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Subtropical high-montane forest climate refuges in Brazil

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ABSTRACT: Climate change represents one of the greatest threats to global biodiversity. We investigate how climate change will affect the future potential distribution of tree species in subtropical high montane habitats in the Atlantic Forest and identify potential climate refuges for these species. The most frequent and exclusive species in this ecosystem were selected and geographic coordinates were compiled. The maximum entropy algorithm was used for climatic niche modeling. Two scenarios for 2061-2080 were considered for future predictions, one low impact (RCP 4.5) and one high impact (RCP 8.5). Isothermality, mean temperature in the driest quarter, mean temperature in the hottest quarter, rainfall in the driest month, and rainfall in the hottest quarter were the variables that best explained the climatic niche of the majority of species. The areas of potential species occurrence were reduced by 48.37 % (± 13.63 %) (RCP 4.5) and 62.49 % (± 21.87 %) (RCP 8.5) on average. The potential area of *Crinodendron brasilense* Reitz & L.B.Sm. decreased the most, by 82.11 % (RCP 4.5) and 90.06 % (RCP 8.5), respectively. High elevation areas in the south of Brazil were identified as priorities for conservation to ensure that climate refuges for high montane forest species are maintained in the future. Climate change events may significantly affect the species evaluated in this study.

Keywords: subtropical Atlantic Forest, climate variables, climate change scenarios, cloud forests

Introduction

The Atlantic Forest is considered a biodiversity hotspot for hosting one of the richest assemblies of biological diversity on the planet. Within the scope of forests classified as high montane in Brazil (IBGE, 2012), tree species richness is relatively lower in higher elevation areas (above 1000 m) due to environmental filters such as low temperatures (Sühs et al., 2019). Despite this lower species richness, the ecological value of high montane forests is high due to their hosting unique species and attributes. Furthermore, these forests are threatened by climate change (Helmer et al., 2019).

Recent studies (e.g., Marchioro et al., 2020) have shown that one of the primary responses of species to climate change is migration from the original native range towards higher elevations. This occurs because, apart from geographical constraints, species native ranges are determined by physiological limits, mainly related to temperature and rainfall (Rodgers et al., 2018; Feng et al., 2022). Considering these premises and potential climate change scenarios, changes in the floristic composition of high montane forests are expected due to the arrival of lower altitude species and the extinction of species that occur exclusively at the highest elevations (Saraiva et al., 2021). Therefore, species that are restricted to the highest elevations, such as those dependent on high montane forest habitats, are at greater risk. For this reason, modeling geographic distribution based on climatic niches is one of the main tools used to predict future climatic adequacy.

Tree species typical of subtropical high montane Atlantic Forests are expected to have narrow climatic niches, which restricts their occurrence to areas of relatively low temperatures. Because the areas of climatic adequacy of these species tend to decrease in response to different climate change scenarios, they may function as indicators of how climate change might influence subtropical high-montane Atlantic Forests. The main hypothesis is that the extension of these forests will decrease due to the fragmentation effect of isolated mountain tops, which restricts species migration capacity. This study aimed to identify climate refuges for high montane species based on determining areas where the necessary climatic conditions for these species to persist will be maintained, so as to avoid future extinctions.

Materials and Methods

A tree species presence/absence database for subtropical high-montane Atlantic Forests ("high-montane forests" hereafter) was created and used to determine the most dependent and representative species. Scientific articles on the flora of these forests were reviewed in search of data. Subtropical forests were defined as forests growing in the Atlantic Domain south of the Tropic of Capricorn. The definition of high-montane was taken from the Brazilian Institute for Geography and Statistics classification (IBGE, 2012), which refers to elevations above 1000 m in latitudes between 24° and 32° S (states in the south of Brazil). Based on these criteria, 26 areas were selected in the Serra do Mar and Serra Geral domains and include high montane forests in Mixed Ombrophilous Forest (Araucaria Forest) and Dense Ombrophilous Forest (Evergreen Rainforest) in the southern states of Brazil (Santos et al. 2022).

