cada región. Medidas sólidas para la mitigación del cambio climático así como escenarios de desarrollo equitativo podrían reducir los impactos en el ecosistema y sustentar la efectividad de la conservación en África.

PALABRAS CLAVE

Cambio global, pastizal, población humana, sabana, uso de suelo

【摘要】

非洲的保护区是非洲大陆独特生物多样性的最后堡垒,但它们越来越受到气候变化、人口大幅增长和土地利用变化的威胁。由于不确定在未来几十年内这些驱动因素相互作用的程度和发生位点,保护规划也面临着挑战。本研究分析了至21世纪末的两种情景下,非洲保护区内气候驱动的植被变化以及人口密度和土地利用未来的综合影响。我们使用了以下两种共享社会经济路径(SSPs)和温室气体代表性浓度路径(RCPs)的组合:“中间路线”情景SSP2-RCP4.5和资源密集型的“化石燃料发展”情景SSP5-RCP8.5。我们用适应性动态全球植被模型(aDGVM)模拟了气候变化对树木覆盖和生物群落类型(即沙漠、草原、稀树草原和森林)的影响。在这两种情景下,大多数保护区都受到了至少一种驱动因素的负面影响,但驱动因素是否共同出现,在很大程度上是地区和情景特异的。aDGVM的预测表明,目前在草原和稀树草原的保护区中,气候驱动的树木覆盖率有大幅增加。我们的分析还表明,西非保护区中气候驱动的植被变化与未来高人口和土地利用压力的热点相重合。除了北非的许多保护区外,未来人口和土地利用压力很少会下降。在大陆尺度上,SSP5-RCP8.5会导致较高的气候驱动的树木覆盖变化和较高的土地利用压力,而SSP2-RCP4.5则会引起较高的未来人口压力。两种SSP-RCP情景都意味着非洲保护区内的生物多样性保护面临越来越多的挑战。我们的发现强调了制定和实施针对区域的保护对策的重要性。大力减缓未来气候变化和公平的发展情景将减少对生态系统的影响,并维持非洲保护工作的有效性。【翻译:胡怡思;审校:聂永刚】

关键词: 适应性动态全球植被模型(aDGVM), 全球变化, 草原, 人群, 土地利用, 温室气体代表性浓度路径(RCPs), 热带草原, 共享社会经济路径(SSP)

INTRODUCTION

African protected areas (PAs) are strongholds of Africa's unique biodiversity (Pacifi et al., 2020) and are fundamental to safeguarding it. A proposed key global goal is to protect 30% of

terrestrial area (action target 3, Convention on Biological Diversity [2021]), but there is increasing evidence that under climate change this target may not be ambitious enough to protect biodiversity (Hannah et al., 2020). Even today, PAs and the biodiversity they conserve are increasingly under pressure from

global change drivers such as climate change (Hannah, 2008), human population growth, and land-use change (Geldmann et al., 2014).

Climate-driven vegetation changes in African PAs have already been observed. Woody encroachment into African savannas in PAs has probably at least partly been driven by fertilization effects of increased atmospheric CO₂ on woody plants (Stevens et al., 2017). Changes in tree cover and thus vegetation structure in savanna and forest biomes imply habitat loss and decreased biodiversity (Aleman et al., 2016; Midgley & Bond, 2015), which impairs the potential of PAs for biodiversity conservation under climate change. Under future climate change, dynamic vegetation models (DVMs) have projected woody encroachment into African grasslands and savannas driven by increasing atmospheric CO₂ and its potential effects on plant physiology and vegetation structure (Martens et al., 2021; Scheiter & Higgins, 2009). In dynamic vegetation simulations for areas with at least 50% protected area, only 2% of Africa remains refugia for biodiversity under climate change (Eigenbrod et al., 2015).

At the beginning of the 21st century, human population growth within the perimeters of African PAs was limited (Geldmann et al., 2019). However, until the end of the century, the human population in sub-Saharan Africa is projected to increase substantially, in contrast to all other global regions (United Nations, 2019). Urbanization in the vicinity of PAs is projected to increase more than 8-fold from 2000 to 2030 across Africa, which implies vast, dynamic changes in future socioeconomic pressures on biodiversity and PAs (Güneralp et al., 2017). In the past, agricultural expansion inside African PAs was stronger than in similar unprotected regions (Geldmann et al., 2019). Deforestation, logging, and fire in the immediate vicinity of PAs often drive changes within PAs (e.g., through ecological edge effects and by predisposing the PA to similar land-use-driven changes) (Laurance et al., 2012). In the future, pressure from commercial agriculture in the vicinity of PAs is expected to increase and intensify (DeFries et al., 2007), likely driven by the expected human population growth and socioeconomic developments.

Increased pressure from a combination of drivers such as human population and intensive agriculture on the majority of African PAs has already been reported for the recent past, although pressure was reduced for several other PAs in Africa (Jones et al., 2018). However, there have been few studies on relationships between climate change impacts (e.g., tree-cover changes) and pressure from socioeconomic drivers (e.g., human population density and agricultural and pasture land use) as they relate to African PAs in the future. Asamoah et al. (2021) estimated that by 2050, ~27% of PAs globally are expected to be in areas with large climate and land-use changes. PAs in tropical moist forests and tropical savanna and grassland biomes are expected to be particularly affected (Asamoah et al., 2021). Both land-use and climate change have been projected to continuously drive a decline of African plant biodiversity in the future for most regions and scenarios (Di Marco et al., 2019).

To assess global change pressure on PAs in Africa until the end of the 21st century, we used projections for climate-driven tree-cover change, human population density, and land

use, including urban, agricultural, pasture, and natural land, under 2 shared socioeconomic pathway (SSP) and representative concentration pathway (RCP) marker scenarios (SSP2-RCP4.5 and SSP5-RCP8.5). For each SSP–RCP scenario, we investigated up to the end of the 21st century which PAs and biomes in PAs were projected to be most affected by climate-change-driven vegetation and habitat loss; which PAs were projected to be particularly affected by population and land-use pressure in their surroundings; and whether population and land-use pressures were projected to co-occur with each other and with climate-change-driven vegetation changes. We also investigated whether the global-change scenarios we considered suggest differing strategies for conservation in different PAs in Africa.

The SSP2–RCP4.5 is the “middle-of-the-road” (O’Neill et al., 2017) scenario in which global inequalities in development and income growth continue with some regional improvements and medium climatic changes (Riahi et al., 2017). In SSP5–RCP8.5, rapid economic and social development is driven by fossil fuel exploitation and associated strong climate change and technological development (“fossil-fueled development”) (Kriegler et al., 2017). We simulated climate-driven vegetation changes with the adaptive dynamic global vegetation model (aDGVM) and used projections of population density (Gao, 2019) and land use (Hurtt et al., 2020) and their respective changes in the surroundings of PAs as proxies for future socioeconomic pressures directly or indirectly exerted on PAs.

METHODS

Scenarios

The RCP and SSP scenarios describe alternative future developments of anthropogenic climate change and its drivers. Emissions associated with possible societal development (SSP) are used as input for RCP scenarios. Radiative forcing from RCP scenarios is used as input for climate model projections. The SSP–RCP scenarios that we used in our analysis, SSP2–RCP4.5 and SSP5–RCP8.5, are designated marker scenarios and part of the Scenario Model Intercomparison Project (ScenarioMIP) for phase 6 of the Coupled Model Intercomparison Project (O’Neill et al., 2016).

The selection of scenario combinations was limited to SSP2–RCP4.5 and SSP5–RCP8.5 by the available climate data for vegetation simulations. Under SSP2–RCP4.5, population is projected to increase by ~157% from 2010 until 2100 for Africa (KC & Lutz, 2017). Cropland is expected to expand by ~51% (~154 Mha) and pastures to decrease by ~7% (58 Mha) from 2020 to 2090 in Africa (based on land-use harmonization [LUH2] data) (Hurtt et al., 2020) (see land-use section under “Data sets and data processing” section). Climatic changes are modest to high and mean annual temperature from 2000–2019 to 2080–2099 is projected to increase by 2.0°C at the continental scale in Africa (derived from Engelbrecht et al. [2015] and Martens et al. [2021]) (details below in “aDGVM and simulation design” section).

