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Original Paper

Taxonomic diversity of Passifloraceae *sensu stricto* along altitudinal gradient and on Serra dos Órgãos mountain slopes in southeastern Brazil

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Abstract
Altitudinal gradients, among other abiotic factors, are directly linked to species' diversity patterns and distributions. Another important factor to be considered is the geographic position of a mountain chain, with oceanic and continental-facing slopes having distinct environmental conditions reflected in distinct phytophysiognomies. We examined the distributions of species of Passifloraceae *sensu stricto* along an altitudinal gradient (varying from 300 to 2,199 m.a.s.l.) in the Serra dos Órgãos National Park (PARNASO) in Rio de Janeiro state, southeastern Brazil. Field excursions were undertaken to record and collect specimens. Maps were prepared of the distribution of sampling efforts, taking into consideration altitudinal gradients and rainfall. The statistical analysis was made to define the patterns of richness and abundance within the altitudinal classes. Analyses of similarity, grouping and NMDS were made of the oceanic and continental slopes. A total of 19 species of Passifloraceae *s.s.* were encountered. The greatest species richness was found at intermediate elevations (1,100–1,300 m.a.s.l). The similarity index between the two exposure slopes was 28%, indicating distinct species compositions on different faces. Our data helps to define the distribution and species composition of Passifloraceae *s.s.* within the PARNASO, and should be useful for conservation actions there.
Key words: Atlantic domain, *Passiflora*, Rio de Janeiro, Serra dos Órgãos National Park.

Resumo
O gradiente altitudinal entre outros fatores abióticos, está diretamente ligado à diversidade e distribuição de espécies. Outro fator importante é o posicionamento da cadeia de montanha, visto que as vertentes continental e oceânica possuem características distintas e podem exercer influência sobre a composição da vegetação. O objetivo deste estudo foi compreender a distribuição dos organismos pertencentes à família Passifloraceae *sensu stricto* em um gradiente de altitude, com variação de 300 a 2.199 m, no Parque Nacional Serra dos órgãos (PARNASO), localizado no estado do Rio de Janeiro, sudeste do Brasil. Foram realizadas expedições em campo para registro e coleta do material nas diferentes altitudes do PARNASO. Mapas de distribuição foram elaborados levando em consideração o esforço amostral, o gradiente de altitude e a pluviosidade. Foram realizadas análises estatísticas para estipular o padrão de riqueza e abundância dentro das classes de altitude. Para as vertentes oceânica e continental foram realizadas análises de similaridade, agrupamento e nMDS. Além disso, foram feitos cálculos de Área de Ocupação e Extensão de Ocorrência para avaliar o status de conservação das espécies. Foram registradas 19 espécies de Passifloraceae. As altitudes intermediárias apresentaram maior riqueza (1.100–1.300 m). A similaridade entre as vertentes foi de 28%, relatando riqueza distinta em ambos os lados da montanha. Os dados encontrados delimitam a distribuição e a composição de espécies de Passifloraceae dentro do PARNASO, tornando-se uma ferramenta colaborativa para ações de conservação do Parque.
Palavras-chave: domínio Atlântico, *Passiflora*, Rio de Janeiro, Parque Nacional Serra dos Órgãos.

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Introduction

The distribution of botanical taxa represents a complex expression of historical evolutionary and ongoing ecological processes (Brown & Lomolino 2006). Factors affecting species richness include total area considered, latitude, elevation, primary productivity, and interactions among them (Lomolino 2001; McCain 2009). In terms of altitudinal gradients, two main abundance patterns have been described: reductions in species richness with increasing elevation, and increased richness at intermediate elevations (Rahbek 1995). The former effect is evident for many plant species (*e.g.*, arboreal vegetation) and can be understood as a response to harsher abiotic conditions at higher elevations (with increased wind and dryness, and lower temperatures and soil nutrient levels); the latter effect has been presented as the mid-domain effect, with intermediate elevations holding higher richness as a natural result of random species distributions.

This view was originally formulated in the context of geographical latitudes rather than elevation, but has since been transformed into an altitudinal gradient framework - following the rationale that higher numbers of species will tend to cluster at intermediate elevations (or middle latitudes in the original proposition) if each species' range is random. In that way, there will be a maximization of overlapping of individual species distribution ranges away from extremes (Colwell & Lees 2000; Colwell *et al.* 2004, 2009; McCain 2004). Another environmental factor evoked to explain species composition and distribution patterns is the polarity of mountain slopes (Hugget 1995). Opposing slopes in a mountain range will experience distinct temperature, wind and precipitation regimes, consequently influencing plant occurrences and distributions (Hugget 1995). A forest's phytophysiognomy is determined by its topographical relief, and can be distinct depending on elevation and latitude (Ivanauskas & Assis 2009).

Most plant species in Brazil are concentrated in dense ombrophilous forest formations, mainly the Amazonian and Atlantic domains (Oliveira-Filho & Fontes 2000). The Atlantic domain is considered one of the most relevant global hotspots of biodiversity, due to its high species richness, high level of endemism, and exposure to high levels of environmental threats (Myers *et al.* 2000; Werneck *et al.* 2011).

The Passifloraceae *sensu stricto* (*s.s.*) family comprises 17 genera and more than 700 species distributed throughout tropical and subtropical regions of the world (Ulmer & MacDougal 2004). Its greatest diversity is found in the Neotropical region, with emphasis on the genus *Passiflora* L. (Ulmer & MacDougal 2004). There are four genera and 166 species of Passifloraceae *s.s.* in Brazil (Bernacci *et al.* 2020). The genera *Mitostemma* Mast. and *Passiflora* occur in the Atlantic Domain, with one and 85 species respectively (Bernacci *et al.* 2020); 40 species have been recorded in Rio de Janeiro (Milward-de Azevedo 2014). Passifloraceae *s.s.* is characterized mainly by vines with alternate leaves, whole or lobed, tendrils and extrafloral nectaries, flowers with an androgynophore, the corona with filaments, and producing fruits, berries or capsules (Milward-de-Azevedo *et al.* 2012).

