RODRIGO GOMES GORSANI

‘*CAMPO DE ALTITUDE*’: CLIMATE CHANGES IN TIME AND SPACE

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Doctor Scientiae*.

Orientador: Andreza Viana Neri

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Andreza Viana Neri
Orientador

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“Se a educação sozinha não transforma a sociedade, sem ela tampouco a sociedade muda.”

"If education alone does not transform society, without it, society also does not change."

Paulo Freire

ABSTRACT

GORSANI, Rodrigo Gomes, D.Sc., Universidade Federal de Viçosa, November, 2023. **'*Campo de Altitude*': Climate changes in time and space.** Adviser: Andreza Viana Neri.

The *Campos de Altitude* are habitats restricted to a narrow eco-orographic strip within the Atlantic Forest domain, which is one of the world's biodiversity hotspots. *Campos de Altitude* are found along the mountain tops of southeastern and southern Brazil, particularly in the *Mantiqueira* and *Mar* Mountains ranges. They generally occur above 2000m in the Southeast region of Brazil, while in the southern regions, their elevation drops to around 1000m. Between 120,000 years before the present (ky BP) and 100 ky BP, the planet underwent its last glacial maximum (LGM), a period during which the average annual temperature was up to 10°C lower than today. This led to a prevalence of grassland vegetation across central Brazil, while forests were restricted to lowlands. Recent decades have seen significant anthropogenic global changes, resulting in various impacts on vegetation. These responses include shifts in geographic distribution, alterations in community composition and dominance, increased extinction risk for mountaintop species, and altitudinal migrations. Biological invasion is one anthropogenic impact that may be exacerbated by climate change, posing a significant threat to areas with high endemism. Beyond its rich biodiversity, *Campos de Altitude* also provide essential ecosystem services such as soil stabilization, maintenance of hydrological properties, and carbon storage. In this context, our objectives were to contribute to the understanding of climate change's impacts on the geographical distribution of *Campos de Altitude* in the *Serra do Mar* and *Mantiqueira* mountain ranges under future global climate change scenarios (Chapter 1). We also aimed to investigate the potential richness of invasive species in areas predicted to be suitable for *Campos de Altitude* under the same future scenarios (Chapter 2). Lastly, we explored the possible paleodistribution of *Campos de Altitude* during various climatic periods of the Quaternary to determine when and if a connection existed between *Campos de Altitude* and the Andean Mountains (Chapter 3). The future projections unmistakably indicate a significant decline in areas both climatically and topographically suitable for *Campos de Altitude* during the 21st century, with substantial losses in nearly all future scenarios. By 2050, the results indicate considerable losses in suitable area (>=95%), with total extinction in other scenarios by 2070. We also identified a potential richness of invasive species of 35 in the current time, and this number is expected to remain closer this in the higher elevation areas of *Campos de Altitude* in future scenarios. Furthermore, we found evidence of a potential historical connection between the Andean mountain range and *Campos de Altitude* through the Cerrado and the southern Amazonian forest approximately 18,000 years before the present. These findings illustrate that *Campos de Altitude* are a product of climatic changes during the Quaternary period, and at the same time, climate change poses the most significant threat to the future of *Campos de Altitude*.

Keywords: High altitude grassland; Global climate change; Species distribution modelling; Biological Invasion; Quaternary

RESUMO

GORSANI, Rodrigo Gomes, D.Sc., Universidade Federal de Viçosa, novembro de 2023. **‘*Campo de Altitude*’: Mudanças climáticas no tempo e espaço**. Orientador: Andreza Viana Neri

O Campos de Altitude são habitats restritos a uma estreita faixa eco-orográfica dentro do domínio da Mata Atlântica, um dos hotspots de biodiversidade do mundo. Os Campos de Altitude são encontrados principalmente nos topos das montanhas do sudeste e sul do Brasil, em particular nas Serras da Mantiqueira e do Mar. Geralmente ocorrem acima de 2000m na região Sudeste, enquanto nas região Sul, também são encontrados a cerca de 1000m de altitude. Entre 120.000 e 100.000 anos antes do presente, o planeta passou pela Último Máximo Glacial (UMG), um período em que a temperatura média anual era até 10°C mais baixa do que hoje. Isso resultou na predominância de vegetação de campos em grande parte do Brasil central, enquanto as florestas eram restritas a regiões de baixa altitude. As últimas décadas testemunharam mudanças globais significativas de origem antropogênica, resultando em diversos impactos na vegetação. As respostas das vegetações incluem mudanças na distribuição geográfica, alterações na composição e dominância das comunidades, aumento do risco de extinção de espécies de montanhas e migrações altitudinais. A invasão biológica é um impacto antropogênico que pode ser exacerbado pelas mudanças climáticas, representando uma ameaça significativa para áreas com alto endemismo. Além de sua rica biodiversidade, os Campos de Altitude também fornecem serviços ecossistêmicos essenciais, como a estabilização do solo, a manutenção das propriedades hidrológicas e a estocagem de carbono. Nesse contexto, nossos objetivos foram contribuir para a compreensão dos impactos das mudanças climáticas na distribuição geográfica dos Campos de Altitude nas cadeias de montanhas da Serra do Mar e Mantiqueira sob cenários futuros de mudanças climáticas globais (Capítulo 1). Também tivemos como objetivo investigar a riqueza potencial de espécies invasoras em áreas previstas como adequadas para os Campos de Altitude nos mesmos cenários futuros (Capítulo 2). Por fim, exploramos a possível paleodistribuição dos Campos de Altitude durante vários períodos climáticos do Quaternário para determinar quando e se existiu uma conexão entre os Campos de Altitude e a Cordilheira dos Andes (Capítulo 3). As projeções futuras indicam claramente uma redução significativa nas áreas tanto climática e topograficamente adequadas para os Campos de Altitude durante o século XXI, com perdas substanciais em quase todos os cenários futuros. Para 2050, os resultados indicam perdas consideráveis na área adequada (>=95%), com extinção total em outros cenários até 2070. Também identificamos uma riqueza potencial de espécies invasoras de 35 nas atuais condições climáticas, e espera-se que esse número se mantenha-se neste patamar alto nas áreas de maior altitude dos Campos de Altitude nos cenários futuros. Além disso, encontramos evidências de uma possível conexão histórica entre a Cordilheira dos Andes e os Campos de Altitude por meio do Cerrado e do sul da Amazônia, há aproximadamente 18.000 anos antes do presente. Essas descobertas ilustram que os Campos de Altitude são um produto de mudanças climáticas durante o período do Quaternário e, ao mesmo tempo, as mudanças climáticas representam a maior ameaça ao futuro dos Campos de Altitude.

Palavras-chave: Campos de Altitude; Mudanças climáticas globais; Modelos de distribuição de espécies; Invasão biológica; Quaternário

SUMÁRIO

Introduction

The *Campos de Altitude* are one of the mountain ecosystems generally treated as part of other biomes or biogeographical regions, and represent a small part of the Brazilian territory, forming a terrestrial archipelago of tiny habitats restricted to a narrow eco-orographic strip included in the Atlantic Forest domain, one of the world's biodiversity hotspots (Benites et al., 2003; Gastauer et al., 2020; Martinelli, 2007; Myers et al., 2000; Safford, 1999a).

Campos de Altitude are found along the mountain tops of southeastern and southern Brazil, with the greatest floristic and geographical development in the *Serra do Caparaó*, *Mantiqueira* and *Mar* Mountains ranges (Safford, 1999b), and some smaller occurrences in the *Serra do Brigadeiro* and southeastern *Minas Gerais*, the southern part of *Mantiqueira* in *Campos do Jordão* in *São Paulo* State, the central part of *Rio de Janeiro* State and on some peaks in *Santa Catarina* and *Paraná* (Iganci et al., 2011; Pillar et al., 2009; Safford, 1999b).

Altitude, temperature, availability of energy for metabolism, species-area effects and shallow, oligotrophic soils are strong environmental filters that determine the composition and structure of plant communities in *Campos de Altitude* (Benites et al., 2003; Gastauer et al., 2020; Neri et al., 2016). It is a vegetation with high environmental heterogeneity and limited dispersal, composed mainly of grasses and shrubs with climatic seasonality, representing the fifth vegetation type with the most endemic angiosperm species in Brazil, 479 (21.8% of the species found in this environment) (BFG, 2015; Safford, 1999a).

The geological substrate on which the *Campos de Altitude* occur varies from medium to highly metamorphosed granites and gneisses to quartzites associated with schists in *Ibitipoca* and silica-poor, feldspar-rich syenites in *Itatiaia* National Park (Benites et al., 2003). The geomorphological surface is similar to plateaus, with rounded and undulating hills, large expanses of bare rock and sometimes cliffs, a product of the rugged terrain and high altitudes (Benites et al., 2003; Safford, 1999b), allowing only shallow soils, sometimes no more than a thin organic layer over the bedrock (Benites et al., 2003). The sparse vegetation cover gives way to grasses and herbaceous plants as the soil becomes thicker, and small patches of forest (*capões de mata*) occur on soils 1 m thick or more (Benites et al., 2003).

Oligotrophism is one of the common characteristics of soils in *Campos de Altitude* and other rupicolous complexes, resulting from high leaching and poor parent material (especially quartzite), as well as yellow hues, sandy texture and high levels of exchangeable aluminium (Benites et al., 2003). The dark colour of the surface horizons is due to the accumulation of organic matter, also caused by the low average temperatures, while the presence of charcoal fragments and the high melanisation of the organic matter suggest the pyrogenic origin of these compounds (Benites et al., 2003).

At 120,000 years before the present (ky BP), the planet experienced its last glacial maximum (LGM), which lasted until about 100 ky BP, a period during which the planet's average annual temperature was as much as 10º C lower than today and caused drastic changes in the vegetation dynamics of South America (Arruda and Schaefer, 2020). In general, glacial periods were not only much colder but also drier, while interglacial periods were significantly warmer and wetter (Safford, 1999b).

During the LGM, grassland vegetation dominated most of central Brazil, with the expansion of Araucaria forests as far as southwestern *Minas Gerais* and an increase in grassland systems in southern and southeastern Brazil (Arruda et al., 2018; Arruda and Schaefer, 2020; Behling, 2002; Behling et al., 2004; Behling and Hooghiemstra, 2001; Carnaval and Moritz, 2008). At the end of the LGM, near the Middle Holocene, 6 ky BP, there were increases in temperature and precipitation, as well as pollen evidence of cloud forests and species of the genus *Podocarpus* in the southeastern highlands, and *Araucaria* forming mosaics with *Campos de Altitude* in southern Brazil (Safford, 1999b).

Anthropogenic global change has been dramatic in recent decades, with an increase in the global mean land surface temperature of 1.5ºC already recorded for the period 2011-2020 compared to the period 1850-1900 (Antonelli et al., 2023; IPCC et al., 2023). Tropical mountains are highly vulnerable to global change and tend to experience more dramatic changes. These habitats are more sensitive to thermal changes in the surface of the oceans, which are already 1.1°C warmer than between 1850 and 1900, and affect the intensity of climate events such as *El Niño* and *La Niña* (Assis and de Mattos, 2016; IPCC et al., 2023; Scarano et al., 2016).

Vegetation impacts and responses to global climate change have been observed, such as changes in geographic distribution, community composition and dominance, ecophysiological and phenological changes, extinction risk for mountaintop species, and altitudinal migration of other species with wider geographic distributions that may seek refuge on mountaintops (Assis and de Mattos, 2016; Scarano et al., 2016). Such responses reflect the search for habitats with more suitable climatic conditions, but this is less likely for endemic species than, for example, native species (Manes et al., 2021). Endemic species, which tend to have smaller geographical ranges, are predicted to be at greater risk of extinction globally (Staude et al., 2020). The world's biodiversity hotspots are projected to lose up to 31% of their current climatic conditions by 2080, affecting an average of 25% of endemic species, and among these habitats, mountain ecosystems are at much greater risk of species loss than lowlands (Manes et al., 2021).

Biological invasion is an anthropogenic impact that may be exacerbated by climate change (Scarano et al., 2016). Areas with high endemism are particularly vulnerable to the introduction of species with invasive potential, especially if endemic species have lower competitive potential compared to invasive species (Manes et al., 2021). In the context of global climate change, with increases in carbon concentration and average temperature, competitive exclusion of native species has been documented on a global scale (Manes et al., 2021; Wang et al., 2019).

In these cases, the continued compression of the geographical distribution of endemic species and their progressive replacement by a few generalist and widespread species can lead to biotic homogenisation (Holl et al., 2022; Manes et al., 2021). This, together with the consequent loss of taxonomic and functional diversity in fragmented anthropogenic landscapes with recurrent disturbances, are positive feedback for biotic homogenisation and therefore a major conservation concern under global climate change scenarios (Holl et al., 2022; Ribeiro and Freitas, 2010; Wang et al., 2019).

In addition to their high biodiversity, *Campos de Altitude* provides ecosystem services such as soil stabilisation and reduction of erosion and landslides, as well as maintaining the hydrological properties of several Brazilian river basins, play an important role as a carbon stock, which is still little understood, and provide diverse natural resources in addition to recreation, tourism and spiritual value for traditional communities (Martinelli, 2007; Overbeck et al., 2022; Ribeiro and Freitas, 2010).

Therefore, in this context of extreme vulnerability to anthropogenic impacts and global climate change, high biodiversity and endemism of a relict flora, and provision of various environmental services, it is necessary to understand how serious the threat of global climate change is for the biogeography of *Campos de Altitude*. It is also essential to recognise the need to include the *Campos de Altitude* in public policies for conservation, preservation, monitoring, inspection, sustainable use and recognition of Brazil's extreme natural wealth (Overbeck et al., 2022, 2015). In this sense, studies with broad approaches that measure aspects of the landscape at a regional scale are important to understand how *Campos de Altitude* will respond in terms of the geographical distribution of its species and biological invasion by exotic species.

Therefore, this thesis aims to contribute to the knowledge of Brazilian tropical mountain ecosystems by filling some gaps regarding the geographical distribution of *Campos de Altitude* on the peaks of *Serra do Mar* and *Mantiqueira* under future scenarios of global climate change (Chapter 1), as well as investigating the potential richness of invasive species in areas predicted to be suitable for *Campos de Altitude* under different future climate change scenarios (Chapter 2). In addition, we sought to understand and map the possible palaeodistribution of *Campos de Altitude* during some different climatic moments of the Quaternary and to determine when and if there was a connection between *Campos de Altitude* and the Andes in the far west of South America (Chapter 3).

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Chapter 1 - *'CAMPOS DE ALTITUDE'* AND GLOBAL CLIMATE CHANGE: TOPO-CLIMATIC MODELS PROJECT MAJOR LOSSES IN THE 21ST CENTURY

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Abstract

Campos de Altitude is a shrub and grassland vegetation found on the highest peaks of the *Mar* and *Mantiqueira* mountain ranges in the Atlantic Forest biome of eastern South America. It is a unique habitat for a rich endemic flora highly threatened by climate change and its consequences such as habitat loss and species migration in search of suitable environmental conditions. To investigate the potential impact of climate change on *Campos de Altitude*, we employed species distribution models using data from eight indicator species of the *Campos de Altitude* as a proxy for this ecosystem to assess the topographic and climatic suitability of the *Campos de Altitude* under current and future Intergovernmental Panel on Climate Change (IPCC) climate change scenarios. We projected models for the future based on Representative Concentration Pathway (RCP) scenarios from the Fifth Assessment Report (AR5) and Shared Socioeconomic Pathways (SSP) scenarios from the Sixth Assessment Report (AR6) of the IPCC. The current projections account for between 22,230.69 and 23,974.12 km² of topo-climatically suitable areas for *Campos de Altitude*. Additionally, we generated a previously unpublished map of *Campos de Altitude* distribution in Brazil. In RCP scenarios, the results indicate near-complete loss of suitable areas by 2050 and the total extinction of *Campos de Altitude* in all scenarios by 2070. Losses in the SSP future scenarios range from 19.15% to 98.65% of suitability for *Campos de Altitude*. Our findings underscore the urgent need for rapid climate change mitigation. Furthermore, we propose that it may be necessary to reconsider strategies for safeguarding the biodiversity of the Brazilian Atlantic montane forest in a rapidly changing world.

Keywords

High Altitude Grasslands, species distribution modelling, habitat loss, mountaintop vegetation, Atlantic Forest

Introduction

Tropical mountains support some of the most biodiverse ecosystems on the planet (Antonelli et al., 2018; Payne et al., 2020; Rahbek et al., 2019). At the same time, tropical montane ecosystems are among the most threatened in the world, by direct human disturbances and by anthropogenic climate change (Rahbek et al., 2019). One of the most endangered areas of tropical montane ecosystems is the Atlantic Forest biome in eastern South America, which has been drastically reduced of its original extent (Rezende et al., 2018; Ribeiro et al., 2009). Aside from extensive areas of montane forest, the Atlantic Forest biome also supports a unique ecosystem type known in Brazil as the *Campos de Altitude*, which are paramo-like shrub- and grasslands found on the highest summits of the Mar and Mantiqueira Mountain ranges (Safford, 1999a; Vasconcelos, 2011). Although most occurrences of *Campos de Altitude* are protected at some level in State and Federal conservation units, they are small, scattered, and highly vulnerable to a suite of human-influenced disturbances and stressors, including fire, grazing, wild plant collecting, and climate change (Assis and de Mattos, 2016; Martinelli, 2007; Safford, 1999a; Scarano et al., 2016).

Climate change is predicted to drive a number of notable changes in Brazilian montane ecosystems, including habitat loss, species migration upwards, invasion of exotic species with higher competitive potential and alteration of vegetation belts along the altitudinal gradient (Assis and de Mattos, 2016; Martinelli, 2007; Scarano et al., 2016; Steinbauer et al., 2018). Changes in taxonomic, functional, and genomic diversity are expected, as well as alterations to unique and important ecosystem services, with potentially important on human populations and economic activities (Steinbauer et al., 2018). Upward migrations, habitat loss and communities structure changes have already been observed in other mountain ecosystems over the last four decades, including the Himalayas (Mohapatra et al., 2019), Alps and Pyrenees (Gottfried et al., 2012), in the Andean páramos (Peyre, 2022; Peyre et al., 2020), the Pantepui Region (Nogué et al., 2009), and campos rupestres ("rocky grasslands") in the highlands of the Brazilian cerrado (Bitencourt et al., 2016; Fernandes et al., 2018).

The |*Campos de Altitude* are located in the highest points of the mountains inserted in the Atlantic Forest (Mar and Mantiqueira Mountain Ranges) and the only representative of the "cold humid tropics" in the eastern half of the continent (Safford, 1999b). *Campos de Altitude* is a refuge habitat for a large number of endemic species, 21.8% (479) of the total plant species found in there (Zappi et al., 2015). As such, the *Campos de Altitude* and their rare and endemic biota are uniquely exposed to the effects of climate warming (Scarano et al., 2016). The most extensive occurrences of *Campos de Altitude* are found above 2000 m elevation, but closer to the ocean and in southern Brazil, *Campos de Altitude* can be found down to c. 1500 m (Safford and Martinelli, 2000). Paleoecological work shows that *Campos de Altitude* were widely distributed in SE Brazil during glacial periods of the Pleistocene, but Holocene warming and generally increased precipitation have greatly reduced their extent due to forest expansion (Behling et al., 2020; Guarinello de Oliveira Portes et al., 2020).

Recent work on *Campos de Altitude*, which is still needed for many regions of its distribution, has highlighted its great taxonomic diversity and addressed the structuring of these unique plant communities (Caiafa and Silva, 2007; Campos et al., 2020, 2018; Cordeiro and Neri, 2019; Mocochinski and Scheer, 2008; Ribeiro et al., 2007; Tinti et al., 2015), as well as describing the soils associated with such formations (Benites et al., 2003) and the influence of vegetation on soil organic matter (Balieiro et al., 2012). The functional ecology, environmental factors and phylogenetic diversity that act to assemble these communities with high diversity and endemism have also been studied (Christmann et al., 2021; Gastauer et al., 2020; Neri et al., 2016), but there is still a lack of work investigating the possible consequences of anthropogenic climate change on *Campos de Altitude* (Martinelli, 2007; Safford, 1999a; Scarano et al., 2016).

Species distribution models (SDM) are one of the tools often used to predict explicit changes in species distribution, based on the observation of species occurrence and statistical relationships with environmental descriptors, projecting the results in geographical space (Elith and Leathwick, 2009; Sánchez-Tapia et al., 2020). In this context, we used SDM to study the impact of global climate change on the distribution of *Campos de Altitude* in the peaks of *Serra do Mar* and *Mantiqueira* under different scenarios of greenhouse gas emissions and mitigation actions. We hypothesize that the *Campos de Altitude* of southeastern and southern Brazil will lose suitable area and may disappear due to global climate change. To test this hypothesis, we will: 1) assess the topographic and climatic suitability of the *Campos de Altitude* under future scenarios of greenhouse gas emissions and mitigation actions; 2) measure the suitable area for the *Campos de Altitude* in southern and southeastern Brazil; 3) quantify how much of the suitable area is within existing protected areas and how much is outside current protected areas; and finally 4) produce a map of topo-climatic suitability for the *Campos de Altitude* at a scale never before done.

Materials and Methods

Study Region

The study area encompasses the South and Southeast political regions of Brazil, where the *Campos de Altitude* are situated, spanning between the coordinates 20º and 30º S and 40º and 52º W. This habitat is closely associated with the *Serra do Mar* and *Serra da Mantiqueira* Mountain ranges, which extend along the eastern coast of Brazil (Fig. 1) and are characterized by a mosaic of shrubs and trees interspersed within a matrix of grasses. They also feature the presence of pteridophytes, bamboo species (Chusquea spp.), and other herbaceous plants, along with rocky outcrops of varying sizes (Caiafa and Silva, 2007; Cordeiro and Neri, 2019).

In the Southeast region (comprising the states of *Espírito Santo, Minas Gerais, Rio de Janeiro,* and *São Paulo*) the *Campos de Altitude* occur between 1800 and 2980 m altitude and are the coldest points in eastern South America often affected by freezing temperatures in winter (Neri et al., 2016; Safford, 1999b; Scarano, 2009) (Fig. 1). *Campos de Altitude* are associated with mountain tops and rocky granite-gneiss outcrops in their great majority, and climates Cfb and Cwb (Overbeck et al., 2022; Safford, 1999b, 1999a). The Cfb (**C**-humid subtropical, **f**-oceanic climate without dry season and **b**-with temperate summer by Köppen's climate classification according Alvares et al., (2013)) climate is characterized by mesothermal with average annual temperature between 12° and 20° C, with moderate winter and mild and humid summer (Overbeck et al., 2022; Safford, 1999b, 1999a). And the Cwb climate (**C**-humid subtropical, **w**-with dry winter and **b**-and temperate summer by Köppen's climate classification according Alvares et al., (2013)) is characterized by an annual average below 12° C, moderately cold winter and cool summer in the mountain tops in which frosts are frequent and snow rarely occurring (Overbeck et al., 2022; Safford, 1999b, 1999a). Annual rainfall varies from 1000 to over 2500 mm (Safford, 1999a).

In the South region of Brazil (composed of *Paraná, Santa Catarina* and *Rio Grande do Sul* states), the *Campos de Cima da Serra* (local name for the *Campos de Altitude*) are associated with the southern Brazilian plateau formed by igneous rocks. They are grouped under the umbrella term *Campos Sulinos* (Iganci et al., 2011; Overbeck et al., 2022). In these areas *Campos de Altitude* ocur from 1000 m to 1800 m altitude at latitudes 24° and 30° S, often forming vegetation mosaics with the Araucaria forests (Iganci et al., 2011; Safford, 1999a, 1999b) (Fig. 1). The climate according to Köppen is humid temperate (Cfb) and humid subtropical (Cfa, **C**-humid subtropical, **f**-oceanic climate without dry season and **b**-with hot summer according Alvares et al., (2013)) with well distributed precipitation during the year, averaging between 1500 and 1700 mm, possibly reaching 2500 mm and annual average temperature 14º to 16º C (Iganci et al., 2011).

The *Campos de Cima da Serra* (Subtropical Highland Grasslands or South Brazilian highland Grasslands - Iganci et al., 2011; Overbeck et al., 2022) despite geomorphological and floristic differences with the *Campos de Altitude* (High Altitude Grasslands/Brazilian *Páramos* or Highland Grasslands - (Overbeck et al., 2022; Safford, 1999a) of southeastern Brazil, hereafter collectively called *Campos de Altitude*, are considered in this study due to the co-occurrence of some species from our vegetation database, as well as their climatic and altitudinal similarity.

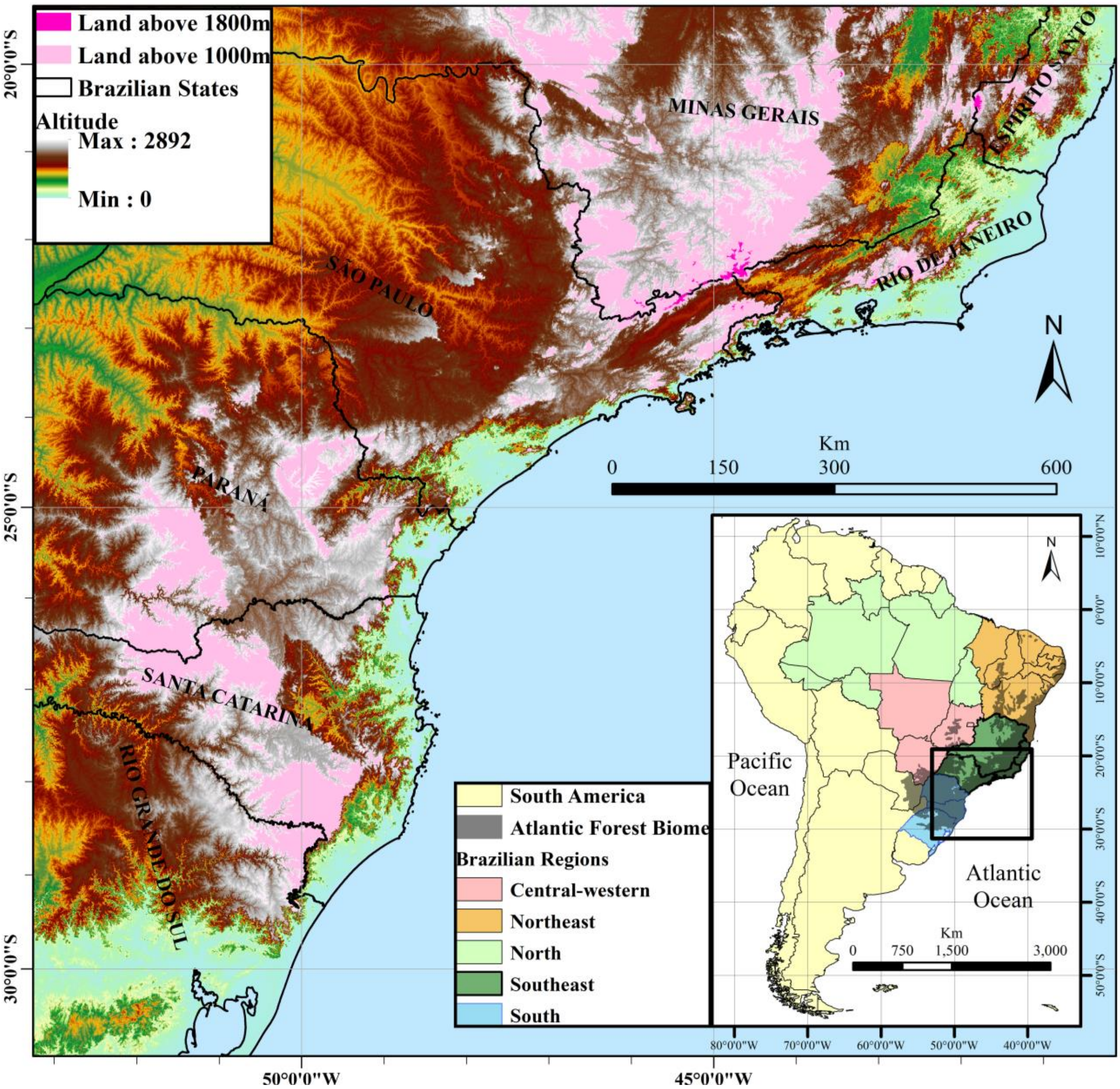


Figure 1: *Campos de Altitude* study area in the South administrative region, highlighted in light blue, where it occurs above 1,000 metres above sea level (areas highlighted in light pink), and in the South-eastern region, highlighted in green, where *Campos de Altitude* occurs above 1,800 metres above sea level (areas highlighted in pink).

Species Dataset

Our dataset includes 131 sites ranging from 5° S to 28º S and 58º W to 35º W along the east of South America, distributed across five Brazilian biomes (Caatinga, Cerrado, Atlantic Forest, Amazon and Pantanal). The ROutVe (Rock Outcrops Vegetation) dataset is a list of species using information available in published literature from four Brazilian rocky outcrop ecosystems: *Campos de Altitude, Inselberg*, *Campo Rupestre* (generally called Rupestrian Grasslands) and *Campo Rupestre Ferruginoso* (Ferruginous Rupestrian Grasslands or *Cangas*) and it is dedicated to understanding the influence of environmental filters and global change scenarios on Rock Outcrops Vegetation of Brazil.

We performed an indicator species analysis, ISA (Dufrene and Legendre, 1997), on this dataset to identify the species that indicate typical *Campos de Altitude* vegetation communities. The ISA is a combination of specificity, which represents the frequency with which the occurrence of the species is observed, and fidelity, which represents the degree of association of a given species with the observed sites (Dufrene and Legendre, 1997) (Table 1). The analysis was performed with software R Statistical Software (R Core Team) using the ‘multipatt’ function in the ‘indicspecies’ package (De Cáceres et al., 2010).

Geographical records of the occurrence of the selected species for the *Campos de Altitude* were retrieved from the Global Biodiversity Information Facility - GBIF portal (GBIF, 2023) and *species*Link Network (specieslink.net/search). These records were filtered by removing repeated points and visually checked individually using satellite imagery at Google Earth Pro to determine whether their coordinates corresponded to locations in the *Campos de Altitude* or to another land use or vegetation type. Additional information on each indicator species is provided in Supplementary Material Table S1.

Table 1: Results from ISA to *Campos de Altitude* in Brazil. IV – indicator value, *p* – statistical significance of the Monte Carlo test between species and *Campos de Altitude* sites from the ROutVe dataset, and NSR – number of species records after filtering.

Indicator Species for *Campos de Altitude* habitats	**IV**	***p***	**Botanic Family**	**NSR**
Gaultheria serrata (Vell.) Sleumer ex Kin.-Gouv.	0.767	0.005	Ericaceae	49
Utricularia reniformis A.St.-Hil.	0.728	0.005	Lentibulariaceae	42
Croton splendidus Mart.	0.717	0.005	Euphorbiaceae	56
Pleroma hospitum (Schrank et Mart. ex DC.) Triana	0.642	0.005	Melastomataceae	56
Abatia americana (Gardner) Eichler	0.608	0.01	Salicaceae	31
Fuchsia regia (Vell.) Munz	0.607	0.025	Onagraceae	68
Clethra uleana Sleumer	0.594	0.01	Clethraceae	23
Agarista niederleinii (Sleumer) Judd	0.594	0.015	Ericaceae	10
			Total Records	**335**

Bioclimatic and topographic variables

We used two different datasets from WorldClim. The standardized bioclimatic variables in the 30-second spatial resolution provided by WorldClim1.4 (Hijmans et al., 2005) based on climate data for 1960-1990, and derived from Coupled Model Intercomparison Project Phase 5 - CMIP5 of the World Climate Research Programme that bases The Physical Science Basis: Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2013) (Table 2).

We also used the same bioclimatic variables from WorldClim2.1 (Fick and Hijmans, 2017) based in climate data for 1970-2000 and are derived from CMIP6 released in 2021, within The Physical Science Basis: Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2021). Both datasets are at the 30 arc-second resolution (0.86 km² at the equator, ~ 1km²) (Table 2). We also used de geology associated with *Campos de Altitude*, such as granitic intrusions, migmatites and gneiss-migmatitic complex, the relief (mountainous and cliff domains), slope (> 25º) and elevation (> 300 m asl), to building a binary variable that predominantly represent the areas associated to *Campos de Altitude*. The shapefiles containing the geological information were obtained from the Brazilian Geological Survey (GEOSGB, 2020) and processed by ArcMap software (ESRI, 2015) with pixel resolution of ~ 1 km² (Table 2). This resolution (<1km) was crucial because we were analysing mountain environments with high variability which is lost at lower resolutions (Hijmans et al., 2005).

All layers have been clipped in the current political-geographical division of the Southeast (states of *Espírito Santo, Minas Gerais, São Paulo,* and *Rio de Janeiro*) and South (states of *Paraná, Santa Catarina,* and *Rio Grande do Sul*), which includes areas of higher elevation and consequent occurrence of *Campos de Altitude* species (Fig. 1).

Table 2: Variables used in the present and future prediction models. The Variable column gives the short name of the variable, the Description column gives the full name and, where applicable, how the variable was obtained, the Source column gives the website where it can be accessed and its respective publication in the Citation column, and finally the spatial resolution used in this study. Variables marked with an asterisk (*) are those that are not used in the CMIP5/Maxent models for future scenarios, nor in the CMIP6/Ensemble models, because they are not projected into the future.

