Original article

Carapichea ipecacuanha (Brot.) Stokes (Rubiaceae): The three last Latin American groups at risk of extinction under pressure from deforestation and climate change

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ABSTRACT

Global climate change is currently a serious threat to biodiversity. The understanding of the effects of climate changes on the flora is urgent. Here, we analyze the effects of future climate change on the spatial distribution of the three remaining groups of *Carapichea ipecacuanha* (Poaia) in the Americas. We built niche-based models for current and optimistic and pessimistic climate scenarios projected for 2050 and 2090. Our findings showed that climatically suitable areas for the Atlantic and Amazon Forest groups will be strongly reduced. The greatest risk of extinction was observed for the Amazon group due to the drastic spatial reduction and abrupt spatial displacement of climate suitability. The climate suitability for the Atlantic Forest group will be reduced, comprising a small suitable area in the transition zone between Minas Gerais and Espirito Santo. The climate suitability for the Panama group remained in an continuous region in Panama and Colombia. Our results encourage future studies that develop conservation management plans in order to ensure the continuation of ecological refugia for this species.

Keywords: Climate suitability, Anthropogenic activities, Poaia, Niche-based models, Future scenarios.

Introduction

Climate change is an important threat to biodiversity (Thomas *et al*. 2004). Assessing the rate of contemporary climate change is a global challenge to ensure the sustainability and subsistence of natural systems on which all life depends (Arthington *et al*. 2018). It is estimated that human-induced activities have already increased the global temperature by 1.0 °C above pre-industrial levels. Global warming is likely to reach 1.5 °C between 2030 and 2052, posing a risk to ecosystems, societies, and economic sectors (IPCC 2021). Human-induced climate changes have caused important habitat changes that led to alterations

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in the spatial distribution of species over the past decades (Parmesan 2006; Diffenbaugh & Field 2013). Thus, there is growing concern to understand the consequences that climate changes can have on biodiversity and related ecosystem services (Diniz-Filho *et al.* 2010; Buckley *et al.* 2010; Hofmann *et al.* 2021), especially the risk of local extinction of species (Román-Palacios & Wiens 2019; Williams *et al.* 2021).

Climate conditions play a key role in the spatial distribution of species that only occur at sites where the environmental conditions are appropriate for their survival (Whittaker *et al.* 2001). Within this context, climate variables can be used as indicators of environmental tolerance to predictions of species distribution (Kearney *et al.* 2010). Thus, modeling the ecological niche of species and predicting their spatial distribution in different climate scenarios (current and future) are feasible.

Niche-based models are gaining space in different fields of study, such as determination of the amplitude of species distribution (Franklin 2010; Nori *et al.* 2011); potential identification of the presence of rare or endangered species (Guisan *et al.* 2006); selection of priority areas for conservation (Araújo *et al.* 2004), and analysis of the effect of climate change on biodiversity and its implications for conservation (Inague *et al.* 2020; Sobral-Souza *et al.* 2021; Bax *et al.* 2021).

The use of Niche-based models to predict the potential effects of climate change on the biodiversity of native (Reis *et al.* 2019) or cultivated plants has proved to be a good strategy (Silva *et al.* 2018; Gomes *et al.* 2020). *Carapichea ipecacuanha* (Brot.) L. Andersson, commonly known as poaia or ipeca, is a plant that deserves attention due to its pharmacological importance and high risk of extinction (Zappi *et al.* 2013). The medicinal and economical value of *C. ipecacuanha* in compounds such as the alkaloids emetine and cephaeline are extracted from the roots and used to treat amoebic dysentery, as well as expectorant, anti-inflammatory, and emetic agents in cases of poisoning and intoxication. Astringent properties have also been reported (Bertolucci *et al.* 2008; Giraldo *et al.* 2015).

During the 1960s and 1970s, poaia was commonly found particularly in the state of Mato Grosso, Brazil. For a long time, "poaieiros" (people who collect poaia) have guaranteed their livelihoods during the rainy months and have moved the state's economy by selling poaia roots (Governo de Mato Grosso 2017; Silva *et al.* 2019).

Poaia is a distylous shrub measuring up to 50 cm in height (Rossi *et al.* 2005) that occurs exclusively in the understory of shady and humid forests (Oliveira & Martins 2002). It has a wide geographic distribution, with records of native populations in Brazil, Colombia, and Central America (Assis & Giulietti 1999; Rossi *et al.* 2005). However, the species shows a disjunct spatial distribution that is considered to be relict and can be explained by the effects of past climate changes (Oliveira *et al.* 2010).

The isolation of populations over large geographic distances, as observed for *C. ipecacuanha*, can be explained by cycles of expansion and retraction of forest areas and areas with dry vegetation formation (related to glacial-interglacial cycles) that have occurred over the last 2 million years in the Neotropical region (Prado & Gibbs 1993; Pennington *et al.* 2000). These cycles, particularly those that occurred in the late period (the last 100,000 years), caused the expansion and retraction of the South American rainforests, which led to several events of isolation and reconnection of these forest biomes (Sobral-Souza *et al.* 2015; Ledo & Colli 2017). In the case of *C. ipecacuanha*, three large population groups have been recognized for their extensive disjunct spatial distribution, one in Central America that predominantly occurs in Panama, another in the southeastern region of the Brazilian Amazon, and the Atlantic Forest population (Oliveira *et al.* 2010).

