


Elevation modulates the impacts of climate change on the Brazilian *Cerrado* flora

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Abstract

Aim: Climate change is causing species distribution to shift across the globe. Lowland taxa are moving upslope with warming, while montane species face extinction. We tested the hypothesis that elevation controls the future distribution of plant species in the Brazilian *Cerrado*, home of 3.5% of the Earth's flowering plants (c. 5000 endemic species) in just 0.4% of the planet's land surface.

Location: *Cerrado* region in Brazil.

Methods: We estimated geographical range shifts of 7398 angiosperm species by 2040 using species distribution models (SDMs). We stacked the SDMs to derive the temporal variations of species richness and composition over the *Cerrado*.

Results: Our results show that between 50 and 52% of the *Cerrado* flora will experience net range loss due to climate change. While montane species were more likely to lose range, range gain was more common among lowland taxa. We estimate that 68–73% of the *Cerrado* extent will face net species losses by 2040. Net species loss was more likely to occur below 743–798 metres above sea level. Virtually the entire *Cerrado* will experience some level of species replacement due to climate change and species turnover will intensify as elevation increases.

Main Conclusions: Our findings suggest that upslope migration allows lowland plants to track climate change ('winners'), whereas montane taxa do not ('losers'). As species move upslope, lowlands become local extinction hotspots and mountains harbour novel plant assemblages. Therefore, elevation exerts a central role in shaping *Cerrado* flora responses to climate change and potentially the long-term efficacy of conservation and restoration efforts.

KEYWORDS

assisted migration, climate refugia, global warming, lowland biotic attrition, MaxEnt, range shifts, tropical savanna, upslope migration

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1 | INTRODUCTION

Climate change is driving shifts in the distribution of species and ecosystems across the globe (Parmesan, 2006; Pecl et al., 2017). Compared to pre-industrial levels, the Earth's surface temperature has increased by 1.1°C and may exceed 4°C by the end of the century (IPCC, 2021). Plant populations occurring outside their climate envelope are likely to undergo mass mortality events, resulting in geographical range loss (Sinervo et al., 2010), a phenomenon that threatens one in six species globally (Urban, 2015). On the other hand, climate change may offer novel habitats for some species to migrate into, leading to range gains (Chen et al., 2011). These contrasting responses to environmental change lead to the 'winner-loser' dichotomy, which has been observed in multiple taxa (Bateman et al., 2016; Brodie et al., 2017; Prugh et al., 2018; Roeder et al., 2021; Smith et al., 2021). However, the drivers of the uneven response of species to the ongoing changes in climate remain unclear.

Elevation plays a key role in shaping how climate change impacts the range dynamics of species. Multiple lines of evidence point that species are shifting their distribution towards higher elevations with global warming, that is, upslope migration (Chen et al., 2009, 2011; Feeley et al., 2011; Freeman et al., 2018; Girish & Srinivasan, 2022; Lenoir et al., 2008; Maharjan et al., 2022; Mamantov et al., 2021; Parmesan & Yohe, 2003; Rumpf et al., 2018; Vitasse et al., 2021). Upslope migration can allow species to track isotherms, but not all species are equally capable of moving upwards. Niche suitability often constrains the leading edge of lowland and mid-elevation species ranges. As climatic envelopes move upslope, such species may find migration opportunities at high elevations, but the distribution of montane species can be physically constrained if the leading edge of their range coincides with the peak of the mountain. Consequently, montane species may have a low migration potential due to the absence of suitable habitats (Bell et al., 2014; Dullinger et al., 2012; Zu et al., 2023). The elevation where a species occurs can underlie, then, whether it will become a 'loser' or 'winner' as climate changes.

Upslope migration can also change the number and identity of species in a given community. Species losses are expected to occur in lowlands if species are synchronously losing range near their lower elevational limit as temperatures increase (Ramirez-Villegas et al., 2014). Similarly, we can anticipate species gains in mountain areas if species are systematically gaining range beyond their upper elevational limit (Peyre et al., 2020; Walther et al., 2005). The net outcome would be species turnover peaking at high elevations due to the immigration of low- and mid-elevation species (Gibson-Reinemer et al., 2015; Thuiller et al., 2011). At the same time, species richness is thought to decline at low elevations due to the loss of emigrant species (i.e. lowland biotic attrition; Colwell et al., 2008; Feeley & Silman, 2010). Evidence for upslope migration shaping species ranges and assemblages under climate change often relies on long-term ecological monitoring, data which are often lacking in the world's most biodiverse regions (Dornelas et al., 2018; Lenoir et al., 2020; Salguero-Gómez et al., 2015).

The Brazilian *Cerrado* host the most species-rich savannas in the globe, but its fate under climate change remains poorly known. *Cerrado* covers only 0.4% of the world's land area but it is home to 3.5% of all vascular plants on Earth (Freiberg et al., 2020). Furthermore, 42% of the c. 12000 flowering plants native to the *Cerrado* are endemic (Reflora, 2020; Zappi et al., 2015). Weather stations spread across the region recorded maximum temperature increases as high as 4°C from 1961 to 2019 (Hofmann et al., 2021). Velasco et al. (2019) estimated that climate change can reduce 34–43% of the historical range of 1553 *Cerrado* angiosperms. An outstanding question is whether elevation may underlie species- and site-specific responses to climate change. The main landforms in the *Cerrado* are plateaus reaching c. 1800m above sea level (henceforth referred to as 'mountains') and depressions starting from sea level (henceforth referred to as 'lowlands'; Lira-Martins et al., 2022; Sano et al., 2019). Elevational gradients played a central role in shaping the origin and maintenance of the *Cerrado*'s remarkable plant diversity (Abadia et al., 2023; Menegat et al., 2019; Mews et al., 2016; Mota et al., 2018). It is less clear, however, whether elevation will also play a role in shaping the responses of the *Cerrado* flora to the contemporary changes in climate.

Here, we aim to unveil whether the effects of climate change on the *Cerrado* angiosperms depend on elevation. To do so, we fitted species distribution models (SDMs) for 7967 *Cerrado* species at the South America scale using the MaxEnt algorithm and seven independent bioclimatic variables averaged from 1981 to 2010. We projected the SDMs to a smaller scale (Brazil) and transferred them to the 2011–2040 timeframe based on the projections of five global circulation models (GCMs). We carried out the analyses considering two shared socioeconomic pathways (SSP): a sustainability scenario limiting warming to 1.5°C (SSP1) and a fossil-fuelled development scenario exceeding warming of 4°C (SSP5). We, then, used the outputs from these simulations to test the following hypotheses.

1. Climate change will shrink the species' range size with net range loss being more pronounced in montane species.
2. Species richness will decline under climate change with net species loss increasing towards lowland sites.
3. Climate change will lead to changes in species composition with temporal turnover increasing with elevation.