Under SSP5–RCP8.5, the evolving global energy-intensive lifestyle and associated greenhouse gas emissions lead to strong

climate changes, with mean annual temperature increasing by 4.5°C from 2000–2019 to 2080–2099 in Africa (based on Engelbrecht et al. [2015] and Martens et al. [2021]). Africa's population in 2100 is projected to be 77% higher than in 2010 (KC & Lutz, 2017). Even though population increase for SSP5–RCP8.5 is only about half the increase for SSP2–RCP4.5, the increased food and feed demand of the changed lifestyle (Hurtt et al., 2020) leads to a similar expansion in cropland (~42%, ~131 Mha) and decrease in pastures (~–7%, ~58 Mha, LUH2 data) from 2020 to 2090 in Africa.

aDGVM and simulation design

The aDGVM is a DVM and was originally developed for tropical vegetation and tree–grass dynamics in Africa. It includes dynamic climate–vegetation–fire feedback processes (Scheiter & Higgins, 2009), which influence tree cover and thus habitats and biome changes in Africa (Midgley & Bond, 2015). Implemented processes at the plant level include photosynthesis, transpiration, and carbon allocation to different plant compartments based on limiting factors, such as light and water availability (Scheiter & Higgins, 2009). Simulated trees compete for light with neighboring trees and for water with all plants at stand scale. Trees are represented as individuals of forest or savanna tree types. Forest trees are shade tolerant but do not cope well with fire, whereas savanna trees are fire tolerant, but shade intolerant. Grasses are represented by superindividuals with C_4 or C_3 photosynthesis growing either below or between tree canopies. Shrubs are not included in aDGVM and thus ecosystems such as the Succulent Karoo or Fynbos in South Africa are not well represented. Fire disturbance occurs in aDGVM depending on available fuel biomass from grasses and tree leaf litter and their moisture content. Ignition events occur randomly. A full model description is in Scheiter and Higgins (2009) and Scheiter et al. (2012).

We used results for potential natural vegetation (i.e., no human land use) from aDGVM simulations in Martens et al. (2021). The aDGVM was forced with an ensemble of climate input from 6 different general circulation models (GCMs) (i.e., ACCESS, CCSM4, CNRM, GFDL, MPI, NorESM1M [Archer et al., 2018]) that were downscaled for Africa with the conformal-cubic atmospheric model (CCAM) (McGregor, 2005) to 0.5° resolution. The mechanistic model CCAM was forced with bias-corrected sea-surface temperature and sea-ice data from the GCMs (Engelbrecht et al., 2015) for RCP4.5 and RCP8.5. Soil properties were derived from Global Soil Data Task Group's (2000) soil data. The aDGVM was run for a spin-up period of 210 years to allow simulated vegetation to reach an equilibrium state. Spin-up was followed by a transient phase with the CCAM climate data for 1971–2099. For each 0.5° grid cell, vegetation in aDGVM was simulated in a 1-ha stand. We scaled the simulation results up to the 0.5° grid by assuming vegetation is homogeneous in each grid cell and that the simulated 1-ha stand is representative for the grid cell. We used the mean across the ensemble of 6 aDGVM simulations for each RCP scenario for our analyses.

Data sets and data processing

We derived geographical location and administrative boundaries of PAs in Africa from the World Database on Protected Areas (WDPA) (UNEP-WCMC & IUCN, 2019). An overview figure of data sets used is in Appendix S1. We excluded PAs smaller than 5 km² from the analysis. Hence, many of the PAs considered in the analysis are smaller than the resolution of the other data sets used (0.5° for vegetation, 0.25° for LUH2). Vegetation in smaller PAs is often characterized by small-scale local microclimatic and topographic conditions, such as steep valleys, that cannot be captured in DVM simulations due to the coarse resolution of climate forcings. We used QGIS 3.10 (QGIS Development Team, 2021) to select African terrestrial PAs of an area greater than 5 km² for the analysis, fill holes in PAs, and identify and fix invalid geometries, such as self-intersecting polygons in the original data set, with the fix geometries algorithm in QGIS. The PAs without spatial polygon data available were excluded from this study as well as PAs with a designation status of proposed or not reported. Coastal PAs that were not covered by the aDGVM data, due to the resolution of simulations, were also removed. In total, 5121 PAs were used for this analysis (72.0% of terrestrial PAs with spatial data and 99.9% of their total PA [Appendix S2]).

Human population pressure was based on Gao's (2019) downscaled projections for SSPs 2 and 5 at 1 km² resolution (Gao, 2017). We used climate data operators' (CDO) remapcon algorithm for first-order conservative remapping (Schulzweida, 2019) to regrid these projections to 0.25° resolution to match the resolution of the LUH2 data set (see below). For each grid cell, decadal population (pop.) densities for 2020 and 2090 were rescaled from 0 to 10 so land-use and population would be on comparable scales. This rescaling assumes a steep increase of population pressure at low population densities that saturates at a population density of 1000/km² (Venter et al., 2016):

$$\text{pop.pressure} = \begin{cases} 3.333 \times \log_{10}(\text{pop.density} + 1) & \text{pop.density} < 1000/\text{km}^2, \\ 10 & \text{pop.density} \geq 1000/\text{km}^2. \end{cases} \quad (1)$$

To estimate land-use pressure, we used annual data for 2020 and 2090 from SSP–RCP marker scenarios SSP2–RCP4.5 and SSP5–RCP8.5 from the LUH2 data set (Hurtt et al., 2020) at 0.25° resolution. The LUH2 data were simulated with different integrated assessment models (IAMs) that combine economic and energy models with agricultural and land-use models and environmental impacts (Hurtt et al., 2020). The SSP2–RCP4.5 data were simulated with the IAM MESSAGE-GLOBIOM and SSP5–RCP8.5 with REMIND-MAgPIE (Hurtt et al., 2020). Each IAM implementation is the marker scenario for the respective SSP and recommended for use in analyses of climate change impact (Riahi et al., 2017).

We grouped the different land-use types in LUH2 into 5 classes (primary vegetation, secondary vegetation, pasture, cropland, urban) and assigned each class a land-use pressure factor from 0 to 10 (Appendix S3) based on an adapted scheme

from Venter et al. (2016). We grouped secondary natural vegetation into young, intermediate, and mature vegetation based on stand age classes (Newbold et al., 2015), where land-use pressure was lower for mature vegetation stands and higher for young stands. In the LUH2 data set, the fractional cover of each land-use type in a grid cell is given. The overall land-use pressure in a grid cell is based on the weighted mean of pressure factors of land-use fractions. A land-use level of 4 is equivalent to pasture. Levels of 4 and higher are considered human dominated (Watson et al., 2016).

Data analyses

Based on simulated tree cover and aboveground biomass, we classified vegetation into desert, grassland, savanna, and forest biomes (simplified from Martens et al., 2021) (Appendix S4). The savanna–forest threshold was chosen at 70% tree cover to reflect observations from remote sensing on the fire- and rainfall-driven bimodality of savanna and forest showing that intermediate tree cover levels of 50–75% rarely occur in Africa (Staver et al., 2011). Subtropical deserts are treeless (Chapin III et al., 2011); therefore, we used biomass to distinguish grasslands from deserts. Biome classification for a PA was based on means for tree cover and aboveground biomass in the PA. Because habitat loss is an important driver of biodiversity loss, we used changes in tree cover as an indicator of habitat loss in forest, savanna (Aleman et al., 2016), and grassland. Tree-cover change does not represent habitat loss and climate-driven vegetation changes well for desert biomes; therefore, we used change in aboveground biomass as indicator of habitat loss in the desert biome (Appendix S5).