Variable	**Description**	**Source**	**Citation**	**Spatial Resolution**
bio_01	Annual Mean Temperature	WorldClim version 1.4 from CMIP5 of the IPCC (2013) for **CMIP5/Maxent Models** AND WorldClim version 2.1 from CMIP6 by IPCC (2021), for **CMIP6/Ensemble Models**. Both are available at https://worldclim.org/data/index.html	CMIP5 data - (Hijmans et al., 2005); CMIP6 data - (Fick and Hijmans, 2017).	0.86 km^2 at the equator (~ $1km^2$)
bio_02	Mean Diurnal Range (Mean of monthly (max temp - min temp))			
bio_03	Isothermality (BIO2/BIO7) (×100)			
bio_04	Temperature Seasonality (standard deviation ×100)			
bio_05	Max Temperature of Warmest Month			
bio_06	Min Temperature of Coldest Month			
bio_07	Temperature Annual Range (BIO5-BIO6)			
bio_08	Mean Temperature of Wettest Quarter			
bio_09	Mean Temperature of Driest Quarter			
bio_10	Mean Temperature of Warmest Quarter			
bio_11	Mean Temperature of Coldest Quarter			
bio_12	Annual Precipitation			
bio_13	Precipitation of Wettest Month			
bio_14	Precipitation of Driest Month			
bio_15	Precipitation Seasonality (Coefficient of Variation)			
bio_16	Precipitation of Wettest Quarter			
bio_17	Precipitation of Driest Quarter			
bio_18	Precipitation of Warmest Quarter			

bio_19	Precipitation of Coldest Quarter			
geology	Geology	http://geosgb.cprm.gov.br/	(GEOSGB, 2020)	~ 1km²
northness	Aspect Northness	http://www.earthenv.org/topography	(Amatulli et al., 2018)	~ 1km²
eastness	Aspect Easteness			~ 1km²
elevation	Elevation			~ 1km²
roughness	Roughness			~ 1km²
slope	Slope			~ 1km²
tpi	Topographic Position Index			~ 1km²
tri	Terrain Ruggedness Index			~ 1km²
Aridity*	Global Aridity Index	https://csidotinfo.wordpress.com/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v3/	(Zomer et al., 2022)	~ 1km²
pot_evapo*	Global Potential Evapotranspiration			~ 1km²
m_an_rad*	Mean Annual Solar Radiation	https://www.worldclim.org/data/worldclim21.html	(Fick and Hijmans, 2017)	~ 1km²
m_an_wspe*	Mean Annual Wind Speed			~ 1km²
ma_evapo*	Mean Annual Actual Evapotranspiration	https://cgiarcsi.community/data/global-high-resolution-soil-water-balance/	(Trabucco and Zomer, 2019)	~ 1km²
mcloud_co*	Mean Annual Cloud Cover	http://www.earthenv.org/cloud	(Wilson and Jetz, 2016)	~ 1km²

Model Construction and validation

The occurrence records of the 8 species obtained by ISA (Table 1) were used as unique taxonomic entity serving as a proxy for the *Campos de Altitude* ecosystem to model the current and future distribution in different climate change scenarios and datasets.

The background modelling layers were the political-geographical divisions of the Southeast and South regions of Brazil, which include the areas of higher elevation and consequent occurrence of *Campos de Altitude* species (Fig. 1). All layers were clipped by this political-geographical divisions for all model groups. In addition, the topographic variables were the same for all future scenarios because these are very unlikely to change during the current century and are fundamental drivers of environmental and microhabitat definition in the *Campos de Altitude* ecosystem.

CMIP5/Maxent

The Maximum entropy approach (Maxent) (Phillips et al., 2017) and CMIP5 dataset were used to generate the first set of models and hereafter referenced as CMIP5/Maxent Models. We choose Maxent because it uses only presence data since data on the absence of species registration are rare and challenging to collect (Phillips and Dudík, 2008).

In the CMIP5/Maxent models, we excluded climate variables with Pearson correlation (ρ) greater than 0.7 (+0.70 and -0.70), and those with reduced ecological importance for *Campos de Altitude*. We used the Correlations and Summary Stats function provided by SDMToolBox (Brown, 2014) for ArcGis (ESRI, 2015). All variables used in the models are described in Table 2.

The current prediction models were projected using 15 climatic variables and 8 topographic variables. The future prediction models were projected using only the topographic and WorldClim variables projected under different scenarios (Table 2). The future models were generated under two future scenarios, the Representative Concentration Pathways (RCPs), RCP4.5 and RCP8.5, defined by the scientific community for the Fifth Assessment Report (AR5) (IPCC, 2013), hereafter referred to as optimistic and pessimistic scenarios, respectively. More details on each scenario can be found in Table 3. Each scenario (RCP4.5 and RCP8.5) projects variables for two time periods 2050 (average for 2041-2060) and 2070 (average for 2061-2080) from two Global Climate Models - GCMs - CCSM4 (Gent et al., 2011) and MIROC5 accounting 9 scenarios in total (WCRP, 2013) (Table 3).

To visualize the possible differences between the GCMs projections we used the GCMeval website, available at https://gcmeval.met.no/ (Parding et al., 2020). This web tool allows the user to evaluate the differences between the GCMs in both RCPs scenarios for the near future (2050) and far future (2100). To the RCP4.5 scenario, both GCMs do not differ from the annual mean climate change from the other GCMs for Southeastern South America, and the same patterns are identified for this RCP in the far future. For the RCP8.5 scenario in the near future, both GCMs do not differ while for the far future, MIROC5 represents a low temperature increase than the annual mean climate change predicted by all other GCMs and CCSM4 is close to the annual mean climate change for temperature and precipitation.

Species occurrence points was used for training (70%) and for testing (30%) with 10 subsample replications. The average models from 10 runs were used to add both GCMs by time-period (2050 and 2070) and RCPs scenarios. We choose the Maximum training sensitivity plus specificity Cloglog threshold to generate the robust binary final map for each scenario (Liu et al., 2005). The final CMIP5/Maxent models were binarized (CCSM4 + MIROC5) using the simple average of the threshold values of both GCMs.

The Area Under the receiving operator Curve (AUC) was used to evaluate the models. The AUC is a single measure of the model performance that do not depend on any choice of threshold and represents a better fit of the model when closer to 1 (Phillips et al., 2006). The final processing steps to calculate the total area suitable to *Campos de Altitude* will be carried to the current and future scenarios performed in ArcGIS ver. 10 (ESRI, 2015).

CMIP6/Ensemble

A second set of models was projected using the CMIP6 dataset and an ensemble approach model was carried out in "modleR" library in R (Sánchez-Tapia et al., 2020) which in the last step allows the user to do an ensemble from different algorithms outputs. This set of models (hereafter CMIP6/Ensemble models) used the same dataset for occurrence points and environmental variables from CMIP5/Maxent models.

To choose the GCMs from the CMIP6 dataset we used again the GCMeval website. In this case, we can evaluate the distribution of precipitation and temperature variation between the GCMs only for the SSP5-8.5 scenario for the near future (2021-2050) and far future (2071-2100). For both moments in the 21st century, the CanESM5 represents high temperature and low precipitation compared to the annual mean climate change from the other GCMs for Southeastern South America. While the MIROC6 represents a lower temperature and high precipitation shifts from other GCMs and BCC-CSM2-MR wherein precipitation and temperature are close to the annual mean climate change from all other GCMs (Table 4). All these multiband layers were clipped by the political-geographic division of Southeast and South Brazil and converted to ascii using R Statistical Software (R Core Team, 2020).

Following the ModleR workflow (Sánchez-Tapia et al., 2020) we first did a data setup (Step 1) where the species occurrence data and all climatic and topographic variables are inserted to prepare a metadata matrix with selected variables and their respective values to project the models in the following step. In step 1, we set a crossvalidation as the partition type, 5 partitions and 10 runs, we also set 500 as the number of pseudoabsenses, disabled options to occurrence data clean and in addition, we set 0.5 as cut off to select the environmental variables.

The Step 2 in ModleR workflow is the fitting the ecological data for each partition and runs (we set 5, in the previous step) and projects them into geographical space for current and future scenarios. In this step, we used the three GCMs defined before in three scenarios by IPCC in AR6 (IPCC, 2021). For AR6 the IPCC included new and better representations of physical, chemical, and biological processes with higher resolution compared with AR5, and are considered in their projections the temporal evolution of pollutants, emissions or changes in land use and land cover, in summary, the Shared Socioeconomics Pathways - SSP (IPCC, 2021). We chose SSP2-4.5, which represents a strong climate change mitigation scenario, SSP3-7.0 which is the middle of the road scenario, and 5-8.5, the worst-case scenario. The scenarios and its details are described in Table 4. In addition, scenarios are projected for four time periods in the 21st century, but we choose the average for 2041-2060 (hereafter 2050) and the average 2081-2100 (hereafter 2090) time periods to represent a moment in middle and at the end of the century (Table 4).

We choose the “spec_sens” threshold because it is the threshold at which the sum of the sensitivity (true positive rate) and specificity (true negative rate) is highest and provides more robust models (Hijmans et al., 2021) which was the same choose in CMIP5/Maxent models. In addition, we also projected the models in five algorithms implemented by ModleR workflow: glm, maxent, maxnet, svmk and rf (Sánchez-Tapia et al., 2020). The third step (Step 3) of the ModleR workflow is to merge the partitions from each algorithm generated in the previous step into a final model of the *Campos de Altitude* ecosystem for each of the different scenarios and time periods. For this, we used the “raw_mean_th” that cuts the models by the mean of the threshold choose in previous step to make a binary model (Sánchez-Tapia et al., 2020). And the final step (Step 4) is producing the final model for *Campos de Altitude* with the best algorithm. And to select the best-performing model we used the AUC evaluation metric available at "dismo" package (Hijmans et al., 2021) implemented by ModleR workflow (Sánchez-Tapia et al., 2020).

Suitable area in Protected Areas

The final processing steps to calculate the total suitable area to *Campos de Altitude* within the Protected Areas (PA) and outside them were carried to the current and future scenarios from both CMIP5/Maxent and CMIP6/Ensemble model groups performed in R Statistical Software (R

Core Team). The available georeferenced data about the Protected Areas in Brazil were obtained on the Ministry of Environment and Climate Change website (available at http://mapas.mma.gov.br/i3geo/datadownload.htm).

Table 3: Characterisation of the Representative Concentration Pathways (RCPs), RCP4.5 and RCP8.5, defined by the scientific community for the Fifth Assessment Report (AR5) (IPCC, 2013), respectively an optimistic and pessimistic scenario, used in this article.

RCPs	***Radiative Forcing***	***Perspectives in emission and mitigation polices***	***CO2 concentration in atmosphere (2100)***	***Average global surface temperature (2100)***	***Time Period***	***GCMs***
4.5	4.5 Wm-2	Optimistic - reality within CO2 emissions stabilize due to greenhouse gas (GHG) emissions reduced by mitigation actions from governments and societies	421 ppm	1.8° C	2050	CCSM4 (Gent et al. 2011)
					2070	MIROC5
					2050	CCSM4 (Gent et al. 2011)
					2070	MIROC5
8.5	8.5 Wm-2	Pessimistic - no mitigation policies and CO2 emissions (and other greenhouse gases) continue to increase	936 ppm	3.7° C	2050	CCSM4 (Gent et al. 2011)
					2070	MIROC5
					2050	CCSM4 (Gent et al. 2011)
					2070	MIROC5

Table 4: Detailed information on the Shared Socioeconomic Pathways (SSPs) as defined by the IPCC in their Sixth Assessment Report (AR6) is provided in this text. The scenarios outlined were employed across two distinct periods of the 21st century and three different GCMs. Additionally, information gained from using the GCMeval web tool was utilized to assess the degree of predicted variability in changes to both temperature and precipitation amongst all GCMs available.

SSPs	***Perspectives in emission and mitigation polices***	***Average global surface temperature range (2100)***	***Time Period***	***GCMs***	***GCMs variation compared with all other available GCMs***
2-4.5	It is a scenario with stronger climate change mitigation and therefore the GHG emissions remain around the current levels until the middle of the century	2.1° C to 3.5° C	2050	CanESM5	-
					-
				MIROC6	-
					-
				BCC-CSM2-MR	-
					-
			2090	CanESM5	-
					-

				MIROC6	-
					-
				BCC-CSM2-MR	-
					-
3-7.0	Represents overall lower GHG emissions (lower than the worst scenario - SSP5-8.5) but CO2 emissions almost double by the year 2100 (compared with current emission levels)	2.8° C to 4.6° C	2050	CanESM5	-
					-
				MIROC6	-
					-
				BCC-CSM2-MR	-
					-
			2090	CanESM5	-
					-
				MIROC6	-
					-
				BCC-CSM2-MR	-
					-
5-8.5	The worst scenario with higher future emissions pathways, where the CO2 emissions double by the year 2050 compared to current levels	3.3° C to 5.7° C	2050	CanESM5	HIGH temperature
					low precipitation
				MIROC6	low temperature
					HIGH precipitation
				BCC-CSM2-MR	close to the average of all GCMs
					close to the average of all GCMs
			2090	CanESM5	HIGH temperature
					low precipitation
				MIROC6	low temperature
					HIGH precipitation
				BCC-CSM2-MR	close to the average of all GCMs
					close to the average of all GCMs

Results

A total of 90 models were generated for CMIP5/Maxent models set considering current climate conditions and all 8 future scenarios (Table 3). The retained variables and their respective contribution to the CMIP5/Maxent models are presented in Supplementary Material Table S2. For Current climate conditions, the models predicted a total suitable area for *Campos de Altitude* around 22,230.69 km². 9,156.13 km² of this area (41.19% of the total predicted area) are inside of official Protected Areas (Fig. 2 and Table 5).

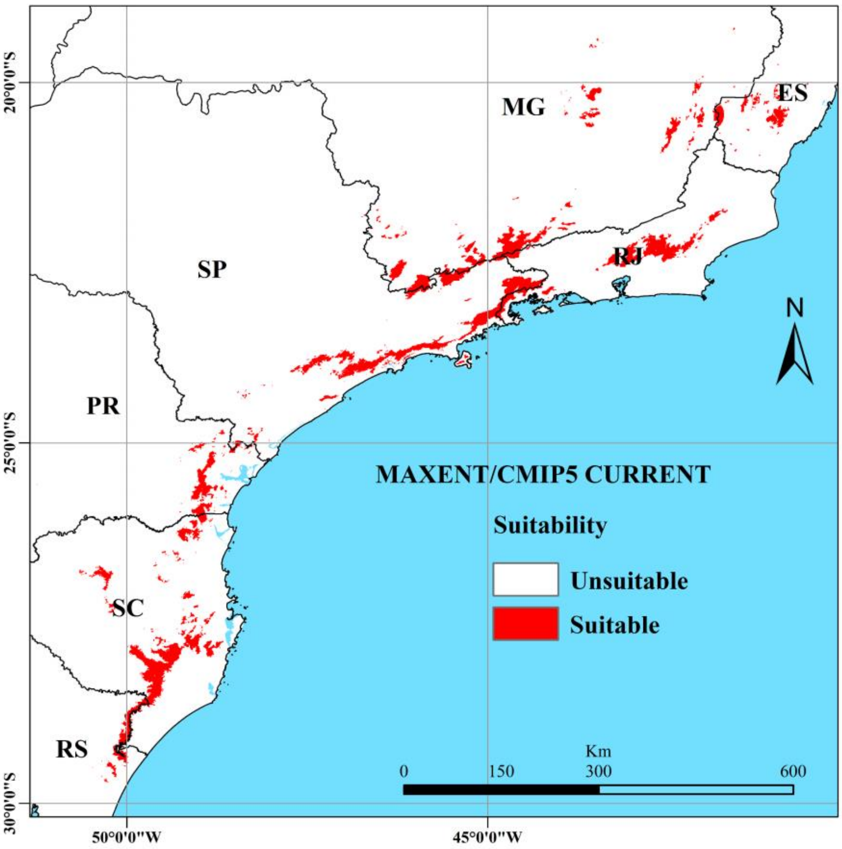


Figure 2: Current topo-climatic predicted distribution of *Campos de Altitude* in the southeastern and southern regions of Brazil, from the CMIP5/Maxent model set. Red areas represent areas suitable for *Campos de Altitude* and white areas unsuitable for *Campos de Altitude*. The acronyms correspond to the political-geographical divisions of the Southeast region of Brazil, which are ES - *Espírito Santo*, MG - *Minas Gerais*, SP - *São Paulo*, RJ - *Rio de Janeiro*, and the southern states are PR - *Paraná*, SC - *Santa Catarina* and RS - *Rio Grande do Sul*.

In the predictions for 2050, both Optimistic and Pessimistic scenarios (RCP4.5 and RCP8.5, respectively) predicted climatic and topographic suitability for *Campos de Altitude*. In the Optimistic scenario 465.01 km² were predicted suitable for *Campos de Altitude* of whom 42.87% (199.34 km²) are inside the existent Protected Areas (Table 5 and Fig. 3). The total predicted loss of suitable area for this scenario was 97.9% compared with the Current Climate *Campos de Altitude* suitable area (Table 5 and Fig. 3). For the pessimistic scenario, whereas in the optimistic scenario most of the predicted areas for *Campos de Altitude* are outside the protected areas, the loss of suitable area is almost complete, 99.58% (Table 5 and Fig. 3).

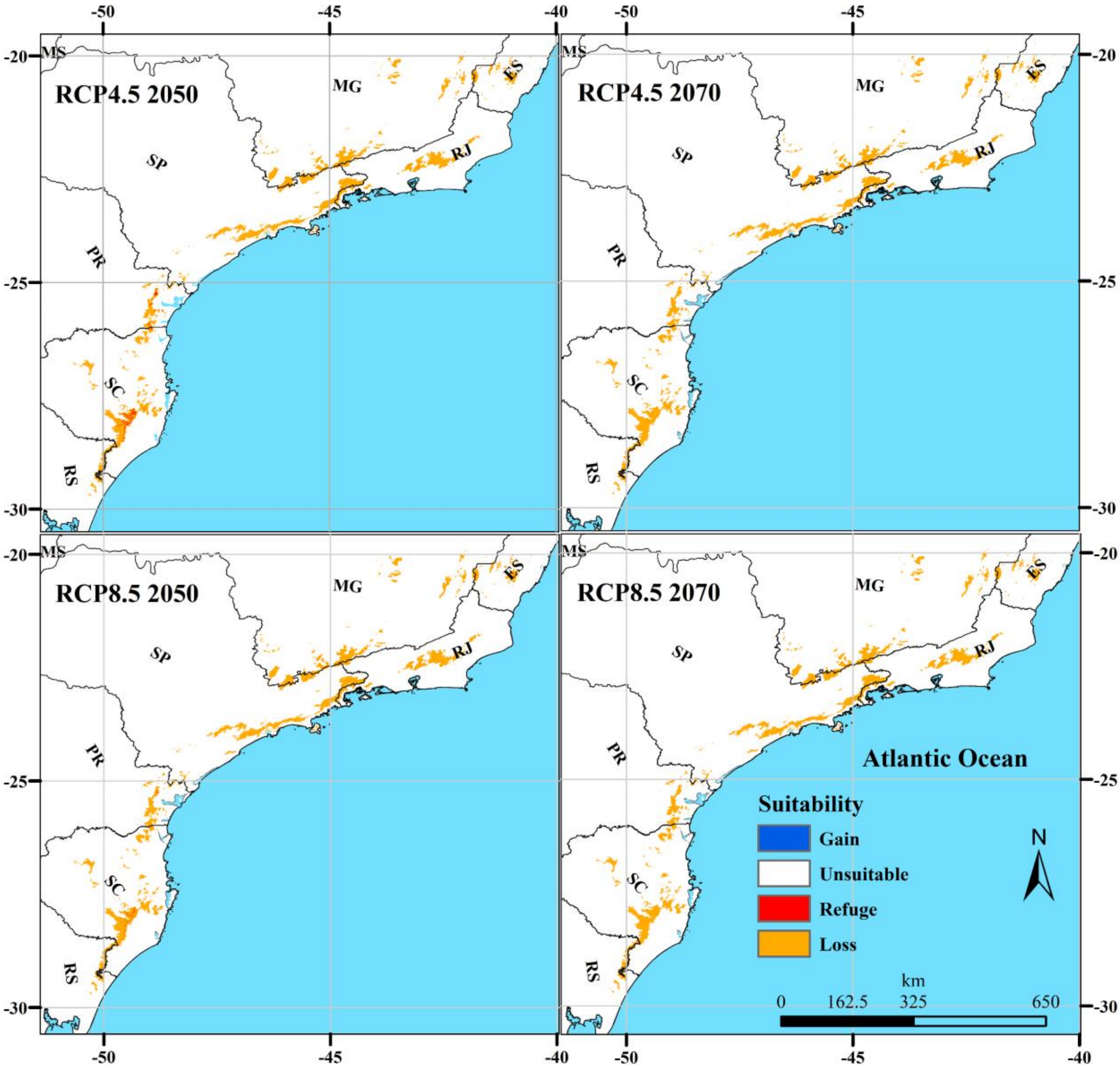


Figure 3: Topo-climatic suitability for *Campos de Altitude* in two future scenarios (RCP4.5 and 8.5) for two time periods (2050 and 2070) showing a decrease in suitability for 2050 and a total loss of suitable areas for *Campos de Altitude* in the second half of the 21st century (2070). The acronyms correspond to the political-geographical divisions of the Southeast region of Brazil, which are ES - *Espírito Santo*, MG - *Minas Gerais*, SP - *São Paulo*, RJ - *Rio de Janeiro*, and the southern states are PR - *Paraná*, SC - *Santa Catarina* and RS - *Rio Grande do Sul*.

For 2070 no suitable areas were predicted for any of the scenarios indicating the possibility of extirpation of *Campos de Altitude* in mountaintops of the south and south-eastern Brazil. As a result, there will be a great loss of taxonomic and functional plant diversity for this mountain environment (Fig. 3 and Table 5).

The evaluation metric AUC clearly shows that CMIP5/Maxent models accurately predicted the *Campos de Altitude* distribution due to 0,98 values verified in all average models (Table 6).

Table 5: Current and future predicted areas (km² and %) of *Campos de Altitude* distribution in southeast and south of Brazil inside and outside existent PAs for each scenario. The bold columns represent the total predicted loss in each scenario for 2050. For 2070 no suitable areas were predicted.

	Current		***2050***					
			RCP4.5			**RCP8.5**		
	km²	**%**	**km²**	**%**	**% loss**	**km²**	**%**	**% loss**
Inside PA	9,156.13	41.19	199.34	42.87	**-97.82**	45.75	49.03	**-99.50**
Outside PA	13,074.55	58.81	265.67	57.13	**-97.97**	47.56	50.97	**-99.64**
Total	**22,230.69**	**100.00**	**465.01**	**100.00**	**-97.91**	**93.31**	**100.00**	**-99.58**

Table 3: Statistical results from Maxent for the *Campos de Altitude* in two GCMs (CCSM4 and MIROC) for two time periods (2050 and 2070) in two different RCPs (4.5 and 8.5). AUC is the receiver operating characteristic (ROC) both in the training and testing steps; Maximum training Threshold is the Maximum training sensitivity plus specificity threshold that was the selected threshold for binarizing the final results, and SM is the simple mean of the selected threshold from the average models by CCSM4 and MIROC Global Circulation Models.

	Training AUC	***Test AUC***	***Maximum training Threshold***
Current Climate	0.9914	0.9894	0.0841
RCP4.5 2050	-	-	-
CCSM4	0.9899	0.9869	0.0713
MIROC	0.9900	0.9843	0.0583
			SM = 0.0648
RCP4.5 2070	-	-	-
CCSM4	0.9902	0.9842	0.0555
MIROC	0.9896	0.9844	0.0914
			SM = 0.0734
RCP8.5 2050	-	-	-
CCSM4	0.9902	0.9874	0.0648
MIROC	0.9899	0.9851	0.0765
			SM = 0.0706
RCP8.5 2070	-	-	-
CCSM4	0.9899	0.9862	0.0633
MIROC	0.9902	0.9817	0.0761
			SM = 0.697

A grand total of 4750 models were produced for the CMIP6/Ensemble set of models, considering both current and potential future climate scenarios, algorithms, and partitions. The following results derive from the Random Forest (rf) models, chosen due to its superior AUC values and other enhanced evaluation metrics as compared to other algorithms (Table 8). The retained variables to the CMIP6/Ensemble models were Mean Diurnal Range (bio_02), Temperature Annual Range (bio_07), Mean Temperature of Driest Quarter (bio_09), Annual Precipitation (bio_12), Precipitation of Warmest Quarter (bio_18), geology, northness (Aspect Northness), eastness (Aspect Easteness), elevation, tpi (Topographic Position Index) and tri (Terrain Ruggedness Index). In the current climate, an area of approximately 23,974.13 km² was predicted as suitable for *Campos de Altitude*. Of this area, 9,138.56 km² (equivalent to 38.12%) is situated within protected areas (Fig. 4 and Table 4).

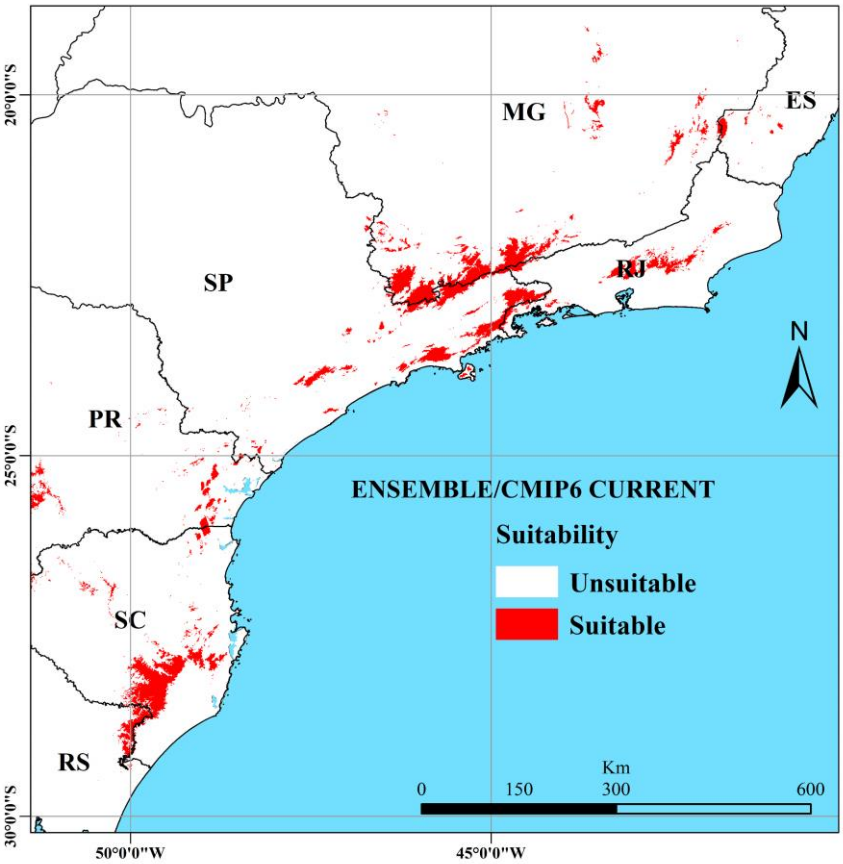
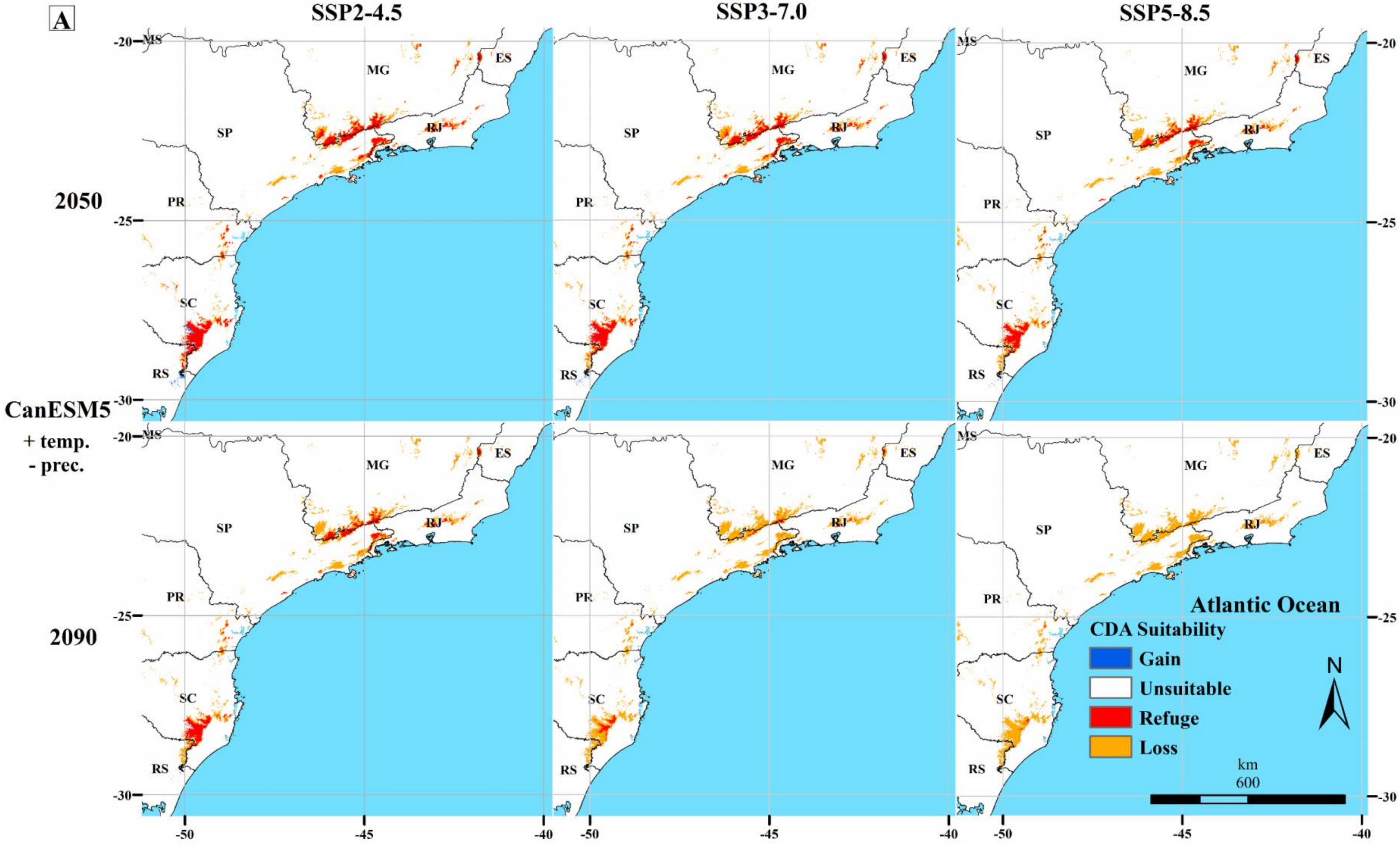