2 | MATERIALS AND METHODS

2.1 | Study area

The *Cerrado* region extends over an area of 1.9 million km² (IBGE, 2019). The average mean annual temperature is 24°C (18–28°C) and the average annual precipitation is 1359mm (800–1831mm; Nascimento & Novais, 2020). Precipitation is seasonal with monthly precipitation >241mm in Dec–Feb and <40mm in Jun–Aug. Elevation ranges from the sea level to 1855m, averaging 494m

(INPE, 2014). Most of the *Cerrado* is comprised of mid-elevation areas, the 1st elevation quantile being 294.4 m and the 3rd quantile being 677.7 m. *Cerrado* mountains fall into the pyramid mountain shape classification sensu Elsen and Tingley (2015), meaning that surface area decreases as elevation increases and mountaintop taxa have no higher-up habitat to migrate (i.e. 'nowhere-to-go' situation). Conversely, mean annual temperature decreases with elevation.

2.2 | Species occurrence and background data

We downloaded occurrence records for all terrestrial plant species (Embryophyta) available in the global biodiversity information facility (GBIF, <https://www.gbif.org/>) and SpeciesLink (<https://specieslink.net/>) across South America. 50% of the occurrences date between 1985 (1st quantile) and 2008 (3rd quantile), the median being 1997. GBIF and SpeciesLink are repositories of herbarium data, which are likely to have georeferencing and taxonomic identification errors (Goodwin et al., 2015; Zizka et al., 2019). We applied a series of filters to minimize the chance of including erroneous occurrence records in our SDMs (See 'Data cleaning' section in the Data S1). We standardized the species names and filtered only angiosperm species according to the APG IV (2016) and those that occur in the Brazilian *Cerrado* using the function 'get.taxa' from the R package 'flora' (Carvalho, 2020) and removed species with ≤ 10 valid occurrence records. The final dataset consisted of 1,988,701 occurrence records (Table S1). We controlled for spatial sampling bias by retaining one presence record per 5 km pixel (i.e. thinning) using the function 'thin' from the R package 'spThin' (Aiello-Lammens et al., 2015). We used the MaxEnt algorithm to fit the SDMs. MaxEnt is a presence-only algorithm, but it requires generating points around the occurrence records (i.e. background points). To further control for bias, we coupled a sampling density map to MaxEnt background point generation to propagate the spatial bias of the presence data into the background data (Phillips et al., 2009; Figures S1 and S2; See 'Bias-corrected background point generation' section in the Data S1).

2.3 | Climatic data

We downloaded 19 bioclimatic variables from CHELSA V2.1 (<https://chelsa-climate.org/>) averaged from 1981 to 2010 (baseline) at 30 arcsecs of resolution (c. 1 km near the equator) (Table S2). We first visually inspected the data and excluded the precipitation of the warmest (BIO18) and coldest quarter (BIO19) due to discontinuities that reflect methodological artefacts rather than biologically meaningful climatic gradients (Booth, 2022). For the 17 remaining variables, we used the Variance Inflation Factor (VIF) to remove highly correlated variables, which controls for collinearity issues and subsequent model overfitting (De Marco & Nóbrega, 2018). We applied the default settings of the function 'vifstep' from the R package 'usdm' (Naimi et al., 2014), which retained seven out of the

17 bioclimatic variables (Table S3). We downloaded the seven independent variables at the 2011–2040 timeframe according to five Global Circulation Models (GCMs): GFDL-ESM4, UK-ESM1-0-LL, MPI-ESM1-2-HR, IPSL-CM6A-LR and MRI-ESM2-0. Approximately 40% of the *Cerrado* flora is composed of herbaceous plants (c. 4800 species), so the 2011–2040 timeframe choice aimed to match the relatively short time to maturation (i.e. from 1 to 2 years to flower) of most *Cerrado* angiosperms. We also considered different scenarios of global change, represented by the Shared Socioeconomic Pathways (SSPs). SSP1 corresponds to the sustainability scenario (optimistic), proportional to RCP2.6. SSP5 corresponds to the fossil-fuelled development scenario (pessimistic), proportional to RCP8.5 (Riahi et al., 2017).

2.4 | SDM training, evaluation, binarization, restriction and transfer

We randomly split the presence data five times for each species into training (80%) and validation (20%) datasets. The five replicates account for the variability due to data splitting. We used the function 'maxent' (default settings) from the R package 'dismo' to fit the SDMs (Hijmans, Phillips, et al., 2021). We fitted the MaxEnt models using the seven independent bioclimatic variables at 30 arcsecs resolution over South America. Even though our study area was the *Cerrado*, fitting the SDMs at this broader scale increases the chances of capturing the species' full climatic niche, which improves the transferability of the SDMs over time (Chevalier et al., 2022; Pang et al., 2022).

We used the Continuous Boyce Index (CBI) to evaluate the goodness of fit of our SDMs. The CBI of each SDM replicate was computed separately. We used the function 'contBoyce' from the R package 'enmSdm' to determine CBI (Smith, 2021). We used $CBI > 0.25$ as the inclusion criteria, which is a conservative cut-off value since $CBI > 0$ would already indicate that the SDM performs better than random.

We projected the models to geographical space at a resolution of 150 arcsecs and across Brazil only to reduce the computational time (Figure S3a). We binarized the niche suitability probability through a threshold that set apart suitable versus unsuitable pixels (Figure S3b). The threshold consisted of the 10th percentile of the niche suitability distribution of the training presence dataset (Radosavljevic & Anderson, 2014). This threshold represents the suitability cut-off that includes 90% of the highest-suitable presence points.

SDMs commonly overpredict the distribution of species. A posteriori spatial restriction routine can reduce SDM overprediction (Mendes et al., 2020). We removed all suitable habitat patches that fell outside the species accessible area (i.e. 250 km radius buffer around presence points; Figure S3c). Biologically, this correction removes habitat patches far from where the species have been observed to occur, that is, areas theoretically less accessible by dispersal.

We projected our SDMs to the 2011–2040 timeframe using the forecasts of GFDL-ESM4, UK-ESM1-0-L, MPI-ESM1-2-HR, IPSL-CM6A-LR and MRI-ESM2-0 GCMs under SSP1 and SSP5 scenarios. Then, we performed the same binarization and spatial restriction routines for the SDMs transferred to the future. Finally, we averaged the SDMs projected using different GCMs into a single ensemble for each SSP.

2.5 | Range size, species richness and species composition

Range size represents the summed area where a given species can be found. We considered the sum of the suitable pixels obtained from the binary SDMs as the potential geographic range size (hereafter referred to as 'range size'). The SDMs were projected across Brazil, hence the range size calculated here corresponds only to the species' distribution within the country. The temporal variation of the range size was expressed as 'Δ range size'. Δ range size was calculated in terms of percentage relative to the baseline (Equation 1).

$$\Delta \text{ range size (\%)} = \frac{\text{Future range size} - \text{Baseline range size}}{\text{Baseline range size}} \times 100 \quad (1)$$

Where the *future range size* and *baseline range size* correspond to the range size estimated in the 2011–2040 and 1981–2010 periods respectively.