Analyses of the impacts of the different drivers on PAs in Africa were conducted in R (R Core Team, 2020). For climate change impacts on PAs, we analyzed simulated vegetation and vegetation changes within PAs and used the R package raster (Hijmans, 2020) to crop data to the boundaries of PAs. Ensemble means of aDGVM simulation results were averaged over 2, 20-year periods, 2000–2019 and 2080–2099, to represent long-term climate-driven vegetation states for both RCP scenarios. We used population and land use within a specified area surrounding PAs (i.e., buffers) (Wittemyer et al., 2008) as a proxy for potential pressures resulting from socioeconomic states and indirect drivers, such as deforestation or overexploitation of ecosystem resources near PAs. We assumed that population and land-use drivers mainly act from outside PAs and omitted communities and land use inside PAs. Population and land use for grid cells intersecting with buffers and the size of the intersecting area were used to derive average pressures from outside a PA. Based on a previous study (Wittemyer et al., 2008) and our minimum PA size of 5 km², we chose 10-km buffers around each PA, but also tested 50-km buffers. Buffer areas were created in QGIS.

To investigate the impacts of climate-driven vegetation changes on biomes in PAs, we compared each biome's share of the total area protected in 2000–2019 and in 2080–2099

and looked at shares of their initial extent affected by habitat loss. To investigate regional differences in the drivers and impacts on PAs, we grouped the PAs by regions of the African Union (Organization of African Unity, 1976) (Appendix S6) and compared them in a box plot. Changes in socioeconomic pressures were calculated as the difference between pressure factors in 2090 and 2020. To determine whether PAs in certain regions were projected to be particularly affected by multiple drivers simultaneously, we plotted population pressure, land-use pressure (and their changes), and climate-driven tree-cover change from 2000–2019 to 2080–2099 against each other for different regions and projected habitat loss of PAs by convex hulls. We investigated relationships between the socioeconomic pressures, population and land use (and their changes), and climate-driven tree-cover change with Spearman's rank correlation for each scenario at continental and regional scale. These analyses required a single indicator of climate change impact on vegetation in PAs. For this purpose, we chose change in mean simulated tree cover because tree cover was also used for the classification of 3 out of the 4 biomes used. Absolute values of tree-cover change were used for Spearman's rank correlation because both negative and positive tree-cover changes represent climate-driven vegetation changes. For population and land-use pressure, actual change values in the buffers were used because increasing values represented increasing pressure. A strong relationship between the different pressure factors may also occur when pressures are low. To analyze differences between the SSP–RCP scenarios, we compared the respective results from the above analyses.

RESULTS

Climate-driven vegetation changes

Model results showed large increases in tree cover until 2080–2099 (Figure 1a,e), which often implied habitat loss in PAs in savanna and grassland regions under both scenarios (Figure 1b,f). The savanna and grassland areas in PAs decreased, and more than 50% of these biomes were projected to lose habitat until the end of the century under both scenarios (Table 1). Forest area in PAs increased under both scenarios (Table 1) and was projected to be less affected by habitat loss (Table 1; Figure 1b,f). Modeled tree cover increases and decreases in PAs were more pronounced under SSP5–RCP8.5 than under SSP2–RCP4.5 (Figure 2a). For both scenarios, tree-cover change in the majority of PAs in Southern and West Africa exceeded the median tree-cover change at the continental scale (Figure 2a).

Future socioeconomic pressures

At the continental scale, PAs were projected to experience higher population pressure in buffers in 2090 under SSP2–RCP4.5 than under SSP5–RCP8.5 (Figure 2b); regional patterns

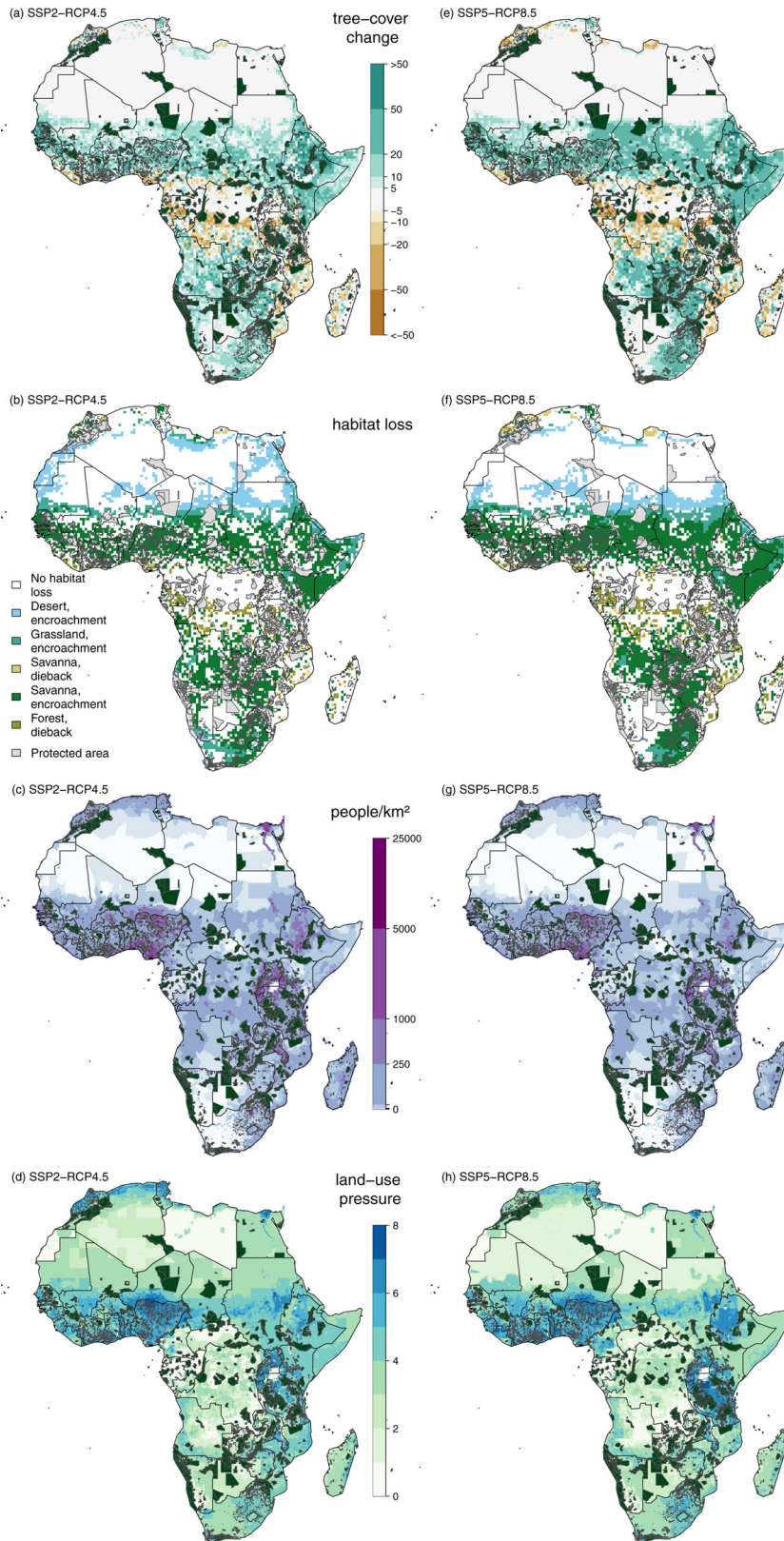


FIGURE 1 Projected (a, e) climate-driven change in tree cover in percentage points, (b, f) habitat loss, (c, g) population density in people per square kilometers, and (d, h) land-use pressure in Africa and protected areas for scenarios (a–d) SSP2–RCP4.5 and (e–h) SSP5–RCP8.5 (RCP, representative concentration pathways; SSP, shared socioeconomic pathways). Projected tree-cover changes (a, e) and derived habitat loss (b, f) (derived from the adaptive dynamic global vegetation model) show the difference between 2000–2019 and 2080–2099 (based on Martens et al. [2021]). For deserts, encroachment was defined as aboveground biomass increase >0.5 t/ha. For grasslands and savannas, encroachment was defined as an increase in tree cover >5 percentage points (p.p.) and >10 p.p., respectively. Dieback for

(Continues)

FIGURE 1 (Continued)

savanna and forest was defined by reductions of tree cover of (>10 and >20 p.p., respectively). Population (based on Gao [2017]) and land-use (based on Hurtt et al. [2020]) pressure are shown for 2090. Land-use pressure factors were based on an adapted scheme from Venter et al. (2016), in which higher numbers represent higher land-use pressure. Protected areas used in this study are mapped on top for each panel. Maps of population density and land-use pressures in 2020 and their projected changes up to 2090 for both SSP–RCP scenarios are in Appendix S8