Carapichea ipecacuanha is a threatened species (Lameira 2002; Vieira *et al.* 2002) and is classified as "vulnerable" by the National Center for Flora Conservation (CNCFlora 2012). The main threats to *C. ipecacuanha* are related to commercial extraction, especially for export due to the pharmacological properties of its roots (Garcia *et al.* 2005). Concern about the maintenance of natural populations of *C. ipecacuanha* was reported at the first meeting of the committee of Conservation of Genetic Resources of Medicinal and Aromatic Plants, where *C. ipecacuanha* was recognized as a priority for conservation studies (Vieira *et al.* 2002).

In 2013, *C. ipecacuanha* was classified as vulnerable to extinction due to the effects of predatory exploitation, trade, and export, the fragmentation and deforestation of its forest habitat, and the requirement for cross-pollination, increasing the rareness of subpopulations and rendering them prone to deleterious stochastic, genetic, population, and environmental effects (Zappi *et al.* 2013).

Situations such as distance from the fragment to the largest population center and in situ and ex situ conservation status are major risk factors for the *C. ipecacuanha* populations in the Atlantic Forest (Oliveira & Martins 2002; Oliveira *et al.* 2010). Anthropogenic factors such as a reduced cluster size, the small number of reproductive plants, habitat loss, and advance of the agricultural frontier jeopardize the maintenance of natural populations of *C. ipecacuanha* in the state of Mato Grosso, Brazil (Silva *et al.* 2019).

These landscape changes can further reduce the populations, rendering them isolated and rare and prone to stochastic deleterious effects (Oliveira & Martins 1998; Zappi *et al.* 2013). In addition, distyly in *C. ipecacuanha* is a limiting morphological factor for reproductive success because it requires the interaction of floral morphs that consists of the reciprocal positioning of stigmas and anthers between two floral morphs that belong to different individuals (Barrett 1992).

Apart from a balanced ratio (1:1) of floral morphs, reciprocal herkogamy of the reproductive organs between the alternative morphs (long-styled and short-styled) is desirable for cross-pollination. This floral polymorphism is usually accompanied by an intramorphic self-incompatibility system and a series of accessory floral features that differ between floral morphs (size of flowers, lobe stigma, number and size of pollen grains) (Ganders 1979). Due to the intramorphic self-incompatibility system, only legitimate pollen from the opposite morph is able to fertilize the ovules and produce viable seeds (Barrett 2002). This reproductive limitation renders this species more vulnerable to the effects of fragmentation and degradation of its native habitat, which is a major complicating factor since in Brazil deforestation for the implementation of agricultural matrices and urban expansion have intensified over the years (TerraBrasilis 2020), increasing the risk of extinction of *C. ipecacuanha*.

Given the eminent scenarios of global climate changes and the medicinal importance and high risk of extinction of *C. ipecacuanha* due to the different reasons mentioned above, studies are needed to assess the implications of climate changes for the potential distribution of this species. Therefore, here we aimed (i) to provide new information on the conservation of *C. ipecacuanha* by building niche-based models to analyze future optimistic and pessimistic climate scenarios of CO_2 emission in 2050 and 2090, and (ii) to apply niche-based models using data from three different poaia groups (Amazon, Atlantic and Panama) separately to analyze and describe the implications of climate change and to quantify the future availability of suitable habitat for these populations with different levels of climate suitability.

Material and methods

Species description

Carapichea ipecacuanha (Brot.) L. Andersson, commonly known as poaia (de Boer & Thulin 2005). Its fresh roots have a ring-like and segmented shape and a yellow or white color (Bertolucci *et al*. 2008). Poaia is distributed throughout Latin America (Skorupa & Assis 1998; Assis & Giulietti 1999). In its natural environment, the species rarely occurs as an individual plant but tends to grow in population clusters. In Brazil, poaia is found in the states of Mato Grosso, Rondônia, Rio de Janeiro, Minas Gerais, Espírito Santo and Bahia, and has been recognized for its sociocultural and economic importance (Lameira 2002; Zappi *et al*. 2013).

Species occurrence data

Occurrence records of poaia were obtained from 10 virtual herbaria (IB - UFMT, RFA, INPA, MBM, JPB, BAH, VIC, NYBG, TANG and IAN. Available at Plataform Species (http://inct.splink.org.br) and by review of the literature (Skorupa & Assis 1998; Oliveira *et al*. 2010). These records were divided into three spatial groups: Amazon, Atlantic Forest, and Panama. After selection and confirmation of the points of occurrence, a filter was applied in order to select only unique occurrences for each environmental cell (2.5 min cell size, approximately 4.5 x 4.5 km resolution at the Equator). This approach prevents inflation of the models, which can cause instability between the number of occurrences and the number of pseudo-absences (Diniz-Filho *et al*. 2003). We also emphasize that some regions such as Pará, Pernambuco and São Paulo were not included in the data since they were temporal decay samplings (1925) and poaia populations could no longer be found in several subsequent expeditions (Assis & Giulietti 1999). Models were built for all points of occurrence of poaia (all data). However, because the three geographical poaia groups (Amazon, Atlantic, and Panama) are spatially isolated, we also built separate models for each poaia group. This was necessary to better understand the effects of future climate change on each spatial group.