The Serra dos Órgãos National Park (PARNASO) is one of the oldest (1939) and most important conservation areas in southeastern Brazil. The park was established on the steep slopes of the Serra do Mar mountain range, which extends for more than 1,500 km. The range includes well-conserved areas of ombrophilous forest of the Atlantic Domain - a phytophysiognomy now limited to only slightly more than 7% of its original cover, and still experiencing increasing anthropic pressure (Coelho *et al*. 2017). According to Park Management Plan (ICMBio 2008) there are nine species of Passifloraceae *s.s.* in PARNASO. No inventory has yet been made of the Passifloraceae *s.s.* in the PARNASO, although it is a relevant group in terms of functional pollination processes and represents a suitable system to test hypotheses of species richness, the mid-domain hypothesis, and slope effects.

This study was designed to analyze the distribution patterns of Passifloraceae *s.s.* species in PARNASO, assess their conservation statuses and extinction threats, and test predictions that: i) the species richness of Passifloraceae *s.s*. follows the mid-domain effect, with peak richness at intermediate elevations; ii) the plant species distribution patterns there can be explained by their continental and oceanic slope distributions.

Materials and Methods

PARNASO (Fig. 1) is an integral protection conservation area located in Rio de Janeiro state, Brazil (22°29'35"S, 43°04'24"W) that encompasses parts of the municipalities of Teresópolis, Guapimirim, Magé and Petrópolis and an area of 20,024 ha, with altitude variation between 80 m.a.s.l. and 2,263 m.a.s.l. (ICMBio 2008). Its topography is characterized by steep relief, with four main types of vegetation cover: Low Montane Ombrophilous Forest (up to 500 m.a.s.l.), Montane Ombrophilous Forest (500–1,500 m.a.s.l.), Upper Montane Ombrophilous Forest (over 1,500 m.a.s.l.) and Highland Fields (above 2,000 m.a.s.l.) (IBGE 2012). It is representative of the Atlantic Forest Domain - one of the most critical areas for global biodiversity conservation; it is considered a Biosphere Reserve by UNESCO, and classified by the Brazilian Ministry of the Environment (MMA) as extremely important to the conservation of that country's flora (ICMBio 2008).

Before collections, data of species were survey from voucher specimens deposited in the R, RB and HB herbaria (acronyms according to Thiers, continuously updated), as well as from virtual collections available on the Species Link (CRIA 2011) and JABOT (2020) websites.

Specimens of Passifloraceae *s.s.* were collected during periodic expeditions (licenses SISBIO 57452-4 and SISGEN A387E5D) between May/2017 and April/2019 in the PARNASO, and included in HCTR* (Instituto Três Rios, Universidade Federal Rural do Rio de Janeiro, Três Rios, Rio de Janeiro, Brazil), HUFSJ and RBR, herbarium acronyms, except marked with an asterisk (*), are according to Thiers, continuously updated. The collect material was photographed and herborized according to the Herbarium Procedures Manual of INCT - Herbário Virtual da Flora e dos Fungos (2013).

The random walk method (Filgueiras *et al.* 1994) on all trails through the PARNASO was used for sampling, noting each specimen's coordinates and elevation (using a handheld GPS).

To evaluate the distribution patterns of Passifloraceae *s.s.* in the PARNASO, the occurrence records of the species (latitude, longitude, and altitude data) were plotted over the PARNASO area using QGIS 2.18 software (QGIS Development Team 2015). The species abundance and richness analyses employed 0.01° × 0.01° grids, allowing the identification of species growing at similar elevations in each grid. That analysis was performed following the phytophysiognomy classification system proposed by IBGE (2012), associated with mean annual rainfall levels (between 1977 and 2006), elevation curves for the PARNASO (IBGE 2010), and the Pluviometric Atlas of Brazil (Serviço Geológico do Brasil <http://www.cprm.gov.br>).

A digital elevation model was also produced using the TIN tool (Triangulated Irregular Network) available with ArcGis 10.1 software (ESRI 2015), to establish altitudinal classes and plot specimens recorded during the fieldwork phase.

To evaluate the distribution amplitude of *Passiflora*, we calculated the Area of Occupancy