TABLE 1 Percentage of overall protected area in 2000–2019 and 2080–2099 and of projected habitat loss by biome under combinations of socioeconomic pathways (SSPs) and representative greenhouse gas concentration pathways (RCPs)^a

	Desert	Grassland	Savanna	Forest
SSP2–RCP4.5				
2000–2019	13.7	9.4	51.2	25.7
2080–2099	9.4	8.2	46.4	36.0
habitat loss ^b	39.0	56.7	67.3	15.0
SSP5–RCP8.5				
2000–2019	16.2	7.0	51.3	25.5
2080–2099	13.9	5.4	40.1	40.7
Habitat loss ^b	19.3	64.2	71.8	21.2

^aSimulated with the adaptive dynamic global vegetation model. Results from Martens et al. (2021) were classified into biomes based on the scheme in Appendix S4. Definitions: SSP2–RCP4.5, intermediate scenario in which global inequalities in development and income growth cont with some regional improvements and medium climatic changes (Riahi et al., 2017); SSP5–RCP8.5, rapid economic and social development driven by fossil fuel exploitation and associated strong climate change and technological development (Kriegler et al., 2017).

^bBased on the scheme to determine habitat loss in Appendix S5.

were similar (Figure 1c,g). For the majority of PAs in North and Southern Africa, population densities decreased by the end of the century under SSP5–RCP8.5 (Figure 2b). Continental-scale projections of land-use pressure generally showed higher pressure under SSP5–RCP8.5 than under SSP2–RCP4.5 in 2090 (Figure 2b). However, in North Africa future land-use pressure in the buffers of PAs was generally lower under SSP5–RCP8.5 than under SSP2–RCP4.5 (Figures 1d,h & 2b). Projected land-use pressure in 2090 for PAs in East and West Africa was high (Figure 1d,h). Increases in land-use pressure for the majority of PAs in Central, East, and West Africa exceeded the continental-scale median increase (Figure 2b). Most PAs in Central Africa were projected to experience lower future population and land-use pressure in their buffers than the continental-scale medians, whereas PAs in East and West Africa were projected to be particularly exposed to both pressures in their buffers under both SSP–RCPs (Figure 2b).

Co-occurrence of climate-driven vegetation changes and future socioeconomic pressures

At the continental scale, 7.1% of PAs under SSP2–RCP4.5 and 8.2% under SSP5–RCP8.5 were projected to experience high future pressure from all 3 global-change drivers (Figure 3a,b; PAs with population and land-use pressure levels >6 and habitat loss). Future population and land-use pressure were positively correlated with each other for both scenarios at the continen-

tal scale and for most regions (Table 2), but future changes in population and land-use pressure on buffers of PAs were only weakly correlated under SSP5–RCP8.5 (Table 2). Climate-driven tree-cover changes in PAs were not correlated with future population, land-use pressures, or their changes (Table 2)

In West Africa, PAs were projected to experience climate-driven habitat loss in combination with elevated future population and land-use pressure in their buffers under both scenarios (Figure 3a,b). These included PAs in savannas and forests of West Africa, where current socioeconomic pressures are already high (Appendix S7). For PAs in East Africa, climate-driven tree-cover change was negatively correlated with future population pressure and its change under both scenarios (Table 2). Future population and land-use changes in East Africa were negatively correlated (Table 2). For Central Africa, future population pressure was lower under both scenarios for PAs affected by habitat loss than for those without (Figure 4a,b), but future land-use pressure was, on average, higher (Figure 5a,b). Future changes in population pressure were generally lower for PAs in Central Africa affected by habitat loss (Figure 4c,d). Many PAs in Southern Africa were subject to habitat loss with low to intermediate future socioeconomic pressures under both scenarios (Figure 3). Under SSP5–RCP8.5, for Southern Africa changes in future population pressure were negatively correlated with changes in future land-use pressure (Table 2). Under SSP2–RCP4.5, PAs with habitat loss in Southern Africa were projected to experience lower population pressure and lower population increases in their buffers than PAs without habitat loss (Figure 4a,c).

North Africa was the only region where many PAs were projected to experience a decrease in both socioeconomic pressures in their buffers and no habitat loss under both scenarios (bottom left quadrants in Figure 3c,d). In North Africa, climate-driven tree-cover changes under both scenarios particularly affected PAs that also experienced elevated future population pressure and under SSP2–RCP4.5 land-use pressures in their buffers (Table 2). However, increases in land-use pressure were negatively correlated with climate-driven tree-cover changes in North Africa under SSP5–RCP8.5 (Table 2).

When considering the combination of all 3 pressures (Figure 3a,b), the continental-scale patterns were broadly the same between the 2 SSP–RCP scenarios. Under both scenarios, many PAs were affected by climate-change-associated habitat loss but experienced regionally varying combinations of future socioeconomic pressures. Under SSP5–RCP8.5, climate-change impacts and future land-use pressure were often higher for PAs and their buffers (Figure 2). In contrast, PAs across all regions experienced higher future population pressure in their buffers under SSP2–RCP4.5. Despite similar spatial patterns, there was a tendency for SSP5–RCP8.5 to have higher overall pressure considering all drivers at the continental scale.

TABLE 2 Spearman's rank correlation (ρ) of pressures in and around protected areas for both SSP–RCP^a scenarios at continental scale and on regional level

Pressure and scenario ^b	Continental (5121 ^c)	Central Africa (187 ^c)	East Africa (1017 ^c)	North Africa (279 ^c)	Southern Africa (1979 ^c)	West Africa (1659 ^c)
TCC & population						
SSP2–RCP4.5						
ρ	−0.06	−0.11	−0.31	0.37	0.01	0.01
p	<0.0005	0.137	<0.0005	<0.0005	0.647	0.598
SSP5–RCP8.5						
ρ	−0.05	−0.14	−0.29	0.51	0.19	−0.07
p	<0.0005	0.055	<0.0005	<0.0005	<0.0005	0.007
TCC & population change						
SSP2–RCP4.5						
ρ	−0.04	−0.14	−0.15	−0.16	−0.09	−0.01
p	0.002	0.062	<0.0005	0.006	<0.0005	0.837
SSP5–RCP8.5						
ρ	−0.02	−0.17	−0.20	−0.14	0.02	0.00
p	0.109	0.024	<0.0005	0.020	0.286	0.988
TCC & land use						
SSP2–RCP4.5						
ρ	0.02	0.02	−0.16	0.30	−0.03	−0.01
p	0.167	0.795	<0.0005	<0.0005	0.212	0.811
SSP5–RCP8.5						
ρ	−0.02	0.05	−0.08	0.08	0.00	−0.10
p	0.112	0.542	0.008	0.163	0.911	<0.0005
TCC & land-use change						
SSP2–RCP4.5						
ρ	0.03	0.17	0.01	0.12	0.02	0.01
p	0.019	0.024	0.776	0.039	0.384	0.566
SSP5–RCP8.5						
ρ	−0.10	0.00	0.11	−0.57	−0.15	−0.11
p	<0.0005	0.938	0.001	<0.0005	<0.0005	<0.0005
Population & land use						
SSP2–RCP4.5						
ρ	0.70	0.57	0.69	0.63	0.17	0.69
p	<0.0005	<0.0005	<0.0005	<0.0005	<0.0005	<0.0005
SSP5–RCP8.5						
ρ	0.67	0.60	0.44	0.18	0.12	0.56
p	<0.0005	<0.0005	<0.0005	0.002	<0.0005	<0.0005
Population change & land use change						
SSP2–RCP4.5						
ρ	0.33	0.22	−0.35	0.07	0.19	−0.23
p	<0.0005	0.003	<0.0005	0.243	<0.0005	<0.0005
SSP5–RCP8.5						
ρ	0.11	−0.05	−0.28	0.36	−0.46	−0.51
p	<0.0005	0.470	<0.0005	<0.0005	<0.0005	<0.0005

^aShared socioeconomic pathway (SSP) and representative concentration pathway (RCP). Pathways are defined in Table 1 and text. Correlations for SSP–RCP scenario combinations SSP2–RCP4.5 and SSP5–RCP8.5 were derived.