Climate and environmental data

We first analyzed the independence of the bioclimatic variables for the current scenario with a resolution of 2.5 min cell size, available from the WorldClim v. 2.1 database (Fick & Hijmans 2017), using a factorial analysis. The first five factor axes that explained 91% of the data variation were selected. The variables with the greatest contribution to each axis were used in the models. The selected variables were: Bio10 = Mean Temperature of Warmest Quarter (31%); Bio17 = Precipitation of Driest Quarter (16%); Bio07 = Annual Temperature Range (22%); Bio18 = Precipitation of Warmest Quarter (7%), and Bio16 = Precipitation of Wettest Quarter (15%).

To predict the models for future climate conditions, we used Four Atmosphere-Ocean General Circulation Models (AOGCMs): Miroc6, CSM2_MR, CNRM_CM6, and CanESMS. For each AOGCM, we predicted the species distribution considering four simulations: future 2050 optimistic (SSP2-4.5) and pessimistic (SSP5-8.5), and future 2090 optimistic (SSP2-4.5) and pessimistic (SSP5-8.5). The 2050 data are the mean from 2041 to 2060 and those for 2090 are the mean from 2081 to 2100. These variables were extracted from the Coupled Model Intercomparison Project (CMIP6), available from WorldClim v.2.1 (http://worldclim.org/data/cmip6/).

The Shared Socioeconomic Pathways (SSPs) are based on a matrix that uses shared socioeconomic pathways. In short, the SSPs describe alternative evolutions of future society in the absence of climate change or climate policy (O'Neill *et al*. 2016). Here, we adopted SSP2-4.5 as optimistic scenarios and SSP5-8.5 as pessimistic scenarios.

The SSP2-4.5 (lower energy demand) represents a "middle-of-the-road" scenario in which trends broadly follow their historical patterns. For these scenarios, global warming will increase the earth's mean temperature by

Robson do Santos Alves da Silva, Celice Alexandre Silva,
Thadeu Sobral-Souza and Ricardo José da Silva

approximately 2.0 °C by 2050 and by 2.7 °C by 2090. This pathway updates the Representative Concentration Pathway (RCP) 4.5. The SSP5-8.5 (maximum power requirement and balanced emissions from fossil fuels and non-fossil fuels) represents the high end of the range of future pathways and updates the RCP 8.5. For these scenarios, global warming will increase the earth's mean temperature by approximately 2.4 °C by 2050 and by 4.4 °C by 2090 (Rogelj *et al.* 2018, IPCC 2021).

Niche-based model building

There are various methods to build niche-based models, which can show variable performance depending on the modeling conditions (Zhu & Peterson 2017). The consensus method or ensemble approach based on several algorithms is more acceptable and indicated (Araújo & New 2007). Here, we used five algorithms for niche-model predictions, including two based only on presence data (**1**) – Bioclim (Nix 1986) and (**2**) – Gower's distance (Carpenter *et al.* 1993) and three using presence/absence data or a pseudo-absence (**3**) – maximum entropy (MaxEnt v3.4.1; Phillips *et al.* 2006); (**4**) – Support Vector Machine (SVM; Tax & Duin 2004), and (**5**) – Random Forest (Breiman 2001). All model were built using the "dismo" and "kernlab" R packages (Karatzoglou *et al.* 2004; Hijmans *et al.* 2015).

We performed 20 repetitions per algorithm and scenario, resulting in 2,000 model runs (20 repetitions x 5 algorithms x 4 scenarios x 4 all data, Amazon, Atlantic and Panama groups). For model evaluation, we randomized the occurrence points into training and test data at a proportion of 75-25%, respectively. This proportion was used to calculate the true skill statistic (TSS). This weighting factor maximizes the point of highest specificity and sensitivity, returning a rank ranging from -1 to 1 for the generated models. This value was used to classify and validate the model. In this study, we only used niche-based models with TSS > 0.5 (Allouche *et al.* 2006)

After construction of the niche-based models, were built using the frequency ensemble approach (Araújo & New 2007). Thus, the higher the frequency of occurrence of the cell in the different models, the higher the habitat suitability of the cell. The ensemble approach was used for present and future (2050 and 2090) data under the optimistic and pessimistic scenarios. This procedure was carried out independently for the four AOGCMs. Finally, an average model was built with the four ensemble approaches for each scenario. This approach is indicated to reduce the effects of data variation resulting from different AOGCMs (Diniz-Filho *et al.* 2009; Diniz-Filho *et al.* 2010). This procedure was adopted for the three groups separately and the ensemble average was used as the final model for the study.

To quantify the implications of climate change for the distribution of poaia, we generated binary maps using the ensemble average model. The following criteria of habitat suitability (threshold) were defined for this purpose: >25, >50 and >75. These binary maps returned areas with 75%, 50% and 25% of climate suitability. Next, the percentage of the number of cells for each binary map was quantified for all scenarios studied. We decided to use the >50% and >75% thresholds for description of the data.

As an exploratory analysis of the climate data, separately for each point of occurrence of the three groups, we built a map for the present scenario using the ensemble average model with a threshold >50% (Fig. 1). All analyses were performed using the R (R Core Team 2021) and Qgis (QGIS 2021) programs.