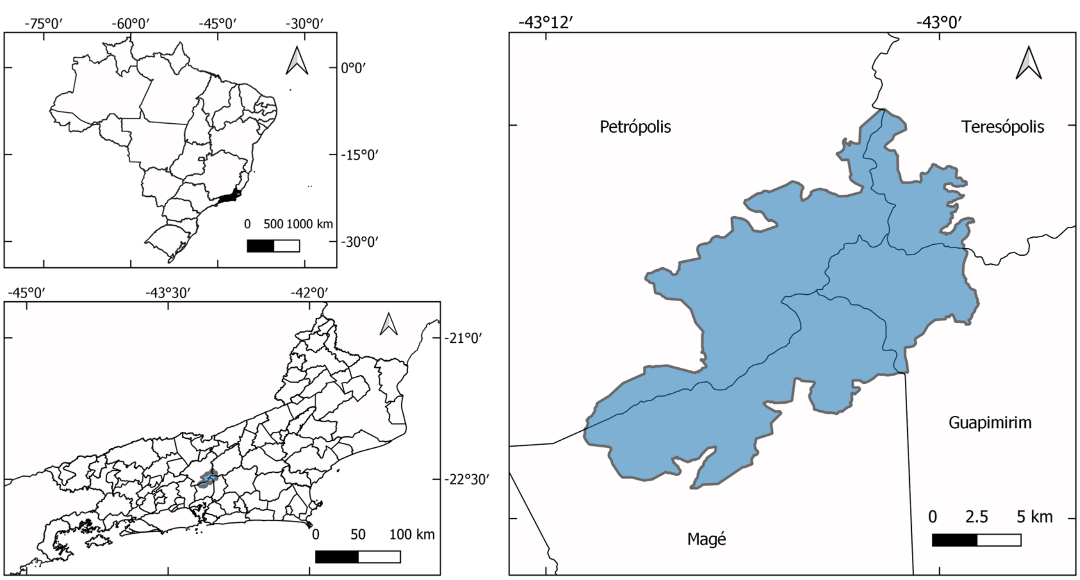

Figure 1 – Delimitation and Geographic localization map of Serra dos Órgãos National Park, Rio de Janeiro, Brazil.

(AOO) and the Extent of Occurrence (EOO) of each of its component species using the GeoCAT tool, considering 2 km cells (Conservation Assessment Tools, available at <http://geocat.kew.org/>) (Moat 2007). Those parameters could not be evaluated for species having only one or two points of occurrence, as they did not form a triangle needed for those calculations; they were accordingly classified as data deficient (DD). The AOO and EOO results were subsequently compared with the categories previously assigned by both national and state red lists.

In order to avoid data bias, and to standardize class sizes, presence/absence matrices were computed for 19 elevational classes spaced at 100 meters intervals, in an altitudinal gradient from 300 to 2,199 (*i.e.* 300–399, 400–499, 500–599, 600–699, 700–799, 800–899, 900–999, 1,000–1,099, 1,100–1,199, 1,200–1,299, 1,300–1,399, 1,400–1,499, 1,500–1,599, 1,600–1,699, 1,700–1,799, 1,800–1,899, 1,900–1,999, 2,000–2,099, 2,100–2,199).

Statistical analyses were performed using R (R Core Team 2015) and SigmaPlot 14 (Systat Software 2011) software, and the data were checked for normality (Shapiro & Wilk 1965). A polynomial quadratic regression was used to test the mid-domain hypothesis for Passifloraceae *s.s.* species in PARNASO. This analysis was also used to test for the abundances of individuals along the gradient.

UPGMA cluster analysis, with the Jaccard index, was used to evaluate the floristic composition of Passifloraceae *s.s.* in PARNASO. The occurrence grids (0.01° × 0.01°) were compared using Biodiverse 2.1 software, which allows cluster analysis of biogeographic data (Laffan *et al*. 2010).

A presence/absence matrix was also elaborated using data for the oceanic and continental slopes of the park. The relationships of floristic similarity between the areas analyzed were calculated using non-metric multidimensional scaling (NMDS) with the Jaccard (Ij) similarity index, using Primer 6.0 software (Clarke & Gorley 2006). The similarity index between the axes was calculated following Magurran (2013).

Taxonomic nomenclature was conferred for all records, following Bernacci *et al.* (2020).

Results

Nineteen species of *Passiflora* were recorded for the PARNASO, belonging to three subgenera: *Passiflora* (13 spp.), *Decaloba* (DC.) Rchb. (four spp.), and *Deidamioides* (Harms) Killip (two spp.), among a total of 427 individuals recorded by collect material, and only one, *P. marginata* Mast., from voucher specimen deposited in herbaria (Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.19620489.v1>).

The species with the most occurrence records was *P. actinia* Hook., with 169 individuals, followed by *P. vellozoi* Gardner and *P. miersii*. Mast. with 37 and 46 individuals respectively. The species with the lowest occurrences were *P. junqueirae* Imig & Cervi, *P. ovalis* Vell. *ex* M.Roem., *P. speciosa* Gardner, and *P. suberosa* subsp. *litoralis* (Kunth) Port.Utl. *ex* M.A.M.Azevedo, Baumgratz & Gonç.-Estev., with two occurrences each, and *P. marginata* Mast., *P. sidifolia* M.Roem., and *Passiflora* sp. with only one. Figure 2 presents the species abundances within the PARNASO, indicating grids 8 and 11 as most representative (with 78 and 64 recorded individuals respectively).

Sampling efforts were concentrated between 300–2,100 m.a.s.l. in the four municipalities composing the PARNASO (Fig. 3). The species found at the lowest elevations were *Passiflora* sp. and *P. actinia*. (345–399 m.a.s.l.), in the municipality of Guapimirim. The species with the widest distribution in PARNASO was *P. actinia* (Tab. S2, available on supplementary material <https://doi.org/10.6084/m9.figshare.19620489.v1>); the only species recorded in Highland Fields were *P. campanulata* Mast., that appear in Upper Montane Ombrophilous Forest from 1,672 to 2,131 m.a.s.l., and *P. marginata*, at elevations up to 2,000 m.a.s.l. (Tab. S3, available on supplementary material <https://doi.org/10.6084/m9.figshare.19620489.v1>).

The three species with the largest areas of distribution (AOO and EOO values) were: *P. actinia* (14 grids), *P. porophylla* Vell. (12 grids), and *P. amethystina* J.C.Mikan (11 grids); 35% of the species had very limited distributions (occurring in only one or two grids) or were considered Data Deficient (Tab. S2, available on supplementary material <https://doi.org/10.6084/m9.figshare.19620489.v1>). No species of *Passiflora* exclusive to the PARNASO has yet been identified.