Botanical names and synonyms were checked before entering the database. Only species of trees and arborescent plants, i.e., adult individuals with a well-developed woody stem structure with a diameter greater than 5 cm at breast height when upright (Sobral et al., 2006), were considered. In addition, based on specific articles (e.g. Enquist et al., 2016), only the species dependent on high montane habitat, i.e., the species with exclusive distribution in these ecosystems, were selected. Ten species were chosen for fitting the selection criteria indicated above and because enough data on them (minimum of 20 points of occurrence) were available for the analysis: *Crinodendron brasiliense* Reitz & L.B.Sm., *Drimys angustifolia* Miers, *Inga lentiscifolia* Benth., *Miconia ramboi* Brade, *Myrceugenia oxisepala* (Burret) D.Legrand & Kausel, *Myrsine altomontana* M.F.Freitas & Kin.-Gouv., *Plinia cardifolia* (D. Legrand) Sobral, *Solanum cassioides* L.B.Sm. & Downs., *Solanum pabstii* L.B. Sm. & Downs and *Tibouchina pilosa* Cogn.

The geographic coordinates of all species were obtained from the BIEN database (Enquist et al., 2016; Maitner et al., 2018; GBIF, 2018) and scientific publications, then submitted to rigorous verification for the removal of inconsistencies related to typing errors or doubtful geographic references (Hijmans and Elith, 2015). As a complement to this approach, a spatial filter was applied to select only one location in an area of 2.5 x 2.5 km because of possible data overlap from herbarium collections, research institutes, or universities (Boria et al., 2014).

Nineteen bioclimatic variables from the WorldClim database (Hijmans et al., 2005) were considered for modeling species geographic distribution. The bioclimatic variables were derived from temperature and rainfall values to represent climatic conditions for developing different life forms on a 2.5-minute resolution grid (~ 5 km²). The climatic variables used were: bio 1 (annual mean temperature), bio 2 (mean diurnal range), bio 3 (isothermality), bio 4 (thermal seasonality), bio 5 (maximum temperature in the hottest month), bio 6 (minimum temperature in the coldest month), bio 7 (annual thermal range), bio 8 (mean temperature in the wettest quarter), bio 9 (mean temperature in the driest quarter), bio 10 (mean temperature in the hottest quarter), bio 11 (mean temperature in the coldest quarter), bio 12 (annual rainfall), bio 13 (rainfall in the wettest month), bio 14 (rainfall in the driest month), bio 15 (rainfall seasonality), bio 16 (rainfall in the wettest quarter), bio 17 (rainfall in the driest quarter), bio 18 (rainfall in the hottest quarter) and bio 19 (rainfall in the coldest quarter). Variance inflation factors of the variables were determined in order to solve problems relating to the multicollinearity of these variables. Highly autocorrelated variables were then removed (VIF > 10). Eight variables (bio2, bio3, bio8, bio9, bio10, bio12, bio14 and bio18) remained for the modeling procedure after multicollinearity was eliminated.

Five global atmospheric circulation models (GCMs: CCSM4, GISS-E2-R, ACCESS1-0, HadGEM2-AO, MIROC5) were defined for the evaluation of predictions of future (2070) impacts of climate change. These GCMs are often used to predict species distributions in South America (Fulgêncio-Lima et al., 2021). Using an ensemble of multiple GCMs reduces the uncertainties of future climate projections. "Emission scenarios" are based on projected future atmospheric concentrations of greenhouse gases. The climate projected for a time in the future, therefore, depends on the model and the emission scenario used, and how the model is run (each model run is different because the climate is a stochastic phenomenon). These models are part of Phase 5 of the Coupled Model Intercomparison Project (CMIP5) of the IPCC fifth assessment (IPCC, 2014). Two climate change scenarios were used: RCP 4.5, considered intermediate, though more optimistic than RCP 8.5, which is pessimistic. Under the optimistic scenario (RCP 4.5), measures to control the emission of greenhouse gases will be adopted, avoiding emissions to the maximum extent possible. Under the pessimistic scenario (RCP 8.5), humanity will not try to reduce or avoid greenhouse gas emissions; thus, emissions will continue and increase. Climatic data of future projections considering the variables mentioned above were also obtained from the WorldClim database (Hijmans et al., 2005).