Results

We compiled 66 points of unique occurrences of Poaia, including 31 points for the Amazon group, 16 points for the Atlantic group and 19 points for the Panama group (Fig. 1). The models for all data and for the individual groups demonstrate that climate change will cause drastic changes in the spatial distributions of this species. The models for 2050 including all data demonstrated a strong reduction in suitable areas for both the optimistic scenario (threshold >50 = -38%; threshold >75 = -65%) and the pessimistic scenario (>50 = -53%; >75 = -76%). The results predicted for 2090 were similar, revealing more alarming rates for both the optimistic scenario (>50 = -60%; >75 = -79%) and the pessimistic scenario (>50 = -87%; >75 = -97%) (Fig. 2 and Figure S1).

The climate data for the Amazon group exhibited the largest variations, with a continuous increase in the "Annual Temperature Range" and "Mean Temperature of Warmest Quarter", reaching a more than 30% increase by 2090 under the pessimistic scenario, as well as a gradual and continuous reduction in "Precipitation of Driest Quarter" and "Precipitation of Warmest Quarter". On the other hand, the smallest differences between the present and future scenarios were observed for the Atlantic group (Figure S2).

Amazon group

The current spatial distribution revealed approximately 67,045,600 ha (for the >50 threshold) and 33,069,150 ha (for the >75 threshold) of suitable areas (Fig. 3). The predictions for 2050 showed a broad reduction in suitable areas for both the optimistic scenario (>50 = -61%; >75 = -83%) and the pessimistic scenario (>50 = -72%; >75 = -90%) (Fig. 2). Similar results were obtained for predictions for 2090; however, the reduction rates were even higher for both the optimistic scenario (>50 = -76%; >75 = -93%) and the pessimistic scenario (>50 = -96%; >75 = -99%) (Fig. 2). In addition, the predictions showed a large displacement to the southeastern region of Brazil, particularly for the 2090 scenarios, with complete disappearance of suitable areas in locations of origin of this group (Fig. 3).

Atlantic group

For the Atlantic group, the present scenario revealed 74,660,900 ha of suitable areas for the >50 threshold and 15,593,950 ha for the >75 threshold (Fig. 3). For 2050, there was a reduction in the areas of climate suitability for both the optimistic scenario (>50 = -56%; >75 = -62%) and the pessimistic scenario (>50 = -75%; >75 = -83%). The results obtained with the 2090 models were similar to the previous scenario but revealed more alarming rates for both the optimistic scenario (>50 = -74%; >75 = -81%) and the pessimistic scenario (>50 = -97%; >75 = -99.4%) (Fig. 2). The models demonstrate that suitable areas are restricted to transition regions in the states of Minas Gerais, Espirito Santo, and a small band in Rio de Janeiro, particularly for the 2090 scenarios (Fig. 3).

Panama group

For the Panama group, the consensus models of the present scenario revealed 269,605,700 ha of suitable areas for the >50 threshold and 33,069,150 ha for the >75 threshold (Fig. 1). The models for 2050 showed a reduction in suitable areas for both the optimistic scenario (>50 = -51%; >75 = -76%) and the pessimistic scenario (>50 =

-66%; >75 = -84%) (Fig. 2). The distribution of this group was restricted to a small band in northern Colombia and the isthmus of Panama and Costa Rica. We also highlight the permanence of small suitable patches along the coast of Suriname and the region of Belém-PR (Fig. 3). Similar results were obtained with the 2090 models for both the optimistic scenario (>50 = -67%; >75 = -86%) and the pessimistic scenario (>50 = -89%; >75 = -97%) (Fig. 2). The distribution of suitable areas obtained for the 2090 optimistic scenario was similar to that observed for the 2050 pessimistic scenario. However, under the pessimistic scenario in 2090, there is a reduction in suitable areas concentrated in southern Panama and the northernmost part of Colombia. A reduction was also observed in southern Nicaragua and throughout Costa Rica (Fig. 3).