Figure 4: Current climate distribution of *Campos de Altitude* in *Serra da Mantiqueira* and *Serra do Mar* mountain ranges of Brazil, from CMIP6/Ensemble set of models. Red areas represent suitable areas for *Campos de Altitude* and the white ones represent climatic and topographic unsuitability for *Campos de Altitude*. The acronyms correspond to the political-geographical divisions of the Southeast region of Brazil, which are ES - *Espírito Santo*, MG - *Minas Gerais*, SP - *São Paulo*, RJ - *Rio de Janeiro*, and the southern states are PR - *Paraná*, SC - *Santa Catarina* and RS - *Rio Grande do Sul*.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SSP3-7.0
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2050
CanESM5
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PR
SC
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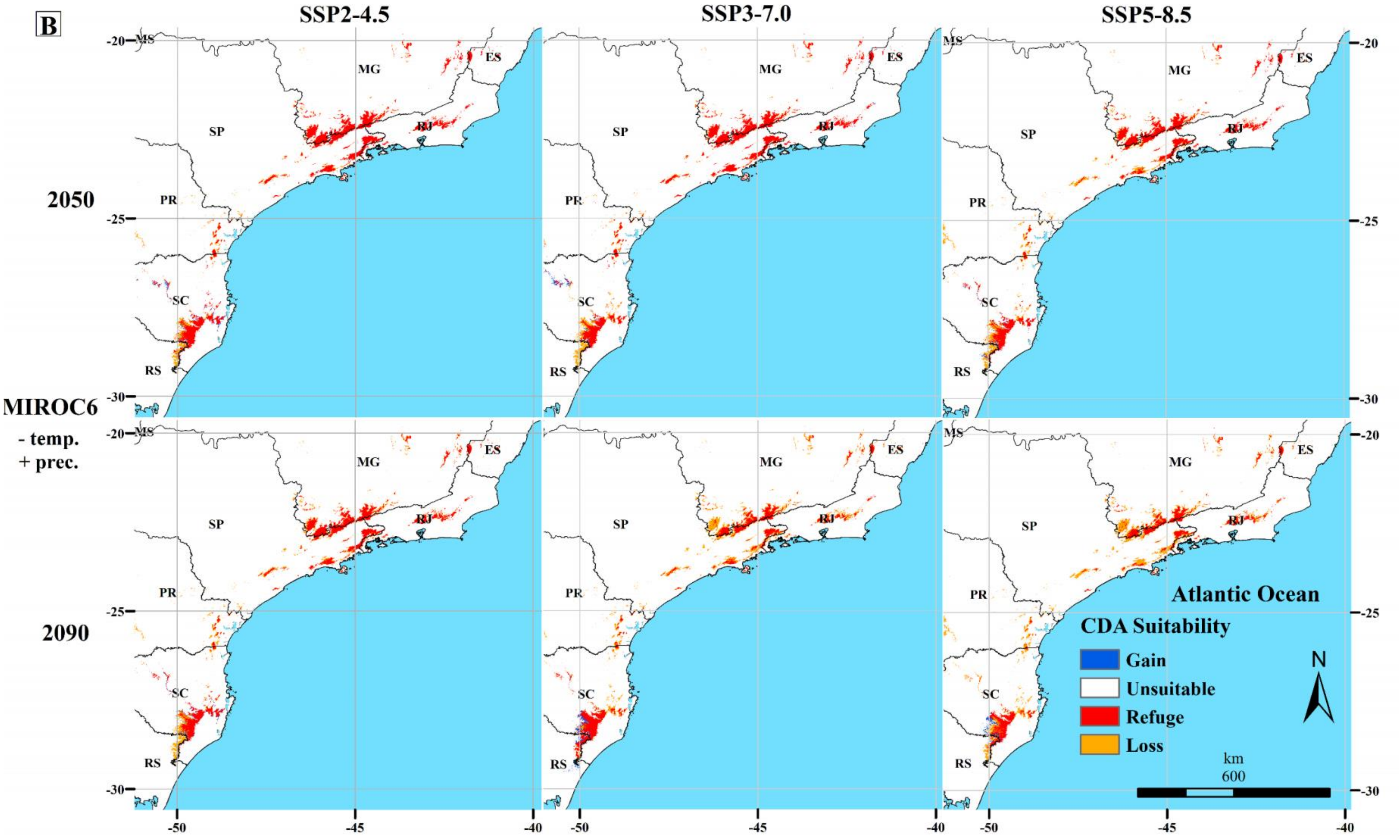
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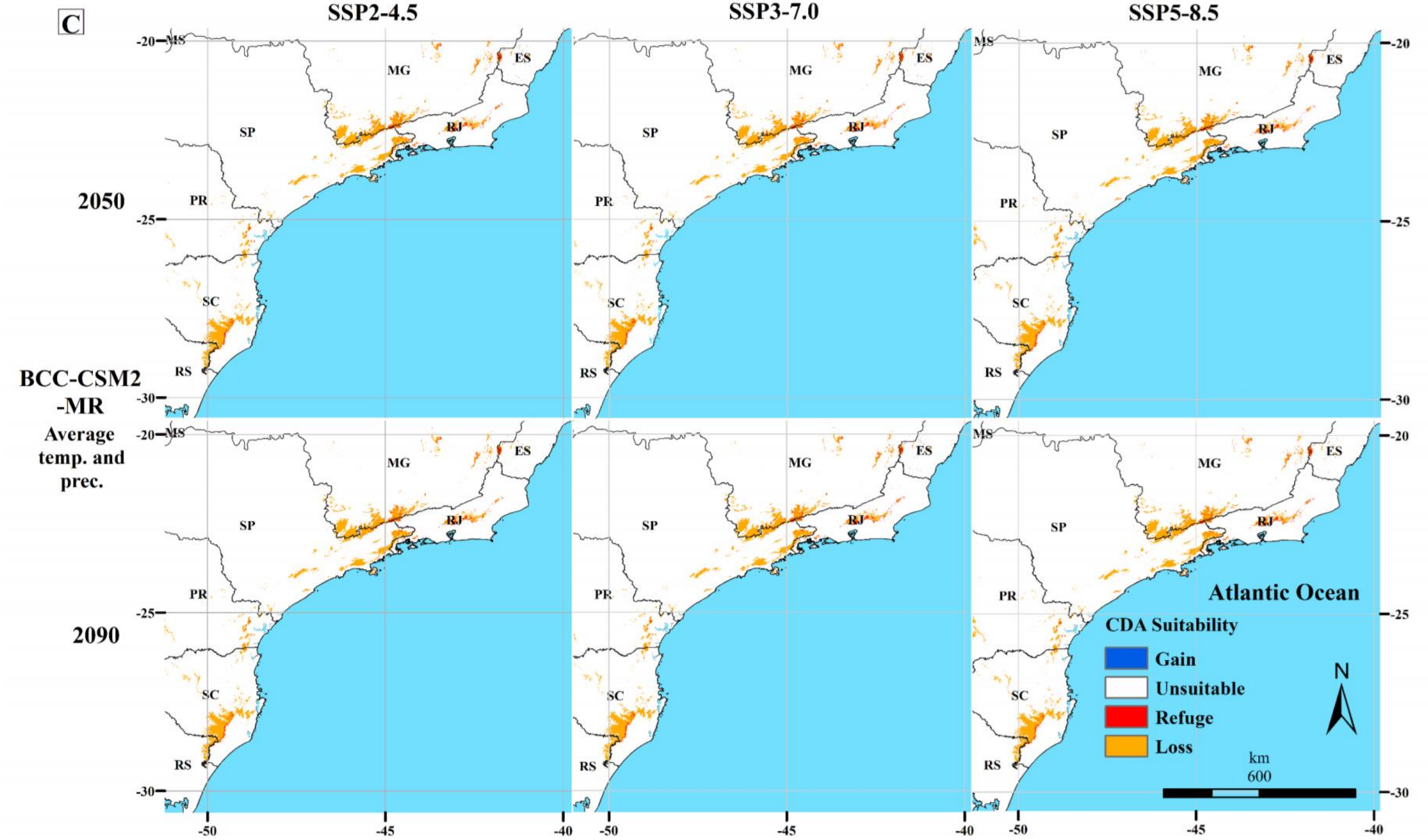

Figure 5: Suitability for *Campos de Altitude* in 18 future scenarios (three IPCC GHG emission and mitigation scenarios, SSPs 2-4.5, 3-7.0 and 5-8.5) for two time periods, 2050 (2041-2060) and 2090 (2081-2100), based on projections from three GCMs used in the IPCC AR6, (A) CanESM5, (B) Miroc6 and (C) BCC-CSM2-MR. The acronyms correspond to the political-geographical divisions of the Southeast region of Brazil, which are ES - *Espírito Santo*, MG - *Minas Gerais*, SP - *São Paulo*, RJ - *Rio de Janeiro*, and the southern states are PR - *Paraná*, SC - *Santa Catarina* and RS - *Rio Grande do Sul*.

The three selected GCMs, CanESM5, Miroc6, and BCC-CSM2-MR predict a decrease in the total suitable area along the different emission and mitigation scenarios from IPCC, 12,438,96 km² in SSP2-4.5, 10,103.00 km² in SSP3-7.0 and 7.639.60 km² in SSP5-8.5, respectively, the scenarios with more greenhouse gas (GHG) emissions mitigation, the middle of the road and the worst-case mitigation scenario (Fig. 5 and Table 7). This decreasing pattern is the same for 2050 and 2090 time periods. The difference is in the GCM BCC-CSM2-MR that in SSP3-7.0 and SSP5-8.5 scenarios showed a little increase in total suitable areas for the 2090 period compared with 2050 (Table 4).

However, there are a few differences between the suitable area predicted for the selected GCMs. Miroc6 representing a low temperature increase and high precipitation increase rates compared to other GCMs, predicted the highest total suitable area compared to other GCMs for all SSPs scenarios and for both time periods (Table 7). Consequently, the percentage loss for this GCM in all scenarios was lower (Table 7). In contrast, the BCC-CSM2-MR was the GCM with the highest projected percentage loss of total suitable area compared to the current climate (over 90% in all scenarios) as the smallest suitable area was predicted in all future scenarios (Table 7).

When we looked at suitable areas inside and outside protected areas, the pattern of loss followed that one predicted by different GCMs. When our models predicted less loss of suitable area, such as models from Miroc6, the areas inside PA are smaller compared to the models with a total suitable area more restricted, such as BCC-CSM2-MR for both time periods (Table 7).

Table 7: Current and future predicted areas (km² and %) of *Campos de Altitude* distribution in southeast and south of Brazil inside and outside existent Protected Areas for 2050 and 2090 and for each SSP scenario from IPCC based in three different GCM. The bold columns represent the total predicted suitable area (km²) for each scenario and its respective percentage loss (%) relative to the current climate coditions.

		In PA		*No PA*		***Total***
		km²	%	km²	%	**km²**
	Current	9,138.56	38.12	14,835.57	61.88	**23,974.13**

		2050						**2090**					
		In PA		*No PA*		***Total***		*In PA*		*No PA*		***Total***	
	GCMs	km²	%	km²	%	**km²**	**% loss**	km²	%	km²	%	**km²**	**% loss**
SSP2-4.5	CanESM5	5,746.78	46.20	6,692.18	53.80	**12,438.96**	**-48.12**	3,771.21	51.15	3,601.48	48.85	**7,372.69**	**-69.25**
	Miroc6	8,424.39	43.46	10,958.26	56.54	**19,382.65**	**-19.15**	7,506.00	46.56	8,613.83	53.44	**16,119.83**	**-32.76**
	BCC-CSM2-MR	1,230.39	58.96	856.26	41.04	**2,086.65**	**-91.30**	1,203.22	61.01	769.01	38.99	**1,972.23**	**-91.77**
SSP3-7.0	CanESM5	5,022.46	49.71	5,080.54	50.29	**10,103.00**	**-57.86**	984.23	60.86	633.06	39.14	**1,617.29**	**-93.25**
	Miroc6	8,350.45	44.82	10,279.19	55.18	**18,629.64**	**-22.29**	5,966.09	43.94	7,610.63	56.06	**13,576.72**	**-43.37**
	BCC-CSM2-MR	1,228.66	59.56	834.09	40.44	**2,062.75**	**-91.40**	1,244.61	59.64	842.28	40.36	**2,086.89**	**-91.30**
SSP5-8.5	CanESM5	3,997.66	52.33	3,641.94	47.67	**7,639.60**	**-68.13**	187.10	57.73	136.98	42.27	**324.08**	**-98.65**
	Miroc6	7,405.73	45.24	8,965.22	54.76	**16,370.95**	**-31.71**	5,554.86	47.94	6,032.60	52.06	**11,587.46**	**-51.67**
	BCC-CSM2-MR	1,224.61	60.22	808.98	39.78	**2,033.59**	**-91.52**	1,240.56	59.74	835.91	40.26	**2,076.47**	**-91.34**

Table 8: All evaluation metrics from five algorithms used in CMIP6/Ensemble models (described in Material and Methods). The best algorithm selected based on metrics is Random Forest.

	glm	***maxent***	***maxnet***	***rf***	***svmk***
kappa	0.438001	0.305138	0.265289	0.429292	0.431853
spec_sens	0.438001	0.305138	0.265289	0.429292	0.426284
AUC	0.993144	0.993136	0.993058	0.996507	0.994137
AUCratio	1.986288	1.986271	1.986116	1.993013	1.988274
pROC	1.930369	1.891818	1.885270	1.939106	1.896927
TSSmax	0.957671	0.961383	0.961886	0.968202	0.949241
KAPPAmax	0.954275	0.957999	0.958738	0.966137	0.947412
F_score	0.972920	0.975114	0.975545	0.979860	0.968551
Jaccard	0.947603	0.951665	0.952491	0.960672	0.939352

Discussion

Our results from both set of models (CMIP5/Maxent and CMIP6/Ensemble sets) clearly show an increasing threat to *Campos de Altitude*, with a possibility of disappearing until the end of the 21st century due to the global climate changes. This confirms our hypothesis and turns on a light alert: we need to change our relationship with biodiversity and natural environments.

The RCPs 4.5 and 8.5 scenarios assume that the increase in the annual mean surface temperature of the planet could vary between 1.8ºC and 3.7ºC, and the SSPs scenarios between 2.1ºC and 5.7ºC. This means that even in the SSP scenario where potentially more mitigation measures are taken and GHG emissions are reduced (SSP2-4.5), the losses range from almost 20% of *Campos de Altitude* suitable area already by 2050, and at least 30% by 2090 compared to the current suitability projection (Table 7). This pattern is maintained in the SSP3-7.0 scenario, where losses of suitable area losses are at least 22% by 2050 and 43% by 2090. The losses are more extreme in the more extreme scenarios in either the CMIP5/Maxent or CMIP6/Ensemble model sets. This pattern demonstrates the clear and glaring threat of anthropogenic global change to the survival of the *Campos de Altitude*.

The AR6 by IPCC (2023) unequivocally shows that human activities, especially the GHG emissions and land use changes already had caused global warming by around 1.1°C in the 2011-2020 decade compared to the pre-industrial global surface temperature. In this context, the RCP4.5 scenario (in which an increase in global average surface temperature of up to 1.8°C is projected) used as a possibility may no longer be feasible. Therefore, the imminent risk for *Campos de Altitude* may be even greater if we follow a path of GHG emissions that leads us to a reality closer to scenarios of greater warming in the surface temperature of the planet. There will consequently be aggravation and intensification of extreme weather events that will contribute to losses and damage to biodiversity and ecosystems as well as the human population (IPCC 2023).

Our models CMIP5/Maxent and CMIP6/Ensemble predicted topo-climatic suitable areas for *Campos de Altitude*, respectively 22,230.69 km² and 23,974.13 km² when the referenced estimates are around 350km² (Safford, 1999b). This difference can be related to the natural uncertainty in projections of species distributions and the high level of microscale heterogeneity commonly found in *Campos de Altitude* environments. Uncertainties for the current and future scenarios of the CMIP6/Ensemble models are available in the supplementary material (Figures S1 and S2). Soils of variable depth, crevices and micro-habitats, small seasonal ponds, very steep slopes, small valleys and basins and rocky outcrops of variable extent locally modify temperature and water availability for example (Caiafa and Silva, 2007; Campos et al., 2018; Cordeiro and Neri, 2019, 2019; Neri et al., 2016). These factors are intrinsic to mountain top environments, but are not available, and their absence may have contributed to the model differences from previous estimates.

Soil depth is an extremely important factor for the delimitation of grassland ecosystems such as the *Campos de Altitude* in the forest matrix of the *Serra do Mar* and *Mantiqueira* mountain ranges (Benites et al., 2003; Garcia and Pirani, 2005). To predict the distribution of plant species, soil variables are essential to capture different parts of the multidimensional niche of these species (Arruda et al., 2017). Thus, soil characteristics are important and should be better represented in high spatial resolution layers for mountain environments and made available to improve the power predictive and accuracy of future phytogeographical investigations.

The uncertainty of suitable areas for *Campos de Altitude* by the projections is why we observed most of the *Campos de Altitude* suitable areas outside existents PAs in CMIP5/Maxent models for Current and future scenarios (Table 4). The CMIP6/Ensemble models in where this pattern repeats itself are for Current and CanESM5 and Miroc6 (future scenarios) that projected larger total areas suitable for *Campos de Altitude* for 2050 and 2090. BCC-CSM2-MR does not show the same pattern because it was the GCM that projected the smallest area for all future scenarios and therefore the *Campos de Altitude* suitable areas were always larger within protected areas (Table 4). This is because we consider an unchanging geographical extent of the protected areas and compare it with suitable areas that have expanded well beyond their borders.

Despite the uncertainty of the suitable area for *Campos de Altitude*, this does not mean that all Protected Areas are completely occupied by *Campos de Altitude*. As described in the Study Region, *Campos de Altitude* are found on mountain tops with shallow soils and rocky outcrops scattered across the montane landscape above the tree line. These are cloud forests of small and twisted trees and shrubs (5 to 12 m tall), usually without clearly defined vegetation strata and great abundance and diversity of epiphytes (Safford, 1999a). It is worth noting that the areas predicted as adequate by both sets of models are mostly already found in the Protected Areas designated by Brazilian legislation.

Miroc6 was the GCM with the highest suitable area predicted for *Campos de Altitude* probably due to its lower temperature increase and greater precipitation compared to the other two GCMs used in this study. And these are good climatic conditions for maintaining *Campos de Altitude* and even expanding its distribution in future scenarios. CanESM5 GCM, where the annual averages of predicted climate change are increases in temperature and no changes in precipitation compared to other GCMs projections, the total area predicted for *Campos de Altitude* was slightly smaller than that predicted in Miroc6 models. This may favour the expansion of tree species because we are in an interglacial period when forests naturally tend to expand into areas of natural grassland. However, it is important to know what the patterns of weather change might be, whether it is the seasonal patterns of temperature or just the annual means that are changing (Assis and de Mattos, 2016; Safford, 1999a).

The BCC-CSM2-MR, which represents a possibility of climate change for precipitation and temperature close to the projected annual mean climate change of all other GCMs, projected a total suitable area for the *Campos de Altitude* ranging from 1970 km² to almost 2100 km², well below the other GCMs. This would be a projection closer to the actual estimated extent of *Campos de Altitude* at present and could be related to the fact that this GCM climate change projections are in the average of all other GCMs.

For a mountain ecosystem with an insular geographic pattern, such as the *Campos de Altitude*, climatic changes are even more intense and can greatly affect these areas (Assis and de Mattos, 2016; Scarano et al., 2016) . The Quaternary climatic changes, especially in the last 20 thousand years, seem to have had a strong impact on the vegetation of the mountains of southern and southeastern Brazil (Behling et al., 2020, 2007; Behling and Safford, 2010). Therefore, understanding these changes from the recent past may shed light on how current anthropogenic global climate change may affect the distribution of *Campos de Altitude* in the near future.

In addition, other factors such as fire appear to have played or at least to have been present in these grassland environments. For example, the abundance of charcoal in the soil in areas of *Campos de Altitude* indicates a forest past that contributed to the formation of the small amount of soil present there today (Benites et al., 2003) . Thus, with recent changes in land use and land cover, increasing temperatures and decreasing rainfall, fire could be another factor putting pressure on areas close to the *Campos de Altitude*. In the same context, invasive alien species may also increase their penetrability (Assis and de Mattos, 2016; Scarano et al., 2016) and be accelerated by the effects of land use and land cover change, i.e. the removal of forest vegetation buffering *Campos de Altitude* areas (Martinelli, 2007).

Our results clearly show that one of the most obvious and expected effects of global climate change on mountain ecosystems, habitat loss, is even more dramatic for *Campos de Altitude*, which, despite it being in Protected Areas, are already located at the highest elevations of southern and southeastern Brazil and therefore have no area available for uphill migration (Scarano et al., 2016). In this context, despite the uncertainty of the predictive models, especially in the more heterogeneous microcondition areas of the Atlantic Forest and *Campos de Altitude*, and the possibility of uphill migration of species that were previously restricted to lower areas, it may be necessary to rethink strategies for preserving biotic heritage.

Studies on the impacts of climate change on biodiversity and protected areas have highlighted the need to identify ecoregions and protected areas that will remain stable and suitable in the future, expand these protected areas, and promote connectivity between biodiversity protection networks (Dobrowski et al., 2021; Wu et al., 2023). In addition, we need to look for co-benefits such as carbon storage and modified areas of the landscape, which will also be important for biodiversity conservation planning under climate change scenarios (Dobrowski et al., 2021; Wu et al., 2023).

Threats to *Campos de Altitude* are also threats to socio-economic sectors, as *Campos de Altitude* provide basic ecosystem services such as regulating the water cycle and maintaining water quality and food security for a large part of the Brazilian population (Aparecido et al., 2018; Assis and de Mattos, 2016; Safford, 1999a). In addition to providing collectable and non-timber products and soil protection, *Campos de Altitude* have potential for recreation, tourism, and environmental education (Martinelli, 2007). Therefore, in addition to a rich natural heritage, they represent a great cultural heritage (Martinelli, 2007; Scarano et al., 2016).

Therefore, hope for the *Campos de Altitude* is found in its high micro-scale heterogeneity, as mentioned above, and the real need to promote adaptation and mitigation measures to ensure sustainable development and quality of life for all in the near-term future.

Actions such as the reforestation of degraded areas around mountains and mountain ranges , the establishment of ecological corridors and the monitoring and promotion of natural regeneration are also fundamental to mitigating anthropogenic impacts, not only climate change (Martinelli, 2007). This need must be addressed quickly and thoroughly in this decade so that we have a chance to move towards a lower warming and lower impact scenario (IPCC, 2023).

Conclusions

Our future projections unequivocally support our hypothesis, indicating a pronounced downward trend in the area both climatically and topographically suitable for *Campos de Altitude* during the 21st century in both model groups. The total area predicted for the current distribution of *Campos de Altitude* was 22,230.69 km² in the CMIP5/Maxent model group results and 23,974.13 km² in the CMIP6/Ensemble model group results. In both sets of projections, there is a more suitable area for *Campos de Altitude* outside protected areas, which is directly linked to the models' uncertainty error, especially in mountainous regions with high environmental heterogeneity at the fine scale, not captured by the resolution of the predictors used. There are significant losses in almost all future scenarios. CMIP5/Maxent showed nearly complete loss of suitable area by 2050 and the total extinction of *Campos de Altitude* in all scenarios by 2070. Losses in CMIP6/Ensemble models for future scenarios ranged from 19.15% to 98.65% of the topo-climatically suitable *Campos de Altitude* area. A map of potential *Campos de Altitude* occurrence was created based on climatic and topographic predictors, which requires further refinement, especially by incorporating more local and high-resolution information to reduce prediction uncertainty and improve the mapping. Our study highlights the pressing need to promptly address the consequences of global climate change on montane Atlantic Forest associated ecosystem biodiversity within this decade. This is crucial to ensure sustainable development and a high quality of life in the near future.

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Supplementary Material

Table S1

Additional information on the indicator species. Botanical family, origin, and endemism in Brazil, different vegetation types where each species occurs, life forms, and substrates. All data were obtained from the Reflora search portal (https://reflora.jbrj.gov.br/consulta).

Species	Family	Origin	Endemism in Brasil	Distribution	Life form	Substrate
Gaultheria serrata (Vell.) Sleumer ex Kin.-Gouv.	Ericaceae	native	Endemic	High Altitude Grassland	shrub/ subshrub	terrestrial
Utricularia reniformis **A.St.-Hil.**	Lentibulariaceae	native	Endemic	High Altitude Grassland, Ombrophyllous Forest (Tropical Rain Forest), Rock outcrop vegetation	herb	Epiphytic/ Rupicolous/ Terrestrial
Croton splendidus **Mart.**	Euphorbiaceae	native	Endemic	High Altitude Grassland, Grassland, Ombrophyllous Forest (Tropical Rain Forest), Coastal Forest (Restinga), Rock outcrop vegetation	Shrub/ Subshrub	terrestrial
Pleroma hospitum **(Schrank et Mart. ex DC.) Triana**	Melastomataceae	native	Endemic	Ombrophyllous Forest (Tropical Rain Forest)	shrub	terrestrial
Abatia americana **(Gardner) Eichler**	Salicaceae	native	Endemic	Ombrophyllous Forest (Tropical Rain Forest)	shrub	terrestrial
Fuchsia regia **(Vell.) Munz**	Onagraceae	native	Not endemic	High Altitude Grassland, Highland Rocky Field, Riverine Forest and/or Gallery Forest, Ombrophyllous Forest (Tropical Rain Forest), Mixed Ombrophyllous Forest	Liana/ scandent-vine/ Shrub	Epiphytic/ Terrestrial
Clethra uleana **Sleumer**	Clethraceae	native	Endemic	Ombrophyllous Forest (Tropical Rain Forest), Mixed Ombrophyllous Forest	shrub/tree	terrestrial
Agarista niederleinii **(Sleumer) Judd**	Ericaceae	native	Endemic	High Altitude Grassland	shrub/tree	terrestrial

Table S2

Table S2: Code and corresponding variable used in the CMIP5/Maxent models and their respective percentage contribution in each projected scenario. (*) Represents those variables with a correlation ≥ +0.75/-0.75 that were not used in the projections. The (-) for future scenarios on the CCSM4 and MIROC global circulation models represents the variables that were not used for future models because they do not have future projections.

			Percent Contribution							
			CCSM4				**MIROC**			
Variable Code		**Current Climate**	4.5 2050	8.5 2050	4.5 2070	8.5 2070	4.5 2050	8.5 2050	4.5 2070	8.5 2070
geology	Geology	33.6	37.3	38.6	38.3	39.8	39.5	36.8	40.2	39
mcloud_co	Mean Annual Cloud Cover	21.8	-	-	-	-	-	-	-	-
bio_10	Mean Temperature of Warmest Quarter	16	24.1	28.8	29	25.5	25.5	31.2	17.5	23.5
elevation	Elevation	8.8	9.2	8.1	5.7	6.3	6.5	6.8	11.7	10.5
bio_05	Max Temperature of Warmest Month	3.4	3.6	4.6	5.2	4.9	5	3.6	6.3	6.4
m_an_wspe	Mean Annual Wind Speed	2.7	-	-	-	-	-	-	-	-
bio_09	Mean Temperature of Driest Quarter	1.9	7.8	3.3	4	5.7	5.3	5.6	3.4	2.7
slope	Slope	1.8	4.3	3	2.8	3.6	3.6	2.2	3.7	2.6
bio_08	Mean Temperature of Wettest Quarter	1.7	2.4	2.3	2.9	2.8	1.7	3.5	2.3	2.8
bio_13	Precipitation of Wettest Month	1.4	1.8	1.8	2.4	1.5	2.1	1.8	2	1.7
bio_07	Temperature Annual Range (BIO5-BIO6)	1.2	1.3	0.8	1.2	1.6	1.2	0.8	1	1
bio_12	Annual Precipitation	1.2	1.1	2	1.4	1	2.2	1.2	2.8	1.4
m_an_rad	Mean Annual Solar Radiation	0.8	-	-	-	-	-	-	-	-
tri	Terrain Ruggedness Index	0.8	1.3	1.2	1.4	1.2	1.1	1	1.9	1.7
ma_evapo	Mean Annual Actual Evapotranspiration	0.7	-	-	-	-	-	-	-	-
bio_18	Precipitation of Warmest Quarter	0.6	1.6	1	0.9	1.6	1.1	0.6	1.5	0.6
roughness	Roughness	0.6	1.9	1.9	1.6	2	2.4	2.2	2.6	2.6
bio_02	Mean Diurnal Range (Mean of monthly (max temp - min temp))	0.5	0.7	1.3	1.6	1.3	1.6	1.3	1.4	2
bio_17	Precipitation of Driest Quarter	0.3	1.1	0.9	1	0.7	0.7	1	1.1	0.9
tpi	Topographic Position Index	0.2	0.3	0.2	0.3	0.1	0.2	0.2	0.3	0.3
bio_06	Min Temperature of Coldest Month	0.1	0.1	0.1	0.2	0.2	0.2	0.1	0.2	0.2
eastness	Aspect Easteness	0	0	0	0.1	0	0	0	0	0
northness	Aspect Northness	0	0	0	0	0	0	0	0	0
pot_evapo*	Global Potential Evapotranspiration	-	-	-	-	-	-	-	-	-
aridity*	Global Aridity Index	-	-	-	-	-	-	-	-	-
bio_1*	Annual Mean Temperature	-	-	-	-	-	-	-	-	-
bio_3*	Isothermality (BIO2/BIO7) (×100)	-	-	-	-	-	-	-	-	-
bio_4*	Temperature Seasonality (standard deviation ×100)	-	-	-	-	-	-	-	-	-
bio_11*	Mean Temperature of Coldest Quarter	-	-	-	-	-	-	-	-	-
bio_14*	Precipitation of Driest Month	-	-	-	-	-	-	-	-	-
bio_15*	Precipitation Seasonality (Coefficient of Variation)	-	-	-	-	-	-	-	-	-
bio_16*	Precipitation of Wettest Quarter	-	-	-	-	-	-	-	-	-
bio_19*	Precipitation of Coldest Quarter	-	-	-	-	-	-	-	-	-

Figure S1

Uncertainty in the current distribution models from CMIP6/Ensemble set of models. Uncertainty in the ModleR workflow is the range of adequabilities (maximum-minimum) for each pixel representing the variation between partitions and algorithms.