^bTCC, tree-cover change simulated with the adaptive dynamic global vegetation model (Martens et al., 2021) for which absolute change values from 2000–2019 to 2080–2099 were used because both negative and positive tree-cover changes represent climate-driven vegetation changes; population, projections derived from Gao (2017); land-use pressure, projections derived from Hurtt et al. (2020). For population and land use, values for 2090 and change from 2020 to 2090 were derived from areas surrounding protected areas.

^cNumber of protected areas considered.

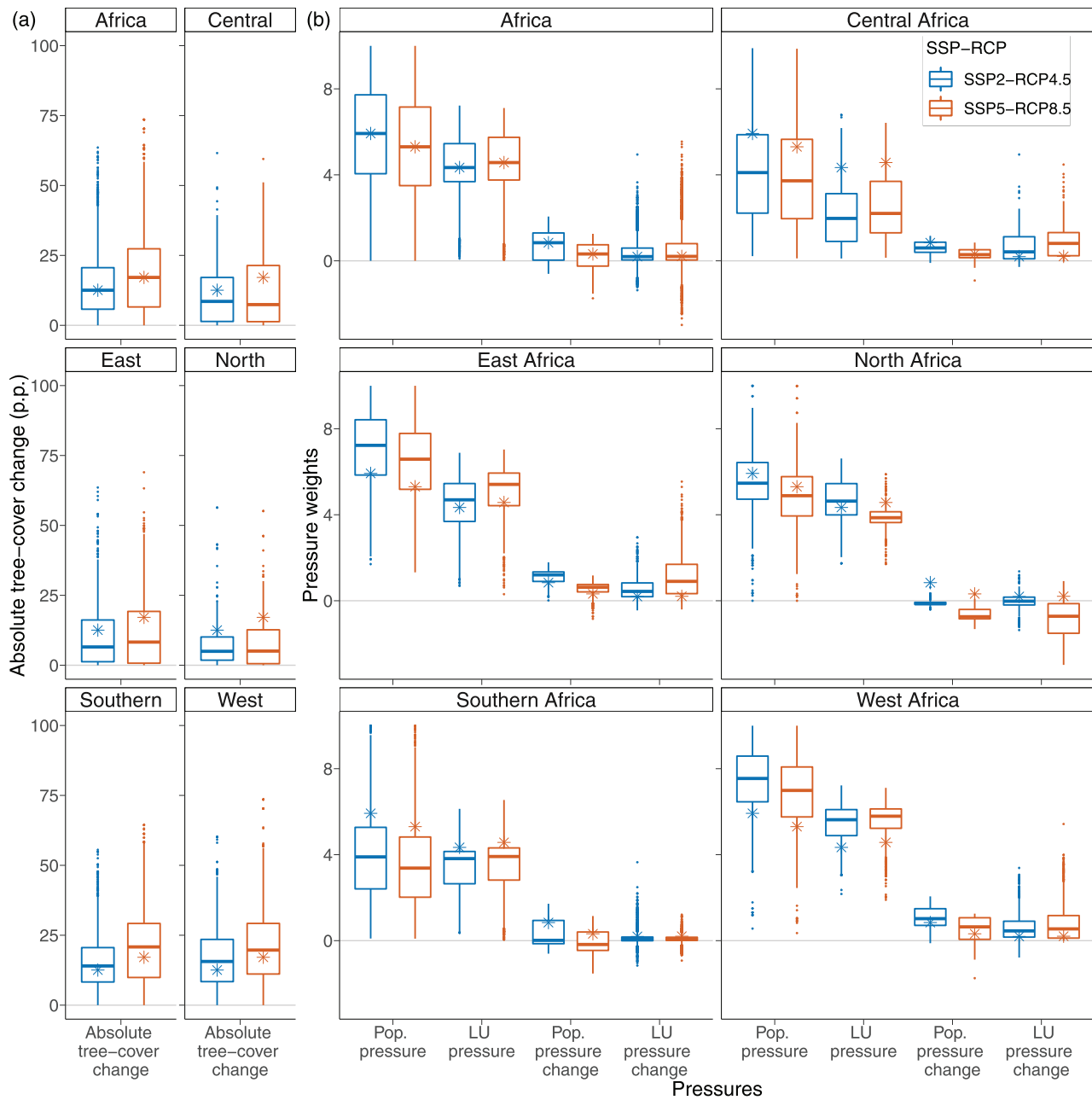


FIGURE 2 (a) Climate-driven change in tree cover in protected areas (derived from adaptive dynamic global vegetation model based on results from Martens et al. [2021]) and (b) socioeconomic pressures in 10-km zones around protected areas by region under SSP2-RCP4.5 (SSP, shared socioeconomic pathways; RCP, representative concentration pathways) and SSP5-RCP8.5 scenarios (defined in Table 1 and text) (p.p., percentage points; pop., population; LU, land use; horizontal lines, median; box ends, 25% and 75% quantile; ends of whisker lines, smallest or largest value, respectively, \geq or ≤ 1.5 times the interquartile range beyond the box ends of protected areas in each group; * continental scale medians from the Africa panel for each pressure and scenario combination). Regions are based on regions defined by the African Union (Appendix S6). Absolute values for tree-cover change from 2000–2019 to 2080–2099 are used because both negative and positive tree-cover changes represent climate-driven vegetation changes. The socioeconomic pressures population (based on Gao [2017]) and land use (based on Hurtt et al. [2020]) in 10-km zones around the protected areas were rescaled from 0 to 10 (Equation 1; Appendix S3) based on Venter et al.’s (2016) scheme. Pressures for protected areas by biome and region under both scenarios are in Appendix S7

DISCUSSION

Our results suggest that the majority of overall PA with grassland and savanna vegetation will be affected by climate-driven increases in tree cover and habitat loss. At the continental

scale, the projected climate-driven tree-cover changes were not correlated with socioeconomic pressures under both scenarios. Except for many PAs in North Africa, PAs across Africa were generally projected to experience increasing pressure from at least 1 of the investigated global change pressures under