Climatic niche models were run using the Maximum Entropy algorithm (Maxent). One hundred pseudo-absences were generated for each species observation (Lobo and Tognelli, 2011) in a radius of 500 km. The data were subdivided into two groups, 70 % for calibration (training) of adjustments and 30 % for evaluation (test) of adjustments. Two rounds of calibration and test were conducted for each pseudo-absence distribution, making a total of 30 adjustments per species (five GCMs x three pseudo-absence distributions x two calibration and test rounds).

The accuracy of the adjustments was evaluated using True Skill Statistics (TSS), which vary from -1 to 1 (Allouche et al., 2006). The closer to 1, the better the adjustment of the model. The classification by Landis and Koch (1977) was adopted, with TSS $\geq$ 0.75 indicating excellent performance adjustments, $0.40 \leq TSS < 0.75$ good performance adjustments, and TSS $<$ 0.40 inadequate performance adjustments.

Binary projections of potential areas of species geographic occurrence in high montane forests were conducted to quantify impacts on the two climate change scenarios for each species. Areas of climatic adequacy were considered those with estimates of the probability of species occurrence higher than 50 %. Shapefiles with data from 2018 were extracted from the SOS Mata Atlântica atlas of natural vegetation remnants (Fundação SOS Mata Atlântica, 2018) and used for this purpose. High montane forest remnants larger than 3 ha in the three southern states (PR, SC, RS) were identified in these shapefiles. Projections for the present and each of the future scenarios (2070) were then overlapped to determine the areas of climatic stability – those where the climate will potentially remain adequate or inadequate – and instability – those where climatic adequacy will potentially be lost or developed in the future. Percentages of reduction in the area of climatic adequacy were calculated for each representative species of high montane forests. Climatic adequacy areas were then overlapped to determine the areas of future climatic refuge for each species. A map was created from the Brazilian Ministry of Environment's shapefile showing the geographic distribution of the Conservation Units of Integral Protection in the region.

All data were analyzed using the R statistics programming language (R Core Team, 2019) with the following packages: dismo (Hijmans et al., 2017), raster (Hijmans, 2020), biomod2 (Thuiller et al., 2020), and BIEN (Maitner et al., 2018).

Results

The geographic distribution of species dependent on the habitat of high montane forests is mainly concentrated in the Serra do Mar and Serra Geral mountain ranges, which are relatively close to the ocean. Climatic adequacy areas or climatic niches in high elevation regions were predicted for these species based on their distribution (Figure. 1).

The modelling results indicated that the variables best explaining the climatic niche of the majority of species were isothermality (bio3), mean temperature in the driest quarter (bio 9), mean temperature in the hottest quarter (bio10), rainfall in the driest month (bio14) and rainfall in the hottest quarter (bio18). The species are more likely to occur in areas where: i) isothermality is lower (bio3); ii) the mean temperature in the driest quarter (bio 9) does not exceed approximately 17 °C; iii); the mean temperature in summer (bio10 – hottest quarter) does not exceed approximately 20 °C; iv) rainfall in the driest month (bio14) is greater than approximately 80 mm; and v) rainfall in the hottest quarter (bio18) is in excess of 500 mm and, for a few species (e.g. *I. lentiscifolia*, *M. oxysepala*, and *D. angustifolia*), is no higher than approximately 800 mm. The potential area of occurrence of typical high montane species is thus characterized by mild temperature summers and the absence of dry periods.

A comparison between the species present area of climatic adequacy in high-montane forests and the potential area indicated by the low (RCP 4.5, Table 1) and high (RCP 8.5, Table 2) impact scenarios based on the five GCM models showed that the potential area of species occurrence is estimated to decrease by 48.37 % (± 13.63 %) and 62.49 % (± 21.87 %) on average, respectively, in the low and high impact scenarios. These losses occur mainly in lower elevation areas.