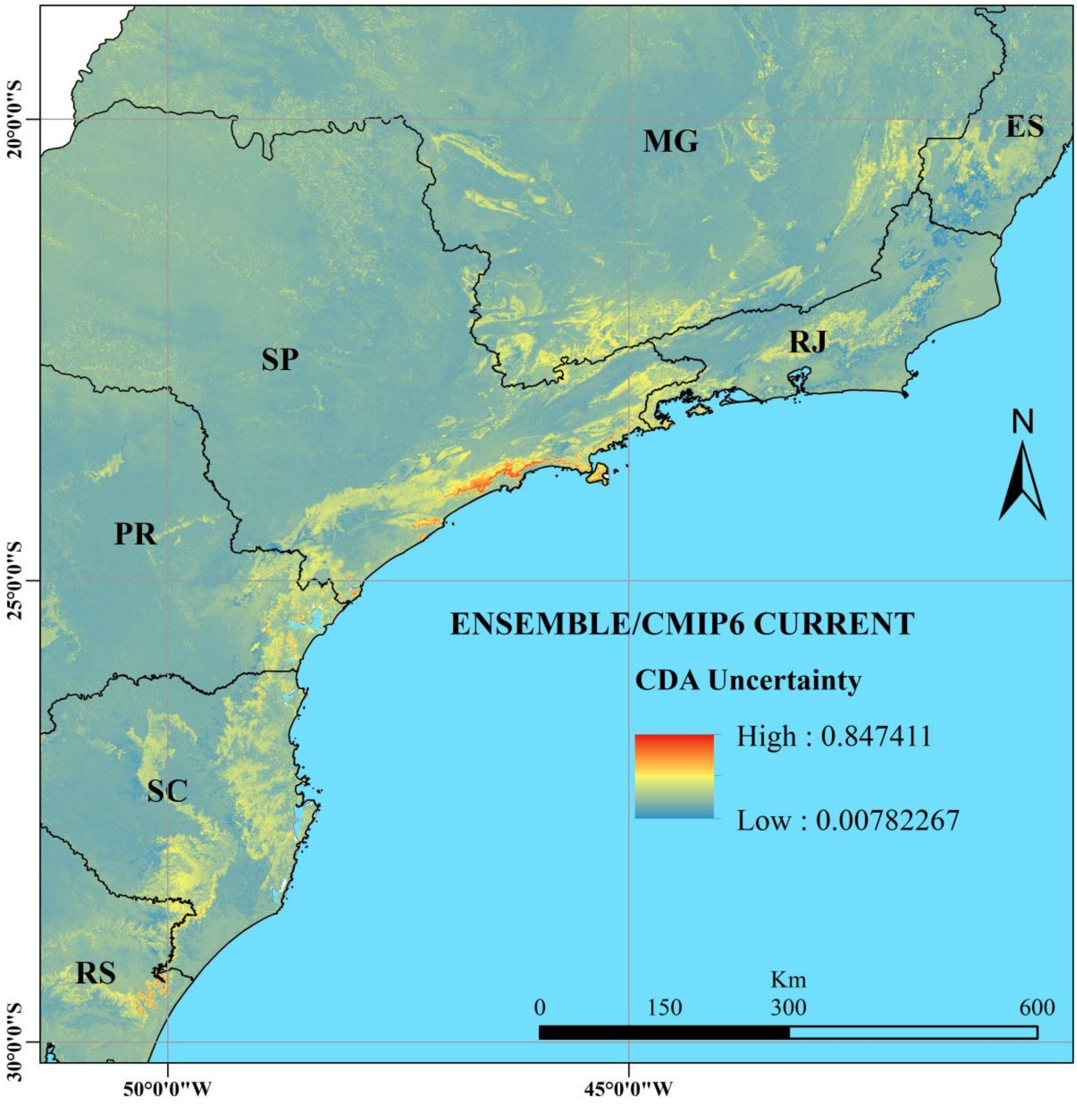
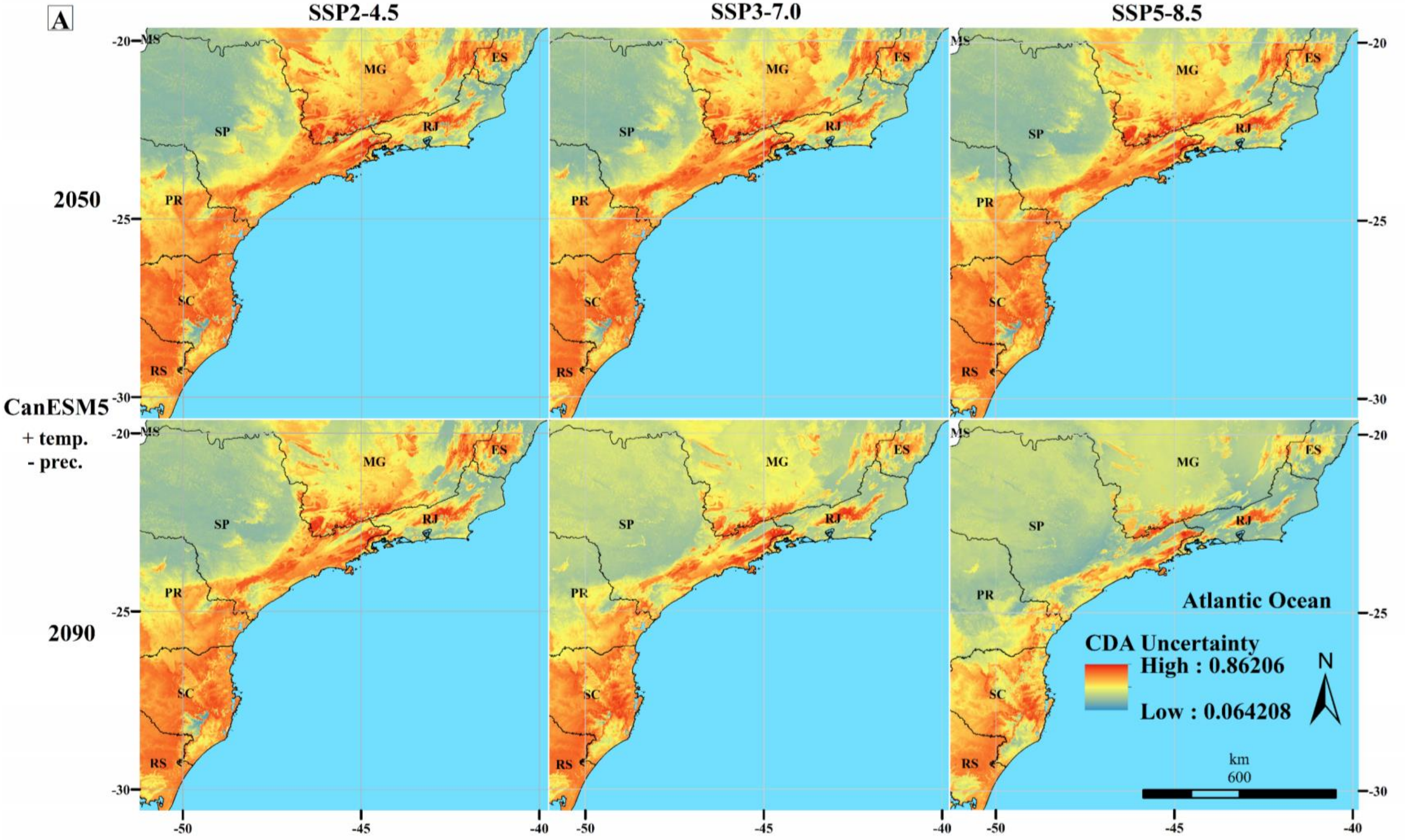
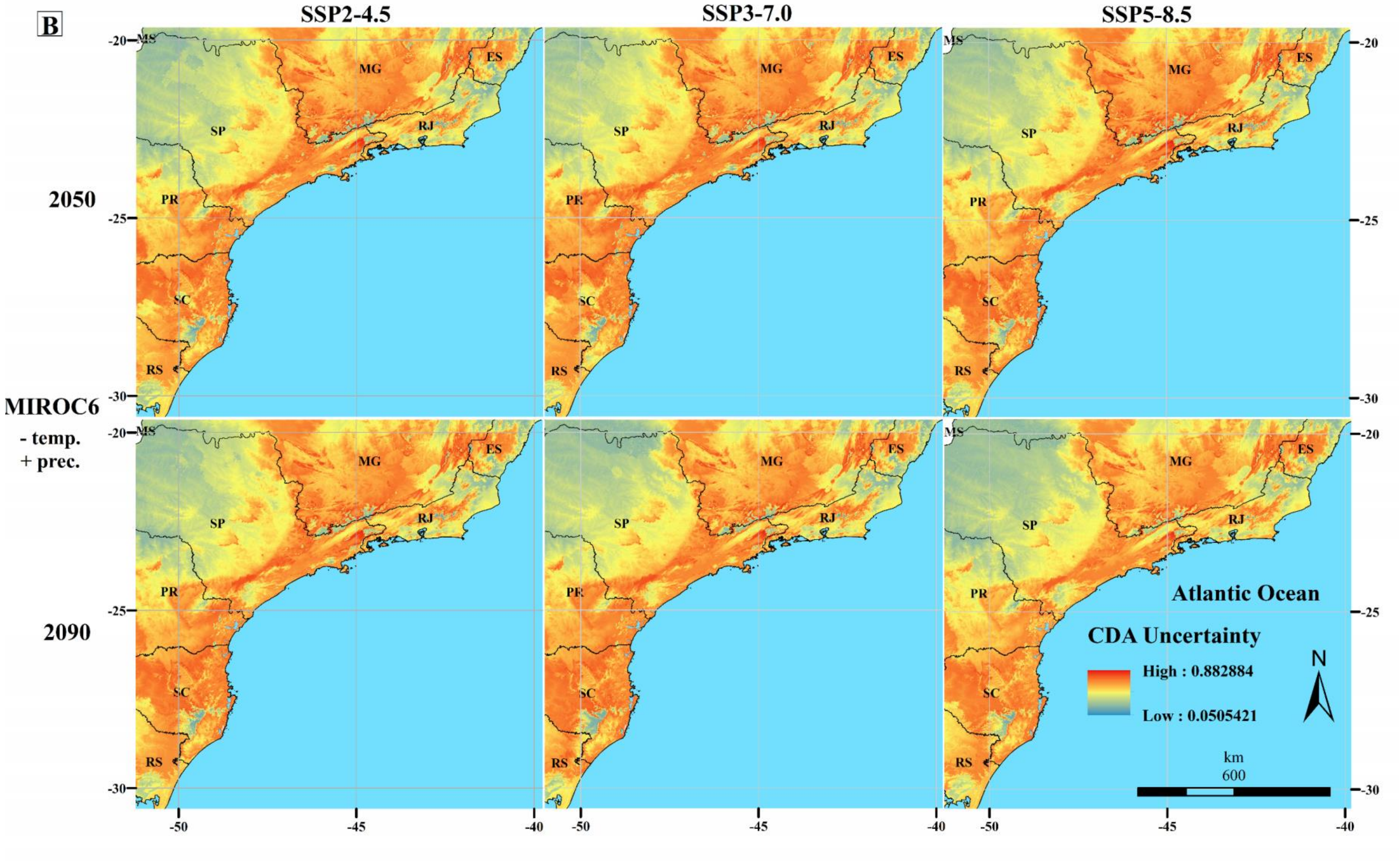


Figure S2

Uncertainty in the future distribution models for results from CanESM5 – A and Miroc6 – B from CMIP6/Ensemble set of models. Uncertainty in the ModleR workflow is the range of adequabilities (maximum-minimum) for each pixel representing the variation between partitions and algorithms.




B
SSP2-4.5
SSP3-7.0
SSP5-8.5
2050
MIROC6
- temp.
+ prec.
2090
MS
MG
ES
SP
RJ
PR
SC
RS
-20
-25
-30
-50
-45
-40
Atlantic Ocean
CDA Uncertainty
High : 0.882884
Low : 0.0505421
N
km
600

Chapter 2 - POTENTIAL PLANT INVASION IN '*CAMPOS DE ALTITUDE*' UNDER CLIMATE CHANGE

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Abstract

Biological invasion occurs when an alien species surpasses its original geographic range, establishing itself in a new region where it reproduces and spreads. This process has numerous impacts on ecosystem structure, functioning, and properties, contributing to biotic homogenization with positive feedbacks on climate change. *Campos de Altitude* is a shrub and grassland ecosystem typically found on mountaintops within the Atlantic Forest, especially in the Mar and Mantiqueira mountain ranges. While it is commonly found above 2000m in the Southeast region of Brazil, in the southern regions of Brazil, it occurs at lower elevations, around 1000m. In this study, we investigate the presence of invasive species within *Campos de Altitude* areas and their potential to expand their distribution into this ecosystem. To achieve this, we employed species distribution models (SDM) under both current and future climate scenarios provided by the Intergovernmental Panel on Climate Change (IPCC). These models were developed using topographic and climatic data from WorldClim. Our findings indicate a maximum potential richness of invasive species (PRIS) at 35 within current *Campos de Altitude* areas. In future scenarios based on the Global Circulation Model (GCM) Miroc6, a higher PRIS of 39 is projected by 2090, while results from GCM CanESM5 predict a lower PRIS (30) by the end of the 21st century. Our results underscore the importance of SDM in predicting potential shifts in the environmental suitability of invasive species. These models should be utilized by managers and stakeholders for planning and monitoring future biological processes within *Campos de Altitude* areas.

Keywords

High altitude grasslands, biological invasion, alien species, montane vegetation, Grasslands

Introduction

The process of biological invasion occurs when an alien species overcomes specific barriers and stages, establishing itself in a region (Blackburn et al., 2011; García-Díaz et al., 2021). It reproduces and spreads progressively farther from its initial point of introduction (Blackburn et al., 2011; García-Díaz et al., 2021). This process involves the intentional or unintentional transportation of species through human activities and ranks among the most significant threats to biodiversity, alongside habitat loss, land-use changes, fragmentation, pollution, and global climate change (Fulgêncio-Lima et al., 2021; IPBES 2023).

The negative impacts of invasive processes by alien species can affect environmental, economic, and social aspects of life across different scales of space and time (García-Díaz et al., 2021). More than 37,000 established alien species induced by human activities exist worldwide, with approximately 3,500 of these species having reported negative impacts (IPBES 2023). Invasive species have contributed to 16% of documented extinctions of animals and plants on the planet. Biotic homogenization, one of the most detrimental impacts of invasive species, has consequences on the structure, functioning, and properties of ecosystems (IPBES 2023).

The economy, as well as food and water security, is significantly impacted by invasive species, with estimated global costs reaching around US$425 billion in 2019 (IPBES 2023). Among the most affected are people involved in activities like fishing and Indigenous Peoples (IPBES 2023). In this context, climate change, coupled with the intensification and expansion of land-use change, can contribute to the spread of invasive species in disturbed habitats, enhance their competitive capacity, or extend suitable areas for them (IPBES 2023).

The *Campos de Altitude* is a shrub and grassland vegetation found in the mountaintops of the Atlantic Forest, especially in the Mar and Mantiqueira mountain ranges, and thus an insular distribution pattern for cold and humid flora in the tropics (Safford, 1999; Vasconcelos, 2011). The most expressive occurrences of *Campos de Altitude* are found above 2000 m; however, closer to the ocean, *Campos de Altitude* can be found down to approximately 1500 m (Safford and Martinelli, 2000). In southern Brazil, its subtropical extension is locally called *Campos de Cima da Serra*, which occurs further down at an elevation of approximately 1000 m (Iganci et al., 2011). *Campos de Altitude* communities have unique flora with a large number of endemic species, comprising 21.8% (479) of the total species found there (Zappi et al., 2015), and are exposed to the effects of climate warming (Martinelli, 2007; Scarano et al., 2016).

The structure of *Campos de Altitude* communities has been studied, and recent works have highlighted their unique taxonomic diversity (Caiafa and Silva, 2007; Campos et al., 2020, 2018; Cordeiro and Neri, 2019; Mocochinski and Scheer, 2008; Ribeiro et al., 2007; Tinti et al., 2015)

Additionally, research has described the soils associated with these mountaintop formations (Benites et al., 2003) and the influence of vegetation and climate on soil organic matter (Balieiro et al., 2012). There are also studies dedicated to understanding the functional ecology, environmental factors, and phylogenetic diversity that contribute to the assembly of *Campos de Altitude* communities (Christmann et al., 2021; Gastauer et al., 2020; Neri et al., 2016). More recently, the first study on the potential effects of climate change on the distribution of *Campos de Altitude* communities has been conducted (Chapter 1), and there is room to improve our knowledge in this context. However, a comprehensive study on the risk of biological invasion by alien species under climate change scenarios across the entire latitudinal range of *Campos de Altitude* distribution is needed (Scarano et al., 2016).

Species distribution modeling (SDM) is one of the most extensively employed tools for studying changes in species distribution (Elith and Leathwick, 2009). It relies on species occurrence data and statistical relationships between environmental descriptors (Elith and Leathwick, 2009). SDM is a widely used tool in ecological research, offering various approaches and interpretations for different research objectives (Araújo and Peterson, 2012; Peterson et al., 2011). These objectives may include species conservation, phylogenetic and evolutionary research, as well as the study of biological invasions by non-native species, where the influence of global climate change can be comprehended (Keppel et al., 2012; Peterson et al., 2011).

In this context, we will first investigate which and how many invasive species already registered in Brazilian territory have confirmed occurrences in the *Campos de Altitude*. The next step was using the SDM to investigate the top-climatic suitability of those invasive species in *Campos de Altitude* areas in the present and in future scenarios of greenhouse gas emissions to understand: A - what are the areas of topographic and climatic suitability for *Campos de Altitude* identified in Chapter 1 with the highest risk of biological invasion? and B - which areas or regions of *Campos de Altitude* have the greatest potential richness of invasive species throughout the distribution of *Campos de Altitude* in southern and southeastern Brazil at present and in future scenarios of global climate change.

Materials and Methods

Study Region

This study covers the entire range of *Campos de Altitude* and *Campos de Cima da Serra* (a related vegetation formation) in the southern region of Brazil, between the coordinates 20º and 30º S and 40º and 52º W, specifically associated with the peaks of the *Serra do Mar* and *Serra da Mantiqueira* mountain ranges, which extend along the eastern coast of Brazil (Fig. 1).

In the Southeast region (the political-administrative region of Brazil, consisting of the states of *Espírito Santo, Minas Gerais, Rio de Janeiro* and *São Paulo*), *Campos de Altitude* occurs between 1800 and 2900 m altitude, associated with rocky granite-gneiss outcrops (Neri et al., 2016; Safford, 1999; Scarano, 2009) (Fig. 1). *Campos de Altitude* is also known as High Altitude Grasslands or Brazilian Páramos, a term introduced internationally by (Safford, 1999). In the southern states of Brazil (*Paraná, Santa Catarina* and *Rio Grande do Sul*), *Campos de Altitude* occurs at altitudes between 1000 m and 1800 m at latitudes 24° and 30° S, often forming vegetation mosaics with Araucaria forests and locally called *Campos de Cima da Serra* (Iganci et al., 2011; Overbeck et al., 2022; Safford, 1999) (Fig. 1).

The climate is subtropical humid mesothermal with an average annual temperature between 12° and 20° C and dry winters and temperate summers (Alvares et al., 2013). Precipitation is well distributed throughout the year, averaging between 1000 and 1700 mm and possibly reaching more than 2500 mm annually (Iganci et al., 2011; Safford, 1999). The *Campos de Altitude* vegetation is found scattered in the mountain tops, consisting of mosaics of shrubs and trees inserted in a matrix of grasses, with the presence of pteridophytes, bamboos (Chusquea spp.) and other herbs, and rocky outcrops of different extent (Caiafa and Silva, 2007; Cordeiro and Neri, 2019). There are also monocotyledonous mats with dense root biomass, which are precursors of primary succession and can be the basis for the growth of even shrub species, and crevices and depressions up to 12 cm deep that accumulate substrate are common microhabitats (Caiafa and Silva, 2007).

In the following, both *Campos de Altitude* and *Campos de Cima da Serra* vegetation will be collectively referred to as *Campos de Altitude*, due to the co-occurrence of some species, as well as their climatic and altitudinal similarity.

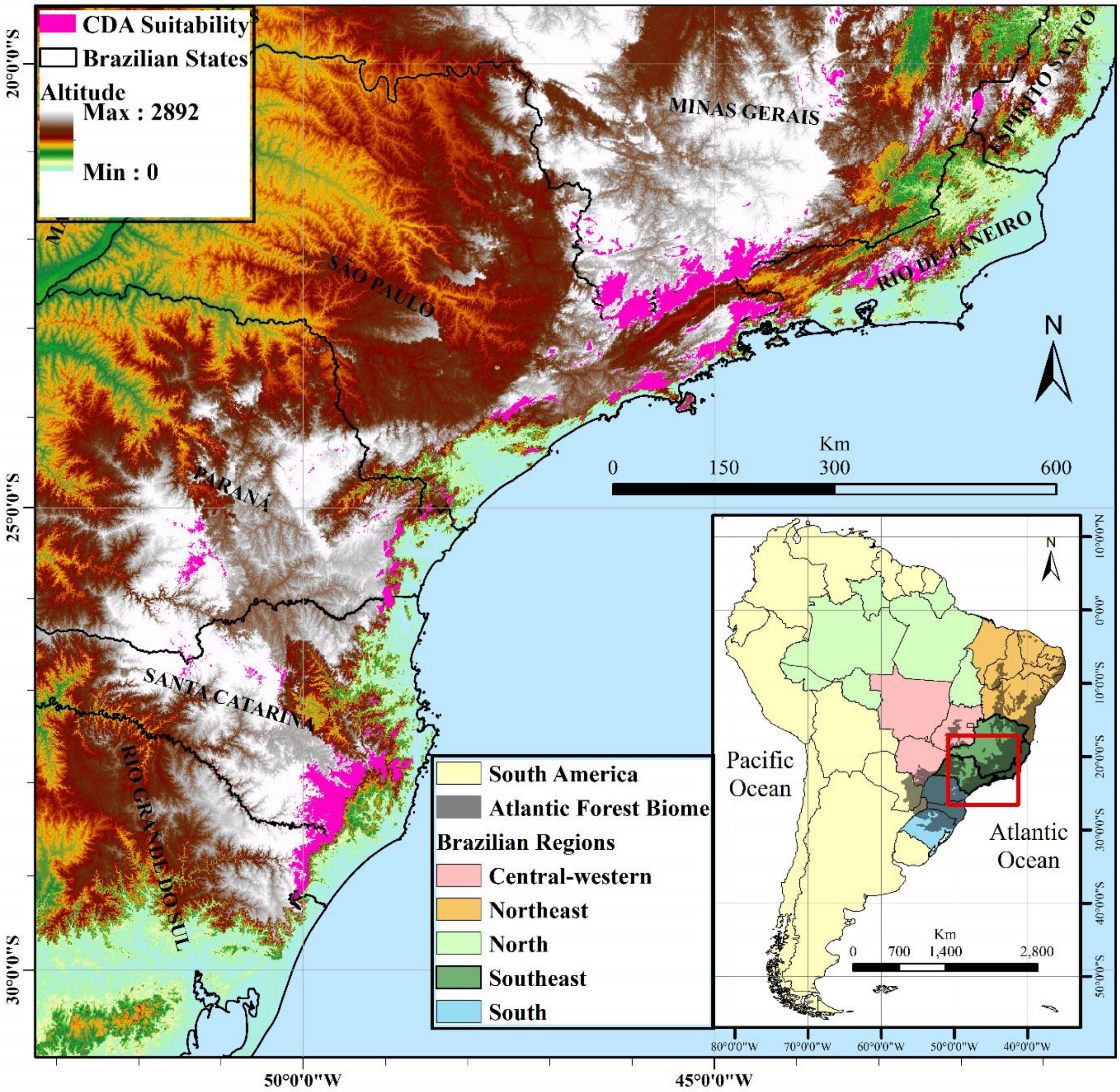


Figure 1: *Campos de Altitude* topographic and climatic suitability study areas, highlighted in pink, located in the Southern Administrative Region, highlighted in light blue, and in the Southeastern Region, highlighted in green. The *Campos de Altitude* is located in the *Serra do Mar* and *Serra da Mantiqueira* mountain ranges, the highest points in eastern South America, and is an ecosystem associated with the Atlantic Forest Biome, defined by Federal Decree No. 6660/2008 and Law No. 11.428/2006, shown in grey. Modified from Chapter 1.

Invasive Species Dataset

To identify invasive species occurring in Brazil and the *Campos de Altitude*, we compared the complete list of invasive species in Brazil provided by the Horus Institute for Environmental Conservation and Development (available at http://bd.institutohorus.org.br) with the list of all species occurring in the *Campos de Altitude* provided by Reflora (available at https://reflora.jbrj.gov.br/consulta/). We found 58 invasive species with confirmed occurrences in the *Campos de Altitude* and registered as invasive species in Brazil (Table S1). For each species, we downloaded the occurrences from the speciesLink network (specieslink.net/search) and the

Global Biodiversity Information Facility - GBIF portal (GBIF, 2023). In the speciesLink portal, we select the option of only consistent geographic coordinates to download occurrence data.

Bioclimatic and topographic variables

We used the 19 bioclimatic variables from WorldClim2.1 (Fick and Hijmans, 2017) based in climate data for 1970-2000 and are derived from Coupled Model Intercomparison Project Phase 6 - CMIP6 released in 2021, within The Physical Science Basis: Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2021) (Table S2).

Were also used topographic variables: Elevation, Slope, Aspect-Eastness, Aspect-Northness, Roughness, Topographic Position Index and Terrain Ruggedness Index (Amatulli et al., 2018). In addition, selected the geology associated with *Campos de Altitude*, such as granitic intrusions, migmatites and gneiss-migmatitic complex, the relief (mountainous and cliff domains), slope (> 25º) and elevation (> 300 m asl), to building a binary variable that predominantly represent the areas associated to *Campos de Altitude* (Table S2). The shapefiles containing the geological information were obtained from the Brazilian Geological Survey (GEOSGB, 2020) and processed by ArcMap software (ESRI, 2015). All variables with pixel resolution of ~ 1 km² that is decisive since we analyzed montane environments with high variability that are lost in smaller resolutions (Hijmans et al., 2005).

All layers have been clipped in the current political-geographic division of the Southeast (states of *Espírito Santo, Minas Gerais, São Paulo,* and *Rio de Janeiro*) and South (states of *Paraná, Santa Catarina,* and *Rio Grande do Sul*) that comprise the areas of higher elevation and consequent occurrence of *Campos de Altitude* species (Fig. 1).

Model Construction and validation

The background modelling layers were the political-geographical divisions of Southeast (States of *Espírito Santo, Minas Gerais, São Paulo* and *Rio de Janeiro*) and South (States of *Paraná, Santa Catarina* and *Rio Grande do Sul*) as mentioned above. In addition, the topographic variables were the same for all future scenarios, as they are very unlikely to change during the current century and are fundamental drivers of environmental and microhabitat definition in the *Campos de Altitude* ecosystem.

To select the global circulation models (GCMs), we used the GCMeval website, available at https://gcmeval.met.no/ (Parding et al., 2020). In this web tool we can visualise the possible differences between the GCM variations for the distribution of precipitation and temperature between the GCMs. For the SSP scenarios, only for the SSP5-8.5 scenario for the near future (2021-2050) and the far future (2071-2100). For both moments in the 21st century, CanESM5 represents high temperature and low precipitation compared to the annual mean climate change of the other GCMs for southeastern South America. MIROC6 represents low temperature and high precipitation shifts from other GCMs, and BCC-CSM2-MR has precipitation and temperature close to the annual mean climate change from all other GCMs. All of these multi-band layers were clipped by the political-geographical division of southeastern and southern Brazil and converted to ascii using R programming environment (R Development Core Team, 2020). This information for each GCM is also shown in Table S3 in the supplementary material.

The models were projected using an ensemble approach model carried out in the "modleR" library in R (Sánchez-Tapia et al., 2020), which in the last step allows the user to make an ensemble of outputs from different algorithms. The first step is a data setup (step 1), where the species occurrence data and all sets of variables are inserted to prepare a metadata matrix with selected variables and their respective values to project the models in the following step. We set the partition type to cross validation, the partition size to 5 partitions and 10 runs, and the number of pseudo-occurrences to 500. Other options for cleaning the occurrence data were 'clean_dupl', which removes points with the same latitude and longitude, 'clean_uni', which keeps only one point per pixel, and 'clean_nas', which removes points outside the boundaries of the environmental rasters and also sets 0.5 as the cut-off for selecting the environmental variables. Despite the user's choice, if there are nine or fewer occurrence points, the package automatically changes the partition type to boostrap and sets the number of partitions equal to the number of clean occurrence points (Table 1).

Step 2 in the ModleR workflow is the adjustment of the ecological data for each partition, running and projecting them in geographical space for each scenario. In this step we used the three GCMs previously defined in three scenarios by the IPCC in AR6 (IPCC, 2021). For AR6, the IPCC included new and improved representations of physical, chemical and biological processes with higher resolution compared to AR5, and consider in their projections the temporal evolution of pollutants, emissions or changes in land use and land cover, in summary the Shared Socioeconomics Pathways - SSP (IPCC, 2021). We chose SSP2-4.5, which represents a strong climate change mitigation scenario, SSP3-7.0 which is the middle of the road scenario, and 5-8.5, the worst-case scenario. The scenarios and their details are described in Table S3 in the supplementary material. In addition, scenarios are projected for four time periods in the 21st century, but we choose the average for 2041-2060 (hereafter 2050) and the average for 2081-2100 (hereafter 2090) to represent a moment in the middle and the end of the century (Table S3).

We have chosen the "spec_sens" threshold because it is the threshold at which the sum of sensitivity (true positive rate) and specificity (true negative rate) is highest and provides more robust models (Hijmans et al., 2021). In addition, we also projected the models in five algorithms implemented by the ModleR workflow: glm, maxent, maxnet, svmk and rf (Sánchez-Tapia et al., 2020). Our choice to keep the same thresholds and algorithms as in Chapter 1 is to make a parallel between the topo-climatic suitable areas for *Campos de Altitude* from Chapter 1 and the potential richness of invasive species in the same climate change scenarios.

The third step (Step 3) of the ModleR workflow is to merge the partitions from each algorithm into a final model per algorithm. To do this, we used 'raw_mean_th', which cuts the continuous models by the mean of the threshold chosen in the previous step to create a binary model (Sánchez-Tapia et al., 2020).

The final step (step 4) we to generate the final model for each invasive species with the algorithm that displayed the best predictive performance. To select the best performing model, we used the AUC evaluation metric available in the "dismo" package (Hijmans et al., 2021) implemented by the ModleR workflow (Sánchez-Tapia et al., 2020).

The final processing step was to produce the potential richness of invasive species (PRIS) raster layer for the *Campos de Altitude* suitable areas from Chapter 1. First, we added the best models of each species for all scenarios and created a species richness raster representing the PRIS in areas of the *Campos de Altitude* under different climate change scenarios. To do this, we selected those species for which the best models had an AUC ≥0.70. An AUC close to 0.5 corresponds to a prediction no better than the random prediction, between 0.6 and 0.7 poor accuracy, 0.7 to 0.8 fair accuracy, 0.8 to 0.9 good accuracy and >0.9 excellent accuracy (Pearce and Ferrier, 2000; Phillips et al., 2006; Swets, 1988). Secondly, in order to present the results, we clipped all the final PRIS maps of the scenarios according to the results of the topo-climatic suitability for *Campos de Altitude* produced in Chapter 1.

Results

We found 58 invasive species with confirmed occurrences in the *Campos de Altitude* and registered as invasive species in Brazil (Table S1). These species belong to 17 different botanical families and almost all of them are herbs, grow in a terrestrial substrate and are already naturalised species in Brazil (Table S1). For two species, *Geranium core-core* and *Ranunculus repens* var. *repens*, no clean points remained after the first step of the modelling workflow (Table S1).

A total of 232,085 models were generated, counting all 56 invasive species confirmed occurrence in the *Campos de Altitude* areas and considering all scenarios, algorithms and partitions. Six species were removed and not included in the final PRIS maps, taking into account the AUC cut-off point of >0.7: *Arenaria groenlandica, Cerastium mollissimum, Cerastium rivulare, Dichondra carolinensis, Digitaria ciliaris* and *Taraxacum campylodes* (Table 1). Other species did not have suitable areas projected by the best algorithm in any of the scenarios and were also removed: *Cenchrus clandestinus, Crocosmia crocosmiiflora, Trifolium incarnatum, Vicia angustifolia* and *Vicia sativa* (Table 1).

The maximum PRIS in the *Campos de Altitude* areas in the current scenario would be 45 species, but the maximum PRIS value was 35 (Table 1 and Figure 2). All evaluation metrics for all algorithms for all species are shown in Table S4 in the supplementary material.

The three selected GCMs, CanESM5, Miroc6, and BCC-CSM2-MR, showed different trends in PRIS for future scenarios. In the CanESM5 results, the PRIS always decreased over the century, being higher in 2050 than in 2090 for all scenarios (Figure 3A). The lower PRIS value in the CanESM5 results was in SSP5-85 in 2090 (30 species) (Figure 3A). In Miroc6, the pattern was the opposite, with PRIS tending to be higher at the end of the century and reaching a higher value in the intermediate scenario (SSP3-7.0) (39 species) (Figure 3B). In the BCC-CSM2-MR results, the PRIS was the same for all future scenarios (20 species) (Figure 3C). The results can be better observed in focal figures presented in Supplementary Material Figures S1, S2, S3, S4, and S5).

The geographical distribution patterns of PRIS in *Campos de Altitude* areas showed almost no differences between the GCMs. Only in CanESM5, which loses three species in the worst-case scenario (SSP5-8.5) in 2090, we can see the loss in the central region of *Campos de Altitude* suitability between *São Paulo, Rio de Janeiro,* and *Minas Gerais* states in the Southeast region of Brazil (Figure S2).

Table 1: Results from species distribution model setup data, the first step of the modleR workflow for 56 invasive species in *Campos de Altitude*. The Partition Type column provides information on what type of partitioning of the data was selected, the Boot-n and CV-partition columns provide the number of bootstrap and croosvalidation partitions, respectively. In addition, the number of runs selected is shown in the CV-n column, as well as the selected predictors for all modelled species and the number of clean occurrences. Species highlighted in bold and with one * were removed by an AUC cut-off value of <0.7 and those highlighted in bold and with two ** are those species for which no suitable areas were predicted by the best algorithm in any scenario and were also removed.