The municipality of Petrópolis (which includes most of the area of the PARNASO) had the highest *Passiflora* species richness (14 species), followed by Teresópolis (9), Guapimirim (3), and Magé (3). Grids 8, 11, 12, 16, and 21, located at elevations between 900 and 1,600 m.a.s.l. in montane ombrophilous forest, had the highest richness (six to eight spp.); only grid 8 occurs in Teresópolis, the others grids are within the municipality of Petrópolis (Fig. 4; Tab. S3, available on supplementary material <https://doi.org/10.6084/m9.figshare.19620489.v1>). Although the continental slope had greater richness in this study, it is important to emphasize that the oceanic slope had greater abundance, mainly caused by the occurrence of *P. actinia* (Fig. 2).

The quadratic regression used to test the mid-domain effect showed a significant fit (R^2 = 62.08%, p = 0.004; gl = 16), implying that elevation satisfactorily explained much of the variation seen in terms of species richness. The elevational classes adopted (every 100 meters) showed greater species richness at intermediate elevations, with the distribution data demonstrating a domed pattern. The greatest species richness was found at elevations between 1,000 and 1,300 m.a.s.l. The highest number of species was observed in the classes 1,100–1,199 and 1,300–1,399 m.a.s.l. (both with 10 of the 19 species found in this study), followed by the 1,000–1,099 class and 1,200–1,299 m.a.s.l. class (both with 8 species each) (Tab. S3, available on supplementary material <https://doi.org/10.6084/m9.figshare.19620489.v1>). The numbers of species increased as intermediate elevations were reached, thereafter decreasing (Fig. 5).The relationship between the elevation levels and the abundances of individuals also had a significant value (R^2 = 36.7%, p = 0.025, gl = 16) (Fig. 6). That data also showed higher values at elevational levels between 1,000–1,300 m.a.s.l., with the highest number of individuals being seen at 1,100–1,199 m.a.s.l. (N = 104), followed by 1,200–1,299 m.a.s.l. (80) and 1,300–1,399 m.a.s.l. (70).

The similarity analysis comparing the grids with species occurrences generated a dendrogram, differentiating species occurring exclusively in continental or oceanic sectors of the PARNASO, widely distributed species and different elevational levels, and species that occurred only in Highland Fields (Fig. 7). The group 1 has species with elevation levels below 500 m.a.s.l., group 2 has species occurring in both slopes, group 3 has species principally in Highland Fields (*P.*

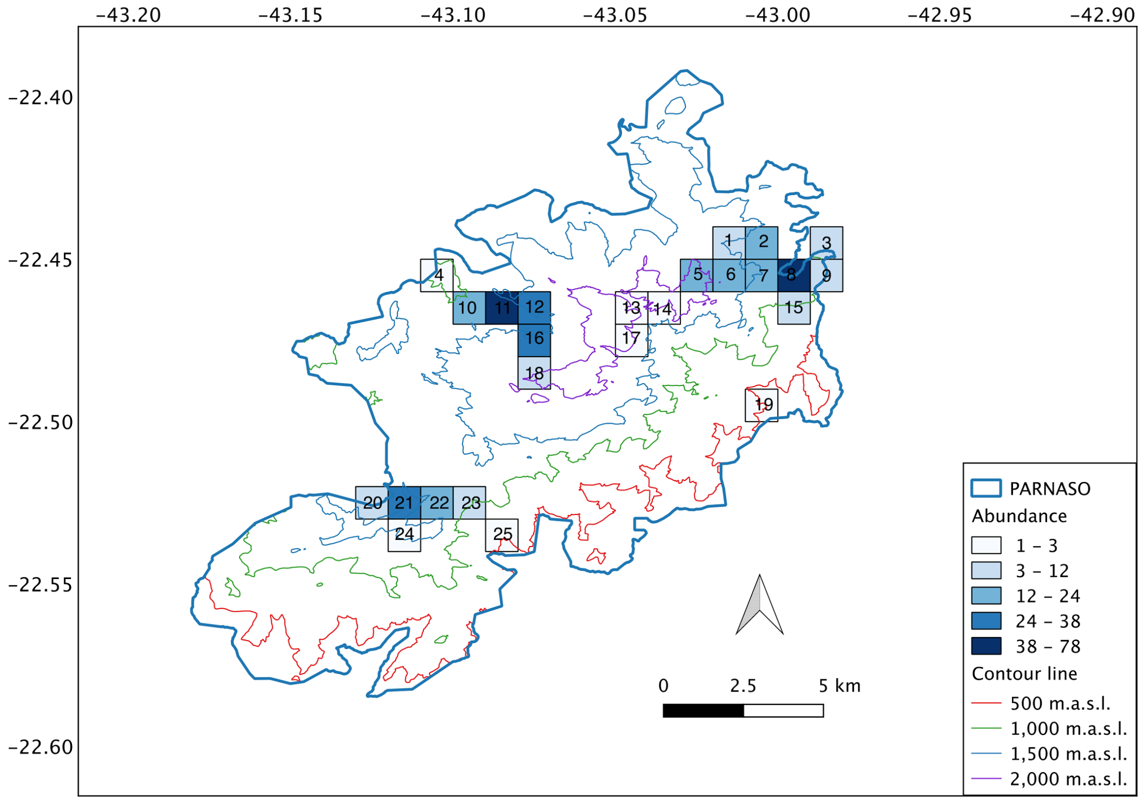

Figure 2 – Collect effort of *Passiflora* species by altitude, in Serra dos Órgãos National Park, Rio de Janeiro, Brazil.

campanulata and *P. marginata*), group 4 has species only in continental slope, group 5 has species in only Upper Montane Ombrophilous Forest (*P. deidamioides* and *P. imbeana*), and group 6 has species with elevation levels below 900 m.a.s.l. and upper 700 m.a.s.l.