Δ range size is the net difference between range size gains and losses. To get insight into Δ range size components, we also calculated range gain by summing the area that was unsuitable in the 1981–2010 period and became suitable in the 2011–2040 period. We calculated range loss using the same logic: the sum of the area that was suitable during 1981–2010 and became unsuitable during 2011–2040.

We stacked the binary SDMs (S-SDM) of all species with CBI > 0.25 into a single object using the 'stack' function from the R package 'raster' (Hijmans, 2021). We used the stacked map to estimate the temporal variation in species richness and composition (temporal turnover). Species richness was calculated by summing all the layers of the S-SDM. The temporal variation of the species richness was expressed as 'Δ species richness' (Equation 2).

$$\Delta \text{ Species richness} = \text{Future species richness} - \text{Baseline species richness} \quad (2)$$

Where the *future species richness* and *baseline species richness* correspond to the species richness estimated in the 2011–2040 and 1981–2010 timeframes respectively.

We used the same S-SDM to estimate the temporal species turnover. We used Simpson's index to quantify potential changes in species composition over time (hereafter referred to as the 'species turnover'; Baselga, 2010). We first converted the S-SDM into a matrix where the rows were the pixels, the columns were the species, and the cells were filled with 1 when the pixel was suitable for the species and 0 when it was not. We contrasted the matrices derived

from the 2011–2040 and 1981–2010 periods using the function 'beta.temp' from the R package 'betapart' (Baselga et al., 2021).

2.6 | Elevation affiliation

We used the elevation affiliation to capture species' preferences across elevational gradients. We defined the elevation affiliation as the elevation where most of the species distribution is concentrated. We estimated the elevation affiliation of each studied species by calculating the median elevation of all valid presence points used to train and validate the SDMs. The elevation affiliation is a continuous index, so it avoids coercing the spectrum of elevation preferences into the binary lowland versus montane classification. The occurrence records reflect only the species' historical elevation affiliation. So, to estimate future upslope migration rates, we first used the binary distribution maps of each species projected to the baseline (1981–2010) and future timeframes (2011–2040) to mask the elevation raster layer. The product represents the range of elevation that a given species is expected to experience over the baseline and future periods. We then extracted the elevation values for each pixel and calculated the 97.5th percentile per timeframe. We used the 97.5th percentile to represent the upper elevational limits of the species. The upslope migration rate consisted of the difference between the 97.5th percentile of the elevation affiliation in the future and the baseline timeframe. Finally, we converted the upslope migration rates to metres per decade by dividing the previous value by three, representing the number of decades between the mean point of baseline (1995) and future horizons (2025). The elevation data used over the entire study originated from the shuttle radar topographic mission (SRTM) retrieved from Brazil's National Institute for Space Research (INPE) Ambdata project (INPE, 2014).

2.7 | Data analysis

We ran a paired Student's *t*-test to contrast the Δ range size, range gain, and range loss between SSP1 and SSP5 scenarios. We fitted linear regressions to test hypothesis 1: elevation affiliation negatively affects Δ range size. The sampling unit was the species. Additionally, we ran linear regressions where elevation affiliation predicts range gain and loss. We also ran paired Student's *t*-tests to compare elevation affiliation in the future versus baseline timeframe.

We ran a paired Student's *t*-test to contrast the Δ species richness between SSP1 and SSP5 scenarios. We fitted linear regressions to test hypothesis 2: elevation positively affects Δ species richness. Elevation may covary with climatic anomalies, which can obscure the effects of elevation on Δ species richness. To account for that covariance, we performed an additional analysis that started by fitting a linear regression where the response was the Δ species richness and the predictors were the anomaly of the seven independent bioclimatic variables used in the study (anomaly = future – baseline). The sampling unit was 150 arcsec pixels across the *Cerrado*. We, then,

fitted a second linear regression where the response variable was the residuals of the previous regression (Δ species richness ~ bioclimatic variables anomaly) and the predictor variable was the elevation. The residual variation of Δ species richness is independent of the climatic anomalies, so it can confirm whether elevation directly affects Δ species richness or not.

We ran a Student's *t*-test to contrast the temporal species turnover (Simpson's index) between SSP1 and SSP5 scenarios. We fitted linear regressions to test hypothesis 3: elevation positively affects species turnover. Same as before, to account for the effects of climatic anomalies on species turnover, we first estimated the effect of the bioclimatic variables' anomaly on the temporal species turnover using linear regressions. We, then, fitted other linear regressions to unveil the effects of elevation on the residuals of the previous regression (species turnover ~ bioclimatic variables anomaly). The sampling unit remained 150arcsec pixels across the *Cerrado*.

3 | RESULTS

3.1 | Modelling species distribution

We fitted satisfactory SDMs (CBI > 0.25) for 7398 species. Nine hundred and fifty two species were removed from the analysis due to poor model fit (CBI ≤ 0.25). The CBI of the 7398 retained species averaged 0.72, indicating good model performance (Figure S4). The 7398 species represent 59.01% of the *Cerrado* angiosperm flora (12,052 species based on Reflora (2020)) and are spread over 174 families (94.05% of the *Cerrado* total). The precipitation of the driest month (BIO14) was the most important variable out of the seven bioclimatic variables used to fit the SDMs, followed by precipitation seasonality (BIO15; Figure S5).

3.2 | Direction and drivers of range shifts (hypothesis 1)

Our analyses predict that half of the studied *Cerrado* species will lose range by 2040. In terms of median values, range loss exceeded range gain under SSP1 (−9% vs. 6%) and SSP5 (−10.1% vs. 7.3%). Consequently, the median Δ range size was negative both under SSP1 (−0.4%) and SSP5 (−1.2%; Figure 1). Δ range size was significantly lower under SSP5 compared to SSP1 ($p = .01$; Table S4). 50.8% of the studied species showed a negative Δ range size under SSP1 (Figure 1). This percentage increased to 52% under SSP5. Our models predict that 152 species (SSP1) and 165 species (SSP5) will experience critical range contraction (i.e. Δ range size < −70%). *Cerrado* endemics accounted for 57.9% of the species with critical range contraction under SSP1 and 58.2% under SSP5.

Elevation affiliation had a negative effect on Δ range size under both scenarios of global change ($p < .001$; Figure 2). While range gain increased, range loss decreased with elevation affiliation ($p < .001$; Table S5; Figure S6). Elevation affiliation had a median value of

587.1 m (95%CI: 103.1–1141.2 m). The subset of species with critical range contraction had a median elevation affiliation of 1041.1 m (SSP1) and 1030.6 m (SSP5). Maximum (97.5th percentile) elevation affiliation increased over time for 75.1% (SSP1) and 77.8% (SSP5) of the studied species. Median upslope migration rates were 5.8 m decade^{−1} under SSP1 and 7.3 m decade^{−1} under SSP5.