Accepted Specie name	Partition Type	Boot-n	CV-partition	CV-n	Selected predictors	Clean occurrences
Achillea millefolium L.	crossvalidation	-	5	10	Annual Precipitation (bio_12), Precipitation of Warmest Quarter (bio_18), Mean Diurnal Range (bio_02), Temperature Annual Range (bio_07), Mean Temperature of Driest Quarter (bio_09), Aspect Easteness, Elevation, Aspect Northness, Geology, Topographic Position Index (tpi), and Terrain Ruggedness Index(tpi).	167
Agrostis capillaris L.	bootstrap	1	4	-		4
Arenaria groenlandica **(Retz.) Spreng.***	**bootstrap**	**1**	**5**	**-**		**5**
Arenaria lanuginosa (Michx.) Rohrb.	crossvalidation	-	5	10		74
Browallia americana L.	crossvalidation	-	5	10		84
Cardionema ramosissima (Weinm.) A.Nelson & J.F.Macbr.	crossvalidation	-	5	10		19
Cenchrus clandestinus **(Hochst. ex Chiov.) Morrone****	**crossvalidation**	**-**	**5**	**10**		**14**
Centaurium erythraea Rafn.	crossvalidation	-	5	10		24
Cerastium dicrotrichum Fenzl ex Rohrb.	crossvalidation	-	5	10		29
Cerastium glomeratum Thuill.	crossvalidation	-	5	10		95
Cerastium humifusum Cambess.	crossvalidation	-	5	10		13
Cerastium mollissimum **Poir.***	**bootstrap**	**1**	**4**	**-**		**4**
Cerastium rivulare **Cambess.***	**crossvalidation**	**-**	**5**	**10**		**34**
Cerastium selloi Schltdl. ex Rohrb.	crossvalidation	-	5	10		10
Cerastium semidecandrum L.	bootstrap	1	5	-		5
Crocosmia crocosmiiflora **(Lemoine) N.E.Br. ****	**crossvalidation**	**-**	**5**	**10**		**53**
Desmodium adscendens (Sw.) DC.	crossvalidation	-	5	10		194
Dichondra carolinensis **Michx.***	**bootstrap**	**1**	**4**	**-**		**4**

Digitaria ciliaris* (Retz.) Koeler	**crossvalidation**	**-**	**5**	**10**		**39**
Digitaria fuscescens (J.Presl) Henrard	crossvalidation	-	5	10		29
Drymaria cordata (L.) Willd. ex Roem. & Schult.	crossvalidation	-	5	10		400
Furcraea foetida (L.) Haw.	crossvalidation	-	5	10		56
Geranium carolinianum L.	crossvalidation	-	5	10		11
Geranium purpureum Vill.	crossvalidation	-	5	10		16
Geranium robertianum L.	crossvalidation	-	5	10		54
Kalanchoe fedtschenkoi Raym.-Hamet & H.Perrier	crossvalidation	-	5	10		23
Lantana camara L.	crossvalidation	-	5	10		57
Melinis minutiflora P.Beauv.	crossvalidation	-	5	10		147
Melinis repens (Willd.) Zizka	crossvalidation	-	5	10		352
Microchloa kunthii Desv.	bootstrap	1	9	-		9
Paronychia brasiliana A.DC.	crossvalidation	-	5	10		13
Phyllanthus urinaria L.	crossvalidation	-	5	10		34
Pinus elliottii Engelm.	crossvalidation	-	5	10		80
Poa annua L.	crossvalidation	-	5	10		166
Polycarpaea corymbosa (L.) Lam.	crossvalidation	-	5	10		35
Polycarpon depressum Nutt.	bootstrap	1	6	-		6
Polycarpon tetraphyllum (L.) L.	crossvalidation	-	5	10		40
Potentilla indica (Andrews) Th.Wolf	crossvalidation	-	5	10		44
Ranunculus muricatus L.	crossvalidation	-	5	10		14
Ranunculus repens L.	bootstrap	1	6	-		6
Sisyrinchium minus Engelm. & A.Gray	crossvalidation	-	5	10		14

Spergularia grandis (Pers.) Cambess.	crossvalidation	-	5	10		40
Stachys arvensis L.	crossvalidation	-	5	10		136
Stellaria media (L.) Vill.	crossvalidation	-	5	10		111
Taraxacum campylodes* G.E.Haglund	**crossvalidation**	**-**	**5**	**10**		**14**
Trifolium campestre Schreb.	crossvalidation	-	5	10		48
Trifolium dubium Sibth.	crossvalidation	-	5	10		25
Trifolium incarnatum* L. *	**crossvalidation**	**-**	**5**	**10**		**14**
Trifolium pratense L.	crossvalidation	-	5	10		77
Trifolium repens L.	crossvalidation	-	5	10		214
Trifolium subterraneum L.	crossvalidation	-	5	10		13
Ulex europaeus L.	crossvalidation	-	5	10		65
Urochloa brizantha (Hochst. ex A.Rich.) R.D.Webster	crossvalidation	-	5	10		68
Verbena officinalis L.	crossvalidation	-	5	10		14
Vicia angustifolia* L. *	**crossvalidation**	**-**	**5**	**10**		**55**
Vicia sativa* L. *	**crossvalidation**	**-**	**5**	**10**		**98**

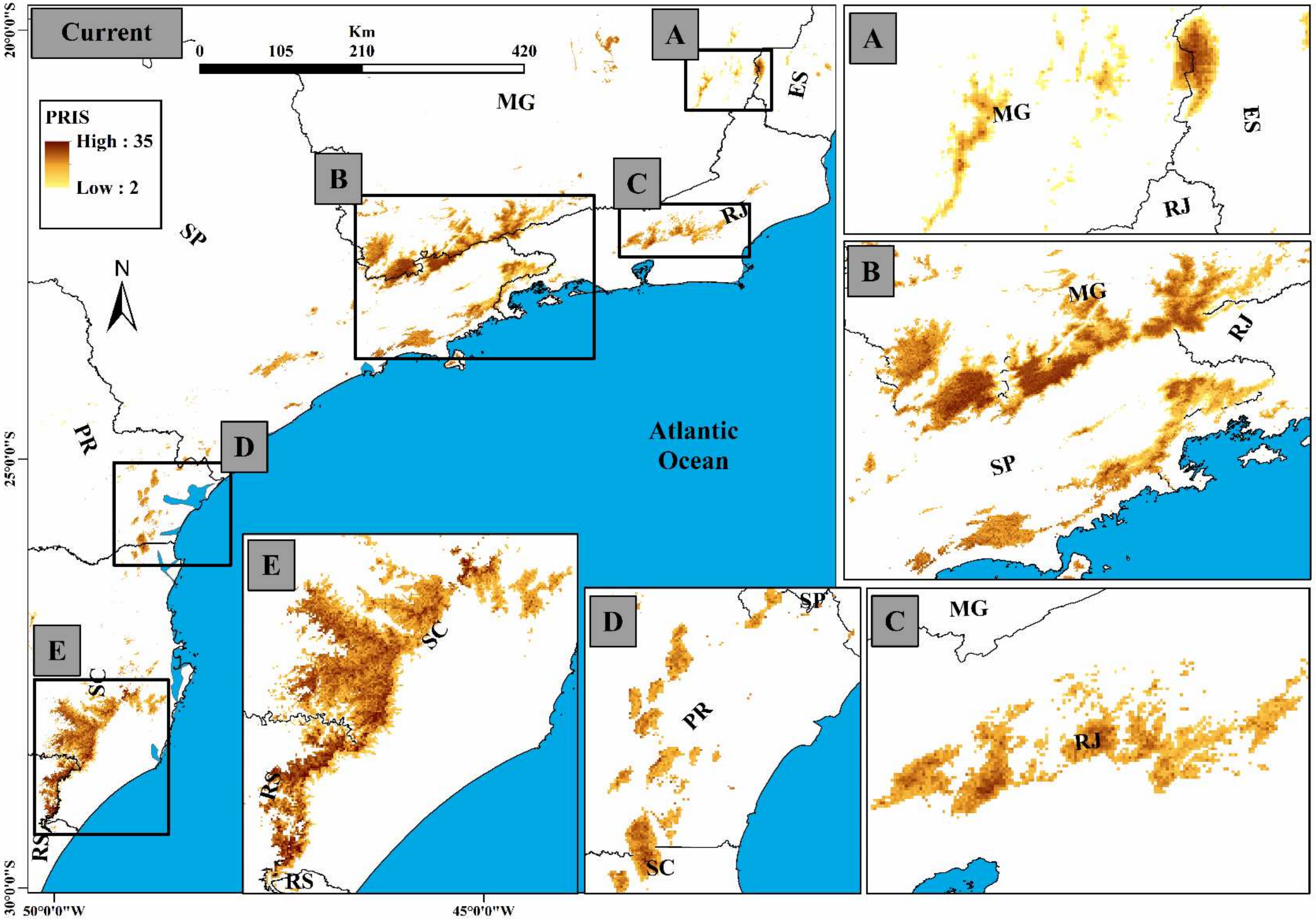
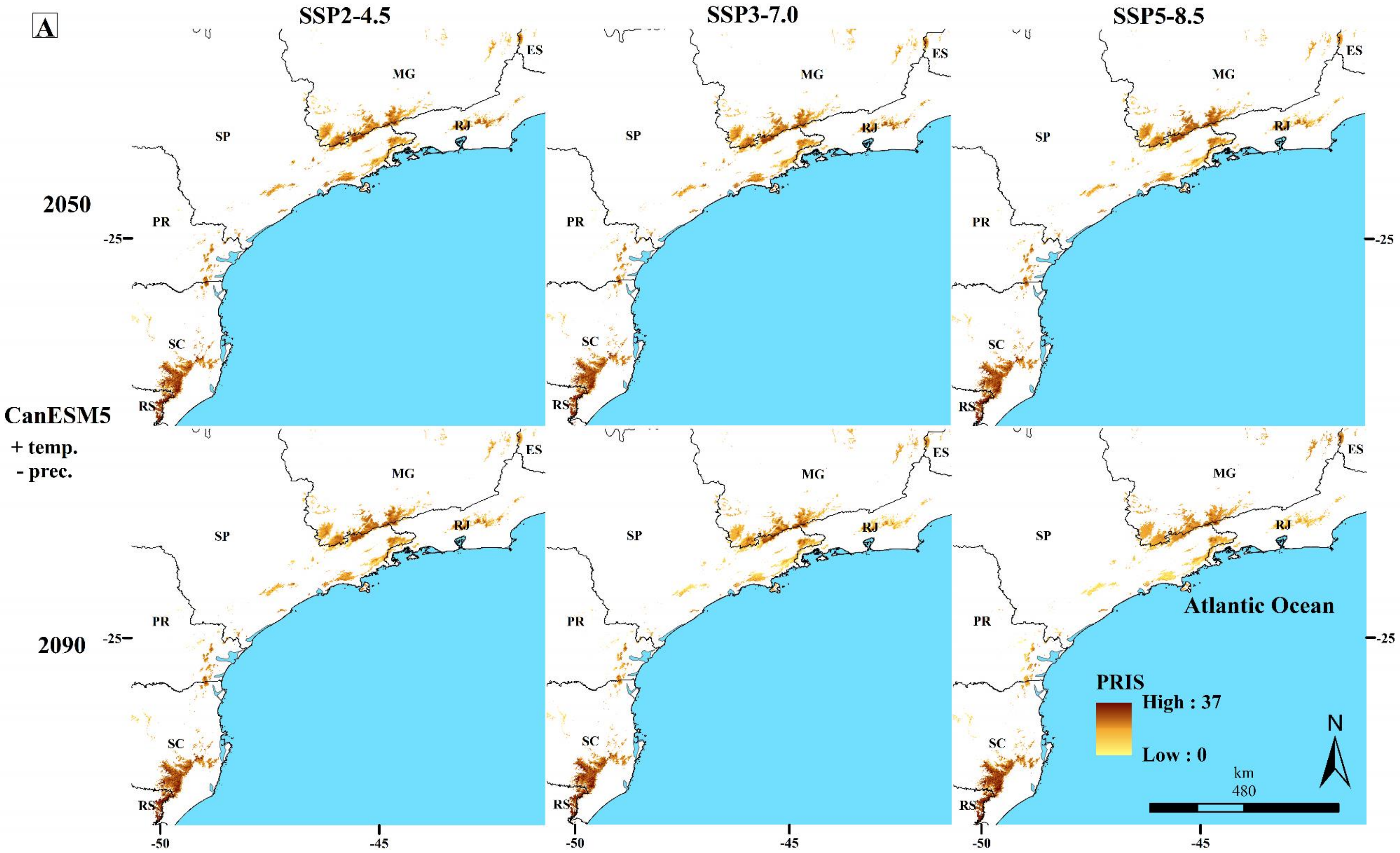


Figure 2: Current topoclimatic distribution of the potential richness of invasive species (PRIS) in areas predicted for the *Campos de Altitude* in *Serra da Mantiqueira* and *Serra do Mar* in Brazil. The acronyms correspond to the political-geographical divisions of the Southeast region of Brazil, which are ES - *Espírito Santo*, MG - *Minas Gerais*, SP - *São Paulo*, RJ - *Rio de Janeiro*, and the states of the South region are PR - *Paraná*, SC - *Santa Catarina*, and RS - *Rio Grande do Sul*. The areas highlighted by zooming in on the main map correspond to the extreme north of the *Campos de Altitude* distribution, in the Caparaó National Park and the Zona da Mata Mineira - A; the central sector of the *Mantiqueira* and *Mar* mountain ranges between *São Paulo*, *Minas Gerais* and *Rio de Janeiro* - B; the central region of the State of *Rio de Janeiro* - C, in the southern region of Brazil, the sector of the State of *Paraná* and the border with the State of *Santa Catarina* - D, and finally the southernmost part of the *Campos de Altitude* in the mountains between *Santa Catarina* and *Rio Grande do Sul* - E.


A
SSP2-4.5
SSP3-7.0
SSP5-8.5
2050
2090
CanESM5
+ temp.
- prec.
ES
MG
SP
RJ
PR
SC
RS
-25
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-45
Atlantic Ocean
PRIS
High : 37
Low : 0
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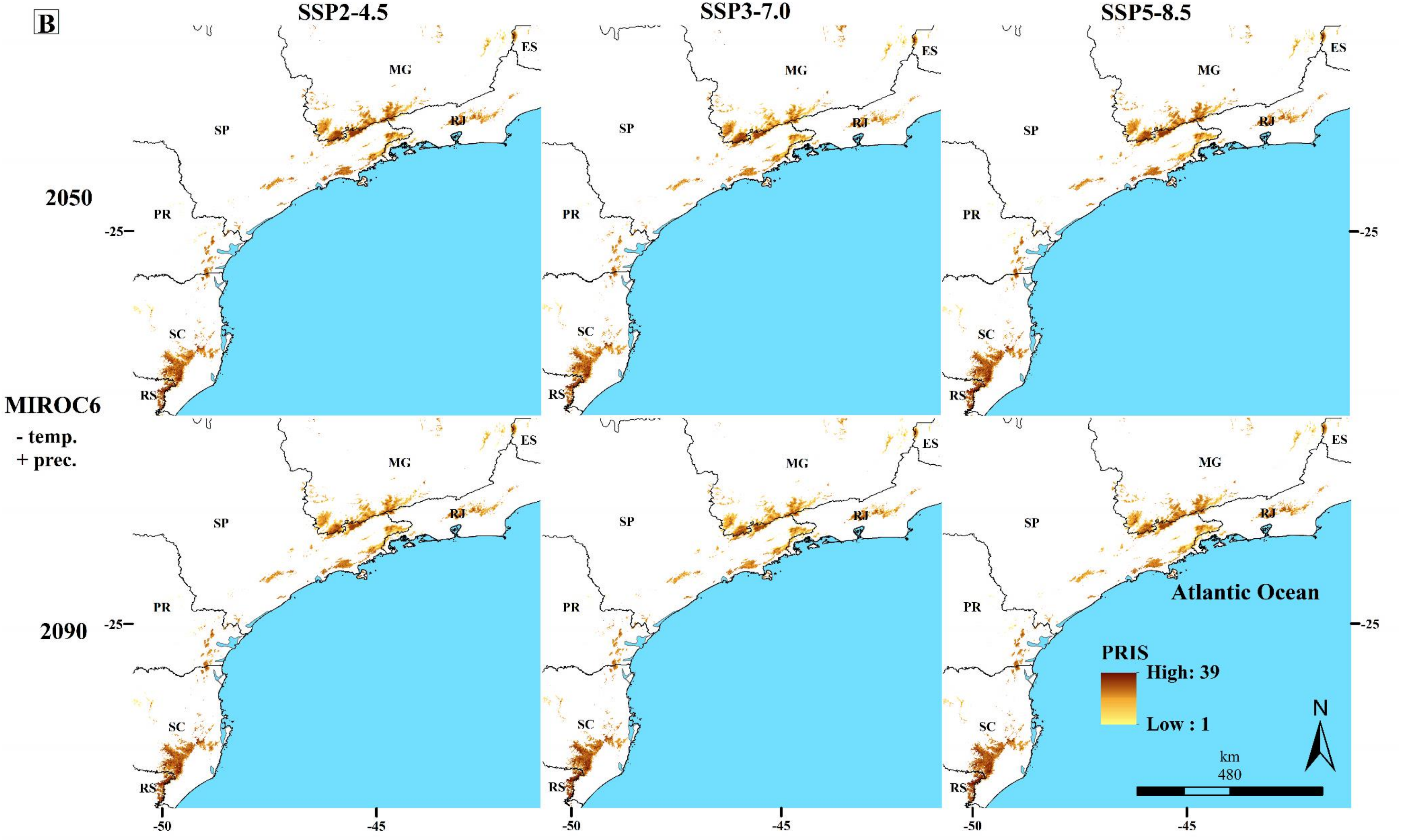
B
SSP2-4.5
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- temp.
+ prec.
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SC
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Low : 1
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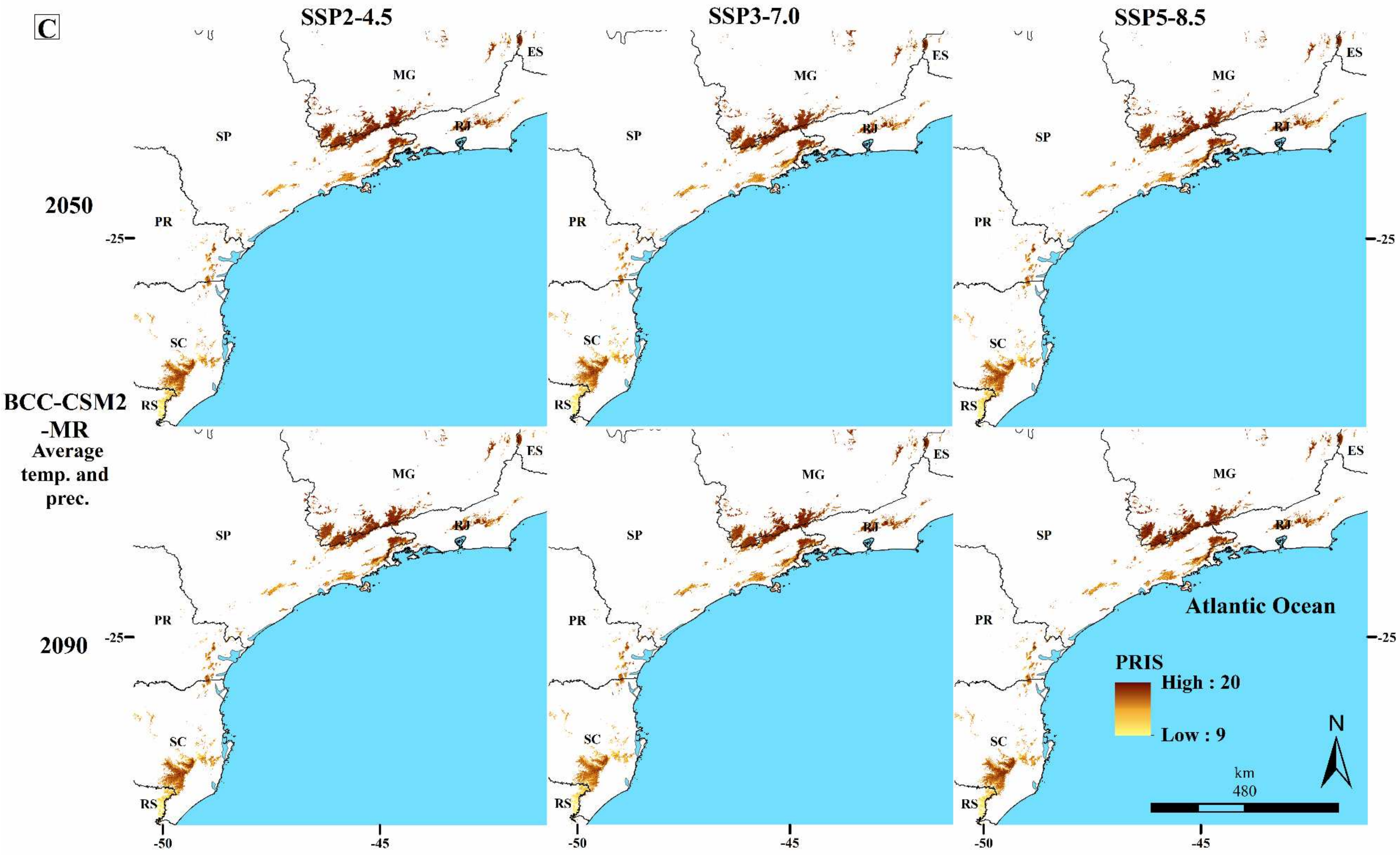

Figure 3: PRIS in *Campos de Altitude* in 18 future scenarios (three GHG emissions and mitigation scenarios by IPCC, SSPs 2-4.5, 3-7.0 and 5-8.5) for two time periods, 2050 (2041-2060) and 2090 (2081-2100) based on projections by three GCMs used in IPCC, CanESM5 - A, Miroc6 - B, and BCC-CSM2-MR - C. The acronyms correspond to the political-geographical divisions of the Southeast region of Brazil, which are ES - *Espírito Santo*, MG - *Minas Gerais*, SP - *São Paulo*, RJ - *Rio de Janeiro*, and the South region states are PR - *Paraná*, SC - *Santa Catarina*, and RS - *Rio Grande do Sul*.

Discussion

Our PRIS results in areas suitable for *Campos de Altitude* clearly indicate the potential for an invasive biological process of intense impacts. The maximum PRIS was 45, however only 35 invasive species exhibited the same topo-climatic suitability as native *Campos de Altitude* species, resulting in a total PRIS of 35 in the current scenario. This is particularly noteworthy when considering that despite the confirmed occurrence of all modeled species in the *Campos de Altitude*, some of them did not have a predicted suitable area that coincided with *Campos de Altitude* suitable areas in all future scenarios.

The PRIS below the expected maximum may be linked with different factors. One of these factors is the current distribution of invasive species. Not all of them are present across the entire latitudinal range of the natural distribution of *Campos de Altitude* in southern and southeastern Brazil. Some have only been confirmed to occur in *Campos de Cima da Serra*, the subtropical extension of the *Campos de Altitude* found in the mountains of the states of Santa Catarina and Rio Grande do Sul, or in the lowlands of Rio Grande do Sul, which are the natural habitat of Campos Sulinos (pampas) (Iganci et al., 2011). On the other hand, some species, despite having a broader distribution across the study area, still exhibit more limited models both in the present and in the future. In any case, certain species maintain their suitable range confined to the coastal lowlands in the Atlantic Forest and southern grasslands (as illustrated in Figure S6), a pattern consistent with findings from another study on biological invasion across all of Brazil's biomes (Fulgêncio-Lima et al., 2021).

In the future scenarios, we identified two contrasting situations. In the results of the CanESM5 GCM, which represents scenarios with a more pronounced increase in temperature compared to the average annual climate change of the other GCMs used, we observed a tendency for the PRIS to decrease over the course of the century. Conversely, in the results of the Miroc6 GCM, which represents a greater increase in precipitation compared to the other GCMs, we noted a slight increase in PRIS towards the end of the century. These trends underscore the strong reliance of *Campos de Altitude* communities on moderate temperatures and very high precipitation levels, exceeding 2000 mm at the summits of *Serra do Mar* and *Mantiqueira* (Safford, 1999). Consequently, these conditions are crucial for some invasive species that are not projected to be suitable in future scenarios.

Another significant focal point for PRIS in both present and future scenarios is the higher elevation regions. The results clearly demonstrate a trend where suitability for invasive species tends to concentrate at the highest points within the *Campos de Altitude*'s occurrence areas (see Figures 2 and 3, as well as Supplementary Figures S1, S2, S3, S4, S5, and S6). This trend aligns with findings from studies conducted in mountainous regions in Switzerland and Australia, where habitat suitability for 48 invasive species was assessed (Petitpierre et al., 2016). In the same study, the authors highlighted that the negative effects of climate change on native species' habitat suitability could be exacerbated by the mutual impacts of invasive species' suitability (Petitpierre et al., 2016). We observed a similar co-occurrence of these patterns in future scenarios for *Campos de Altitude* communities, which is a cause for significant concern in terms of conservation planning and strategies.

Ten years ago, in a survey conducted exclusively within Brazil's Federal Protected Areas, Sampaio and Schmidt (2013) discovered that 125 of these protected areas already harbored invasive species, with 43 of them located in the Atlantic Rainforest, representing the highest number among all Brazilian biomes. Furthermore, the highest concentration of invasive species was identified in Protected Areas within the Atlantic Forest biome, with three protected areas in this biome ranking among the top 10 locations with the most recorded invasive species. Notably, the National Parks of Itatiaia had 34 invasive species, while *Serra da Bocaina, Aparados da Serra,* and *Serra Geral* each had 22 records of invasive species (Sampaio and Schmidt, 2013). Our current results indicate an increase over the past decade, particularly in the case of *Serra da Bocaina* National Park and *Aparados da Serra* and *Serra Geral* National Parks.

The growing PRIS at higher elevations will necessitate more comprehensive planning and preventive measures from protected areas managers (Wu et al., 2023). In general, international protocols and laws use strategies for the control of invasive species based on the negative impacts they cause, such as population control on the abundance or population size of invasive species or by considering priority species and areas for management (García-Díaz et al., 2021). However, this one-dimensional view of invasive species management practices has not proven to be the most effective (García-Díaz et al., 2021).

It is necessary a continuous planning and management in medium and long terms that considers the effectiveness of measures adopted, monitoring the outcomes of management practices or projects, positive and negative impacts on various sectors and the costs of all of these aspects must be consider maximizing the cost-efficiency (García-Díaz et al., 2021; Sampaio and Schmidt, 2013; Soto et al., 2023). In addition, the involvement of society, political sectors, and decision-makers (García-Díaz et al., 2021) in an integrated governance approach that acknowledges the interactions between invasive alien species and other drivers, including climate change, direct exploitation of natural resources, pollution, and land-use changes, alongside human, animal and plant health, can identify where to best direct policy alignment and mutually supportive efforts (IPBES, 2023).

Further studies need to be conducted to incorporate the biotic aspects of invasive species, as our work has focused solely on topo-climatic models. Incorporating biotic dimensions and interactions, including species dispersal, landscape connectivity, land use, and the competitive potential of invasive and native species, will enhance the predictive capabilities of the models and reduce the inherent uncertainties in the method (Dormann et al., 2018; Elith and Leathwick, 2009). These efforts will provide a foundation for monitoring potential invasions and taking immediate action to prevent and manage invasive processes by exotic species.

Conclusions

We identified a maximum PRIS of 35 species in areas currently suitable for *Campos de Altitude*. In the future scenarios, we observed two distinct trends. The first trend showed an increase in PRIS over the 21st century in scenarios derived from the GCM Miroc6, with 39 invasive species projected. Meanwhile, in the results from GCM CanESM5, there was a slight decrease in PRIS until 2090, with 30 species predicted. Notably, no significant variations in PRIS were detected across the latitudinal range of *Campos de Altitude* distribution. Despite numerical variations in the results between different GCMs, both in the present and future scenarios, there is a prevailing trend of increasing PRIS in higher areas, which are often already encompassed by Protected Areas. Our findings underscore the valuable utility of tools such as species distribution models in predicting the suitability of invasive species. These models provide a crucial foundation for environmental managers, society, and governments in planning and implementing consistent control and management measures aimed at addressing the presence of invasive species in areas suitable for *Campos de Altitude*.

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Supplementary Material

Table S1

List of invasive species with confirmed occurrences in the *Campos de Altitude* and registered as invasive species in Brazil, from the Horus Institute and Reflora databases. All information was confirmed in the Reflora search portal, available at < http://floradobrasil.jbrj.gov.br/.

Accepted Specie name	Botanical family	Origin	Life form	Substrate
Furcraea foetida (L.) Haw.	Asparagaceae	Naturalized	herb	-
Achillea millefolium L.	Asteraceae	Cultivated	herb/subshrub	terrestrial
Taraxacum campylodes G.E.Haglund	Asteraceae	Naturalized	herb	terrestrial
Arenaria groenlandica (Retz.) Spreng.	Caryophyllaceae	Naturalized	herb	terrestrial
Arenaria lanuginosa (Michx.) Rohrb.	Caryophyllaceae	Naturalized	herb	terrestrial
Cardionema ramosissima (Weinm.) A.Nelson & J.F.Macbr.	Caryophyllaceae	Naturalized	herb	terrestrial
Cerastium dicrotrichum Fenzl ex Rohrb.	Caryophyllaceae	Naturalized	herb	terrestrial
Cerastium glomeratum Thuill.	Caryophyllaceae	Naturalized	herb	terrestrial
Cerastium humifusum Cambess.	Caryophyllaceae	Naturalized	herb	terrestrial
Cerastium mollissimum Poir.	Caryophyllaceae	Naturalized	herb	terrestrial
Cerastium rivulare Cambess.	Caryophyllaceae	Naturalized	herb	terrestrial
Cerastium selloi Schltdl. ex Rohrb.	Caryophyllaceae	Naturalized	herb	terrestrial
Cerastium semidecandrum L.	Caryophyllaceae	Naturalized	herb	terrestrial
Drymaria cordata (L.) Willd. ex Roem. & Schult.	Caryophyllaceae	Naturalized	herb	terrestrial
Paronychia brasiliana A. DC.	Caryophyllaceae	Naturalized	herb	terrestrial
Polycarpaea corymbosa (L.) Lam.	Caryophyllaceae	Naturalized	herb	terrestrial
Polycarpon depressum Nutt.	Caryophyllaceae	Naturalized	herb	terrestrial
Polycarpon tetraphyllum (L.) L.	Caryophyllaceae	Naturalized	herb	terrestrial
Spergularia grandis (Pers.) Cambess.	Caryophyllaceae	Naturalized	herb	terrestrial
Stellaria media (L.) Vill.	Caryophyllaceae	Naturalized	herb	terrestrial
Dichondra carolinensis Michx.	Convolvulaceae	Naturalized	herb	terrestrial
Kalanchoe fedtschenkoi Raym.-Hamet & H.Perrier	Crassulaceae	Naturalized	herb/subshrub/ succulent	rupicolous/ terrestrial

Desmodium adscendens (Sw.) DC.	Fabaceae	Naturalized	subshrub	terrestrial
Trifolium campestre Schreb.	Fabaceae	Naturalized	herb	terrestrial
Trifolium dubium Sibth.	Fabaceae	Naturalized	herb	terrestrial
Trifolium incarnatum L.	Fabaceae	Cultivated	herb	terrestrial
Trifolium pratense L.	Fabaceae	Naturalized	herb	terrestrial
Trifolium repens L.	Fabaceae	Naturalized	herb	terrestrial
Trifolium subterraneum L.	Fabaceae	Cultivated	herb	terrestrial
Ulex europaeus L.	Fabaceae	Naturalized	shrub	terrestrial
Vicia angustifolia L.	Fabaceae	Naturalized	herb	-
Vicia sativa L.	Fabaceae	Naturalized	herb/liana-scandent-vine	-
Centaurium erythraea Rafn.	Gentianaceae	Naturalized	herb	terrestrial
Geranium carolinianum L.	Geraniaceae	Naturalized	herb	terrestrial
Geranium core-core* Steud.	**Geraniaceae**	**Naturalized**	**herb**	**terrestrial**
Geranium purpureum Vill.	Geraniaceae	Naturalized	herb	terrestrial
Geranium robertianum L.	Geraniaceae	Naturalized	herb	terrestrial
Crocosmia crocosmiiflora (Lemoine) N.E.Br.	Iridaceae	Naturalized	herb	terrestrial
Sisyrinchium minus Engelm. & A.Gray	Iridaceae	Naturalized	herb	terrestrial
Stachys arvensis L.	Lamiaceae	Naturalized	herb	terrestrial
Phyllanthus urinaria L.	Phyllanthaceae	Naturalized	herb/shrub	terrestrial
Pinus elliottii Engelm.	Pinaceae	Naturalized	tree	terrestrial
Agrostis capillaris L.	Poaceae	Naturalized	herb	terrestrial
Cenchrus clandestinus (Hochst. ex Chiov.) Morrone	Poaceae	Naturalized	herb	terrestrial
Digitaria ciliaris (Retz.) Koeler	Poaceae	Naturalized	herb	terrestrial
Digitaria fuscescens (J.Presl) Henrard	Poaceae	Naturalized	herb	terrestrial
Melinis minutiflora P.Beauv.	Poaceae	Naturalized	herb	terrestrial
Melinis repens (Willd.) Zizka	Poaceae	Naturalized	herb	terrestrial
Microchloa kunthii Desv.	Poaceae	Naturalized	herb	terrestrial/ rupicolous

Poa annua L.	Poaceae	Naturalized	herb	terrestrial
Urochloa brizantha (Hochst. ex A.Rich.) R.D.Webster	Poaceae	Naturalized	herb	terrestrial
Ranunculus muricatus L.	Ranunculaceae	Naturalized	herb	aquatic/ terrestrial
Ranunculus repens L.	Ranunculaceae	Naturalized	herb	aquatic/ terrestrial
Ranunculus repens* L. var. *repens*	**Ranunculaceae**	**Naturalized**	**herb**	**aquatic/ terrestrial**
Potentilla indica (Andrews) Th.Wolf	Rosaceae	Naturalized	herb	terrestrial
Browallia americana L.	Solanaceae	Naturalized	herb	terrestrial
Lantana camara L.	Verbenaceae	Naturalized	Shrub	terrestrial
Verbena officinalis L.	Verbenaceae	Naturalized	herb	terrestrial

Table S2

Variables used in the current and future prediction models. The Variable column gives the short name of the variable, the Description column gives the full name and, where applicable, how the variable was obtained, the Source column gives the website where it can be accessed, and the spatial resolution used in this study.

Variable	Description	Source	Spatial Resolution
bio_01	Annual Mean Temperature	WorldClim version 2.1 from CMIP6 by IPCC (2021) available at https://worldclim.org/data/index.html	0.86 km² at the equator (~ 1km²)
bio_02	Mean Diurnal Range (Mean of monthly (max temp - min temp))		
bio_03	Isothermality (BIO2/BIO7) (×100)		
bio_04	Temperature Seasonality (standard deviation ×100)		
bio_05	Max Temperature of Warmest Month		
bio_06	Min Temperature of Coldest Month		
bio_07	Temperature Annual Range (BIO5-BIO6)		
bio_08	Mean Temperature of Wettest Quarter		
bio_09	Mean Temperature of Driest Quarter		
bio_10	Mean Temperature of Warmest Quarter		
bio_11	Mean Temperature of Coldest Quarter		
bio_12	Annual Precipitation		
bio_13	Precipitation of Wettest Month		
bio_14	Precipitation of Driest Month		
bio_15	Precipitation Seasonality (Coefficient of Variation)		
bio_16	Precipitation of Wettest Quarter		
bio_17	Precipitation of Driest Quarter		
bio_18	Precipitation of Warmest Quarter		
bio_19	Precipitation of Coldest Quarter		
geology	Geology	http://geosgb.cprm.gov.br/	~ 1km²
northness	Aspect Northness	http://www.earthenv.org/topography	~ 1km²
eastness	Aspect Easteness		~ 1km²

elevation	Elevation		~ 1km²
roughness	Roughness		~ 1km²
slope	Slope		~ 1km²
tpi	Topographic Position Index		~ 1km²
tri	Terrain Ruggedness Index		~ 1km²

Table S3

Detailed information on the Shared Socioeconomic Pathways (SSPs) as defined by the IPCC in their Sixth Assessment Report (AR6) is provided in this text. The scenarios outlined were employed across two distinct periods of the 21st century and three different GCMs. Additionally, information gained from using the GCMeval web tool was utilized to assess the degree of predicted variability in changes to both temperature and precipitation amongst all GCMs available.