The species distribution map shows that the northeastern portion of the park as distinct from the northwestern section, reflecting the presence of peaks reaching above 1,500 m.a.s.l. between Pedra do Sino (Guapimirim) and Castelos do Açú (Petrópolis). The northeastern section has a mean annual rainfall rate of 2,200–3,000 mm, with the highest peak of the park receiving from 2,300–2,500 mm/year; the northwestern section of the park, on the other hand, has a lower mean annual rainfall rate (1,600–2,200 mm) (Figs. 8; 9).

Those differences in precipitation in different park sectors are reflected in differences in their respective species compositions. *P. edulis* Sims, *P. ovalis* Vell. *ex* M.Roem., *P. truncata* Regel, and *Passifora* sp. are found exclusively in the northeastern sector of the park, while *P. capsularis* L., *P. junqueirae*, *P. miersii*, *P. sidifolia*, *P. speciosa*, *P. suberosa* subsp. *litoralis*, and *P. vellozoi* are exclusive to the northwestern sector (Fig. 3). The high elevations of the mountains, with their vegetation coverage of upper montane ombrophilous forest and Highland Fields (primarily occupied by *P. campanulata* and *P. marginata*) impede the passage of montane ombrophilous forest species.

The southern/southwestern sector of the PARNASO principally contains species that are widely distributed within the park: *P. actinia*, *P. alata* Curtis, *P. amethystina*, and *P. porophylla* at elevations of approximately 1,500 m.a.s.l. with montane and upper montane ombrophilous forests, in addition to *P. deidamioides* Harms and *P. imbeana* Sacco that also occur in the northwestern

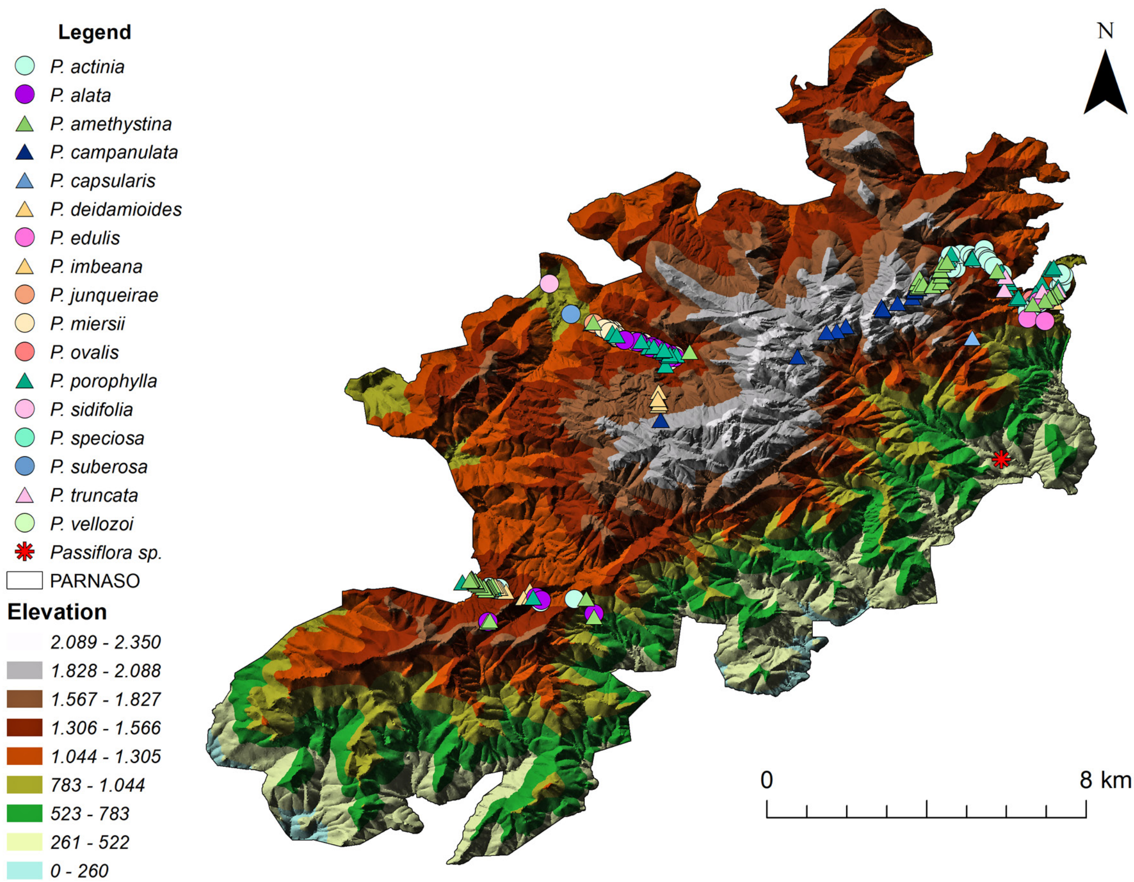

Figure 3 – Distribution of *Passiflora* species on a thematic elevation map according to the occurrence records in the Serra dos Órgãos National Park, Rio de Janeiro, Brazil.

sector of the park at elevations of 1,340 to 1,760 m.a.s.l. (Fig. 3). That distribution is probably favored by a dense Atlantic Forest corridor growing in an area with a mean annual rainfall rate between 1,900 and 2,000 mm (Figs. 8-9). It is important to note that species demonstrating wide distributions are capable of adapting to areas with high rainfall rates as well as to areas with approximately 47% less rainfall (as seen in the northeastern sector of the PARNASO). Among the widely distributed species in the PARNASO, only *P. actinia* does not occur in the northwestern sector.