3.3 | Direction and drivers of species richness change (hypothesis 2)

Our models suggest that c. 70% of the *Cerrado* is expected to face climate-driven net species loss by 2040. Negative Δ species richness was projected to occur in 68.4% of the *Cerrado* area under SSP1 and 73.9% under SSP5 (Figure 3). The median potential species richness was 3721 species per 150arcsec pixel at the baseline timeframe. The median Δ species richness dropped from −71 species per 150arcsec pixel under SSP1 (95%CI: −435–210 spp. pixel^{−1}) to −95 spp. pixel^{−1} under SSP5 (95%CI: −469–204 spp. pixel^{−1}; $p < .001$; Table S6). Examples of regions with Δ species richness < −200 were the *Cuiabá* Depression (*Depressão Cuiabana*) and *Araguaia* Floodplain (*Planície do Araguaia*) lowlands. In contrast, the *Parecis* Plateau (*Serra dos Parecis*) and *Veadeiros* Plateau (*Chapada dos Veadeiros*) mountains represent regions with Δ species richness > 200 species.

Elevation had a positive effect on Δ species richness under SSP1 and SSP5 ($p < .001$; Figure 4). The regression line predicted Δ species richness of −254.9 (SSP1) and −291.3 (SSP5) at sea level (i.e. elevation = 0; Table S7). Δ species richness tended to increase by one species when elevation increased by 2.9 m (SSP1) and 2.7 m (SSP5). Δ species richness was predicted to cross the zero at an elevation of 743.2 m (SSP1) and 798.9 m (SSP5). The positive relationship between Δ species richness and elevation remained statistically significant even after controlling for the effect of climatic anomalies on Δ species richness variation (Table S8).

3.4 | Direction and drivers of species temporal turnover (hypothesis 3)

We predict a shift in the composition of *Cerrado* angiosperm flora under climate change. The Simpson's turnover index was higher under SSP5 (median of 0.08) compared to SSP1 (median of 0.07; $p < .001$; Figure 5). The median turnover index was 5.5 (SSP1) and 5.1 times (SSP5) higher than the median nestedness index (Figure S7). Regions showing the highest species turnover (> 0.1) included the Upper *São Francisco* Plateaus (*Serras do Alto São Francisco*) and *Parecis* Plateau (*Serra dos Parecis*). Meanwhile, the *Araguaia* Floodplain (*Planície do Araguaia*) and *Paraná* Depression (*Vão do Paraná*) illustrate regions displaying the lowest species turnover values (< 0.05).

Elevation had a positive effect on species turnover under both SSPs ($p < .001$; Figure 6). Pixels at sea level (i.e. elevation = 0) tended to have a turnover index of 0.06 under SSP1 and SSP5 as inferred by the regression intercept (Table S7). Species turnover increased

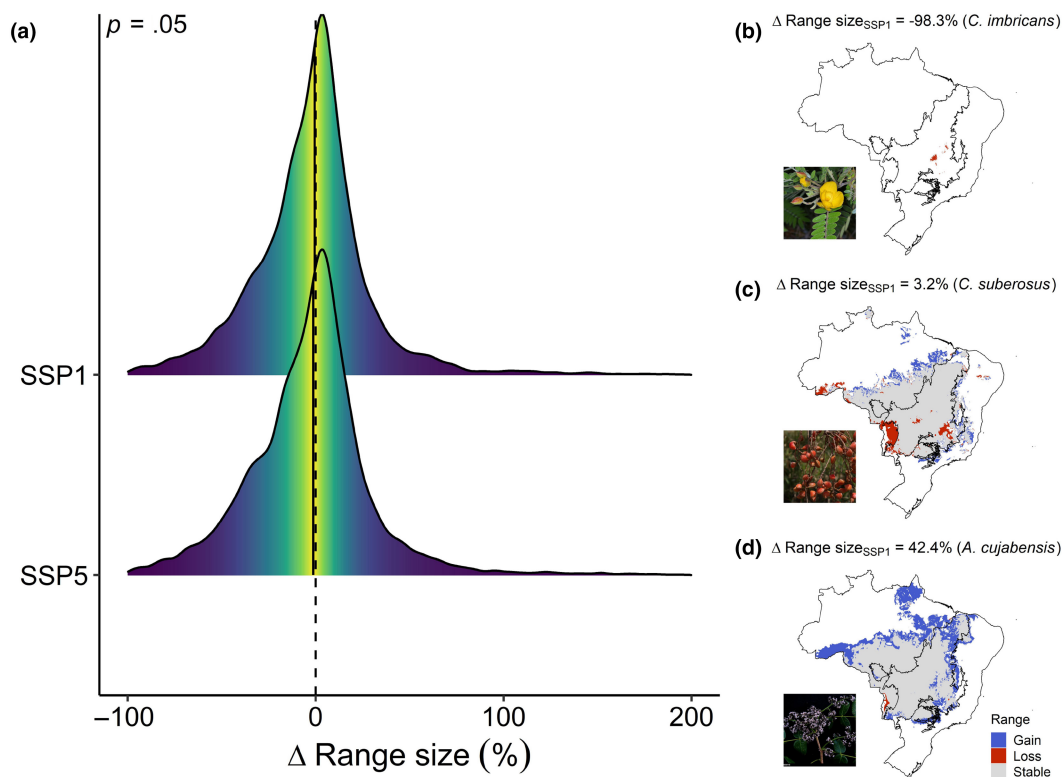


FIGURE 1 Climate change impacts on the range size of Cerrado flowering plants. (a) The distribution of Δ range size for the 7398 studied species and (b–d) species-specific examples. Δ range size represents the change in the potential geographic range size in the future (2011–2040) compared to the baseline (1981–2010) at the Brazil scale. Δ range size > 0 suggests range gain and Δ range size < 0 range loss. Δ range size was expressed in percentage relative to the baseline range size. The upper distribution in panel (a) corresponds to an optimistic scenario of global change (SSP1) and the lower distribution to a pessimistic scenario (SSP5). The distribution charts in panel (a) were coloured according to the tail probabilities. The dashed line marks the zero, that is, no net change. The solid line indicates the median of the distribution. The x-axis of panel (a) was limited to 200% to improve visualization which concealed 55 outlier species. The p -value at the panel (a) top right corner refers to the paired t-test comparing Δ range size under SSP1 versus SSP5. Stable, gained, and lost range of (b) *Chamaecrista imbricans*, (c) *Connarus suberosus*, and (d) *Andira cujabensis* in the future versus baseline timeframe. *C. imbricans* is a montane species (elevation affiliation = 1067 m), *C. suberosus* a mid-elevation species (elevation affiliation = 521.8 m), and *A. cujabensis* a lowland species (elevation affiliation = 391.6 m). The outer polygon depicts the Brazil border and the inner polygon the Cerrado limits. Δ Range size_{SSP1} in panels (b–d) corresponds to the Δ range size under the SSP1.

at a rate of 2.4×10^{-5} per metre above sea level under SSP1 and 3.1×10^{-5} under SSP5. The effect of elevation on species turnover remained positive and statistically significant after accounting for the effects of climatic anomalies on the turnover index (Table S8).