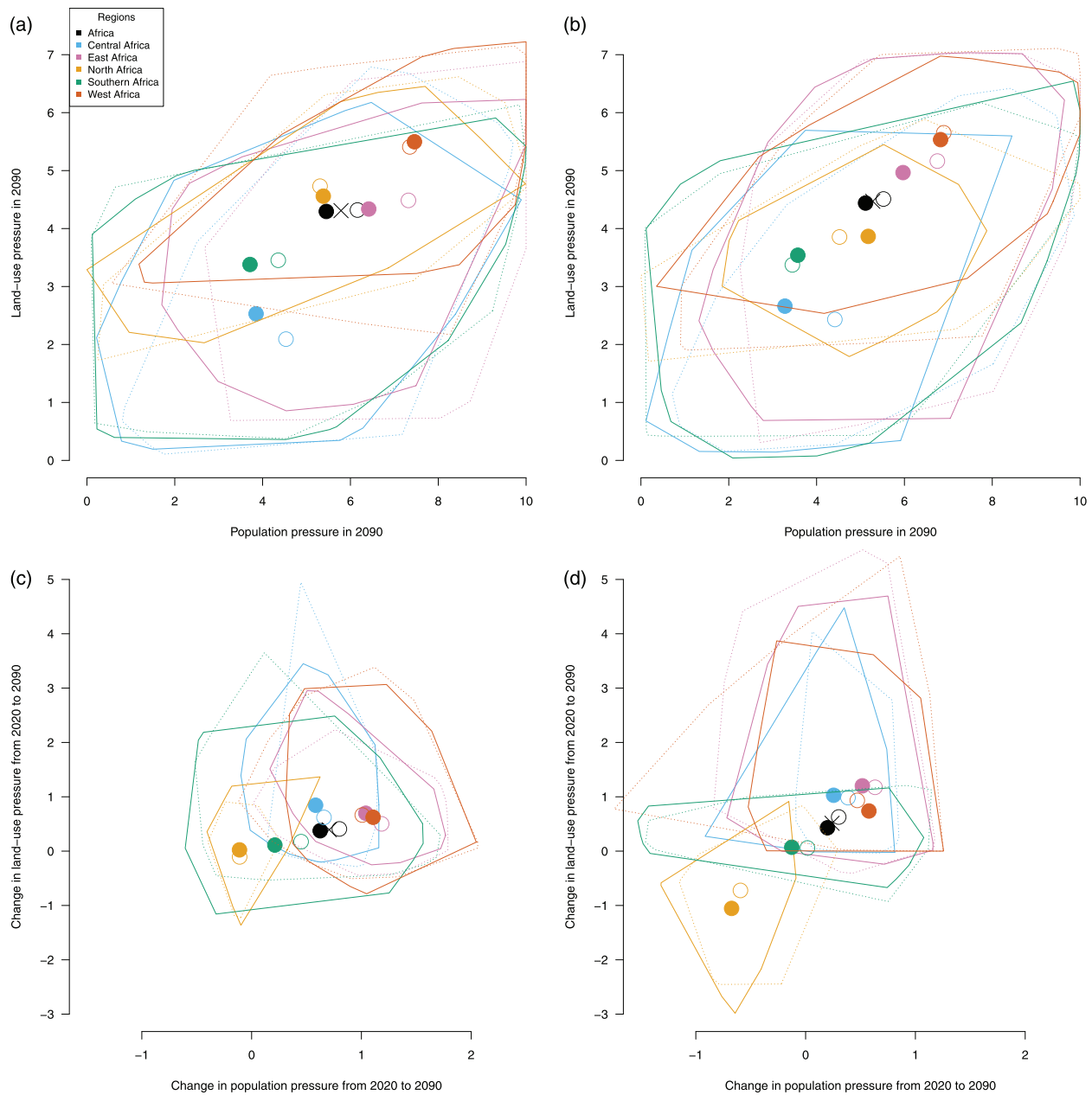


FIGURE 3 (a, b) Population and land-use pressure in 10-km zones around protected areas and (c, d) their change for (a, c) SSP2–RCP4.5 and (b, d) SSP5–RCP8.5 scenarios (defined in Table 1 and text) and habitat loss by region and biome (p.p., percentage points; cross, continental mean across protected areas; polygons, convex hulls of subgroups of protected areas; solid lines and filled circles, subgroups of protected areas projected to show habitat loss and their means; dashed lines and circles, subgroups of protected areas without habitat loss and their means). Land use (based on Hurtt et al. [2020]) and population density (based on Gao [2017]) pressures in 10-km zones surrounding protected areas were scaled based on an adapted scheme from Venter et al. (2016). Pressure plots showing all individual protected areas and regions for SSP2–RCP4.5 and SSP5–RCP8.5 are in Appendices S9 and S10. Pressure-change plots showing individual protected areas and regions for SSP2–RCP4.5 and SSP5–RCP8.5 are in Appendices S11 and S12.

both SSP–RCP scenarios. Particularly strong pressure from all 3 drivers was projected for PAs in West Africa. Overall, impacts from SSP5–RCP8.5 were slightly stronger than under SSP2–RCP4.5, even though increases in population pressure were generally lower under SSP5–RCP8.5.

Climate change impacts on PAs

The aDGVM results suggested high vulnerability of grasslands and savannas to climate- and CO₂-driven habitat loss in African PAs; effects were stronger under SSP5–RCP8.5, which

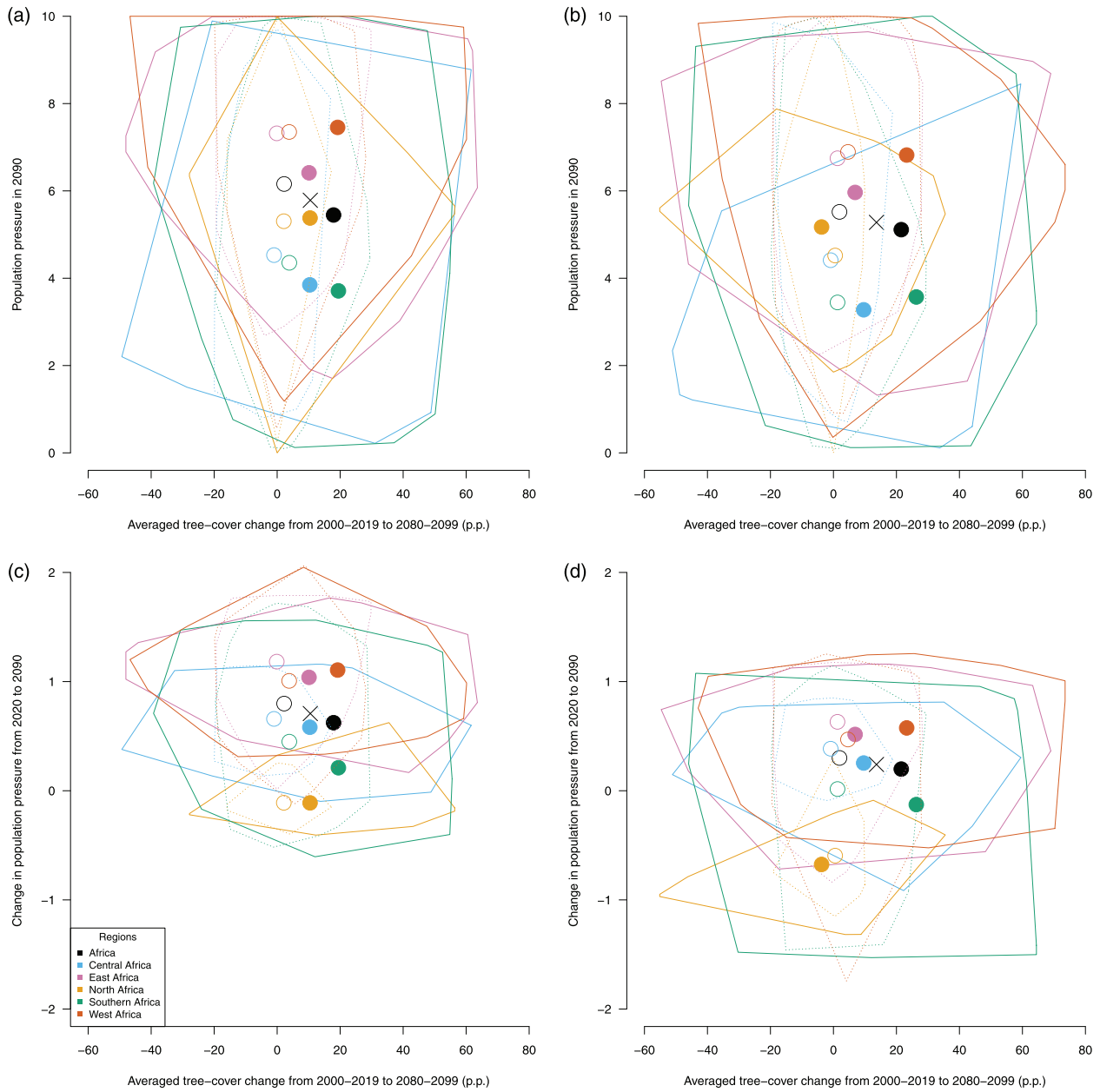


FIGURE 4 Climate-driven (a, b) tree-cover change in protected areas and population pressure in 10-km zones surrounding protected areas and (c, d) population pressure change in 10-km zones surrounding protected areas for (a, c) SSP2-RCP4.5 and (b, d) SSP5-RCP8.5 scenarios (defined in Table 1 and text) and habitat loss by region and biome (p.p., percentage points; cross, continental mean across protected areas; polygons, convex hulls of subgroups of protected areas; solid lines and filled circles, subgroups of protected areas projected to show habitat loss and their means; dashed lines and circles, subgroups of protected areas without habitat loss and their means). Tree-cover change derived from simulations with the adaptive dynamic global vegetation model (Martens et al., 2021). Population density (based on Gao [2017]) in 10-km zones surrounding protected areas was scaled from 0 to 10 based on an adapted scheme from Venter et al. (2016). Pressure plots showing all individual protected areas and regions for SSP2-RCP4.5 and SSP5-RCP8.5, respectively, are in Appendices S13 and S14. Pressure-change plots showing individual protected areas and regions for SSP2-RCP4.5 and SSP5-RCP8.5, respectively, are in Appendices S15 and S16

is consistent with continental-scale biome change projections of Martens et al. (2021). This previous analysis also showed that physiological effects of increasing atmospheric CO₂ have a large impact on simulated climate-driven vegetation changes and are a main source of uncertainties in the simulations (Martens et al., 2021).