Discussion

Our findings suggest that future climate change scenarios will lead to drastic spatial reductions in the three geographic poaia groups. Furthermore, there will be a spatial rearrangement of the suitable climate conditions for the Amazon group to Atlantic Forest areas in southeastern
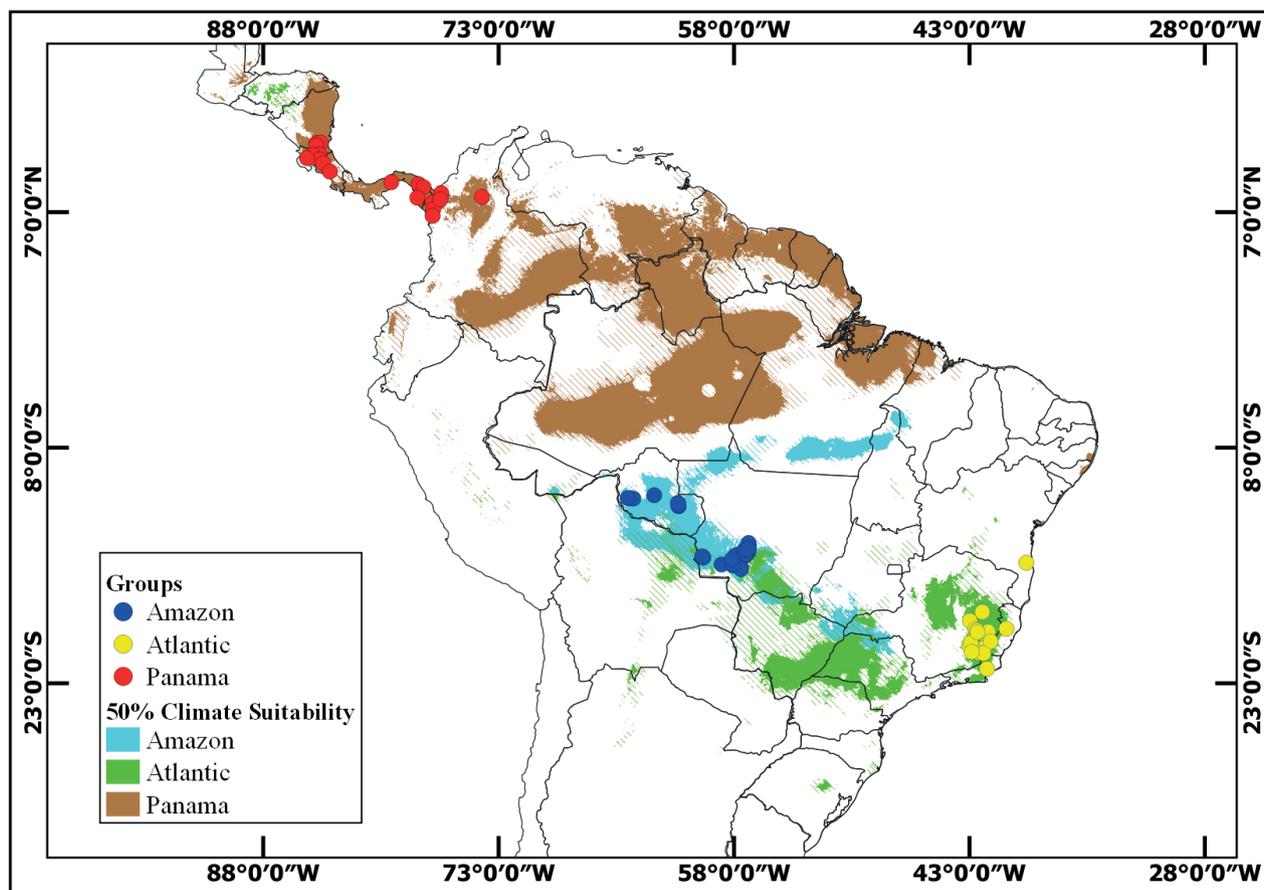
Figure 1. Occurrence of three groups of *Carapichea ipecacuanha* (Poaia) in Latin America, showing the present scenario of climate suitability (threshold >50%).

Brazil, which are already suffering strong anthropic pressure (Ribeiro *et al.* 2009). This fact will exert strong extinction pressures on the native populations of poaia. Apparently, climate change related to global warming, especially under the pessimistic scenarios, will have major effects on the local vegetation structure. Regarding the Brazilian vegetation, few studies have addressed these dynamics and there is wide variation in the literature in terms of the origin of climate data used for modeling the scenarios of CO_2 emission and the algorithms used. However, large losses of climatically suitable areas have generally been observed for species and/or groups of species, for example, Atlantic Forest trees

(Colombo & Joly 2010), coffee (Gomes *et al.* 2020), *Ilex paraguariensis* (Silva *et al.* 2018), *Connarus suberosus* (Reis *et al.* 2019), and 1,553 Cerrado plant species in Bolivia, Brazil and Paraguay (Velazco *et al.* 2018).