Six groups were formed in the NMDS analysis (Fig. 10), which corresponds well to the cluster analysis (Fig. 7). The similarities between the treatments are relating those species to different elevational levels highlighting for *P. sidifolia*, *P. suberosa* subsp. *litoralis* and *Passiflora* sp., and corresponding to: groups of species exclusive to each axis (*P. edulis*, *P. ovalis*, *P. truncata* and *Passiflora* sp. / *P. capsularis*, *P. deidamioides*, *P. junqueirae*, *P. miersii*, *P. speciosa*, *P. sidifolia*, *P. suberosa* subsp. *litoralis*, *P. truncata* and *P. vellozoi*), a group formed by both axes (*P. actinia*, *P. alata*, *P. amethystina* and *P. porophylla*), and a group of species principally occurring in Highland Fields, grids 5, 13, 14, 17 and 18 (*P. campanulata* and *P. marginata*). The difference between the two treatments is that in NMDS if there was no differentiation between the slope symbols, we would have related data of elevational levels. The similarity index was 0.28, indicating low similarity between the two axes analyzed.

Discussion

We found twelve more species that had not previously been cited in the park management plan (ICMBio 2008), because two species mentioned in this plan were not found in PARNASO, and added new records of Passifloraceae *s.s.* to the PARNASO as a whole, complementing the floral surveys undertaken in Rio de Janeiro state by Pessoa (1994, 1997) and Milward-de-Azevedo & Valente (2004), as well as the plant list for Rio de Janeiro (Milward-de-Azevedo 2014). Among

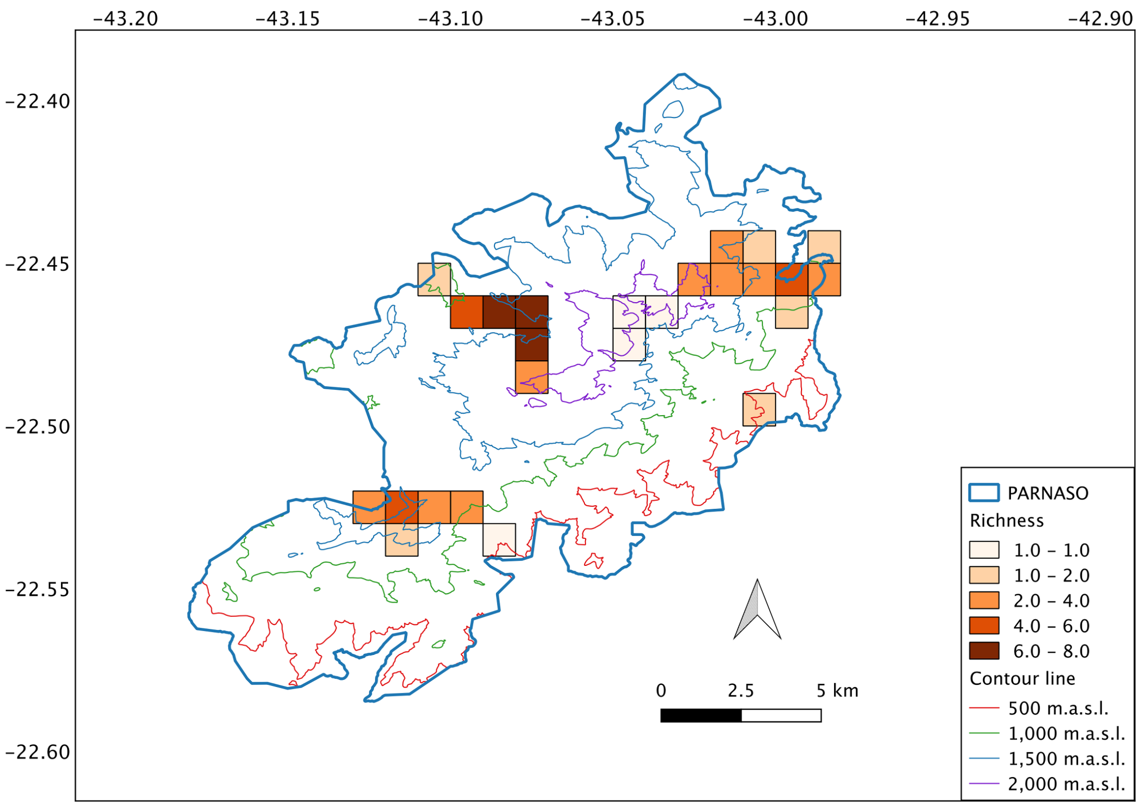

Figure 4 – *Passiflora* species distribution along the altitude gradient in the Serra dos Órgãos National Park, Rio de Janeiro, Brazil.

all of the species evaluated, only P. *marginata* was not collected during our expedition; the single record of that species, in Highland Fields (Bernacci *et al.* 2020), was encountered in the IAC herbarium (L.C. Bernacci & M. Peixoto 4669). Data concerning the other species were gathered during our study expeditions.

Among the *Passiflora* species occurring in PARNASO, 15 are endemic to Brazil and 10 are endemic to the Atlantic Forest domain, while *P. imbeana* is endemic to Rio de Janeiro State (Bernacci *et al.* 2020). Considering conservation statuses, only *P. imbeana* is classified as endangered (EN), according to the CNCFlora (2012), Mezzonato-Pires *et al.* (2018) and (Milward-de-Azevedo & Fernandes 2021); it is also included in Annex 1 of the Brazilian List of Endangered Plant Species (MMA 2008) and in Ordinance No. 443 of December 17, 2014 - the Official Brazilian National List of Endangered Plant Species (MMA 2014).