The modeling results show that climate change affected all the species evaluated, especially those endemic to high montane forests, such as *Crinodendron brasiliense*. According to the results, the potential area of occurrence of this species will undergo the greatest decrease under both low and high impact scenarios (RCP 4.5, RCP 8.5, Tables 1, 2): 82.11 % (± 9.26 %) and 90.06 % (± 11.72 %), on average, respectively.

Consensual projection of priority areas for the conservation of the species evaluated was obtained from overlapping future areas of climatic adequacy for the group of species that considered two scenarios (RCP 4.5 and RCP 8.5) and five GCMs. These potential climate refuges (Figure 2) are shown in darker shades of green, representing the highest values on the scale. These are the areas with a higher overlap of potential future climatic adequacy for species in the subtropical high montane Atlantic Forest in southern Brazil and represent the best chances of future survival of the species typical of high montane forests. When considering species conservation under the different climate change scenarios, the importance of conservation units of

Table 1 – Future decrease (2061-2080) in % of areas of climatic adequacy in a low impact scenario (RCP 4.5) for species typical of subtropical high-montane Atlantic Forest based on five different global atmospheric circulation models (GCMs) (CC = CCSM4, GS = GISS-E2-R, AC = ACCESS1- 0, HD = HadGEM2-AO, MC = MIROC5).

Species	RCP4.5					Mean
	AC	CC	GS	HD	MC	
Crinodendron brasiliense	–83.50	–89.56	–65.32	–91.47	–80.70	–82.11
Myrsine altomontana	–45.21	–84.46	–42.82	–85.65	–85.29	–68.69
Drimys angustifolia	–70.18	–64.79	–30.24	–55.79	–50.89	–54.38
Plinia cardifolia	–37.44	–64.79	–24.39	–74.13	–64.20	–52.99
Solanum cassioides	–50.37	–67.03	–28.81	–72.47	–31.77	–50.09
Miconia ramboi	–39.61	–50.90	–10.36	–59.84	–39.91	–40.12
Myrceugenia oxisepala	–42.37	–45.14	–20.90	–44.18	–38.13	–38.14
Solanum pabstii	–33.48	–45.28	–15.13	–58.41	–37.52	–37.96
Tibouchina pilosa	–39.34	–43.07	6.52	–46.80	–45.56	–33.65
Inga lentiscifolia	–16.78	–38.50	–2.00	–46.31	–24.43	–25.60
Mean	–45.83	–59.35	–23.30	–63.50	–49.84	–48.37