SSPs	Perspectives in emission and mitigation polices	Average global surface temperature range (2100)	Time Period	GCMs	GCMs variation compared with all other available GCMs
2-4.5	It is a scenario with stronger climate change mitigation and therefore the GHG emissions remain around the current levels until the middle of the century	2.1° C to 3.5° C	2050	CanESM5	HIGH temperature low precipitation
				MIROC6	low temperature HIGH precipitation
				BCC-CSM2-MR	close to the average of all GCMs close to the average of all GCMs
			2090	CanESM5	HIGH temperature low precipitation
				MIROC6	low temperature HIGH precipitation
				BCC-CSM2-MR	close to the average of all GCMs close to the average of all GCMs
3-7.0	Represents overall lower GHG emissions (lower than the worst scenario - SSP5-8.5) but CO2 emissions almost double by the year 2100 (compared with current emission levels)	2.8° C to 4.6° C	2050	CanESM5	HIGH temperature low precipitation
				MIROC6	low temperature HIGH precipitation
				BCC-CSM2-MR	close to the average of all GCMs close to the average of all GCMs
			2090	CanESM5	HIGH temperature low precipitation
				MIROC6	low temperature HIGH precipitation
				BCC-CSM2-MR	close to the average of all GCMs

					close to the average of all GCMs
5-8.5	The worst scenario with higher future emissions pathways, where the CO2 emissions double by the year 2050 compared to current levels	3.3° C to 5.7° C	2070	CanESM5	HIGH temperature
					low precipitation
				MIROC6	low temperature
					HIGH precipitation
				BCC-CSM2-MR	close to the average of all GCMs
					close to the average of all GCMs
			2090	CanESM5	HIGH temperature
					low precipitation
				MIROC6	low temperature
					HIGH precipitation
				BCC-CSM2-MR	close to the average of all GCMs
					close to the average of all GCMs

Table S4

Evaluation metrics for five algorithms used in PRIS assessment models. The best algorithm selection was based on the AUC metric. The results for each species are presented in descending order, from the best algorithm (highlighted in bold) to the lowest AUC value.

Species name	algorithm	kappa	AUC	AUCratio	pROC	TSSmax	KAPPAmax	F_score	Jaccard
Achillea_millefolium	**rf**	**0.38118933**	**0.79928984**	**1.59857968**	**1.46191560**	**0.51124920**	**0.48103435**	**0.61502628**	**0.44654921**
Achillea_millefolium	maxnet	0.47822105	0.78225116	1.56450232	1.29971375	0.48574545	0.44466677	0.59277529	0.42280574
Achillea_millefolium	maxent	0.61693968	0.78107611	1.56215223	1.30299825	0.48279465	0.44074665	0.58819744	0.41807201
Achillea_millefolium	svmk	0.18346659	0.74653868	1.49307736	1.43400733	0.45753119	0.41798209	0.57521684	0.40539772
Achillea_millefolium	glm	0.34079400	0.73379857	1.46759715	1.46075065	0.41246738	0.36455185	0.54479004	0.37554854
Agrostis_capillaris	**svmk**	**0.01135616**	**0.90800000**	**1.81600000**	**1.69894973**	**0.90800000**	**0.27504863**	**0.28516043**	**0.17840909**
Agrostis_capillaris	rf	0.02307799	0.86000000	1.72000000	NA	0.86000000	0.23972863	0.25076856	0.17026144
Agrostis_capillaris	maxent	0.37393817	0.82600000	1.65200000	1.98114322	0.82600000	0.15363960	0.16611958	0.09758105
Agrostis_capillaris	maxnet	0.30134816	0.82600000	1.65200000	1.98401209	0.82600000	0.15363960	0.16611958	0.09758105
Agrostis_capillaris	glm	0.24989999	0.62100000	1.24200000	NA	0.24800000	0.16577540	0.17847769	0.13095238
Arenaria_groenlandica	**svmk**	**0.00423560**	**0.53400000**	**1.06800000**	**1.89131578**	**0.53200000**	**0.05331824**	**0.07142141**	**0.03776431**
Arenaria_groenlandica	rf	0.00664000	0.50500000	1.01000000	NA	0.43800000	0.04020141	0.05867066	0.03079662
Arenaria_groenlandica	glm	0.00364949	0.42200000	0.84400000	NA	0.40200000	0.01541016	0.03457091	0.01761369
Arenaria_groenlandica	maxnet	0.40948181	0.34800000	0.69600000	1.38935722	0.34600000	0.01173078	0.03099760	0.01575420
Arenaria_groenlandica	maxent	0.50247534	0.34600000	0.69200000	1.38972663	0.34600000	0.01173078	0.03099760	0.01575420
Arenaria_lanuginosa	**rf**	**0.31705867**	**0.85339619**	**1.70679238**	**1.80013467**	**0.62929524**	**0.51502291**	**0.51205400**	**0.34946745**
Arenaria_lanuginosa	glm	0.35671929	0.83565714	1.67131429	1.83812694	0.61120952	0.55484779	0.57320274	0.40866066
Arenaria_lanuginosa	maxnet	0.52785121	0.81584476	1.63168952	1.66217102	0.58562857	0.53829686	0.56050121	0.39576334
Arenaria_lanuginosa	maxent	0.67191598	0.81471238	1.62942476	1.64326058	0.58569524	0.53437994	0.55433937	0.38933033
Arenaria_lanuginosa	svmk	0.14532983	0.80618667	1.61237333	1.81654741	0.57937143	0.50119138	0.51890210	0.35502686
Browallia_americana	**rf**	**0.33944133**	**0.89488456**	**1.78976912**	**1.80799158**	**0.72004706**	**0.62204746**	**0.65234260**	**0.48959859**
Browallia_americana	maxent	0.58923647	0.88940809	1.77881618	1.69377194	0.71064118	0.60336450	0.62961556	0.46463933

Browallia_americana	maxnet	0.46335145	0.88929044	1.77858088	1.69716186	0.70979706	0.60155493	0.62319490	0.45782815
Browallia_americana	glm	0.27143308	0.87300294	1.74600588	1.78112257	0.67132059	0.54171444	0.59185003	0.42574762
Browallia_americana	svmk	0.16628940	0.84734118	1.69468235	1.88076178	0.63888235	0.52493276	0.56503022	0.39637499
Cardionema_ramosissima	**maxent**	**0.77729229**	**0.90862862**	**1.81725724**	**1.95483262**	**0.79679798**	**0.60147735**	**0.40160550**	**0.27888548**
Cardionema_ramosissima	maxnet	0.61346582	0.90737862	1.81475724	1.95664887	0.79159394	0.59396881	0.38893798	0.26433399
Cardionema_ramosissima	glm	0.21442928	0.85583805	1.71167609	1.91509917	0.71300808	0.37404346	0.26882179	0.15997409
Cardionema_ramosissima	rf	0.23541549	0.82135084	1.64270168	1.95595617	0.71021616	0.52502660	0.45623037	0.32365489
Cardionema_ramosissima	svmk	0.05936039	0.81502424	1.63004848	1.76284119	0.66333939	0.40042881	0.29858781	0.18373656
Cenchrus_clandestinus	**maxnet**	**0.57639836**	**0.75220000**	**1.50440000**	**1.74438704**	**0.62073333**	**0.27226744**	**0.22894140**	**0.13790061**
Cenchrus_clandestinus	maxent	0.73629669	0.75193333	1.50386667	1.73654410	0.62033333	0.27205198	0.22872977	0.13777942
Cenchrus_clandestinus	glm	0.07092512	0.71833333	1.43666667	1.98656039	0.58946667	0.19830842	0.20167115	0.11491476
Cenchrus_clandestinus	rf	0.11985931	0.70686667	1.41373333	1.97192185	0.54693333	0.24657902	0.19142989	0.10993054
Cenchrus_clandestinus	svmk	0.03842740	0.70173333	1.40346667	1.89938968	0.53980000	0.34094402	0.25628760	0.15935331
Centaurium_erythraea	**rf**	**0.26638677**	**0.88267000**	**1.76534000**	**1.97077016**	**0.76500000**	**0.40102898**	**0.33638000**	**0.20877694**
Centaurium_erythraea	glm	0.25287966	0.84687000	1.69374000	1.96834932	0.70940000	0.34554235	0.29943495	0.17988838
Centaurium_erythraea	svmk	0.04995411	0.83406000	1.66812000	1.96659625	0.67940000	0.40884931	0.31655415	0.19794844
Centaurium_erythraea	maxnet	0.61164373	0.82475000	1.64950000	1.69771313	0.65540000	0.37941759	0.28089096	0.16775446
Centaurium_erythraea	maxent	0.76989931	0.82145000	1.64290000	1.68232832	0.64980000	0.37365145	0.27581508	0.16355217
Cerastium_dicrotrichum	**rf**	**0.19197067**	**0.81364667**	**1.62729333**	**1.91667039**	**0.63413333**	**0.32247766**	**0.28258866**	**0.16665044**
Cerastium_dicrotrichum	maxent	0.78888346	0.76775333	1.53550667	1.66481430	0.53953333	0.35912871	0.28786656	0.17476477
Cerastium_dicrotrichum	maxnet	0.63870137	0.76768667	1.53537333	1.67343392	0.54153333	0.36397857	0.28836745	0.17491144
Cerastium_dicrotrichum	glm	0.20963482	0.73083000	1.46166000	1.96215898	0.51593333	0.28232333	0.26358391	0.15619518
Cerastium_dicrotrichum	svmk	0.04110332	0.71618667	1.43237333	1.81220686	0.48606667	0.27603283	0.25997643	0.15417096
Cerastium_glomeratum	**rf**	**0.34658867**	**0.86264211**	**1.72528421**	**1.73397674**	**0.62104211**	**0.53773651**	**0.57837329**	**0.41175804**
Cerastium_glomeratum	glm	0.30093446	0.85445263	1.70890526	1.72059805	0.64475789	0.49205612	0.56197650	0.39346583
Cerastium_glomeratum	maxnet	0.46409307	0.85281053	1.70562105	1.62998520	0.63767368	0.53455008	0.58667190	0.42013652
Cerastium_glomeratum	maxent	0.59340782	0.85110526	1.70221053	1.61689294	0.63912632	0.53256164	0.58695318	0.41989587
Cerastium_glomeratum	svmk	0.15822298	0.83358947	1.66717895	1.74630356	0.59202105	0.50224392	0.54967965	0.38336938
Cerastium_humifusum	**maxent**	**0.78121441**	**0.77346667**	**1.54693333**	**1.90230314**	**0.65533333**	**0.34320255**	**0.27671787**	**0.17979063**

Cerastium_humifusum	maxnet	0.61456352	0.77330000	1.54660000	1.90230845	0.65493333	0.34320255	0.27585420	0.17914581
Cerastium_humifusum	glm	0.16395708	0.75760000	1.51520000	1.96895899	0.64726667	0.29802835	0.25145773	0.15674571
Cerastium_humifusum	rf	0.15348596	0.74750000	1.49500000	1.85170047	0.58173333	0.28368356	0.20702471	0.12083863
Cerastium_humifusum	svmk	0.01921674	0.59146667	1.18293333	1.63765988	0.42313333	0.23632823	0.20655602	0.12427483
Cerastium_mollissimum	**maxent**	**0.45476473**	**0.63400000**	**1.26800000**	**1.69511458**	**0.63400000**	**0.18990617**	**0.20205191**	**0.14327088**
Cerastium_mollissimum	maxnet	0.37017148	0.63400000	1.26800000	1.70643316	0.63400000	0.18990617	0.20205191	0.14327088
Cerastium_mollissimum	rf	0.02110000	0.55600000	1.11200000	NA	0.42400000	0.17487007	0.18736120	0.13554720
Cerastium_mollissimum	glm	0.03842146	0.53300000	1.06600000	NA	0.25400000	0.16587294	0.17857294	0.13100077
Cerastium_mollissimum	svmk	0.00328192	0.53000000	1.06000000	1.95241320	0.51800000	0.03831131	0.05318264	0.02773728
Cerastium_rivulare	**rf**	**0.20852447**	**0.67085476**	**1.34170952**	**1.91046628**	**0.41216190**	**0.22357430**	**0.23201454**	**0.13268026**
Cerastium_rivulare	maxnet	0.64653968	0.65151429	1.30302857	1.53587533	0.41661905	0.29885216	0.31056912	0.19132046
Cerastium_rivulare	maxent	0.83275923	0.65073333	1.30146667	1.52101716	0.41716190	0.29779440	0.30478253	0.18690656
Cerastium_rivulare	svmk	0.03066162	0.64106190	1.28212381	1.37429928	0.36906667	0.17192265	0.21080453	0.11927971
Cerastium_rivulare	glm	0.10877006	0.60886429	1.21772857	1.87103374	0.36926667	0.15588204	0.22232642	0.12664841
Cerastium_selloi	**svmk**	**0.01597395**	**0.87000000**	**1.74000000**	**1.78279196**	**0.86600000**	**0.36612138**	**0.38748168**	**0.28066667**
Cerastium_selloi	rf	0.09060136	0.76000000	1.52000000	NA	0.72200000	0.47595538	0.49435897	0.42736984
Cerastium_selloi	glm	0.12584145	0.71800000	1.43600000	NA	0.70600000	0.37808853	0.40019231	0.33029584
Cerastium_selloi	maxent	0.61094348	0.70800000	1.41600000	1.66496907	0.70800000	0.31016496	0.33458877	0.25348035
Cerastium_selloi	maxnet	0.47921708	0.70800000	1.41600000	1.66502967	0.70800000	0.31016496	0.33458877	0.25348035
Cerastium_semidecandrum	**svmk**	**0.00447904**	**0.71200000**	**1.42400000**	**1.42764566**	**0.70600000**	**0.08412386**	**0.10140289**	**0.05529642**
Cerastium_semidecandrum	rf	0.01888000	0.70400000	1.40800000	NA	0.69800000	0.12680001	0.14296919	0.08068833
Cerastium_semidecandrum	glm	0.00254788	0.24600000	0.49200000	NA	0.14600000	0.00397976	0.02347163	0.01187946
Cerastium_semidecandrum	maxent	0.24129612	0.14400000	0.28800000	NA	0.14400000	0.00362615	0.02312824	0.01170134
Cerastium_semidecandrum	maxnet	0.20412124	0.14200000	0.28400000	NA	0.14200000	0.00356412	0.02306801	0.01167048
Crocosmia_crocosmiiflora	**maxnet**	**0.46598688**	**0.88730000**	**1.77460000**	**1.68095378**	**0.71530909**	**0.49263453**	**0.48392164**	**0.32247990**
Crocosmia_crocosmiiflora	maxent	0.60221338	0.88633273	1.77266545	1.66946900	0.70892727	0.49285375	0.47625626	0.31597474
Crocosmia_crocosmiiflora	rf	0.30514400	0.87813727	1.75627455	1.84571392	0.67421818	0.53854096	0.51578693	0.35535870
Crocosmia_crocosmiiflora	glm	0.27361517	0.87754909	1.75509818	1.86295079	0.67963636	0.48704325	0.46396772	0.30628336
Crocosmia_crocosmiiflora	svmk	0.12314110	0.80257818	1.60515636	1.96048915	0.57532727	0.49352864	0.46057444	0.30715443

Desmodium_adscendens	**rf**	**0.39797600**	**0.86557976**	**1.73115951**	**1.63681482**	**0.65827881**	**0.62207469**	**0.72985546**	**0.57618994**
Desmodium_adscendens	maxent	0.54818003	0.84921943	1.69843887	1.48528177	0.62337787	0.57954193	0.70325840	0.54344261
Desmodium_adscendens	maxnet	0.44344585	0.84715547	1.69431093	1.49347632	0.61842402	0.57600746	0.70110020	0.54076200
Desmodium_adscendens	glm	0.31972643	0.83376248	1.66752497	1.57584598	0.61019703	0.55487114	0.69125899	0.52934138
Desmodium_adscendens	svmk	0.24527682	0.82340688	1.64681377	1.53939652	0.59174251	0.55433412	0.68756014	0.52491766
Dichondra_carolinensis	**rf**	**0.00243453**	**0.49100000**	**0.98200000**	**NA**	**0.42200000**	**0.01634781**	**0.03171479**	**0.01614636**
Dichondra_carolinensis	svmk	0.00252875	0.48600000	0.97200000	1.86643079	0.48000000	0.02481072	0.03998466	0.02053931
Dichondra_carolinensis	glm	0.00536854	0.40800000	0.81600000	NA	0.36000000	0.10056671	0.11424846	0.06969414
Dichondra_carolinensis	maxent	0.15247839	0.19600000	0.39200000	NA	0.19600000	0.00416824	0.01981851	0.01001002
Dichondra_carolinensis	maxnet	0.13380874	0.19600000	0.39200000	NA	0.19600000	0.00416824	0.01981851	0.01001002
Digitaria_ciliaris	**svmk**	**0.10377174**	**0.69050357**	**1.38100714**	**1.72537307**	**0.41710000**	**0.35176768**	**0.30606705**	**0.18549336**
Digitaria_ciliaris	glm	0.26960162	0.67414286	1.34828571	1.88019420	0.41317143	0.31767880	0.31889359	0.19391497
Digitaria_ciliaris	maxnet	0.70166978	0.67133571	1.34267143	1.47075107	0.39697143	0.33574275	0.29723972	0.17830233
Digitaria_ciliaris	rf	0.34238578	0.67079464	1.34158929	1.85613434	0.43165714	0.37213347	0.34274730	0.21184986
Digitaria_ciliaris	maxent	0.84354124	0.66818214	1.33636429	1.43911751	0.39621429	0.33258766	0.30304977	0.18271411
Digitaria_fuscescens	**glm**	**0.33624726**	**0.75582667**	**1.51165333**	**1.95029609**	**0.51793333**	**0.34460184**	**0.24328231**	**0.14030013**
Digitaria_fuscescens	maxent	0.71470178	0.74830000	1.49660000	1.64141693	0.52593333	0.32850925	0.28128823	0.16820360
Digitaria_fuscescens	maxnet	0.58715749	0.74758000	1.49516000	1.65331347	0.52580000	0.32699658	0.28075802	0.16779332
Digitaria_fuscescens	rf	0.26078657	0.71611333	1.43222667	1.94538600	0.48966667	0.38090073	0.30060965	0.18302098
Digitaria_fuscescens	svmk	0.07513521	0.61874667	1.23749333	1.93600244	0.38560000	0.34253466	0.31553399	0.19975961
Drymaria_cordata	**rf**	**0.51813600**	**0.83713750**	**1.67427500**	**1.30840165**	**0.56965000**	**0.57711025**	**0.75263637**	**0.60425493**
Drymaria_cordata	maxnet	0.45730291	0.82912000	1.65824000	1.20832055	0.52905000	0.53422895	0.73201125	0.57835767
Drymaria_cordata	maxent	0.57386456	0.82690750	1.65381500	1.20265287	0.52410000	0.52999058	0.72673079	0.57175023
Drymaria_cordata	svmk	0.45127903	0.80691250	1.61382500	1.23481871	0.51655000	0.52094243	0.72454234	0.56917029
Drymaria_cordata	glm	0.49353540	0.80617750	1.61235500	1.29260107	0.49870000	0.50017097	0.72091730	0.56432065
Furcraea_foetida	**maxent**	**0.68565791**	**0.86409091**	**1.72818182**	**1.72684874**	**0.65964242**	**0.58320686**	**0.51888818**	**0.35705892**
Furcraea_foetida	maxnet	0.54598169	0.86399545	1.72799091	1.72772257	0.66101212	0.58369153	0.51584500	0.35469232
Furcraea_foetida	rf	0.38349067	0.83625758	1.67251515	1.88769749	0.62540000	0.59533236	0.52722991	0.36771812
Furcraea_foetida	svmk	0.22609010	0.80107576	1.60215152	1.93587404	0.60159394	0.57590056	0.54143680	0.37976109

Furcraea_foetida	glm	0.37989543	0.78055758	1.56111515	1.86005647	0.55965455	0.54533177	0.53484695	0.37430329
Geranium_carolinianum	**glm**	**0.05471478**	**0.74751818**	**1.49503636**	**1.98826112**	**0.64688687**	**0.19875526**	**0.18683704**	**0.10766064**
Geranium_carolinianum	maxent	0.72239194	0.73310202	1.46620404	1.66773939	0.60664444	0.17518746	0.15956483	0.08901436
Geranium_carolinianum	maxnet	0.56448645	0.73306936	1.46613872	1.66542786	0.60664444	0.17518746	0.15956483	0.08901436
Geranium_carolinianum	rf	0.04751942	0.58488586	1.16977172	NA	0.45960000	0.12856889	0.11053145	0.06265282
Geranium_carolinianum	svmk	0.00904565	0.43913165	0.87826330	1.85504068	0.29423030	0.05152036	0.07905787	0.04203795
Geranium_purpureum	**glm**	**0.20706767**	**0.72458333**	**1.44916667**	**1.97138545**	**0.53220000**	**0.36052702**	**0.23049462**	**0.13855543**
Geranium_purpureum	rf	0.10969384	0.65138333	1.30276667	1.98813027	0.48013333	0.18781471	0.16218803	0.09015645
Geranium_purpureum	svmk	0.01643920	0.61193333	1.22386667	1.95004696	0.42900000	0.10637142	0.13385153	0.07273550
Geranium_purpureum	maxnet	0.48628668	0.60215000	1.20430000	1.67887520	0.43180000	0.10436230	0.13665267	0.07427719
Geranium_purpureum	maxent	0.61281744	0.60208333	1.20416667	1.67969970	0.43126667	0.10390495	0.13501347	0.07332439
Geranium_robertianum	**rf**	**0.25766067**	**0.83868909**	**1.67737818**	**1.85080851**	**0.62136364**	**0.41521762**	**0.41162329**	**0.26181255**
Geranium_robertianum	glm	0.27109821	0.81300182	1.62600364	1.90942696	0.57149091	0.37533691	0.40137038	0.25461774
Geranium_robertianum	maxnet	0.58033740	0.81218364	1.62436727	1.74148592	0.56896364	0.41714340	0.39443317	0.24927360
Geranium_robertianum	maxent	0.75459147	0.81154182	1.62308364	1.73488849	0.56903636	0.41747609	0.39655573	0.25079813
Geranium_robertianum	svmk	0.08450918	0.77610000	1.55220000	1.54799974	0.51801818	0.41751257	0.39849382	0.25537824
Kalanchoe_fedtschenkoi	**rf**	**0.22251043**	**0.82090500**	**1.64181000**	**1.95585422**	**0.65800000**	**0.40130956**	**0.29833119**	**0.18210002**
Kalanchoe_fedtschenkoi	svmk	0.06633121	0.74980000	1.49960000	1.86527662	0.55700000	0.38811275	0.28902685	0.18189528
Kalanchoe_fedtschenkoi	maxnet	0.64785836	0.74728000	1.49456000	1.70933277	0.54920000	0.37986570	0.27447691	0.17250737
Kalanchoe_fedtschenkoi	maxent	0.80801866	0.74719000	1.49438000	1.70108753	0.54880000	0.37897214	0.26859207	0.16831343
Kalanchoe_fedtschenkoi	glm	0.18165716	0.70803000	1.41606000	1.95469351	0.47520000	0.27651301	0.23005443	0.13408481
Lantana_camara	**maxent**	**0.68711857**	**0.81612424**	**1.63224848**	**1.55837775**	**0.58680000**	**0.46032575**	**0.46333110**	**0.30750722**
Lantana_camara	maxnet	0.54612368	0.81560455	1.63120909	1.56531797	0.58766667	0.45749994	0.46159866	0.30594200
Lantana_camara	rf	0.24909800	0.81198636	1.62397273	1.79408590	0.58938788	0.42891984	0.44999117	0.29453101
Lantana_camara	glm	0.19314366	0.76053409	1.52106818	1.81719694	0.52304848	0.35699278	0.39975025	0.25216932
Lantana_camara	svmk	0.06662595	0.72818636	1.45637273	1.47213363	0.48083030	0.33624931	0.39465410	0.24885974
Melinis_minutiflora	**rf**	**0.36221400**	**0.80681126**	**1.61362253**	**1.55117944**	**0.54635172**	**0.48928370**	**0.60830290**	**0.43933065**
Melinis_minutiflora	maxent	0.59441901	0.79284391	1.58568782	1.33797138	0.50617701	0.43797781	0.56991300	0.39965166
Melinis_minutiflora	maxnet	0.47513664	0.79123425	1.58246851	1.34345078	0.49985287	0.43517524	0.56677659	0.39648843

Melinis_minutiflora	glm	0.32722344	0.78380391	1.56760782	1.52107199	0.48838391	0.42830143	0.56778327	0.39789310
Melinis_minutiflora	svmk	0.17811838	0.74841747	1.49683494	1.66059023	0.46487816	0.42894826	0.55877193	0.38909540
Melinis_repens	**rf**	**0.46932133**	**0.73866543**	**1.47733087**	**1.17099789**	**0.41541167**	**0.42064152**	**0.65322700**	**0.48638084**
Melinis_repens	maxnet	0.48814255	0.69751018	1.39502036	1.06624997	0.34820644	0.35093491	0.61460396	0.44489912
Melinis_repens	maxent	0.61496865	0.69506429	1.39012857	1.06038053	0.34421610	0.34597216	0.61510396	0.44532759
Melinis_repens	svmk	0.42153764	0.67410249	1.34820499	1.14455646	0.31068048	0.32190174	0.56736760	0.39801078
Melinis_repens	glm	0.44467731	0.66311477	1.32622954	1.10628896	0.28508732	0.28237282	0.60011460	0.43030142
Microchloa_kunthii	**glm**	**0.22952143**	**0.89112554**	**1.78225108**	NA	**0.89112554**	**0.54898061**	**0.56297272**	**0.49089707**
Microchloa_kunthii	maxent	0.72437378	0.88899711	1.77799423	1.96204081	0.88899711	0.60239123	0.61494431	0.55911817
Microchloa_kunthii	maxnet	0.59333661	0.88899711	1.77799423	1.96677690	0.88899711	0.60239123	0.61494431	0.55911817
Microchloa_kunthii	rf	0.17081482	0.81630592	1.63261183	NA	0.80216450	0.58953960	0.60249723	0.54581129
Microchloa_kunthii	svmk	0.02748443	0.81024531	1.62049062	1.92860761	0.81024531	0.60752331	0.62058758	0.59262710
Paronychia_brasiliana	**rf**	**0.14767858**	**0.73016667**	**1.46033333**	**1.48542176**	**0.59393333**	**0.32468574**	**0.25446889**	**0.15827789**
Paronychia_brasiliana	glm	0.19086143	0.68226667	1.36453333	1.64578144	0.51520000	0.33614294	0.28434795	0.18237399
Paronychia_brasiliana	maxent	0.76147346	0.65490000	1.30980000	1.70143761	0.49433333	0.32751621	0.21802874	0.13410580
Paronychia_brasiliana	maxnet	0.62339668	0.65476667	1.30953333	1.70826011	0.49393333	0.32748618	0.21802984	0.13412913
Paronychia_brasiliana	svmk	0.01255818	0.42970000	0.85940000	1.26553474	0.28106667	0.12863998	0.13703701	0.07957996
Phyllanthus_urinaria	**glm**	**0.23646727**	**0.84855238**	**1.69710476**	**1.94166831**	**0.67668571**	**0.48046222**	**0.41645726**	**0.27216979**
Phyllanthus_urinaria	rf	0.30017666	0.84344048	1.68688095	1.93223764	0.67811429	0.48179819	0.42239779	0.27534464
Phyllanthus_urinaria	maxnet	0.50082643	0.84060000	1.68120000	1.84854815	0.69153333	0.50595874	0.46444864	0.30979011
Phyllanthus_urinaria	maxent	0.63139764	0.84031905	1.68063810	1.84336118	0.69044762	0.50570628	0.46407589	0.31116329
Phyllanthus_urinaria	svmk	0.06372116	0.83204286	1.66408571	1.75459090	0.65133333	0.45966868	0.43582929	0.28580486
Pinus_elliottii	**rf**	**0.30039067**	**0.80575000**	**1.61150000**	**1.74980948**	**0.55280000**	**0.45210682**	**0.49416613**	**0.33227487**
Pinus_elliottii	glm	0.22014214	0.78337500	1.56675000	1.74716332	0.52155000	0.35867440	0.44994429	0.29218180
Pinus_elliottii	svmk	0.08394683	0.77536250	1.55072500	1.41112500	0.51235000	0.41480530	0.47280492	0.31225621
Pinus_elliottii	maxent	0.64142288	0.76958750	1.53917500	1.44743054	0.50235000	0.38712632	0.45753322	0.29900331
Pinus_elliottii	maxnet	0.51126380	0.76950000	1.53900000	1.45235594	0.50195000	0.38266481	0.45976691	0.30117805
Poa_annua	**rf**	**0.45286667**	**0.86353494**	**1.72706988**	**1.58657214**	**0.59707594**	**0.56349783**	**0.66141058**	**0.49560395**
Poa_annua	maxnet	0.45238588	0.85331907	1.70663815	1.49708177	0.61422709	0.56195587	0.67298522	0.50887759

Poa_annua	maxent	0.56019026	0.85218396	1.70436791	1.49894099	0.61615365	0.56077453	0.67299071	0.50894486
Poa_annua	glm	0.37293984	0.84489002	1.68978004	1.58926848	0.60593512	0.52926549	0.65426642	0.48748961
Poa_annua	svmk	0.35568190	0.82595740	1.65191480	1.66016599	0.57166774	0.53543572	0.64458164	0.47693855
Polycarpaea_corymbosa	**rf**	**0.23281877**	**0.84537143**	**1.69074286**	**1.90605754**	**0.63688571**	**0.49161075**	**0.41790957**	**0.27551375**
Polycarpaea_corymbosa	maxnet	0.61363555	0.82020000	1.64040000	1.67818857	0.61840000	0.44697243	0.37221388	0.23570481
Polycarpaea_corymbosa	maxent	0.78708821	0.82017143	1.64034286	1.69513373	0.61948571	0.44393811	0.37291227	0.23522879
Polycarpaea_corymbosa	svmk	0.03582064	0.77985714	1.55971429	1.58715207	0.59568571	0.36271813	0.36459441	0.22837886
Polycarpaea_corymbosa	glm	0.17826315	0.73172857	1.46345714	1.95517846	0.49985714	0.26242486	0.26371243	0.15360448
Polycarpon_depressum	**maxent**	**0.63733003**	**0.75332282**	**1.50664563**	**1.82520975**	**0.75332282**	**0.18235459**	**0.20000305**	**0.11725225**
Polycarpon_depressum	maxnet	0.50148666	0.75332282	1.50664563	1.82567183	0.75332282	0.18235459	0.20000305	0.11725225
Polycarpon_depressum	svmk	0.00759744	0.73532224	1.47064448	NA	0.72932205	0.22052546	0.23738761	0.15550868
Polycarpon_depressum	glm	0.02054086	0.72535380	1.45070759	1.98579555	0.72138554	0.13569147	0.15469862	0.08667892
Polycarpon_depressum	rf	0.01154827	0.49120291	0.98240581	NA	0.43703385	0.03864182	0.06076084	0.03170052
Polycarpon_tetraphyllum	**maxent**	**0.68424805**	**0.88295000**	**1.76590000**	**1.84182754**	**0.71150000**	**0.48527998**	**0.42383059**	**0.27235425**
Polycarpon_tetraphyllum	maxnet	0.53424441	0.87807500	1.75615000	1.82535244	0.70590000	0.46993910	0.41285924	0.26329499
Polycarpon_tetraphyllum	glm	0.25972541	0.85270000	1.70540000	1.91540937	0.67450000	0.43044186	0.40050778	0.25416108
Polycarpon_tetraphyllum	rf	0.19304608	0.82507500	1.65015000	1.89533310	0.63070000	0.40492583	0.39332014	0.24766720
Polycarpon_tetraphyllum	svmk	0.04326697	0.78115000	1.56230000	1.58031572	0.57420000	0.35371959	0.35029334	0.21521958
Potentilla_indica	**maxent**	**0.66895674**	**0.89725556**	**1.79451111**	**1.83364500**	**0.71016667**	**0.59811398**	**0.50773743**	**0.35514835**
Potentilla_indica	maxnet	0.53146769	0.89645278	1.79290556	1.83519668	0.70806667	0.59000895	0.49670548	0.34234886
Potentilla_indica	rf	0.32201678	0.89249028	1.78498056	1.92376584	0.73803333	0.60124740	0.55769270	0.39795838
Potentilla_indica	glm	0.38934072	0.86105000	1.72210000	1.92222615	0.63754444	0.53432056	0.42764802	0.27929654
Potentilla_indica	svmk	0.13071491	0.85135556	1.70271111	1.93157182	0.67580000	0.57902999	0.50616642	0.34809645
Ranunculus_muricatus	**svmk**	**0.02526130**	**0.75460000**	**1.50920000**	**1.85863623**	**0.58946667**	**0.35214200**	**0.24812351**	**0.15043549**
Ranunculus_muricatus	maxent	0.63927567	0.74530000	1.49060000	1.77094594	0.63013333	0.19941891	0.16653311	0.09189634
Ranunculus_muricatus	maxnet	0.51061618	0.74530000	1.49060000	1.78487247	0.63033333	0.19945475	0.16660280	0.09193683
Ranunculus_muricatus	rf	0.12456759	0.73633333	1.47266667	1.93424084	0.58306667	0.27700522	0.22058389	0.13267863
Ranunculus_muricatus	glm	0.04235385	0.65208333	1.30416667	NA	0.48780000	0.11098758	0.12285572	0.06614416
Ranunculus_repens	**svmk**	**0.01262223**	**0.92582234**	**1.85164467**	**1.92304053**	**0.92381430**	**0.41104695**	**0.42328042**	**0.33373555**