The high vulnerability of grasslands and savannas also confirms Eigenbrod et al.'s (2015) results: protected tropical grasslands and tropical woodlands are among the global biomes most vulnerable to climate-driven biome shifts. Differences between our results and Eigenbrod et al. (2015) included a lower vulnerability of forests in PAs to climate-driven vegetation changes in

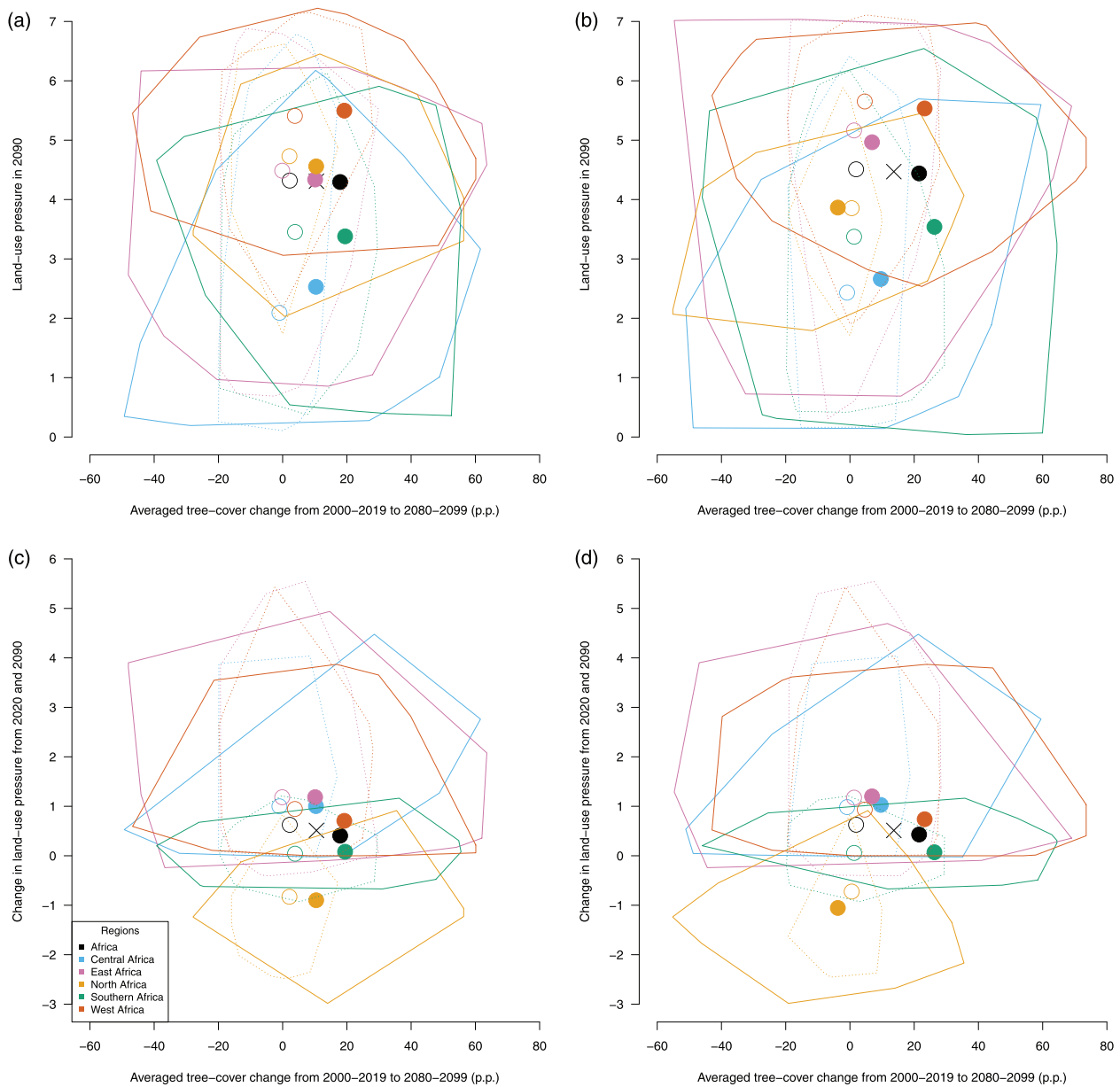


FIGURE 5 Climate-driven (a, b) tree-cover change in protected areas and land-use pressure in 10-km zones surrounding protected areas for (a, c) SSP2–RCP4.5 and (b, d) SSP5–RCP8.5 scenarios (defined in Table 1 and text) and habitat loss by region and biome (p.p., percentage points; cross, continental mean across protected areas; polygons, convex hulls of subgroups of protected areas; solid lines and filled circles, subgroups of protected areas projected to show habitat loss and their means; dashed lines and circles, subgroups of protected areas without habitat loss and their means). Tree-cover change derived from simulations with the adaptive Dynamic Global Vegetation Model (Martens et al., 2021). Land-use (based on Hurtt et al. [2020]) pressure factors in 10-km zones surrounding protected areas were scaled from 0 to 10 based on an adapted scheme from Venter et al. (2016). Pressure plots showing all individual protected areas and regions for SSP2–RCP4.5 and SSP5–RCP8.5, respectively, are in Appendices S17 and S18. Pressure change plots showing individual protected areas and regions for SSP2–RCP4.5 and SSP5–RCP8.5, respectively, are in Appendices S19 and S20

our results. This may be due to differences in climate input data and DVMs, in climate change impacts on simulated future vegetation states at global scale compared with the African scale, and in applied biome classification schemes. In addition, we focused on habitat loss rather than biome change, where habitat loss may occur without a biome change and vice versa.

In our DVM-based projections of vegetation changes under climate change, habitat loss in PAs was more widespread under SSP5–RCP8.5 than SSP2–RCP4.5. This is consistent with projections from species distribution models (SDMs) (e.g., Hannah et al., 2020), which are the basis for calls to limit climate change and expand the PA network to reduce species extinction risk.

The widespread habitat loss projected for all biomes in our simulations supports the view that the current extent of African PAs might not be sufficient to prevent species loss. Using DVM results as input for SDMs could improve representation of climate change impacts and ecosystem feedbacks among fire dynamics, CO₂ fertilization of C₃ photosynthesis, and related tipping points (Midgley & Bond, 2015) for species and their habitat.

Socioeconomic change impacts on PAs

The projected general increase in population density in the vicinity of most African PAs until the end of this century under both scenarios (Gao, 2017) is consistent with urbanization trends projected to 2030 (Güneralp et al., 2017). Although rural to urban migration may reduce pressure on PAs, increased food and resource demands (Güneralp et al., 2017) (e.g., through resource-intensive lifestyles under SSP5–RCP8.5) can lead to increased land-use pressure on PAs. This particularly affects PAs in urban catchments and near good transportation links to cities (Rudel, 2013). Increases in human population in combination with socioeconomic development may also increase societal pressure to downgrade PAs to allow, for example, human settlements and livestock herding (Lindsey et al., 2017) or renewable energy facilities (Rehbein et al., 2020) in PAs. This is expected to increase conflicts between achieving conservation goals and meeting human needs (DeFries et al., 2007). In IAMs, PAs are usually excluded from conversion into cropland or pastures (Stehfest et al., 2019) and land-use types from industrial activities are not explicitly included apart from urban land (Hurt et al., 2020). We used the developments of human population and land use in the vicinity of PAs as a proxy for these types of developments and associated impacts on PAs.