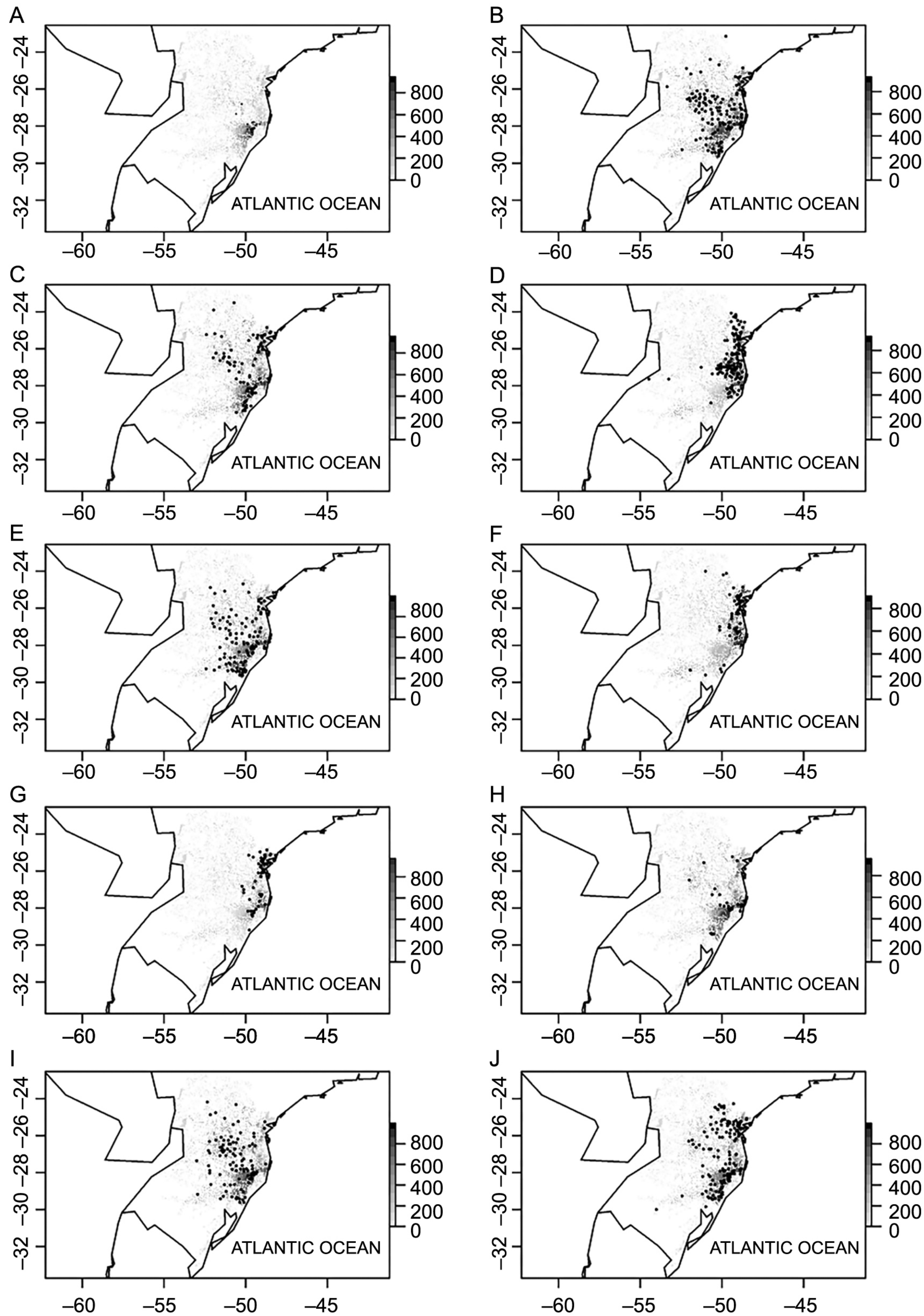

Figure 1 – Present climatic adequacy areas for species typical of subtropical high-montane Atlantic Forest: (a) *Crinodendron brasiliense*, (b) *Inga lentiscifolia*, (c) *Miconia ramboi*, (d) *Tibouchina pilosa*, (e) Myrceugenia oxisepala, (f) Plinia cardifolia, (g) *Myrsine altomontana*, (h) *Solanum cassioides*, (i) *Solanum pabstii*, and (j) *Drimys angustifolia* based on the mean probability of all adjustments. Shades of gray, from darker to lighter, represent the gradient of higher to lower climatic adequacy for the species (%).

Table 2 – Future decrease (2061-2080) in % of areas of climatic adequacy under a high impact scenario (RCP 8.5) for species typical of subtropical high-montane Atlantic Forest based on five different global atmospheric circulation models (GCMs) (CC = CCSM4, GS = GISS-E2-R, AC = ACCESS1- 0, HD = HadGEM2-AO, MC = MIROC5).