According to the List of Plant Species in São Paulo State Threatened with Extinction (Bernacci 2003; SMA-SP 2016), *P. campanulata* is classified as extinct in the wild (EW). *Passiflora actinia* and *P. amethystina* (Rio Grande do Sul state), *P. deidamioides* and *P. miersii* (São Paulo), and *P. sidifolia* (Espírito Santo) are listed as "Vulnerable" (VU); *P. porophylla* is listed in Rio Grande do Sul as "Endangered" (EN) (CONSEMA 2002; Bernacci 2003; Fraga *et al.* 2019). *Passiflora deidamioides* and *P. truncata* are considered "Endangered" (EN), based on available material analyzed in virtual herbaria by Milward-de-Azevedo & Fernandes (2021). *Passiflora miersii* and *P. campanulata* are classified as "Rare" in the Red List of Plants in Paraná State Threatened with Extinction (SEMA/GTZ-PR 1995).

Passiflora junqueirae is registered in the red list of Espírito Santo state in the category "Critically Threatened" (CR) (Fraga *et al.* 2019), as it was only known from that state (Bernacci *et al.* 2020). Its current geographic distribution has since been amplified, and its status can now be considered "Endangered" (EN), as cited by Milward-de-Azevedo & Fernandes (2021). *Passiflora marginata* is considered "Endangered" (EN) in the Flora of São Paulo (Bernacci *et al.* 2003).

Our results indicate *P. junqueirae*, *P. marginata*, *P. ovalis*, *P. sidifolia*, *P. speciosa*, *P. suberosa* subsp. *litoralis*, and *Passiflora* sp. as data deficient in terms of their respective distribution ranges in PARNASO (Tab. S2, available on supplementary material <https://doi.org/10.6084/m9.figshare.19620489.v1>), as each has only one or two collection records. *Passifora suberosa* subsp. *litoralis* has a wide distribution in Brazil, occurring in areas of dense ombrophilous forest, savanna, steppe, and restinga phytophysiognomies (Milward-de-Azevedo *et al.* 2012). It demonstrates a restricted distribution in PARNASO, however, probably because it does not normally occur at high elevations. The other species have more limited distributions, with most of them occurring only in states in the southeastern region of Brazil, except *P. sidifolia*, which also occurs in the northeastern state of Bahia (Bernacci *et al.* 2020).

In spite of the low AOO values of *P. alata*, *P. capsularis*, and *P. edulis* (Tab. S2, available on supplementary material <https://doi.org/10.6084/

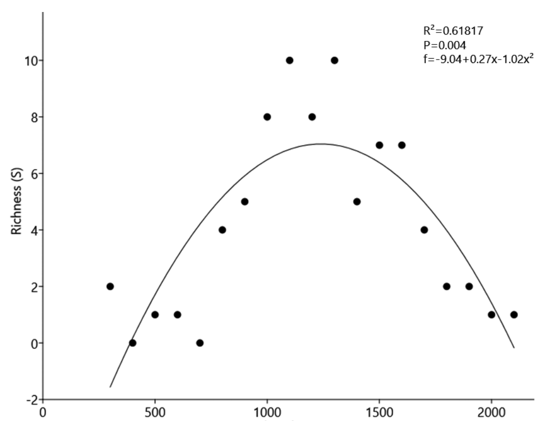

Figure 5 – Species richness of *Passiflora* by classes of altitude in the Serra dos Órgãos National Park, Rio de Janeiro, Brazil.

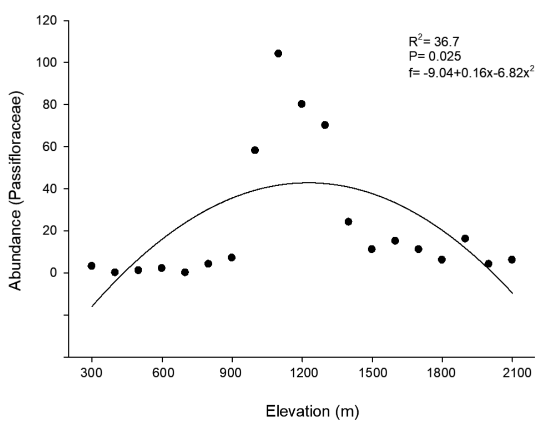

Figure 6 – Occurrence records of *Passiflora* species by altitude gradient in the Serra dos Órgãos National Park, Rio de Janeiro, Brazil.

m9.figshare.19620489.v1>), they demonstrate ample distributions in Brazil, occurring principally in regenerating forests and forest borders, and can be found in dense ombrophilous forests to areas of Restinga vegetation (Bernacci *et al.* 2020; Cervi 1997; Milward-de-Azevedo *et al.* 2012). Although *P. actinia* is widely distributed in PARNASO (as can be seen in Tables S2 and S3, available on supplementary material <https://doi.org/10.6084/m9.figshare.19620489.v1>), it is principally common in the northeastern sector of the park (and less so in other areas). The other species demonstrated restricted distributions and, for that reason, may be classified as having some level of threat in national or state-level lists; those lists therefore corroborate our results for *P. campanulata*, *P. deidamioides*, *P. imbeana*, *P. miersii*, *P. truncata*, and *P. vellozoi* (Tab. S2, available on supplementary material <https://doi.org/10.6084/m9.figshare.19620489.v1>).

The increase in species richness and abundance observed at intermediate altitudes supports the hypothesis that the greatest diversity would be in the median section of that gradient. It is important to note that R^2 was high for the species richness analysis and demonstrated a better fit to the model than the abundance data.