4 | DISCUSSION

Our results show that half of Cerrado plant species will experience range contraction by 2040. These range shifts translate to species losses, gains and replacements at the community level. Elevation plays a key role in regulating how Cerrado angiosperms may respond to future climate change because as the ranges of montane species decrease, those of lowland species will increase. Up to three-quarters of Cerrado flowering plants will most likely have their ranges centred at higher elevations by 2040. Upslope migration rates are estimated at around 5–7 m decade⁻¹. At the community level, net species loss is predicted to peak in the lowlands, but mountains are likely to have

a net species gain and be the hotspots of temporal species turnover. Finally, the more pessimistic climate change scenario (SSP5) leads to more net range loss, net species loss and species replacement in the Cerrado relative to the more optimistic scenario (SSP1). We discuss below whether our data support our hypotheses and how our findings can inform conservation and restoration decision-making.

4.1 | Montane species are more vulnerable to climate change than lowland species

We show that climate change will drive range shrinkage among Cerrado angiosperms and therefore data support hypothesis 1. However, the difference between species experiencing range loss versus gain was small, only 0.8% (SSP1) to 2% (SSP5). At the global scale, the proportion of climate ‘winners’ and ‘losers’ tends to be similar across taxonomic groups and biomes (Dornelas et al., 2019). Elevation affiliation emerges as a key modulator of how climate

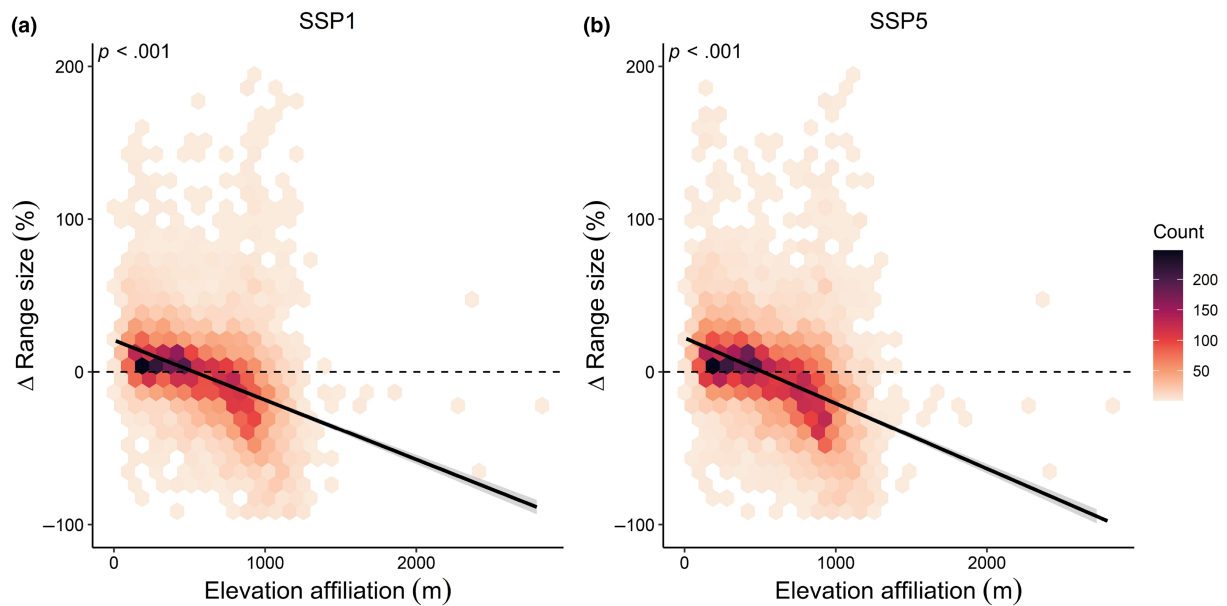


FIGURE 2 Relationship between range shift and elevation affiliation across *Cerrado* flowering plants. Δ range size was expressed in percentage relative to the baseline range size. Δ range size was calculated based on an (a) optimistic (SSP1) and (b) a pessimistic scenario of global change (SSP5). The solid line depicts the linear model fit. The p -value is shown at the top right corner. Each observation corresponds to a species. The hexagons' colour is proportional to the density of species in that area. The dashed line marks the zero, that is, no net change. m.a.s.l. stands for metres above sea level. The X-axis was limited to 200% to improve visualization which concealed 32 outlier species.

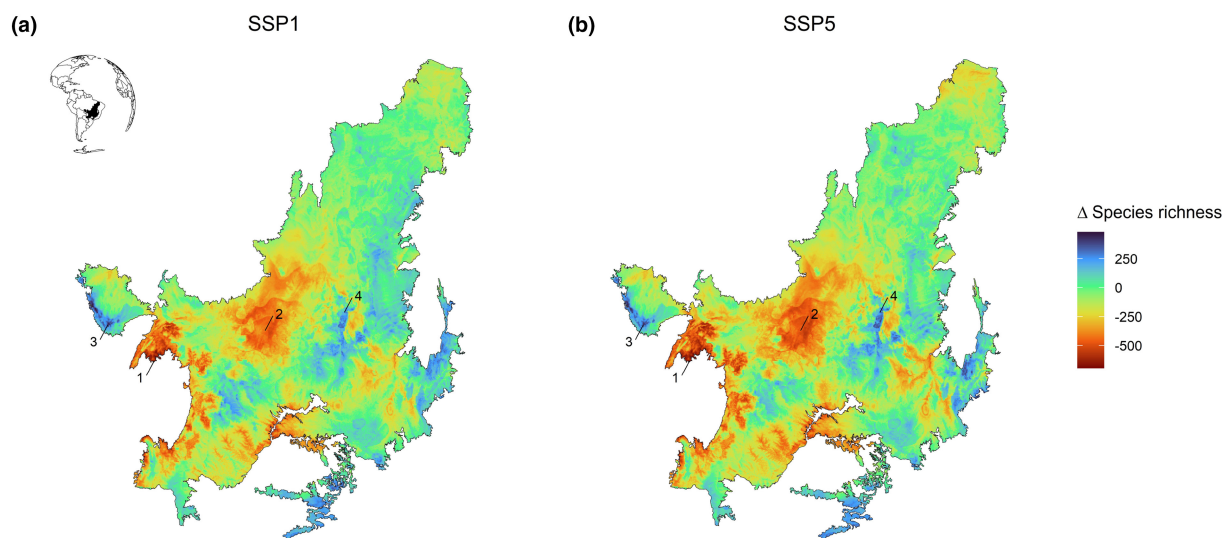


FIGURE 3 Temporal variation of floristic richness under climate change in the *Cerrado*. Δ species richness represents the change in potential species richness in the future (2011–2040) compared to the baseline (1981–2010). Δ species richness >0 suggests species gain and Δ species richness <0 species loss. Δ species richness was estimated based on an (a) optimistic (SSP1) and (b) a pessimistic scenario of global change (SSP5). Site-specific examples are labelled as follows: (1) *Cuiabá* Depression (*Depressão Cuiabana*) and (2) *Araguaia* Floodplain (*Planície do Araguaia*) exemplify lowlands with negative Δ species richness and (3) *Parecis* Plateau (*Serra dos Parecis*) and (4) *Veadeiros* Plateau (*Chapada dos Veadeiros*) exemplify mountains with positive Δ species richness.