Ranunculus_repens	rf	0.04979444	0.79154714	1.58309428	1.99951841	0.78953911	0.27913427	0.29460784	0.20597805
Ranunculus_repens	maxnet	0.43319209	0.73859725	1.47719449	1.84973454	0.73859725	0.10816013	0.12803060	0.07042477
Ranunculus_repens	maxent	0.54022560	0.73264487	1.46528973	1.84996824	0.73264487	0.10788615	0.12776605	0.07028808
Ranunculus_repens	glm	0.01058930	0.58944110	1.17888220	NA	0.57252821	0.06175093	0.08311011	0.04407518
Sisyrinchium_minus	**glm**	**0.15265311**	**0.73400000**	**1.46800000**	**1.96062017**	**0.59213333**	**0.36578998**	**0.30242662**	**0.20508154**
Sisyrinchium_minus	rf	0.15370045	0.71916667	1.43833333	1.95874393	0.56120000	0.37250810	0.27558135	0.18272020
Sisyrinchium_minus	maxnet	0.62455310	0.69836667	1.39673333	1.75917795	0.56053333	0.36078805	0.29136773	0.19189203
Sisyrinchium_minus	maxent	0.78786009	0.69830000	1.39660000	1.75163720	0.56033333	0.35875848	0.29128170	0.19184277
Sisyrinchium_minus	svmk	0.01797580	0.58183333	1.16366667	1.65414149	0.42393333	0.21400185	0.19848897	0.11649559
Spergularia_grandis	**maxent**	**0.68424805**	**0.88295000**	**1.76590000**	**1.84182754**	**0.71150000**	**0.48527998**	**0.42383059**	**0.27235425**
Spergularia_grandis	maxnet	0.53424441	0.87807500	1.75615000	1.82535244	0.70590000	0.46993910	0.41285924	0.26329499
Spergularia_grandis	glm	0.25972541	0.85270000	1.70540000	1.91540937	0.67450000	0.43044186	0.40050778	0.25416108
Spergularia_grandis	rf	0.19304608	0.82507500	1.65015000	1.89533310	0.63070000	0.40492583	0.39332014	0.24766720
Spergularia_grandis	svmk	0.04326697	0.78115000	1.56230000	1.58031572	0.57420000	0.35371959	0.35029334	0.21521958
Stachys_arvensis	**rf**	**0.38195800**	**0.85252513**	**1.70505026**	**1.60966367**	**0.58965291**	**0.53829624**	**0.61729163**	**0.44870831**
Stachys_arvensis	maxnet	0.45769816	0.82122275	1.64244550	1.48889318	0.54676296	0.49638727	0.59814093	0.42906095
Stachys_arvensis	maxent	0.58777140	0.82049074	1.64098148	1.46396731	0.54301587	0.49612186	0.59467930	0.42531571
Stachys_arvensis	svmk	0.26181728	0.81909630	1.63819259	1.50760936	0.56171217	0.52382995	0.61467187	0.44551069
Stachys_arvensis	glm	0.33073673	0.80904365	1.61808730	1.63830813	0.54302222	0.46315954	0.58557173	0.41598164
Stellaria_media	**glm**	**0.33911608**	**0.81593123**	**1.63186245**	**1.69662322**	**0.55080474**	**0.47234814**	**0.55827032**	**0.38985554**
Stellaria_media	maxnet	0.48794019	0.81448893	1.62897787	1.51861453	0.53968775	0.48870964	0.56309864	0.39470286
Stellaria_media	maxent	0.60331564	0.81190830	1.62381660	1.49310449	0.53858182	0.48766866	0.56314023	0.39472994
Stellaria_media	rf	0.32947521	0.81139684	1.62279368	1.65571038	0.53919526	0.47636184	0.56148083	0.39352577
Stellaria_media	svmk	0.15629575	0.79736601	1.59473202	1.76103879	0.52879209	0.46817849	0.55164004	0.38291398
Taraxacum_campylodes	**maxent**	**0.69395078**	**0.67880000**	**1.35760000**	**1.58015900**	**0.51546667**	**0.22292462**	**0.15967951**	**0.08926296**
Taraxacum_campylodes	maxnet	0.54934068	0.67826667	1.35653333	1.59565052	0.51466667	0.22152811	0.15832270	0.08835100
Taraxacum_campylodes	rf	0.08045256	0.66510000	1.33020000	1.96552842	0.49620000	0.21515587	0.19773289	0.11649703
Taraxacum_campylodes	glm	0.08230903	0.65836667	1.31673333	NA	0.48786667	0.17344428	0.15027576	0.08335369
Taraxacum_campylodes	svmk	0.02009498	0.62490000	1.24980000	1.66728717	0.44146667	0.18112598	0.17802765	0.10228277

Trifolium_campestre	**rf**	**0.28084467**	**0.88530889**	**1.77061778**	**1.92479708**	**0.70782222**	**0.55040648**	**0.51904289**	**0.36042824**
Trifolium_campestre	maxent	0.67225212	0.88450000	1.76900000	1.83329280	0.71326667	0.56721172	0.50651512	0.34463314
Trifolium_campestre	maxnet	0.52779682	0.88360222	1.76720444	1.83719164	0.70886667	0.56693793	0.49982261	0.33757350
Trifolium_campestre	svmk	0.08088713	0.85517556	1.71035111	1.60820240	0.63408889	0.46601885	0.41036836	0.26254235
Trifolium_campestre	glm	0.30752471	0.83829778	1.67659556	1.92051407	0.61133333	0.41921230	0.39219268	0.24805128
Trifolium_dubium	**rf**	**0.13128180**	**0.72280000**	**1.44560000**	**1.94523297**	**0.50920000**	**0.21165359**	**0.21570924**	**0.12267567**
Trifolium_dubium	maxnet	0.46445154	0.71488000	1.42976000	1.69187346	0.53100000	0.18289131	0.21228379	0.11981026
Trifolium_dubium	maxent	0.58555172	0.71268000	1.42536000	1.67425494	0.53260000	0.18445110	0.21528995	0.12167652
Trifolium_dubium	glm	0.11158783	0.69604000	1.39208000	1.93260211	0.50160000	0.20989003	0.20089087	0.11367028
Trifolium_dubium	svmk	0.02355334	0.63512000	1.27024000	1.55191910	0.40260000	0.12795999	0.16795625	0.09236288
Trifolium_incarnatum	**maxnet**	**0.57115799**	**0.75003333**	**1.50006667**	**1.76018319**	**0.60253333**	**0.27087523**	**0.21582283**	**0.12546953**
Trifolium_incarnatum	maxent	0.71790317	0.74993333	1.49986667	1.75492722	0.60233333	0.27079727	0.21575037	0.12543000
Trifolium_incarnatum	glm	0.09884711	0.72440000	1.44880000	1.96066925	0.58200000	0.25786415	0.17659047	0.10056323
Trifolium_incarnatum	rf	0.12526244	0.70806667	1.41613333	1.95426951	0.52753333	0.27598707	0.20935389	0.12642583
Trifolium_incarnatum	svmk	0.01742979	0.61033333	1.22066667	1.75155392	0.41293333	0.16447275	0.14597218	0.08137410
Trifolium_pratense	**rf**	**0.38511533**	**0.90692833**	**1.81385667**	**1.85223029**	**0.71481667**	**0.64850419**	**0.60321854**	**0.43937720**
Trifolium_pratense	maxnet	0.46136105	0.90476667	1.80953333	1.79017743	0.72333333	0.62663626	0.62447072	0.45951251
Trifolium_pratense	maxent	0.58494095	0.90343250	1.80686500	1.78199969	0.72261667	0.62649603	0.61548041	0.44974632
Trifolium_pratense	glm	0.30905370	0.88953000	1.77906000	1.85125157	0.70035000	0.53993553	0.56877929	0.40185914
Trifolium_pratense	svmk	0.25242665	0.88097250	1.76194500	1.89384585	0.66755000	0.61649812	0.57147949	0.40643837
Trifolium_repens	**rf**	**0.41102400**	**0.87575836**	**1.75151672**	**1.60258926**	**0.63318228**	**0.59242359**	**0.72147665**	**0.56596774**
Trifolium_repens	maxent	0.49396910	0.86069745	1.72139491	1.53426560	0.62775681	0.57593404	0.71501643	0.55825630
Trifolium_repens	maxnet	0.41182361	0.86046711	1.72093422	1.54859032	0.62179158	0.57318784	0.71231692	0.55508819
Trifolium_repens	glm	0.38151497	0.84908206	1.69816412	1.61146360	0.62362968	0.56785533	0.71356984	0.55632901
Trifolium_repens	svmk	0.40606300	0.84771484	1.69542968	1.53327673	0.60848726	0.57885905	0.70998195	0.55174964
Trifolium_subterraneum	**rf**	**0.11672591**	**0.80636667**	**1.61273333**	**1.97544100**	**0.67373333**	**0.28568164**	**0.19468460**	**0.11105454**
Trifolium_subterraneum	glm	0.08291220	0.76356667	1.52713333	NA	0.64813333	0.21736906	0.18018015	0.10165284
Trifolium_subterraneum	svmk	0.01912351	0.74276667	1.48553333	1.70030877	0.58173333	0.26709299	0.19233260	0.11445569
Trifolium_subterraneum	maxnet	0.57677799	0.73963333	1.47926667	1.70376060	0.63180000	0.22356086	0.17917104	0.09993023

Trifolium_subterraneum	maxent	0.72455971	0.73960000	1.47920000	1.70193813	0.63200000	0.22421301	0.17928500	0.09999690
Ulex_europaeus	**maxent**	**0.70182809**	**0.88044615**	**1.76089231**	**1.77239279**	**0.65435385**	**0.60701824**	**0.54170009**	**0.38203135**
Ulex_europaeus	maxnet	0.56011884	0.87818462	1.75636923	1.77936445	0.64883077	0.60331320	0.53711904	0.37784955
Ulex_europaeus	glm	0.36720447	0.87440000	1.74880000	1.87130278	0.67613846	0.56948808	0.54140988	0.37658962
Ulex_europaeus	rf	0.37379733	0.85960000	1.71920000	1.89457209	0.63812308	0.60235049	0.56269585	0.40050960
Ulex_europaeus	svmk	0.22429517	0.81232308	1.62464615	1.91472589	0.57818462	0.57068726	0.54230314	0.37991018
Urochloa_brizantha	**rf**	**0.27125067**	**0.74946484**	**1.49892967**	**1.73021794**	**0.48024176**	**0.35276583**	**0.40827006**	**0.25969155**
Urochloa_brizantha	maxnet	0.50192111	0.73267692	1.46535385	1.38397642	0.48007253	0.28110939	0.37757710	0.23437966
Urochloa_brizantha	maxent	0.62726503	0.72792637	1.45585275	1.38166374	0.47431648	0.27695991	0.37533689	0.23268418
Urochloa_brizantha	glm	0.19040409	0.72359011	1.44718022	1.72733556	0.44049231	0.28199419	0.36051747	0.22124804
Urochloa_brizantha	svmk	0.06908254	0.65525934	1.31051868	1.29195090	0.34119121	0.24603774	0.33007878	0.19925601
Verbena_officinalis	**glm**	**0.10631435**	**0.78976667**	**1.57953333**	**1.99170500**	**0.65773333**	**0.23475810**	**0.18103255**	**0.10240044**
Verbena_officinalis	maxent	0.72178686	0.76793333	1.53586667	1.65321119	0.64320000	0.23397613	0.17975157	0.10233723
Verbena_officinalis	maxnet	0.56909906	0.76786667	1.53573333	1.65808174	0.64340000	0.22941471	0.17984353	0.10239014
Verbena_officinalis	svmk	0.01862166	0.66226667	1.32453333	1.50362237	0.47953333	0.20804898	0.15718405	0.08842385
Verbena_officinalis	rf	0.05657264	0.62483333	1.24966667	1.95293115	0.43553333	0.12340298	0.12971968	0.07051794
Vicia_angustifolia	**maxnet**	**0.51700270**	**0.82749091**	**1.65498182**	**1.76090645**	**0.61225455**	**0.40971412**	**0.43090588**	**0.27824730**
Vicia_angustifolia	maxent	0.64830906	0.82712727	1.65425455	1.75079724	0.61103636	0.40844560	0.43197237	0.27949932
Vicia_angustifolia	rf	0.23564363	0.81620000	1.63240000	1.81792039	0.57718182	0.39725893	0.42475188	0.27299243
Vicia_angustifolia	glm	0.21386240	0.80630000	1.61260000	1.88164906	0.59121818	0.37178525	0.41079075	0.26098302
Vicia_angustifolia	svmk	0.05188463	0.77990909	1.55981818	1.60716942	0.54465455	0.35219400	0.38954751	0.24390896
Vicia_sativa	**maxnet**	**0.48506040**	**0.87398000**	**1.74796000**	**1.65250451**	**0.64721053**	**0.55770274**	**0.59409274**	**0.42644324**
Vicia_sativa	maxent	0.61156249	0.87379158	1.74758316	1.65526717	0.64926316	0.55905986	0.59593055	0.42844873
Vicia_sativa	glm	0.30887565	0.85662737	1.71325474	1.73163788	0.63153684	0.50066425	0.57078174	0.40222957
Vicia_sativa	rf	0.37330000	0.85619974	1.71239947	1.77633281	0.60858947	0.54902271	0.56493065	0.39692636
Vicia_sativa	svmk	0.15395111	0.82655421	1.65310842	1.70528267	0.61062105	0.53569525	0.57440026	0.40634488

Figure S1

Northernmost area of *Campos de Altitude* distribution and PRIS distribution in current and future scenarios.

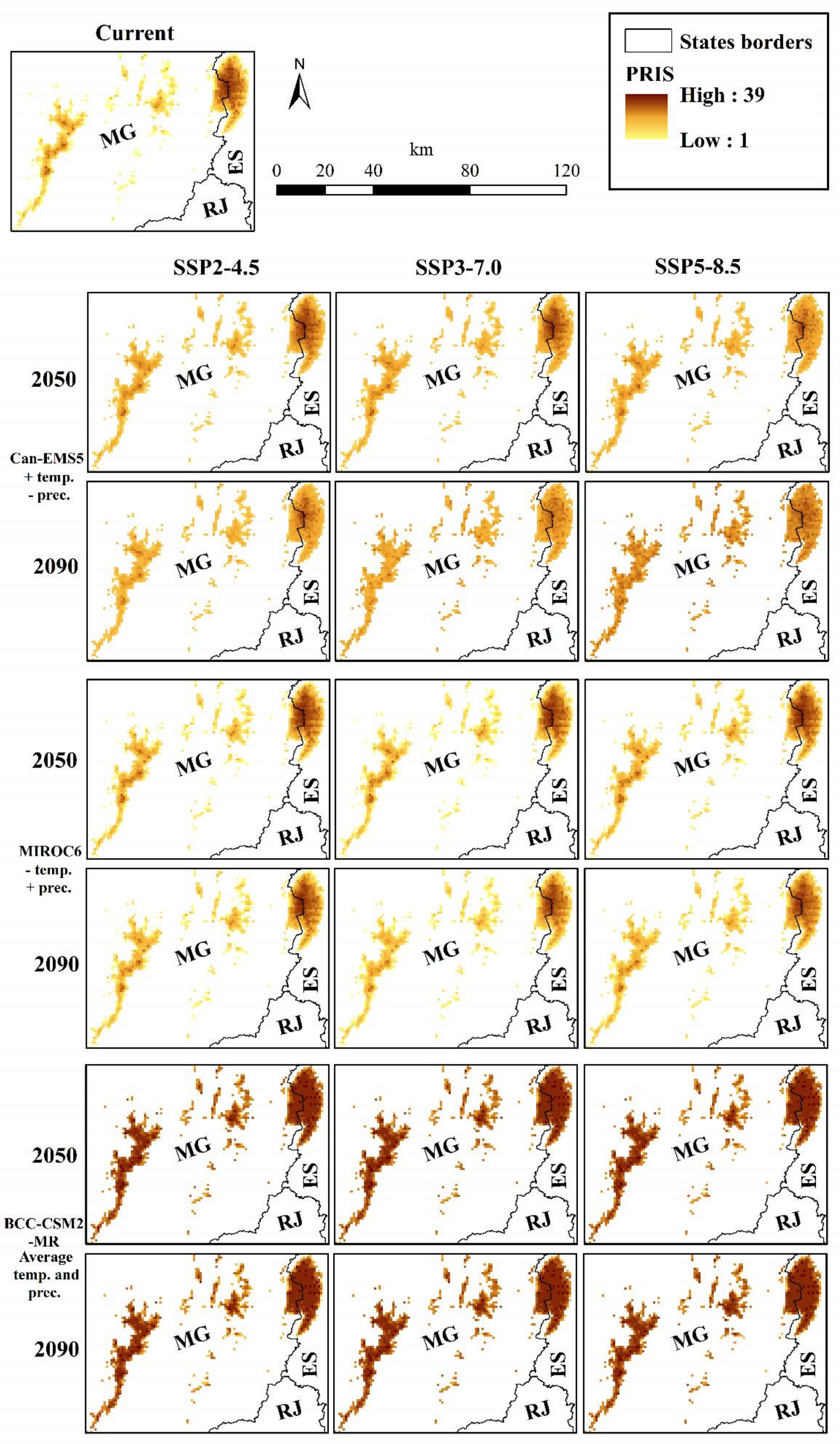


Figure S2

Central area of *Campos de Altitude* distribution and PRIS distribution in current and future scenarios.

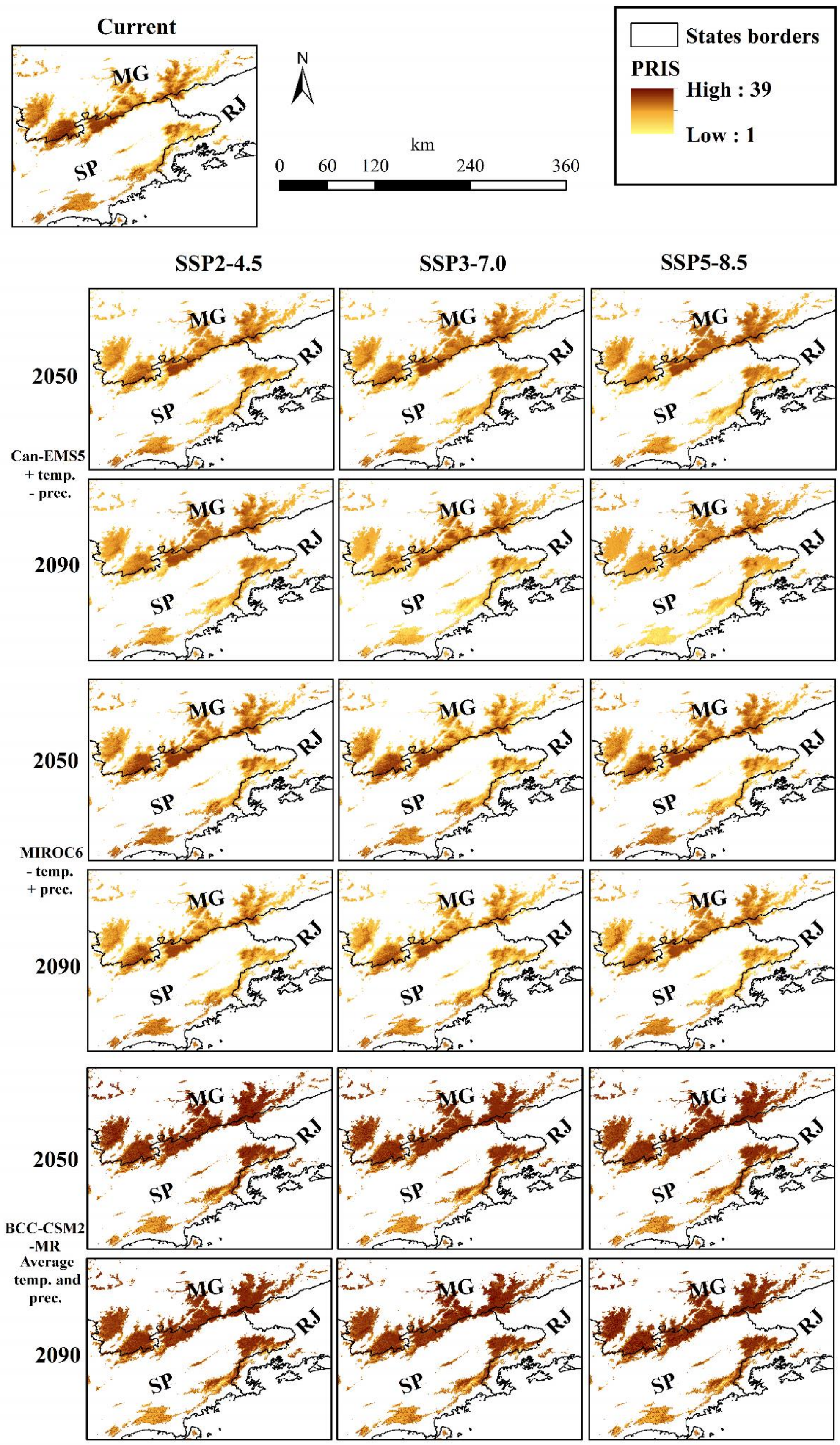


Figure S3

Central area of *Campos de Altitude* distribution in *Rio de Janeiro* state and PRIS distribution in current and future scenarios.

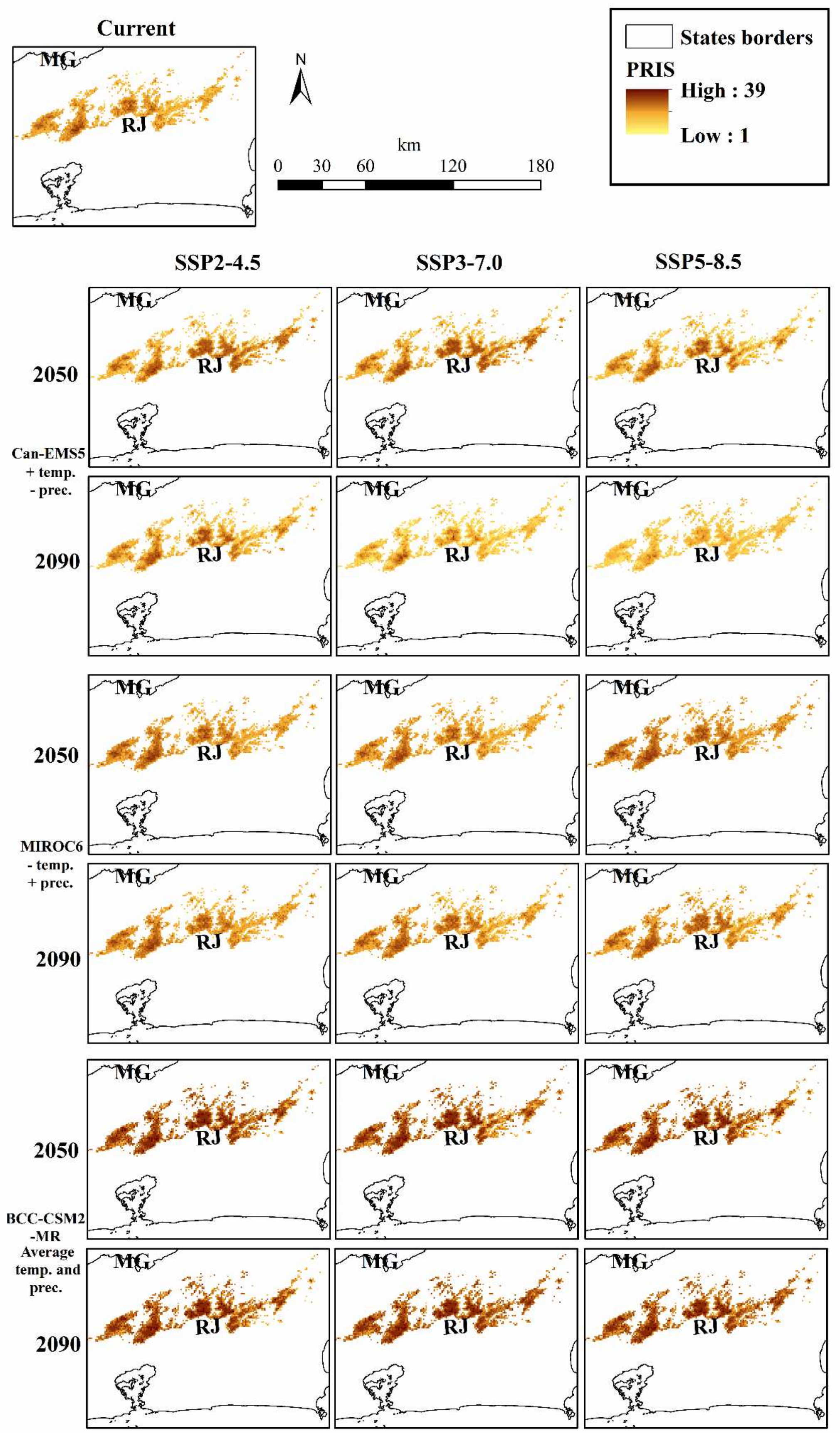


Figure S4

Paraná state areas of *Campos de Altitude* distribution and PRIS distribution in current and future scenarios.

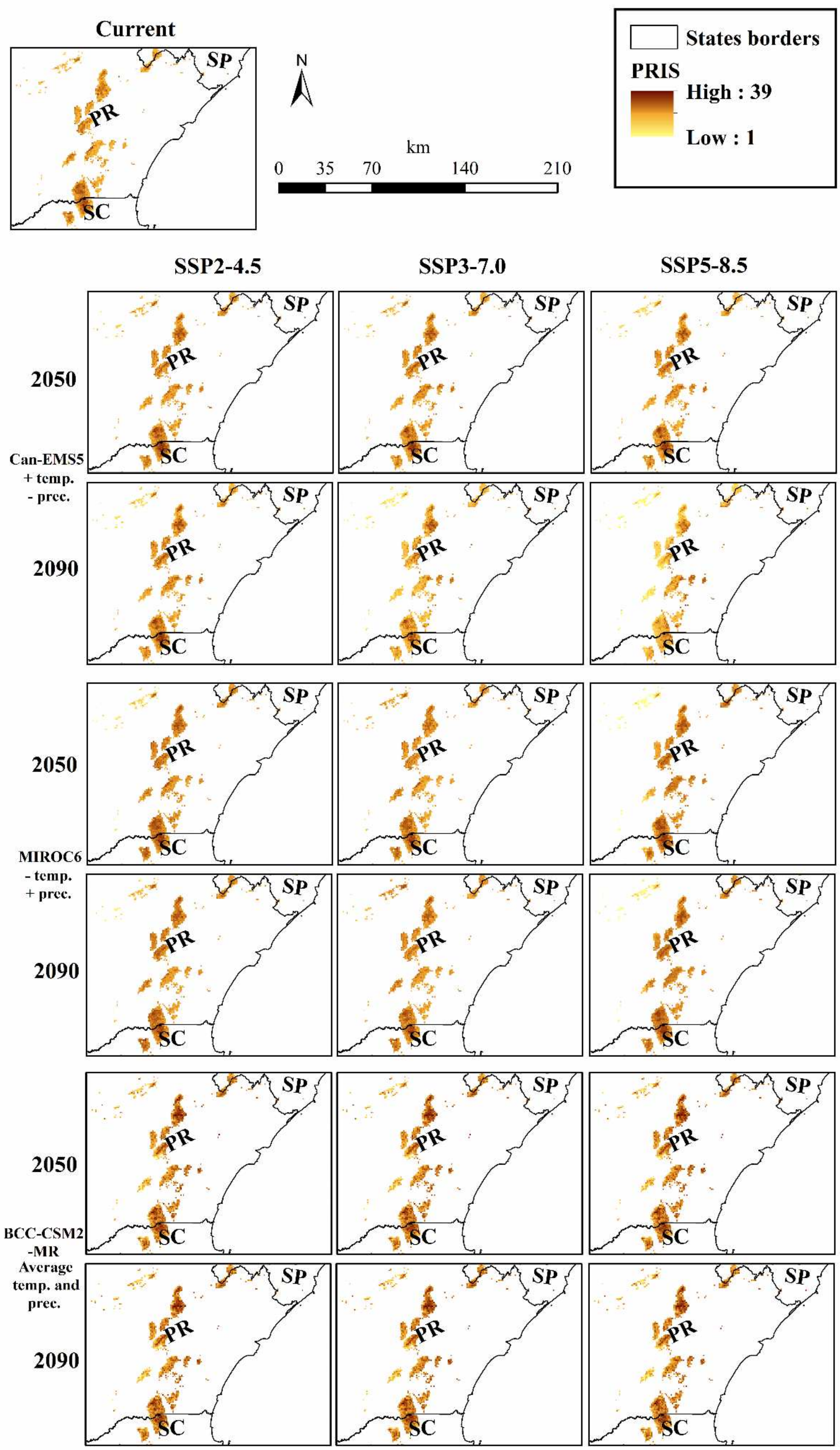


Figure S5

Southernmost area of *Campos de Altitude* distribution and PRIS distribution in current and future scenarios.