Species	RCP8.5					Mean
	AC	CC	GS	HD	MC	
Crinodendron brasiliense	–96.97	–97.87	–67.90	–99.21	–88.33	–90.06
Myrsine altomontana	–85.05	–90.77	–29.42	–93.57	–86.69	–77.10
Solanum cassioides	–71.93	–83.68	–32.04	–84.96	–65.62	–67.65
Drimys angustifolia	–83.74	–75.40	–33.22	–87.14	–58.36	–67.57
Plinia cardifolia	–85.77	–73.76	10.30	–93.18	–75.39	–63.56
Miconia ramboi	–76.67	–64.21	–9.22	–80.13	–60.52	–58.15
Solanum pabstii	–42.92	–74.01	–17.56	–74.01	–65.27	–54.75
Myrceugenia oxisepala	–58.30	–67.17	–26.06	–62.63	–45.48	–51.93
Tibouchina Pilosa	–85.01	–44.91	16.83	–88.51	–49.17	–50.15
Inga lentiscifolia	–43.20	–62.31	1.96	–72.56	–43.81	–43.98
Mean	–72.96	–73.41	–18.63	–83.59	–63.86	–62.49

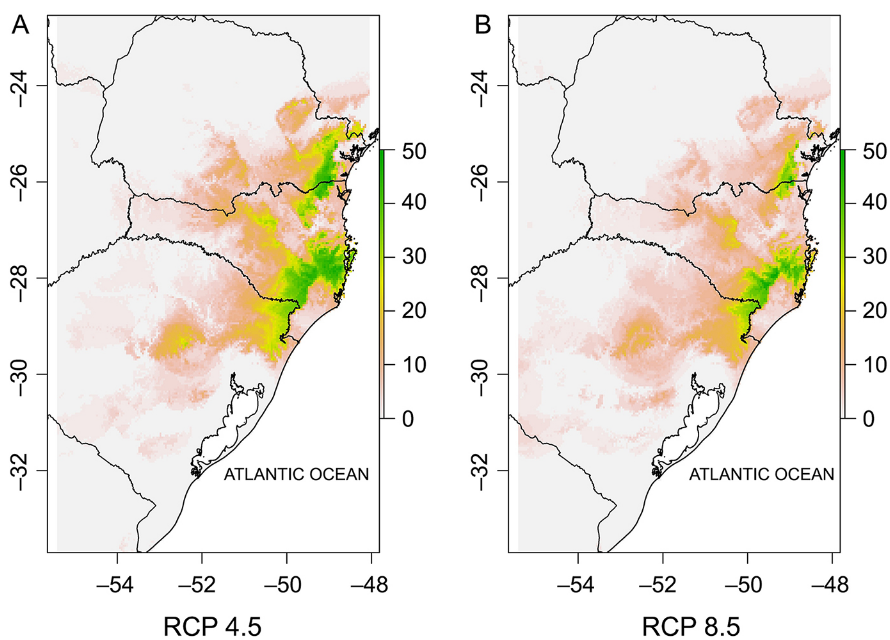

Figure 2 – Indication of priority areas for the conservation of subtropical high-montane Atlantic Forest species in southern Brazil considering all the species evaluated and two climate change scenarios of low and high impact (a - RCP 4.5 and b - RCP 8.5) based on five different global atmospheric circulation models (GCMs) (CC = CCSM4, GS = GISS-E2-R, AC = ACCESS1- 0, HD = HadGEM2-AO, MC = MIROC5). Darker shades of green, or higher values on the scale: areas with a higher overlap of potential future climatic adequacy for subtropical high-montane Atlantic Forest species in South Brazil, i.e., where a larger number of the five models used as well as a higher number of the ten species overlap.

integral protection (Figure 3) should be emphasized, especially in the plateaus and mountainous regions near the sea which are most likely to serve as climate ref ugia (e.g., Parque Nacional Guaricana, Parque Nacional de São Joaquim, Parque Estadual do Tabuleiro, Parque Nacional Aparados da Serra, Reserva Biológica da Serra Geral).

Exceptionally reduced climate refuge areas were determined for a number of species such as *C. brasiliense*. The mean area of future climatic adequacy for this species compared with the present area (Table 3) should decrease from 6,237.4 km² to 1,115.9 km² and to 620.2 km² under both the low and high impact scenarios, respectively.