Amazon and atlantic groups

For the Amazon group, the combination of drastic reduction and the broad displacement of climatically suitable areas classifies this group as the one with the highest risk of local extinction. Regarding the displacement of the predicted area, similar results have been reported in a study
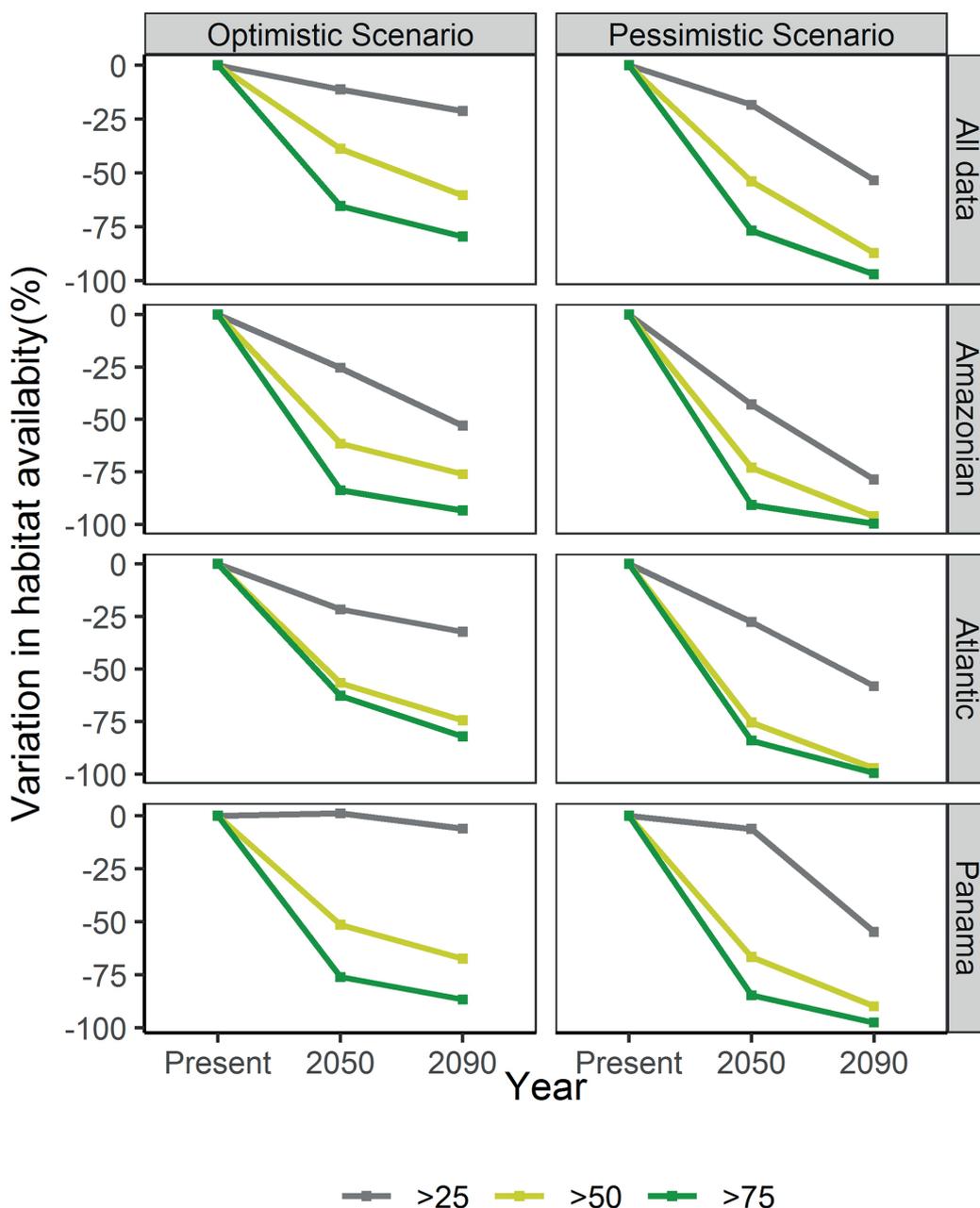
Figure 2. Variation in habitat availability for *Carapichea ipecacuanha* (Poaia) under the present and 2050 and 2090 (optimistic and pessimistic) scenarios using all data and data for the three groups separately. Grey = climate suitability >25%; yellow = climate suitability >50%; green = climate suitability >75%.

determining the geographic distribution of tree species of the Atlantic Forest. The authors observed displacement of the potential area to southern Brazil, in agreement with the present study in which the potential area was found to be reduced and displaced to southeastern Brazil (Colombo & Joly 2010). A similar pattern has been reported for *Connarus suberosus*, with large reduction and displacement of climate suitability to the Atlantic Forest (Reis *et al.* 2019).

Here, the 2050 and 2090 pessimistic scenarios demonstrate that climate suitability for the Amazon and Atlantic Forest groups of poaia will only occur in areas with current remnants of the Atlantic Forest in São Paulo, Minas