The co-occurrence of population and land-use pressure under both scenarios is in line with population pressure being a key driving force of land-cover change in West Africa (Herrmann et al., 2020). However, for changes in these socioeconomic pressures, co-occurrences were variable: positive, negative, and no correlation depending on region and scenario. This can be attributed to a combination of scenario-dependent local patterns of population pressure, the physical environment, socioeconomic conditions, policies (Herrmann et al., 2020), and links to international markets (Kriegler et al., 2017).

Combined socioeconomic and climate change impacts on PAs

At the continental scale, no clear overall patterns in relationships between climate-driven vegetation changes and socioeconomic pressures emerged from our analysis. This is not surprising because climate-driven vegetation changes and socioeconomic drivers are spatially independent global change drivers and socioeconomic developments vary regionally such that different regions will be subject to different combinations of pressures. The majority of PAs in West Africa might face chal-

lenges coping with elevated pressures from climate change impacts together with population and land-use pressure. In East Africa, socioeconomic pressure factors will need to be considered in management plans of PAs. In Southern Africa, climate change adaptation in PAs will be the main challenge, whereas socioeconomic pressures are weaker than in other regions.

Our results largely confirmed regional patterns of climate and land-use change under SSP5–RCP8.5 in African PAs identified by Asamoah et al. (2021). However, our climate-driven DVM simulations included dynamic fire–vegetation feedbacks and plant-physiological effects of increasing atmospheric CO₂ concentrations. As Martens et al. (2021) showed, CO₂ fertilization may partially compensate for adverse climate-change impacts on vegetation. This explains why climate-change impacts on forest PAs in Central Africa in our analysis were weaker than those presented by Asamoah et al. (2021).

Patterns of increased land-use pressure until 2090 in our analysis for SSP5–RCP8.5 are in line with Di Marco et al.'s (2019) LUH2-driven statistical modeling projections of declining plant biodiversity persistence until 2050. Compared with these global land-use-only projections, climate-change impacts increased the number of species estimated to go extinct by a factor of 4.5 (Di Marco et al., 2019), which underlines the importance of combining climate and socioeconomic projections when analyzing global-change impacts on ecosystems and PAs. Even under the high mitigation SSP1–RCP2.6 scenario, impacts on biodiversity from land use alone were projected to increase by a factor of 3.7 when climate change impacts were included (Di Marco et al., 2019).

Study limitations

Our data were derived from model projections. Models inherently come with assumptions and uncertainties, such as the implementation of the CO₂-fertilization effect (Martens et al., 2021), country- or regional-level assumptions for population or land use (Riahi et al., 2017), and limited data resolution, and can only be evaluated against observational data (e.g., Scheiter & Higgins [2009] for aDGVM). To study potential future dynamics at larger scales, models are, however, the only feasible option. We included PAs that were smaller than the size of grid cells in the data sets we used. Hence, heterogeneity of, for example, environmental conditions within PAs or differences inside and outside of smaller PAs were not represented. This simplification allowed us to study regional patterns of pressures for PAs rather than providing specific estimates for individual PAs.

In conservation science, the effectiveness of PAs is often analyzed using a matching approach, in which environmental states in a PA are compared with those of a matching site outside the PA (e.g., Geldmann et al., 2019). We used buffers as proxies for potential future socioeconomic influences on PAs because this study was based entirely on model results and could not be tested against observational data. Land-use and population changes in PAs depend on factors, such as management capacities, resource availability, and socioeconomic level (Lindsey et al., 2017), that are difficult to project into the future

across larger scales. We argue that PAs are usually not isolated from their surrounding areas, neither ecologically nor socioeconomically. Using the matching approach to identify sites similar to the PA would introduce additional parameters to our analysis and increase uncertainty.

We acknowledge uncertainties of the applied buffer approach. Where the ecosystem in a PA is very different from the surrounding area, developments in the buffer do not adequately represent developments of the PA (Joppa & Pfaff, 2011). Therefore, we do not assume that the developments in buffer areas are representative of developments within PAs, but rather that they represent potential indirect socioeconomic influences on PAs as well as the potential isolation of PAs from other natural areas. We expected that the size of the buffer may influence our results; however, the analysis with 50-km instead of 10-km buffers yielded similar results (Appendix S21).

Future studies could also include other SSP–RCP scenario combinations, including a high mitigation sustainability scenario to give a wider overview of consequences of societal pathways and could thus help motivate policies beneficial for conservation. For example, high climate change mitigation under SSP2–RCP2.6 (Riahi et al., 2017) may come at the cost of large increases in bioenergy croplands, which would affect biodiversity (Hof et al., 2018). These biodiversity impacts can have similar magnitudes, as in a scenario with higher climate change but lower land-use impacts (SSP2–RCP6.0; Hof et al., 2018).

Implications for conservation and management

The high vulnerability of grasslands and savannas in PAs to climate- and CO₂-driven habitat loss may require well-conceived conservation measures. Active management practices that include fire and browsing to maintain grasslands and savannas (Midgley & Bond, 2015) may help safeguard their unique, ancient biodiversity (Bond, 2016). Where future environmental conditions do not support grasslands and savannas in their current locations, intensive management might not be sufficient to conserve these ecosystems. Therefore, future anthropogenic climate and CO₂ change may lead to the loss of these old-growth ecosystems and their biodiversity. The controversial method of managed translocation of species to new or other PAs (Corlett & Westcott, 2013) to recreate old-growth grassland communities might not be appropriate for these systems because old-growth grasslands are very slow to establish and are distinct from secondarily established grasslands (Veldman et al., 2015). Managed translocation also bears the risk of potentially introducing invasive species to local ecosystems (Schwartz et al., 2012). In addition, over time costs of maintaining PAs and their connectivity under climate change increase and their effectiveness decreases (Hannah, 2008). We conclude that limiting climate change is the most promising path to conserving these unique ecosystems.

Projected associations of multiple pressures for African PAs differed by region and biome as well as by socioeconomic and climate change scenario. This implies that challenges for conservation differ by region and biome, depending on

socioeconomic and climatic developments. To account for these differences, conservation strategies need to be regionally and locally adapted. A solid understanding of the individual socioeconomic and ecological conditions as well as existing or potential conflicts builds an important foundation for planning (DeFries et al., 2007). Developing regional narratives in the context of the global SSP scenarios (Palazzo et al., 2017) can ensure that projections and policy development are based on regionally appropriate and relevant scenarios.

For PAs with high population pressure in heavily fragmented regions, fencing together with sufficient resources and management capacities can effectively prevent increasing human influence within PAs and human–wildlife conflicts (Lindsey et al., 2017). Multiuse buffer areas with low-intensity land use and community engagement that surround the main PAs can also support conservation goals and local communities (Wittemyer et al., 2008). At the same time, introducing buffer zones around PAs with high population density or intensive land use often leads to local imbalances of power, land, and resource access and to conflicts due to relocation and evictions (Neumann, 1997).

For PAs with communities that rely heavily on local food and energy resources in their vicinity, the main challenge for conservation remains to develop livelihood alternatives that improve human well-being, reduce pressure on natural resources (DeFries et al., 2007), and thus reduce pressure on the PA. Under the scenarios we investigated, socioeconomic pressures in the vicinity of PAs increased, which emphasizes that future conservation strategies need to account for the socioeconomic situation and changes in the surroundings of PAs. Community-managed PAs (Grantham et al., 2020) with a strong focus on long-term awareness strategies (Nzau et al., 2020), participatory decision-making processes, and benefit sharing that consider socioeconomic and power structures and interests of local communities (Neumann, 1997) are important to develop strategies that account for conservation and community needs. Indigenous knowledge, which is increasingly being lost, formal education, awareness raising, and equitable access to resources are important contributing factors for the success of these strategies (Nzau et al., 2020).

Despite the large variation between scenarios and regions, it can be concluded that climate-change impacts on vegetation will likely be exacerbated by socioeconomic pressures for most PAs and regions in Africa. This combination of pressures challenges conservation aspirations, such as protecting 30% of land areas (post-2020 global biodiversity framework; Convention on Biological Diversity, 2021). Our results suggest that efforts to strongly mitigate climate change combined with measures that promote equitable, wealth-distributing, and sustainable development (Crist et al., 2017) are key for the success of ecosystem conservation in this century.

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SUPPORTING INFORMATION

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