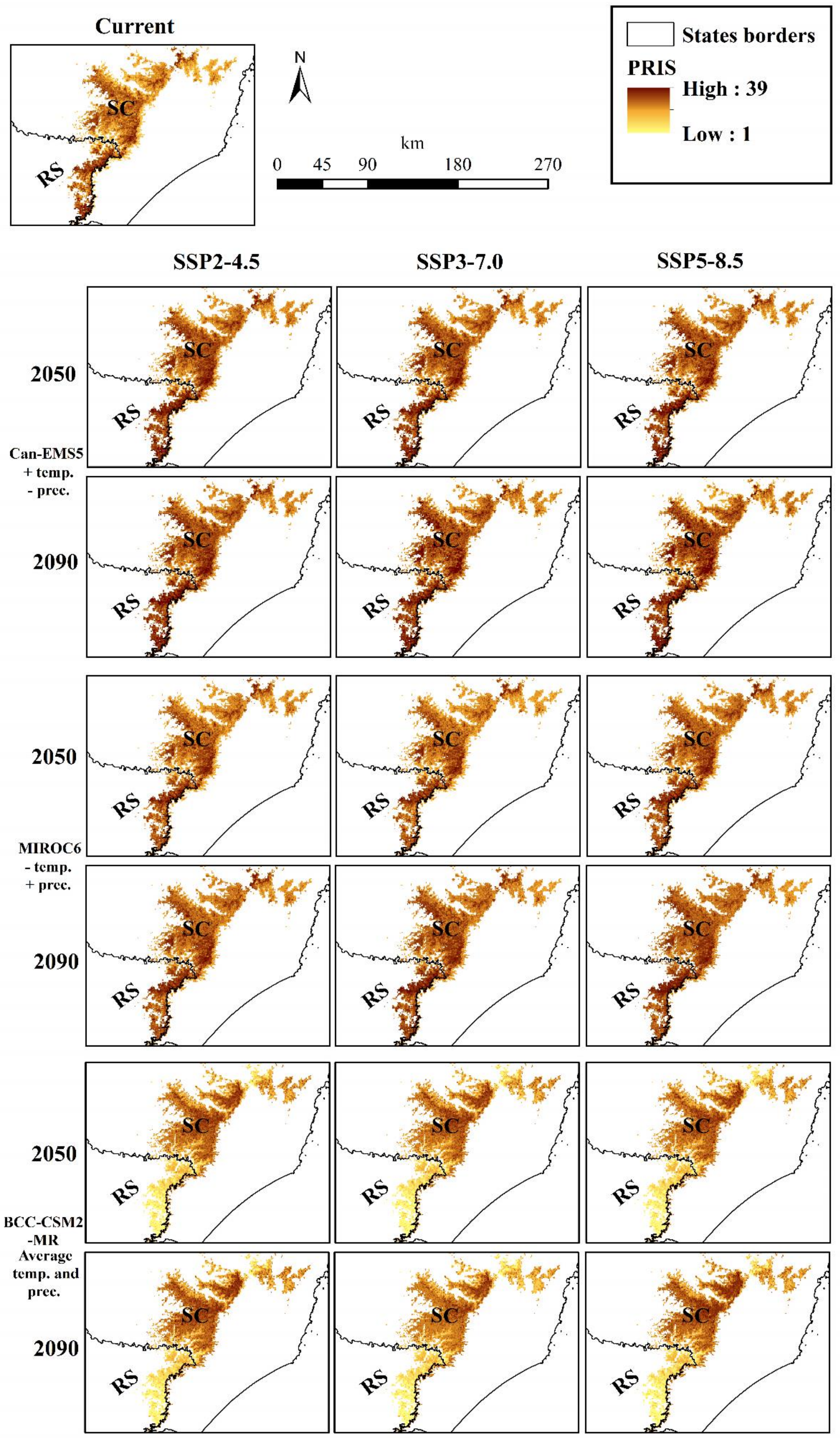
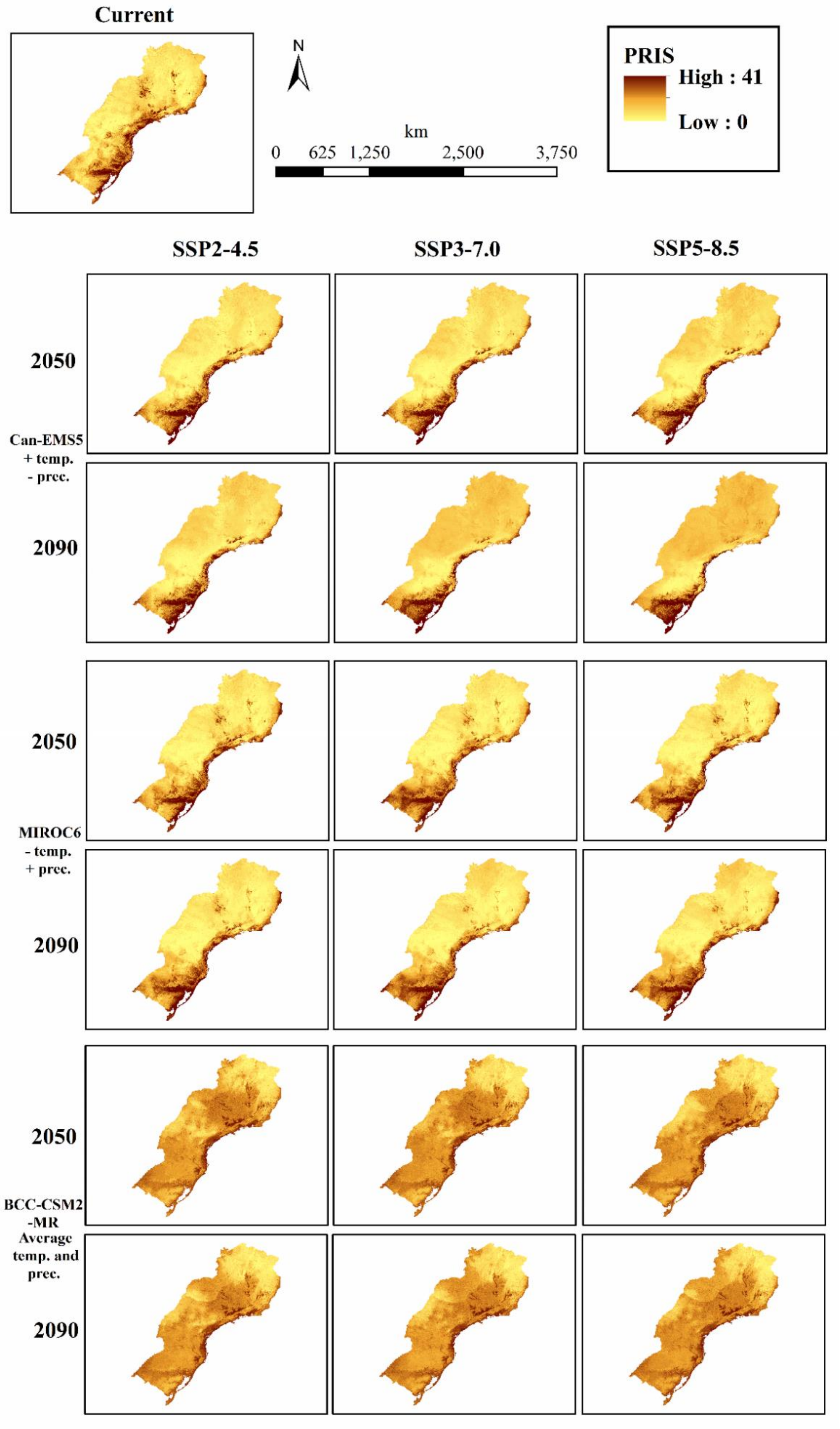


Figure S6

Southeast and South political regions of Brazil and the PRIS distribution in current and future scenarios.



Preliminary results

Chapter 3 - BRAZILIAN MOUNTAINTOP VEGETATION *'CAMPOS DE ALTITUDE'* IN THE QUATERNARY

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Introduction

During the last 420 ky (ky - thousands of years), the planet has experienced four glaciations, of which the Last Glacial Maximum (LGM) began 120 ky BP (ky BP - thousands of years before present) and lasted about 100 ka. In general, the interglacial periods (between glacial periods) of the Pleistocene were distinctly warm and wet, while the glacial periods were colder and drier. During the Last Interglacial, Antarctic ice core data indicate that temperatures were about 3°C above the current average, reaching nearly -10°C during the LGM period (Anthelme and Peyre, 2020; Arruda and Schaefer, 2020).

These climatic dynamics in the LGM, with a reduction in precipitation of between 35 and 55 per cent, allowed the dominance of grassland vegetation in most of central Brazil, the northward expansion of *Araucaria* forests (up to the *Triângulo Mineiro*) and an increase in the distribution of grassland systems in southern and southeastern Brazil (Arruda et al., 2018; Arruda and Schaefer, 2020; Behling, 2002; Behling et al., 2004; Behling and Hooghiemstra, 2001; Carnaval and Moritz, 2008; Safford, 1999). In proportion to the expansion of grassland systems, there has been a retreat of ombrophilous forests and their replacement by semi-deciduous formations, a reduction in the drainage network in seasonal channels and, consequently, the dominance of physical erosion processes (Arruda and Schaefer, 2020; Safford, 1999).

In general, the opposite processes played a leading role during the interglacial periods, when climatic conditions favoured the formation of deep soils, the advance of forests and fluvial erosion processes that desiccated the highlands (Arruda and Schaefer, 2020; Safford, 1999). Progressively from about 12 ky BP to the Middle Holocene, about 6 ky BP, there was an increase in temperature and precipitation near the Brazilian Atlantic coast and the first evidence of coastal cloud forest pollen, while the interior of the continent continued to experience colder temperatures and some water stress until about 7 ky to 5ka BP (Safford, 1999). From 3 ka BP, Araucaria and Podocarpus began to become more abundant in the highlands of southeastern Brazil, indicating a slight increase in the rainfall regime, which by 1.5 ka BP was closer to current standards, still wetter and slightly cooler, allowing the advance of Araucaria forests and the formation of the field and forest mosaics that exist today in the southern latitudinal maximum of the *Campos de Altitude* (Safford, 1999).

In mountain ecosystems, during glacial periods, vegetation belts tend to move down the mountain, allowing mountain species to radiate while lowland species tend to form refugia, while during interglacial periods the opposite occurs, contributing to the formation of biogeographic islands in the mountains (Anthelme and Peyre, 2020). These are important processes that contribute to the patterns of endemism in South American mountain ecosystems today, such as the

Páramos in the far north of the Andes, the richest tropical alpine phytogeographic province in the world (5000 plant species, 60% of which are endemic), and the *Campos de Altitude* in the far east of the continent (Anthelme and Peyre, 2020).

In the *Campos de Altitude*, patterns of endemism suggest climate-driven allopatric speciation processes in a history of climate change and long-distance migration in favourable environments (Safford, 2007). This argument is based on elements of a neotropical flora (*Tibouchina, Pleroma, Clethra*) from drier, more open environments and initially restricted to forests, which are also currently part of the *Campos de Altitude* communities (Safford, 2007). There are also elements of a temperate flora (*Weinmannia, Araucaria, Podocarpus, Fuchsia, Gaultheria, Cortaderia, Sisyrinchium*), often cosmopolitan, which arrived in the mountains of south-eastern Brazil by migration during the Quaternary climate change and contribute to the high floristic similarity between the *Campos de Altitude* and other Brazilian montane ecosystems and the Andes (Safford, 2007).

Palynological evidence from the Pleistocene-Holocene boundary indicates a decrease in the dominance of grasses and an increase in forest taxa at rates that accelerate as the Holocene approaches, accompanying the increase in precipitation across South America (Safford, 2007). There is also evidence of forested areas between 700 and 1000 m asl occupied by *Campos de Altitude* during the LGM (Safford, 2007). Thus, *Campos de Altitude* appear to have been climatic refugia since the LGM. The term *refugium* has primarily been used to describe sites of limited spatial extent to which plant species retreat and can survive during periods of climate change, and subsequently expand into the surrounding landscape when ideal conditions return (Keppel et al., 2012).

Identifying these relict areas is, therefore, a priority for conservation efforts, especially in the context of rapid anthropogenic global climate change (Keppel et al., 2012). Following this theoretical framework, we aim to answer the question: when and where did the connectivity pathway between the *Campos de Altitude* of southeastern Brazil and the Andes emerge, facilitating the migration of flora between these mountain ecosystems? To find the answer, we will use species distribution models at different times in the Holocene and Pleistocene to map the palaeodistribution of the *Campos de Altitude* across South America and try to identify when and what was the connection between the Andes and the *Campos de Altitude* of southeastern Brazil.

Materials and Methods

Study Region

To investigate possible connections between the *Campos de Altitude* and the Andes during different Quaternary time slices, we use the whole of South America as a potentially suitable area for the *Campos de Altitude*. The current distribution of the *Campos de Altitude* encompasses the South and Southeast political regions of Brazil, especially associated with the *Serra do Mar* and *Serra da Mantiqueira* Mountain ranges which extend along the Brazilian east coast and is an ecosystem associated with the Atlantic Forest biome (Fig. 1). More details about Campos de Altitude are described in Chapter 1 of this Thesis.

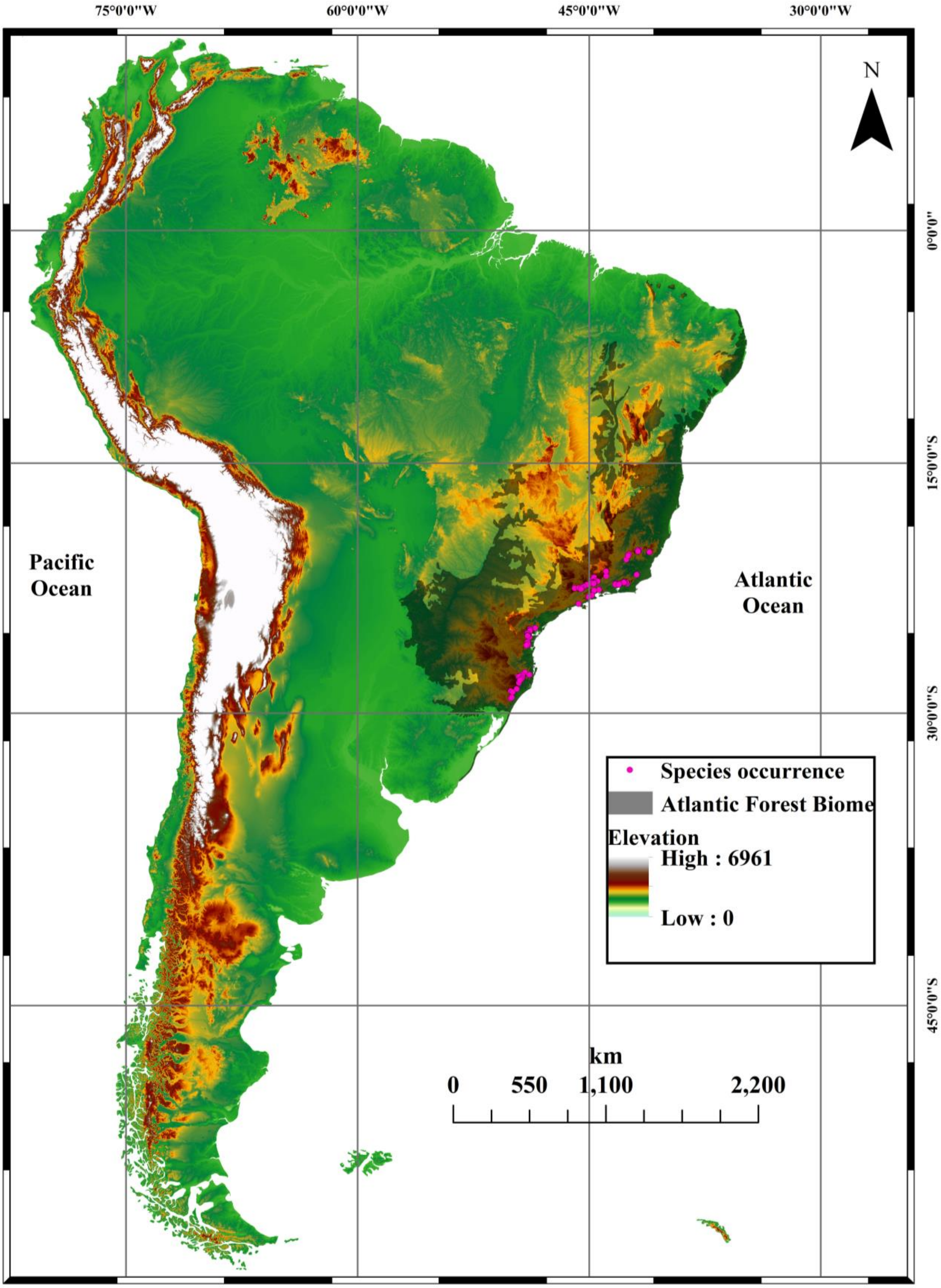

Figure 1: *Campos de Altitude* study area in the South America. It is an ecosystem located in the *Serra do Mar* and *Serra da Mantiqueira* Mountain ranges, the highest points in eastern South America, and is an ecosystem associated with the Atlantic Forest Biome, defined by Federal Decree No. 6660/2008 and Law No. 11.428/2006, shown in grey.

Species Dataset

Our dataset included 131 sites ranging from 5° S to 28º S and 58º W to 35º W along the east of South America, distributed across five Brazilian biomes (Caatinga, Cerrado, Atlantic Forest, Amazon, and Pantanal). The ROutVe (Rock Outcrops Vegetation) dataset is a list of species from four Brazilian rocky outcrop ecosystems: *Campos de Altitude*, *Inselberg*, *Campo Rupestre* (generally called Rupestrian Grasslands) and *Campo Rupestre Ferruginoso* (Ferruginous Rupestrian Grasslands or *Cangas*). The dataset was compiled using information available in the published literature and is dedicated to understanding the influence of environmental filters and global change scenarios on Rock Outcrops Vegetation of Brazil.

We performed an indicator species analysis, ISA (Dufrene and Legendre, 1997), on this dataset to identify species that indicate typical *Campos de Altitude* vegetation communities. The ISA is a combination of specificity, which represents the frequency with which the occurrence of a species is observed, and fidelity, which represents the degree of association of a given species with the observed sites generating an Indicator Value (IV) (Dufrene and Legendre, 1997) (Table 1). The analysis was performed with software R Statistical Software (R Core Team, 2020) using the ‘multipatt’ function in the ‘indicspecies’ package (De Cáceres et al., 2010) and retaining the species with the highest IV.

The next step was to download the geographical records of the occurrence of the indicator species for *Campos de Altitude*. This information was obtained from the Global Biodiversity Information Facility (GBIF) portal (GBIF, 2023) and the speciesLink Network (specieslink.net/search). The records were filtered by removing duplicates and visually checked individually using satellite imagery to check the correspondence with the *Campos de Altitude* or to another land use or vegetation type. Additional information on each indicator species is provided in Supplementary Material, Table S1 of Chapter 1.

Table 1: Results from ISA to *Campos de Altitude* in Brazil. IV – indicator value, *p* – statistical significance of the Monte Carlo test between species and *Campos de Altitude* sites from the ROutVe dataset, and NSR – number of species records after filtering.

Indicator Species for *Campos de Altitude* habitats	**IV**	***p***	**Family**	**NSR**
Gaultheria serrata (Vell.) Sleumer ex Kin.-Gouv.	0.767	0.005	Ericaceae	49
Utricularia reniformis A.St.-Hil.	0.728	0.005	Lentibulariaceae	42
Croton splendidus Mart.	0.717	0.005	Euphorbiaceae	56
Pleroma hospitum (Schrank et Mart. ex DC.) Triana	0.642	0.005	Melastomataceae	56
Abatia americana (Gardner) Eichler	0.608	0.01	Salicaceae	31
Fuchsia regia (Vell.) Munz	0.607	0.025	Onagraceae	68
Clethra uleana Sleumer	0.594	0.01	Clethraceae	23
Agarista niederleinii (Sleumer) Judd	0.594	0.015	Ericaceae	10
			Total Records	**335**

Bioclimatic and topographic variables

We used the 19 bioclimatic variables from the CHELSA-TraCE21k (Karger et al., 2023). The resolution of 30 arcseconds (0.86 km² at the equator, ~ 1km²) was crucial because we were analysing montane environments with high variability, which is lost at smaller resolutions (Hijmans et al., 2005). CHELSA-TraCE21k is a dataset obtained by downscaling TraCE-21k data using the "Climatologies at high resolution for the earth's land surface areas" (CHELSA) V1.2 algorithm. The aim was to produce global monthly climatologies for temperature and precipitation at 30 arcsec spatial resolution in 100-year time steps for the last 21,000 years (Karger et al., 2023) (Table 2).

We downloaded the bioclimatic variables and elevation for eight different Quaternary time slices: Present time, 500 years BP, 2, 6, 10, 14, 18 and 21 ky BP (Table 2). Chelsa datasets were clipped to the current political-geographical division of South America using *terra* package (Hijmans, 2023) in the R statistical environment (R Core Team, 2020). This geographical region may include the potential areas for *Campos de Altitude* species occurrence at Quaternary time slices (Fig. 1).

Table 2: Variables description and Quaternary time slices used in past projections. The Source column gives the website where the data can be accessed and downloaded, the Time slice and k years BP columns give the name used for each Quaternary time slice, the GCMs and Resolution columns give the name and resolution of each GCM used, and the Variables column gives the short name and description of each variable used in this study. The numbers superscript indicates the variables that were selected for ChelsaTraCE21k models.

Source	**Time period**	**k years Before Present (BP)**	**GCMs**	**Resolution**	**Variables**		
					shortname		**Description**
Chelsa TraCE21k available at https://chelsa-climate.org/chelsa-trace21k/	Current	0y BP	CCSM3	30 arc-sec (~ 1km² at the equator)	dem and bioclimatic	bio1	Annual Mean Temperature
						bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
						bio3	Isothermality (BIO2/BIO7) (×100)
	16th Century (1500-1599)	0.4y BP				**bio4**^{1}	Temperature Seasonality (standard deviation ×100)
						bio5	Max Temperature of Warmest Month
						bio6	Min Temperature of Coldest Month
	Late Holocene	2ky BP				bio7	Temperature Annual Range (BIO5-BIO6)
						bio8	Mean Temperature of Wettest Quarter
	Mid Holocene	6ky BP				bio9	Mean Temperature of Driest Quarter
						bio10^{1}	Mean Temperature of Warmest Quarter
						bio11	Mean Temperature of Coldest Quarter
	Early Holocene	10ky BP				bio12	Annual Precipitation
						bio13	Precipitation of Wettest Month
	Late Pleistocene	14ky BP				bio14	Precipitation of Driest Month
						bio15^{1}	Precipitation Seasonality (Coefficient of Variation)
		18ky BP				bio16	Precipitation of Wettest Quarter
						bio17	Precipitation of Driest Quarter
						bio18^{1}	Precipitation of Warmest Quarter
	Last Glacial Maximum (LGM)	21ky BP				**bio19**^{1}	Precipitation of Coldest Quarter
						dem	Surface elevation above sea level

Model Construction, validation, and selection

The occurrence records of the 8 species obtained through ISA (Table 1) were treated as a single taxonomic unit, serving as a proxy for the Campos de Altitude ecosystem, to model past distributions in various Quaternary time slices. The background modelling layers were the entire extent of South America, including potentially suitable areas for *Campos de Altitude* species (Fig. 1). All layers were clipped by South America for all model sets.

We used an ensemble approach model that is run in the 'modelR' library in R. (Sánchez-Tapia et al., 2020). This workflow was explained in detail in Chapter 1 of this thesis, so only the essential parameters will be detailed here. The first step is to do a data setup where we set a crossvalidation as the partition type, 5 partitions and 10 runs, we also set 500 as the number of pseudoabsences, disabled options to clean occurrence data and additionally set 0.5 as cut off to select the environmental variables.

Step 2 in the ModleR workflow is to fit the ecological data for each partition and runs set in the previous step, and project them in geographic space for different selected time slices of the Quaternary according to Table 2. We chose the 'spec_sens' threshold because it is the threshold at which the sum of sensitivity (true positive rate) and specificity (true negative rate) is highest and provides more robust models (Hijmans et al., 2021). In addition, we also projected the models in five algorithms implemented by the ModleR workflow: glm, maxent, maxnet, svmk and rf (Sánchez-Tapia et al., 2020). In the third set of models, we have added three more algorithms, bioclim, brt and svme, which are also implemented in the ModleR workflow and will be presented in the supplementary material of this preliminary chapter.

Step 3 of the ModleR workflow is to merge the partitions from each algorithm generated in the previous step into a final model for each algorithm. For this, we used the "raw_mean_th", which cuts the models by the mean of the "spec_sen" threshold to create a binary model (Sánchez-Tapia et al., 2020).

The final step (step 4) is to produce the final ensemble model for *Campos de Altitude* with the best algorithm and 0.5 consensus of all algorithms. To select the best-performing model, we used the AUC evaluation metric available in the "dismo" package (Hijmans et al., 2021) implemented by the 'modelR' workflow (Sánchez-Tapia et al., 2020). To classify the models based on AUC evaluation metric we can used the following classes: AUC close to 0.5 corresponds to a prediction no better than the random prediction, between 0.6 and 0.7 poor accuracy, 0.7 to 0.8 fair accuracy, 0.8 to 0.9 good accuracy and >0.9 excellent accuracy (Pearce and Ferrier, 2000; Phillips et al., 2006; Swets, 1988).

Results

The evaluation metrics for the ChelsaTraCE21k based results showed excellent accuracy for all implemented algorithms. We first created a map layout showing the results only for the best algorithm, which was rf (AUC = 0.99534435) (Figure 2). However, as all algorithms showed excellent performance, we also show the results of a 0.5 consensus between all implemented algorithms (Figure 3). Considering all partitions, algorithms, and scenarios were projected for the first set of models a total of 2000 models.

Table 3: Evaluation metrics from all algorithms used to project the distribution of *Campos de Altitude* in the past. The best algorithm is highlighted in bold.

algorithm	kappa	spec_sens	AUC	AUCratio	pROC	TSSmax	KAPPAmax
rf	**0.448625334**	**0.373933556**	**0.99534435**	**1.990688699**	**1.792474646**	**0.959863539**	**0.952028588**
maxnet	0.204149063	0.177379171	0.993247335	1.98649467	1.841743326	0.948933902	0.94207933
maxent	0.352496764	0.309231086	0.992697228	1.985394456	1.84342524	0.94584435	0.939016885
svmk	0.466567854	0.400463876	0.991714286	1.983428571	1.704299688	0.957153518	0.952045434
glm	0.539209286	0.356133033	0.990211087	1.980422175	1.413229913	0.924654584	0.920666507

These preliminary results were crystal-clear, showing a connection around 18 ky BP that follows the current distribution path of the Brazilian *Cerrado* biome and the highlands of central Brazil (Figure 2 and 3). This pathway formed a corridor between the eastern part of South America and the Andes, connecting areas currently occupied by other mountain ecosystems, such as the *Campos Rupestres*, to the *Cerrado* domain and its diverse vegetation types. The current distribution of the *Cerrado* borders the Amazon Rainforest at its southern limit, and it seems that the connection followed this path, where the states of *Mato Grosso* and *Rondônia* in Brazil and the northern regions of Bolivia and southern Peru are located today (Figure 2 and 3). In addition, we can observe that the currently suitable areas for *Campos de Altitude* have been climatic refuges since the LGM (Figure 2 and 3).

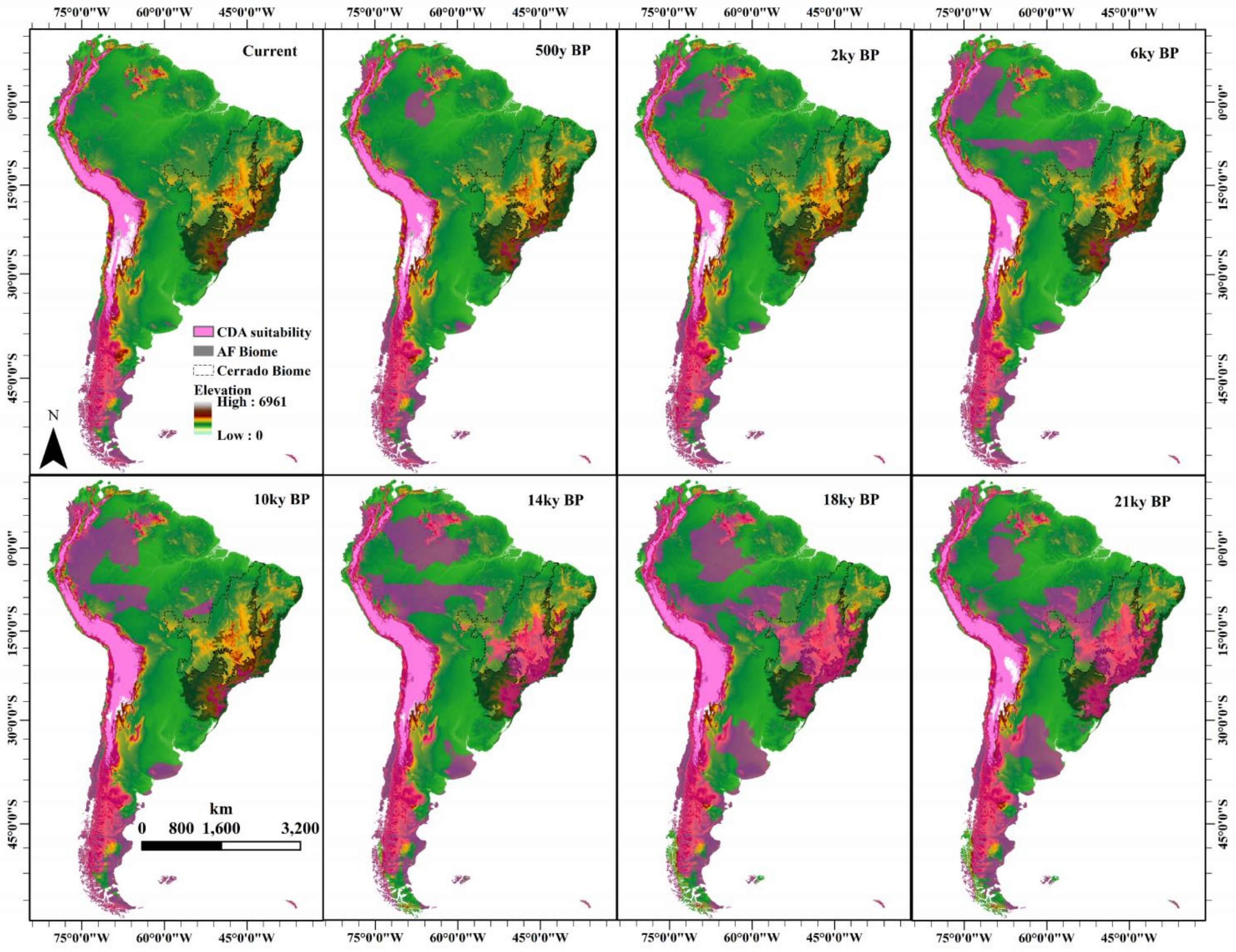

Figure 2: Present and past climatically predicted distributions of proxy species representing *Campos de Altitude*, using the best algorithm in South America, during seven different Quaternary time slices.Light pink areas represent suitable areas for *Campos de Altitude*, and the elevational gradient of the continent is shown in a colour gradient. Atlantic Forest and *Cerrado* Biome are shown to guide the interpretation of paleodistribution.

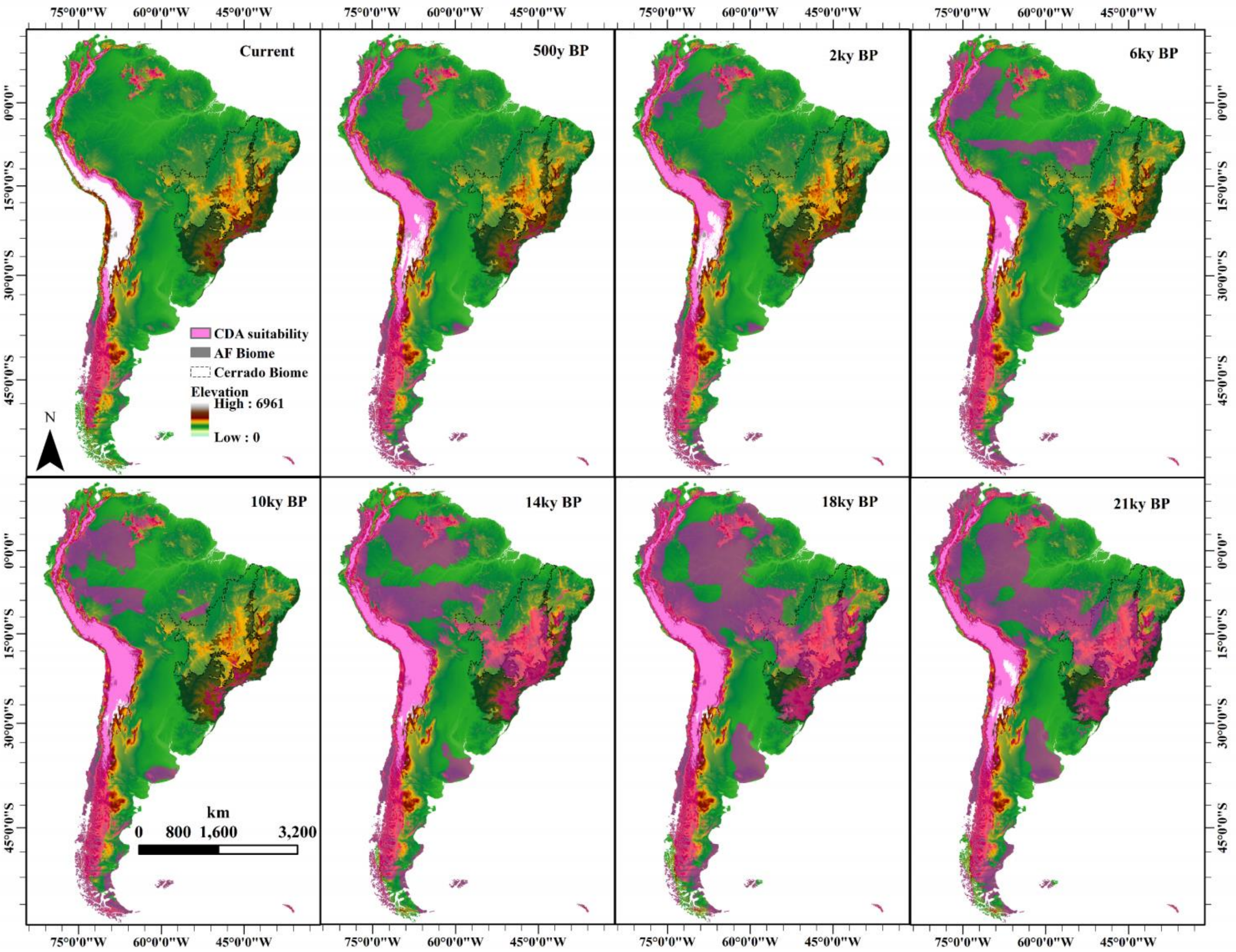

Figure 3: Present and past climatically predicted distribution of proxy species representing *Campos de Altitude* from 0.5 consensus between algorithms in South America, during seven different Quaternary time slices. Light pink areas represent suitable areas for *Campos de Altitude*, and the elevational gradient of the continent is shown in a colour gradient. Atlantic Forest and *Cerrado* Biome are shown to guide the interpretation of paleodistribution.

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Conclusion

Our findings illustrate that *Campos de Altitude* is a product of climatic changes during the Quaternary period. Simultaneously, climate change poses the most significant threat to the future of *Campos de Altitude*. The results of this study, and the impact of climate change on all of us, highlight the pressing need to promptly address the consequences of global climate change on montane ecosystem biodiversity within this decade. This is crucial to ensure sustainable development and a high quality of life in the near future.

Additionally, our findings underscore the valuable utility of tools such as species distribution models in predicting the climatic and topographic suitability of both native and invasive species. These models provide a crucial foundation for environmental managers, society, and governments in planning and implementing consistent policies to mitigate the negative impacts of climate change and its positive feedbacks. They also form the basis for strategies of control and management measures aimed at addressing the presence of invasive species in native ecosystems.

The significant utility of modeling tools for studying the historical distribution of species should also be emphasized. With the assistance and external validation of other biotic dimensions, such as palynological and phylogenetic information, it enables us to make inferences and draw parallels to comprehend the present diversity patterns of plant communities. Understanding the biogeographic origins and driving factors of our current reality will also provide insights into the future.