Gerais, Rio de Janeiro, and Espirito Santo. Currently, more than 148 million people live in the region of influence of the Brazilian Atlantic Forest, corresponding to approximately 67% of the Brazilian population (WWF 2017). The Atlantic Forest is therefore the biome with the highest anthropic pressure in Brazil and only 11.6% of its original forest cover remains (Ribeiro *et al.* 2009). Furthermore, it is one of the three biodiversity hotspots most vulnerable to the impacts of climate change (Bellard *et al.* 2014). This landscape is already under strong anthropic pressure. According to estimates for 2050, these areas will suffer the strongest
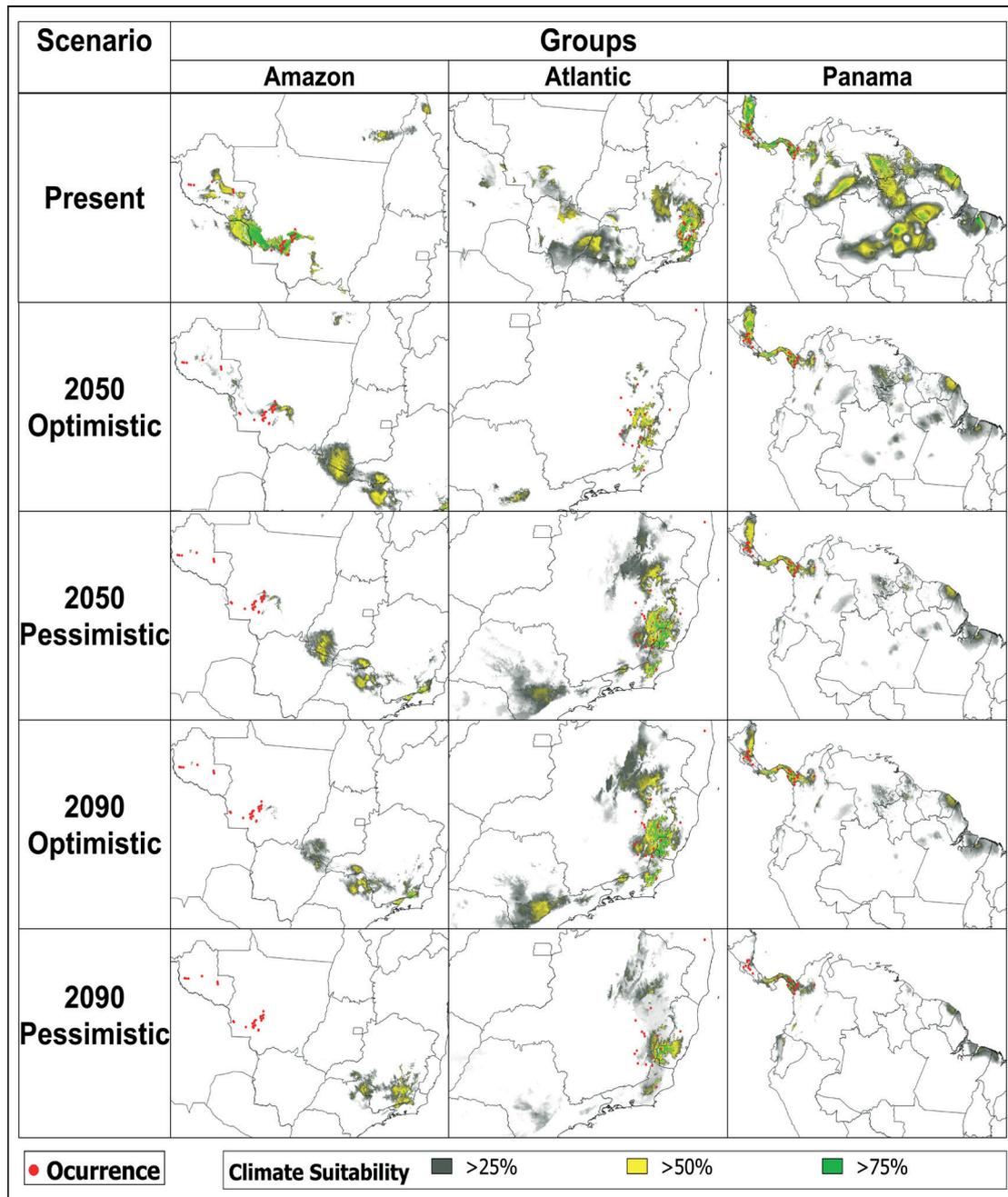
Figure 3. Separate distribution of the three groups of *Carapichea ipecacuanha* (Poaia) under the present and 2050 and 2090 scenarios (optimistic and pessimistic). Grey = climate suitability >25%; yellow = climate suitability >50%; green = climate suitability >75%.

anthropic pressure in the world, mainly because of the expansion of agricultural areas (Williams *et al.* 2021).

The increase in human-induced pressures on landscapes will possibly lead to a reduction in the area of different remnants and/or fragmentation of continuous areas. This fragmentation and creation of a landscape with small habitat patches promote biotic homogenization, mainly caused by local extinction and the inability to recolonize specialized species in the forested area (Solar *et al.* 2015; Bilyaminu *et al.* 2020). Since poaia is found exclusively in the understory of shady and humid forests, it becomes highly susceptible to the effects of fragmentation and its populations tend to decline rapidly when exposed to forest edge environments (Oliveira & Martins 2002). Fragmented areas are characterized by various disturbance factors that can aggravate the structure of poaia populations, including an increase in luminosity, temperature and wind speed that cause drying and mortality of plants not adapted to these conditions (Didham 1998). Poaia does not tolerate solar radiation and is found only in locations with >70% of shade (Lameira 2002).

Another factor impairing the maintenance of populations in fragmented landscapes formed by small remnant patches is that poaia is a distylous species. This is an important aggravating factor for reproductive success because it requires the interaction of floral morphs belonging to different individuals (Barrett 1992; Silva *et al.* 2019). In the absence of occurrence of the two morphs at the same location, populations tend to collapse, causing local extinction. Furthermore, small fragments only support a small number of individuals, a fact that can reduce the genetic diversity of the population. Thus, the isolation of poaia populations in these patches that are embedded in an inhospitable matrix tends to increase the rates of long-term local extinction since the decrease in the size of native areas reduces the size of the resident populations. Isolation and population decline, in turn, reduce gene flow and increase the likelihood of genetic drift and inbreeding depression (Hedrick & Kalinowski 2000; Fahrig 2003). The loss of genetic variability as a result of population isolation renders the population more susceptible to environmental stochasticity (Matthies *et al.* 2004), which can increase the risks of local and regional extinction (Hanski *et al.* 2004). These characteristics of poaia, associated with its low tolerance to climatic variations, high habitat specialization and low dispersal ability (dependent on birds), increase the vulnerability of the species to future climate change (Trew & Maclean 2021).

Panama group

Although our results demonstrate a future decline in the suitable area for the Panama group, this reduction may be understood as an artifice caused by inflation of the model for the present scenario. The models for this group showed the greatest extrapolation to areas without occurrence

of the species. This fact can be explained by the almost nonexistence of strict endemism of the species in Panama (Powell *et al.* 2018). The diversity of the fauna and flora in the Panama region originates from and is influenced by the biodiversity of South America, while the biodiversity of the Nicaragua and Costa Rica region is of North American origin (Duivenvoorden *et al.* 2002). However, this range of diversity eventually fuses at some point, characterizing the Panama environment (Stiles 1985; Wilson 1990).