change impacts the range of *Cerrado* plant species. Range contractions are more likely to occur among montane species, potentially the future 'losers' (Dullinger et al., 2012). In the *Cerrado*, species facing a high risk of extinction (i.e. range contraction $>70\%$) were affiliated to elevations around 1000m (e.g. *Chamaecrista imbricans*, Figure 1b),

but range expansion was common among species that typically occur at lower elevations (e.g. *Andira cujabensis*, Figure 1d), potentially the future 'winners'. The land area often decreases as elevation increases in pyramid-shaped mountain ranges (the case of *Cerrado*). Hence, the lack of habitat higher up constrains the ability of montane

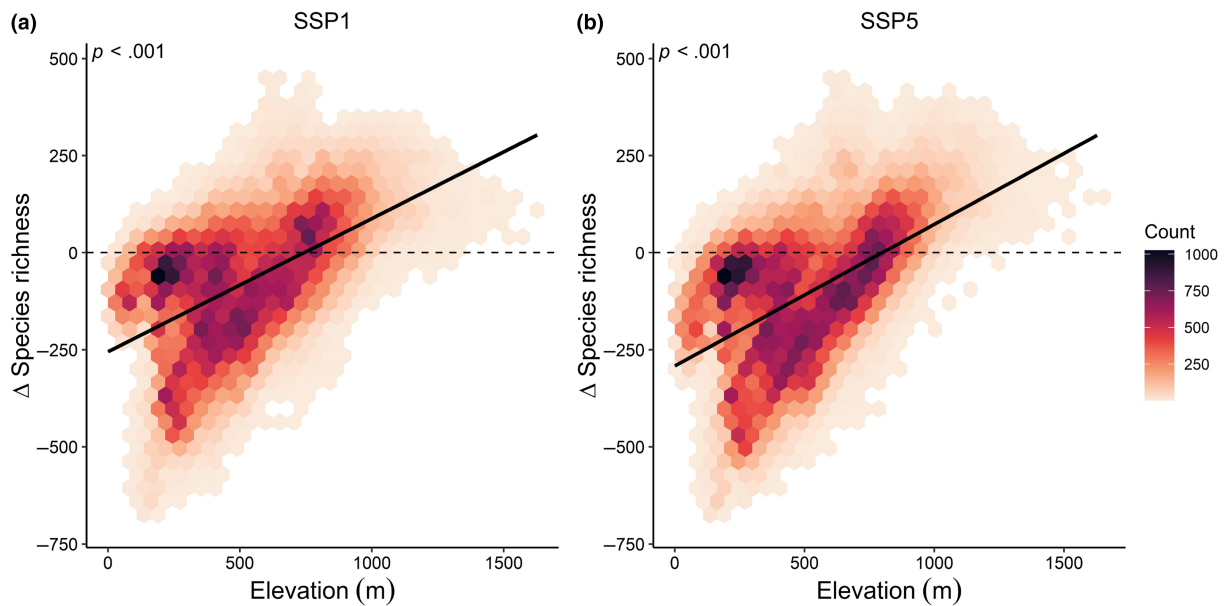


FIGURE 4 Effect of elevation on the temporal variation of floristic richness in the *Cerrado*. Δ species richness represents the change in potential species richness in the future (2011–2040) compared to the baseline (1981–2010). Δ species richness >0 suggests species gain and Δ species richness <0 species loss. Δ species richness was calculated based on an (a) optimistic (SSP1) and (b) a pessimistic scenario of global change (SSP5). The solid line depicts the line fitted to the relationship between the Δ species richness and the elevation. The p -value is shown at the top right corner. Each observation corresponds to a species. The hexagons' colour is proportional to the density of species in that area. The dashed line marks zero.

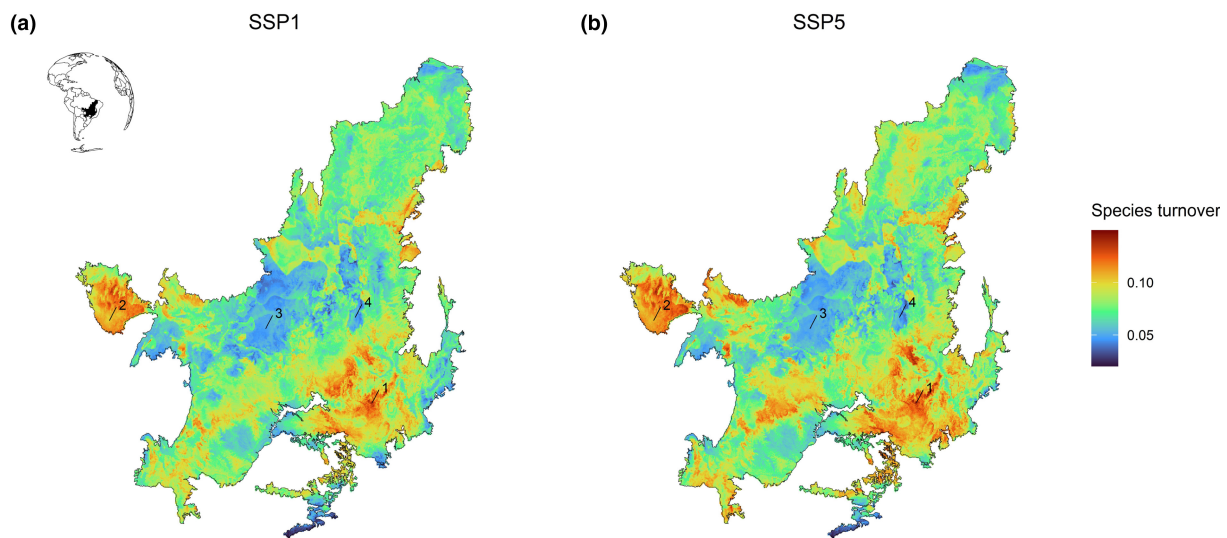


FIGURE 5 Temporal floristic turnover under climate change in the *Cerrado*. Species turnover represented by Simpson's index which reflects the species replacement in the future (2011–2040) compared to the baseline horizon (1981–2010). Turnover = 0 suggests no change in species composition and turnover = 1 suggests complete species replacement. Species turnover was estimated based on an (a) optimistic (SSP1) and (b) pessimistic scenario of global change (SSP5). Site-specific examples are labelled as follows: (1) Upper São Francisco Plateaus (*Serras do Alto São Francisco*) and (2) Parecis Plateau (*Serra dos Parecis*) exemplify mountains with high species turnover and (3) Araguaia Floodplain (*Planície do Araguaia*) and (4) Paranã Depression (*Vão do Paranã*) exemplify lowlands with low species turnover.

species to migrate upslope at the rates that lowland species may do (Bell et al., 2014; Benito Garzón et al., 2008). Alternatively, montane taxa could migrate to new mountains where they can find suitable habitats. However, mountain ranges are often disconnected (Flantua et al., 2019), which tends to drive the patchy distribution of most

montane species (Rahbek et al., 2019). In the *Cerrado*, this habitat discontinuity constrains the ability of montane species to keep up with climate change by migrating latitudinally or longitudinally. Therefore, habitat shortage and patchiness probably synergistically drive the vulnerability of montane species to climate change in the *Cerrado*.