Discussion

In general, the results suggest a significant future decrease in areas of climatic adequacy for species dependent on subtropical high montane Atlantic Forest habitat in the south of Brazil. Considering that the species evaluated are indicators of this forest type,

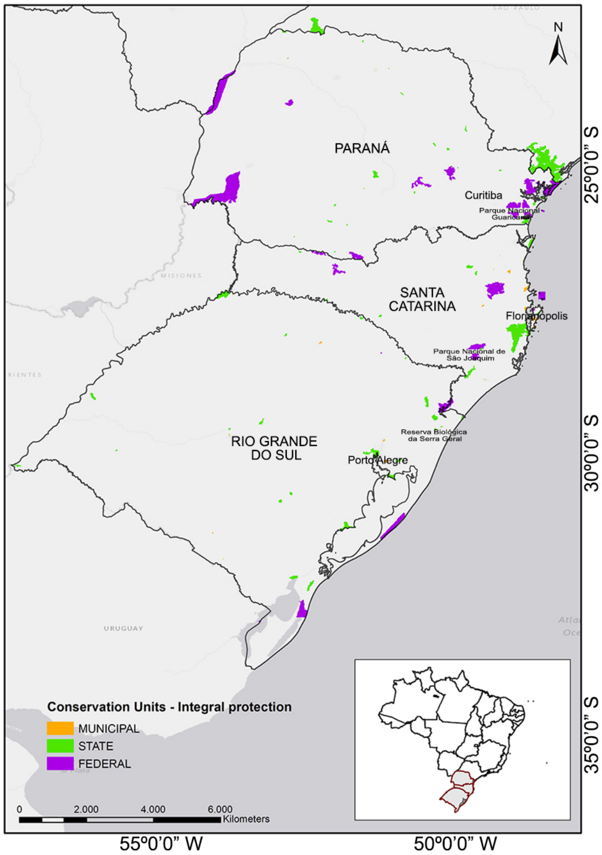

Figure 3 – Conservation Units of Integral Protection that currently exist in the southern region of Brazil.

Table 3 – Size of present and future areas of climatic adequacy for subtropical high-montane Atlantic Forest species in southern Brazil considering two climate change scenarios of low and high impact (RCP 4.5, RCP 8.5) based on the mean and consensus of five global atmospheric circulation models (GCMs) (CC = CCSM4, GS = GISS-E2-R, AC = ACCESS1- 0, HD = HadGEM2-AO, MC = MIROC5).

Species	Present area	RCP 4.5 area	RCP 8.5 area
	km^2		
Crinodendron brasiliense	6237.4	1115.9	620.2
Myrsine altomontana	11753.7	3407.8	2566.4
Plinia cardifolia	9443.6	3407.8	2573.4
Solanum cassioides	10423.6	5145.3	3323.8
Tibouchina pilosa	11816.7	6808.6	4884.9
Drimys angustifolia	16878	7479.3	5279.7
Solanum pabstii	17858.1	10629.5	7785.9
Miconia ramboi	20889.3	12456.6	8498.5
Myrceugenia oxisepala	16654	10300.4	9149.6
Inga lentiscifolia	20693.3	13832.9	10929.1

the results corroborate the hypothesis of a decrease in the area of subtropical high montane Atlantic Forest. Furthermore, such results confirm that the distribution of species is highly correlated with higher elevations in the Serra do Mar and Serra Geral mountain ranges in the southern region of Brazil, and that the potential impacts of future climate changes threaten these species.

Among the species evaluated in this study, *C. brasiliense* and *Drimys angustifolia* may be considered endemic. *D. angustifolia* is very abundant in high montane forests in the southern region of Brazil (Sühs et al., 2019), and has adapted very well to this habitat. These results corroborate the idea that species may function as indicators in studies that quantify the impacts of climate change and help determine priority areas for conservation.

The mean decrease estimated in the potential distribution area of the species evaluated is 48.37 % under the optimistic scenario and 62.49 % under the pessimistic scenario. The potential mean area of climatic adequacy for several species, such as *C. brasiliense*, *D. angustifolia*, *Myrsine altomontana*, *Solanum cassioides*, and *Plinia cordifolia* decreased by more than 50 % under both climate change scenarios, showing how sensitive these ecosystems are to the effects of climate change.