This strong South American influence on Panama's biodiversity may be linked to the shared environmental and climate characteristics (ANAM 2010), which may have influenced the models to large part of northern South America. Few large areas of primary forest remain intact, which occur only in large reserves such as in eastern Panama along the Internacional La Amistad Park, and particularly in the Biológica La Selva Reserve (~1,500 ha) along northeastern Costa Rica that is connected to the Braulio Carrillo National Park (Powell *et al.* 2018). This connection is the last intact gradient of primary forest from sea level to 2,900 m (Lieberman *et al.* 1996). These forest blocks retain almost all vertebrate species in this ecoregion, including most large predators (Stiles 1985). These mountain forest refugia are the sites where climatically suitable areas, in almost all scenarios, remain in future climate scenarios (Fig. 3).

In addition to its small size, most of Panama's territory is anthropized due to the construction of cities, highways, power plants, and cultivated areas. Consequently, the remaining natural areas have been reduced and fragmented by rapid deforestation throughout the 20th century and extending to the 21st century (Kapos *et al.* 2015). The parks themselves face enforcement problems of environmental protection, including the Tortuguero National Park and the Barra de Colorado Wildlife Refuge, both in Costa Rica. Deforestation for logging, banana monocultures and opening up lands for grazing are some of the anthropic factors that threaten the biodiversity in the Panama region (Powell *et al.* 2018). Although large areas of intact habitat still exist, lowland forests have been seriously fragmented (Sánchez-Azofeifa *et al.* 1999). The evergreen forest areas are the least protected in Costa Rica (Stiles 1985), representing an additional threat to the poaia populations that occur in those areas. Another factor that does not provide hope for the expansion of already protected areas is the difficult economic situation in Panama for investments in the environmental sector (Powell *et al.* 1992). The climate models for the Colombian poaia population tend to maintain climate suitability under all scenarios, decreasing after 2090.

Landscape roughness and climate refugia

The topographic complexity of the terrain is a local factor that can mitigate the effects of global warming by acting as a buffer for climate variables (Trew & Maclean 2021). Regions with a more heterogeneous relief, including the

presence of mountains and valleys, provide a greater variety of habitats because a wide range of micro- and mesoclimatic conditions is available on a small spatial scale (Badgley *et al.* 2017). Thus, the southeastern region of Brazil, particularly the state of Minas Gerais due to its higher terrain roughness indices (Amatulli *et al.* 2018), can be considered the most resistant to climate change among the regions of the three populations studied here.

On the other hand, the Amazon region shows the lowest terrain roughness indices (Amatulli *et al.* 2018) and can therefore be considered the region with the highest susceptibility to climate change. This topographic homogeneity limits habitat availability; thus, the species do not have climate refugia, increasing the risk of local extinction (Trew & Maclean 2021). Furthermore, locations with less topographic complexity, such as the Amazon region, exhibit a higher climate velocity, which is the rate of climate movement in the landscape, calculated as the rate of climate change over time (°C per year or mm of precipitation per year) divided by the rate of climate change in space (IPCC 2014). Thus, the climate velocity is generally high in flat areas because the rate of temperature variation in relation to space is low (Chen *et al.* 2011). Species that occupy extensive flat landscapes are particularly vulnerable because they must disperse over longer distances than species in mountainous regions in order to find climate refugia. Therefore, the Amazon group is at high risk of extinction since climate change occurs at a speed greater than its migration capacity. Although there is no migration rate for poaia, we can infer that this rate of displacement is slow, as observed for all herbaceous plants (Kinlan & Gaines 2003), and will not be sufficient to ensure the migration of these species to areas with a favorable climate. This fact contributes to the prospect of future extinction of the Amazon population.

Conclusion

Our findings showed that the suitable areas for the three geographic poaia groups will be spatially reduced in the future. However, the three groups exhibited different geographic rearrangements in future scenarios. We can consider the Amazon and Atlantic Forest groups to be at higher risk of extinction because of the drastic reduction and geographic displacement of the areas predicted for the future to locations distant from the location of origin. In addition, future suitable areas will be located in the Atlantic Forest in southeastern Brazil, an area that currently suffers strong anthropic pressure.

An important result was the relationship between lower landscape roughness in the Amazon group and high rates of climate change. This is a matter of great concern since extensive forest and Cerrado areas have a low topographic complexity, a fact that renders these landscapes highly

susceptible to the effects of climate change. We therefore encourage future studies to investigate the relationship between landscape roughness and the creation of climate refugia. We also emphasize the importance of future studies that develop conservation management plans in order to ensure the continuation of native forests, especially for groups in Brazil.

Supplementary material

The following online material is available for this article: Figure S1 - Distribution of *Carapichea ipecacuanha* (Poaia) obtained for the present scenario and for the 2050 and 2090 optimistic and pessimistic scenarios using all data. Figure S2 - Variation in bioclimatic variables used for individual modeling of the three *Carapichea ipecacuanha* (Poaia)groups between the present scenario and the 2050 and 2090 optimistic and pessimistic scenarios.

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