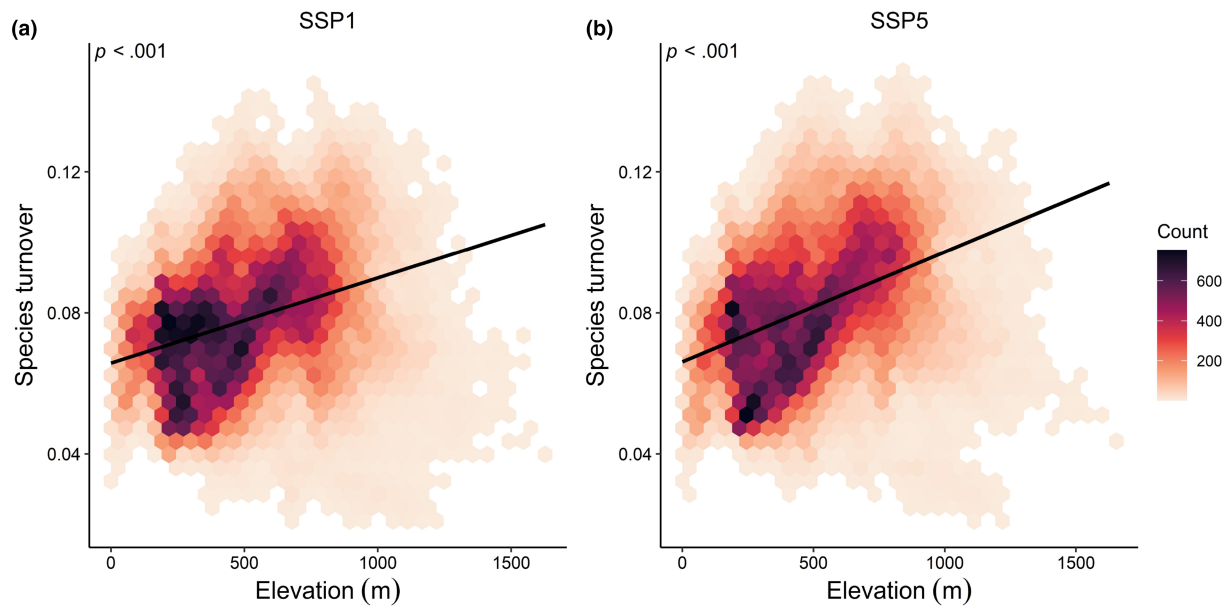


FIGURE 6 Effect of elevation on *Cerrado* temporal floristic turnover. Species turnover represented by Simpson's index which reflects the species replacement in the future (2011–2040) compared to the baseline horizon (1981–2010). Turnover=0 suggests no change in species composition and turnover=1 suggests complete species replacement. Species turnover was calculated based on (a) an optimistic (SSP1) and (b) a pessimistic scenario of global change (SSP5). The solid line depicts the line fitted to the relationship between the species turnover and the elevation. The p -value is shown at the top right corner. Each observation corresponds to a species. The hexagons' colour is proportional to the density of species in that area.

Cerrado flowering plants will need to move from five to seven metres upslope per decade to track climate change. This estimate aligns with a recent global systematic review reporting an average upslope migration rate of 6.9 m decade^{-1} for plants (Rubenstein et al., 2023). Even though lowland species show potential for migrating upwards, three factors may constrain their movement. First, dispersal and colonization limitations are common features of *Cerrado* plant assemblages (Arruda et al., 2021; Le Stradic et al., 2018). For instance, some typical *Cerrado* families, such as the Poaceae and Melastomataceae, display a suite of traits that limit propagule movement and establishment. These include fire-triggered flowering (Fidelis & Zironi, 2021; Fontenele & Miranda, 2022; Pilon et al., 2018; Zironi et al., 2021), a high proportion of embryoless seeds (Fontenele et al., 2020; Kolb et al., 2016; Le Stradic et al., 2015) and seed dormancy (Dayrell et al., 2017; Escobar et al., 2018; Silveira et al., 2012). Second, several *Cerrado* plants are edaphic specialists and adapted to acidic, aluminium-rich, phosphorus-impooverished quartzite soils, typical of much of the *Cerrado* (Abrahão et al., 2019; Haridasan, 2008; Oliveira et al., 2015; Teodoro et al., 2019). These species may find suitable climate upslope, but not suitable edaphic conditions for their establishment and growth (Van De Ven et al., 2007). Third, half of the *Cerrado* native vegetation cover has been converted to alternative land uses, mainly monoculture pastures and crops (Mapbiomas, 2021; Souza et al., 2020), and the remaining native vegetation is often embedded in fragmented landscapes (Aguar et al., 2016; Rosan et al., 2022). The lack of habitat quantity and connectivity can further hamper the chance of propagules

dispersing to new sites. Therefore, upslope migration in the *Cerrado* will depend not only on the elevational affiliation of the species, but also on its dispersal abilities, edaphic requirements and landscape configuration.

4.2 | Lowlands are prone to climate-driven local extinctions

Net species losses will be widespread across the *Cerrado* by 2040 and particularly intense at lower elevations, in line with hypothesis 2. The range expansion predicted to happen among lowland species does not imply that lowlands will benefit from climate change. Lowland/mid-elevation species will lose range at low elevations, where they historically occurred, and expand their range upslope (e.g. *Conarus suberosus*) (Rumpf et al., 2018). The result is net range gain for migrant species, but species richness declines for the assemblage from which these species migrated. The southwest part of the *Cerrado* offers a good example of these phenomena. Even though species losses were widespread across the region, net species losses were more intense at low elevations (e.g. *Cuiabá* Depression) compared to high-elevation areas (e.g. *Parecis* Plateau; Figure 3). The *Cerrado* lowland flora is, therefore, likely to harbour a subset of its historical species pool under climate change, supporting the lowland biotic attrition hypothesis (Bertrand et al., 2011; Colwell et al., 2008; Freeman et al., 2018).

Two processes could offset future biotic attrition in the *Cerrado*'s lowlands. First, migration from other biomes leading to the arrival of non-*Cerrado* species adapted to warmer climates (see Anderson

et al., 2012). Second, niche truncation where the modern climatic envelope of lowland species does not reflect their true fundamental niche (Feeley & Silman, 2010). Successful migrations of species from other biomes, such as seasonally tropical dry forests in the *Caatinga*, are unlikely as they do not possess fire and edaphic adaptations needed to thrive in fire-prone and P-impooverished savannas that cover c. 80% of the *Cerrado* (Simon & Pennington, 2012). Furthermore, even correcting for realized versus fundamental niche mismatch was not enough to prevent widespread species losses in Amazon lowlands (Feeley & Silman, 2010). Assuming low cross-biome migration potential and low niche truncation, our findings suggest that climate change threatens low-elevation *Cerrado* areas by the erosion of local species pools as a consequence of upslope migration.