This pattern of decrease corroborates former studies showing that one of the responses of terrestrial species to climate change was to migrate to higher elevations and latitudes (Marchioro et al., 2020). This tends to occur because the geographic distribution of species is often determined by physiological limits related mainly to temperature and rainfall (Rodgers et al., 2018; Feng et al., 2022). However, as the species evaluated in this study are already restricted to higher elevations, this response is not feasible or is at least very limited in scope. Furthermore, not all species can migrate fast enough (e.g., those with low dispersal capacity) to keep up with the pace of climate change (Dagnino et al., 2020). These species may be, therefore, even more susceptible to the impacts of climate change.

The characterization of species climatic niches indicated a preference for areas of mean low temperatures, especially in the summer, and the absence of severe dry periods, particularly in the summer. Therefore, the potential distribution area was generally characterized by mild summers without dry periods.

Other ecological factors, apart from climate play an important role in species distributions such as biotic interactions (Zvereva and Kozlov, 2021) and anthropogenic disturbance (Escobar et al., 2015). The negative effects of anthropogenic activities on terrestrial ecosystems, such as habitat fragmentation, are among the main causes of species extinctions (Luther et al., 2020). If inadequate areas (e.g., agriculture, pastures for cattle, urbanization) are not included in distribution models, the projected available areas may be overestimated. Moreover, a chronic disturbance may result in the biological homogenization of forests (Zwiener et al., 2018) and should not be neglected. Forests (including high montane forests) in southern

Brazil have been subjected to intense disturbance (e.g., fragmentation, selective wood exploitation, and cattle ranching) since the beginning of the 20th century. It is reasonable to suppose that both factors can potentially influence species distribution and should not be overlooked when planning conservation strategies.

While the present area of climatic adequacy for many of the species evaluated in this study is naturally restricted, the future potential area tends to be even more reduced. This is true in the case of the future climatic adequacy area for *C. brasiliensis*, expected to decrease by 82.11 % and 90.06 % on average under the optimistic and pessimistic scenarios, respectively. This implies a risk of extinction of this species in the coming centuries. Priority areas for the conservation of these species were identified from the overlap of future potential distribution maps in both scenarios and areas of future climatic adequacy. These high elevation, lower temperature areas must be considered potential climate refuges of significant relevance in the case of subtropical high montane Atlantic Forests, especially those located in the southern and eastern plains (Planalto Sul and Leste) in the state of Santa Catarina state, east of the state of Paraná, and those along the Serra Geral and Serra do Mar mountain ranges. However, for species and populations at risk of losing their natural habitat due to climate change, other measures should be considered such as rescue for *ex situ* conservation and assisted colonization (Schlaepfer and Lawler, 2022).

In conclusion, the results of this study demonstrated that the species, as well as the associated ecosystem, the subtropical high montane Atlantic Forest in southern Brazil are threatened by potential impacts of future climate change. Potential climate refuges, such as high elevation areas in mountain ranges in the southern region of Brazil (the Serra Geral and Serra do Mar) should be prioritized for protection and conservation. Furthermore, the adoption of public policies to protect high-montane forest ecosystems, the establishment of protected areas for climate refugia in areas identified for this purpose, and measures to reduce the rate of climate change are urgently needed.

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Authors' Contributions

Conceptualization: Santos, G.N.; Silva, A.C.; Higuchi, P. **Formal analysis**: Santos, G.N. **Investigation**: Santos, G.N.; Silva, A.C.; Higuchi, P. **Writing-Original Draft**: Santos, G.N. **Resources**: Silva, A.C. **Writing-Review & Editing**: Santos, G.N.; Silva, A.C.; Higuchi, P. **Visualization**: Santos, G.N.; Silva, A.C.; Higuchi, P. **Supervision**: Silva, A.C. **Project administration**: Silva, A.C. **Funding acquisition**: Silva, A.C. **Methodology**: Higuchi, P. **Software**: Higuchi, P. **Data Curation**: Santos, G.N.; Silva, A.C.; Higuchi, P.

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