4.3 | Mountains are likely to harbour a novel flora in a warmer world

Climate change will drive species replacement across the *Cerrado*, especially at higher elevations, consistent with hypothesis 3. The fact that mountains had net species gains coupled with species turnover further suggests that these regions can be refugia for species tracking climate change. Previous studies using hind-casted species distribution models suggested that *Cerrado* mountains played a role as refugia over past climatic events (Bueno et al., 2017; Werneck et al., 2012). Examples are the *Veadeiros* and Upper *São Francisco* Plateaus (Figures 3 and 5). However, Bueno et al. (2017) proposed refugia areas based on species affiliated with mid-elevation areas (500–700 m), such as *C. suberosus*, affiliated to elevations c. 522 m. The *Cerrado*'s mountain ranges may have provided climatic refugia primarily to low- and mid-elevation species, instead of montane ones, in the past. Our findings extend this idea to future climate change. While lowland species find climatic refugia upslope, mountains become unsuitable to present-day montane taxa, exposing them to extinction risk (Dullinger et al., 2012; Freeman et al., 2018).

The models suggest that the number of immigrating lowland species will exceed the number of montane species becoming locally extinct, leading to a net species gain in the *Cerrado* mountains. Transplant experiments and process-based simulations demonstrate that lowland species may outcompete montane species as they move uphill and lead to biotic homogenization (Alexander et al., 2015; Svenning et al., 2014). Our estimates of species richness in the *Cerrado* mountains can be considered optimistic since our SDMs do not account for new competitive interactions that may emerge from upslope migration. *Cerrado* mountains are, therefore, prone to undergo a floristic turnover in the future, characterized by the arrival of lowland 'refugee' taxa due to upslope migration and the decline of mountaintop 'resident' taxa due to climatic suitability loss and potentially competitive exclusion.

4.4 | Model assumptions and scope

Ecological models are simplified, yet useful representations of natural systems and SDMs are no different (Elith & Leathwick, 2009). We consider our predictions best-case scenarios due to two underlying assumptions. First, we assumed that *Cerrado* flowering plants can colonize new habitats by 2040 as long as they are within 250 km of a known occurrence point. Both unrestricted and no-dispersal scenarios are unrealistic, as no plant has either infinite or zero dispersal potential (Cain et al., 2000; Nathan, 2006). The 250 km threshold lies in between unlimited and zero dispersal scenarios and is optimistic given maximal seed dispersal distance tends to be below 100 km (Poulsen et al., 2021, megafauna dispersal). Second, we assumed that only climatic suitability and proximity to an occurrence point constrain the movement of species through the landscape. It is known, however, that vegetation loss and fragmentation, which are extensive in the *Cerrado*, will certainly limit species dispersal (de Barros Ferraz et al., 2021; Sousa et al., 2021). Since the scope of our SDMs was to represent optimistic assumptions, we can then foresee the effects of climate change on the *Cerrado* flora under the best-case scenario. We show that climate change will put *Cerrado* angiosperms at risk even if there were no affiliation to particular soils and fire regimes or if these plants could move freely over an extensive area. Failing in the transition to a sustainable future (SSP1) will further intensify the impacts of climate change on the *Cerrado* flora. Specifically, range contractions, local extinctions and species replacement are expected to occur even if we limit global warming to 1.5°C (SSP1). All these responses will escalate in a 4°C warmer future (SSP5). Global action towards climate change mitigation is, therefore, fundamental to reduce biodiversity loss that will happen in places such as the *Cerrado*.

4.5 | Perspectives for conservation and restoration planning

Our data can assist conservation and restoration decision-makers in adapting to climate change. The species-specific distribution maps are useful to tailor conservation actions to species that are vulnerable to climate-driven extinction. We flagged up to a hundred species facing range contractions exceeding 70% until 2040. For instance, the legume *C. imbricans* is expected to lose 98.3% of its range (Figure 1b), which will be restricted to a small habitat patch in Brazil's Central Plateau (*Planalto Central*). Conservation planners can target regions where the distribution of climate 'loser' species, such as *C. imbricans*, will remain stable for the creation of protected areas (Groves et al., 2012; Sales & Pires, 2023). Besides, the SDMs generated here can also guide assisted migration programmes, that is, tracking climate change by introducing species in newly suitable habitats (Guisan et al., 2013; Hällfors et al., 2017; McKone & Hernández, 2021; McLachlan et al., 2007).

Historical baselines may offer limited insight for selecting species for ecosystem restoration as species numbers and identities are

changing over time due to climate change (Harris et al., 2006; Higgs et al., 2014; Hobbs et al., 2009). S-SDMs can offer practitioners lists of species that will persist over time in a given area, thus boosting climate change resilience in restoration projects (Butterfield et al., 2017; Fremout et al., 2020). The species selection for restoration can be further refined by crossing S-SDM recommendations with the species available on the market as seeds and seedlings (Coutinho et al., 2023; Silva et al., 2022). We have made available an R script based on the analyses presented here for (1) conservationists to visualize the current and future distribution of all the 7398 species studied here, and (2) restoration practitioners to generate lists of species prone to occur in a specified coordinate in the future (2040).

5 | CONCLUSION

Elevation mediates how *Cerrado* flora will respond to climate change. Approximately half of the species will lose range and half will gain range, meaning a balance between climate 'winners' and 'losers'. Moreover, range loss is more intense among montane species ('losers') than lowland species ('winners') since the latter can migrate upslope while the former cannot. Under climate change, lowlands are left with a diminished species pool as species losses surpass species gains. Conversely, the arrival of new species at high elevations outstrips the number of species going locally extinct, resulting in a net species gain and compositional turnover in the mountains. We anticipate that our predictions capture the best-case scenario of how climate change may impact *Cerrado* angiosperms. The realized impact will depend, among other factors, on whether we limit global warming to 1.5°C as well as the dispersal ability of species and habitat quantity and connectivity. Climate change mitigation is key for safeguarding the integrity of *Cerrado* ecosystems in the long term. Additionally, we urge the incorporation of climate adaptation measures into conservation and restoration decision-making to increase climatic resilience in the *Cerrado*.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13832>.

DATA AVAILABILITY STATEMENT

The data and code used to perform the analyses in this study are available on the Figshare online repository. Access to full data on https://figshare.com/projects/Divers_Distrib/183343 or the individual files on <https://doi.org/10.6084/m9.figshare.24559669.v2>, <https://doi.org/10.6084/m9.figshare.24559897.v2> and <https://doi.org/10.6084/m9.figshare.24559651.v1>.

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BIOSKETCH

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Author contributions: MS, LR, RTP and PT designed the study. MS performed the analysis and drafted the manuscript. All the authors contributed to the final version of the article and approved its submission.

SUPPORTING INFORMATION

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

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