That altitudinal effect could be explained, in part, by the fact that environmental parameters show major changes at higher altitudes, mainly in terms of greater variations of atmospheric pressure and temperature (Körner 2007). With each kilometer of elevation gain, temperatures become reduced by 5.5 ºC (Barry 1992). As temperatures decrease, the air is not able to maintain the same humidity as at lower elevations, which leads to water balance deficits in high-altitude areas (Stephenson 1990).

We sought to test the mid-domain effect through a regression to a dome-shaped curve model (a negative quadratic parabola), where the extremes (lower and higher elevations) show less species richness than intermediate elevations. According to the mid-domain effect, geometric restrictions also contribute to the explanation of why species richness is lower at lower elevations,

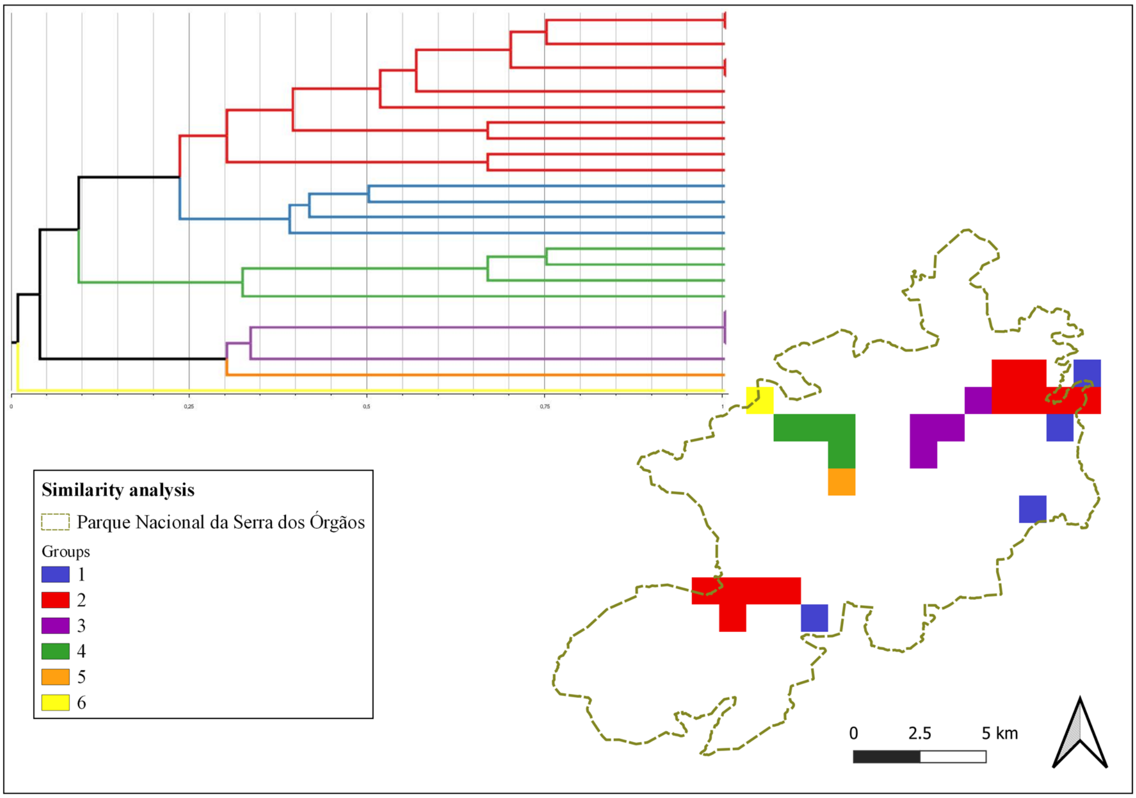

Figure 7 – Floristic similarity of *Passiflora* species obtained by UPGMA linkage method between grids occurrence in the Serra dos Órgãos National Park, Rio de Janeiro, Brazil.

as random species distributions will result in greater overlapping at intermediate elevations (Grytnes 2003). Additionally, studies in the Atlantic Domain have reported decreasing species richness at lower elevations as compared to higher elevations, mainly in areas closer to the coast, due to persistent fog cover (Grubb 1971; Flenley 1995; Caglioni *et al*. 2018).

Many studies have discussed the causes of decreasing species richness and abundance as a function of altitude, pointing out the influences of factors such as: a more rigorous climate, lower productivity, reductions of available area, and reductions of habitat heterogeneity (Rahbek 1995; Contreras & Huerta 2001; Heaney 2001; Lomolino 2001).

The PARNASO has lower temperatures in relation to average temperatures in the surrounding region, mainly at elevations above 800 m.a.s.l., where temperatures do not exceed 19 ºC, and can reach 1 ºC in July and August (ICMBio 2008). In Highland Fields above 2,000 m.a.s.l., temperatures can reach -5 ºC (IBDF & FBCN 1980).

Temperature is a relevant environmental factor that can restrict vine distributions in an elevational gradient (Parthasarathy *et al*. 2004). According to Schnitzer & Bongers (2002), liana diversity (such as Passifloraceae *s.s.*) usually increases at lower latitudes and lower elevations. This is in accordance with the decreases in species richness observed at elevations above 1,500 m.a.s.l., as temperatures tend to decrease at higher elevations and few lianas are tolerant of very extreme conditions (Meeussen 2017). Even with a capable vascular system, very low temperatures can affect xylem vessels and impede water conduction (Ewers 1985), and lianas are better adapted to warmer, low elevation locations (Hu and & Riveros-Iregui 2016).

Moraes *et al*. (2018) reported a similar result in their study at Serra do Brigadeiro State Park (Minas Gerais) in an elevational gradient between 900 and 2,000 m.a.s.l., with Passifloraceae *s.s.* species having greater richness and abundance at intermediate altitudes (between 1,100 and 1,600 m.a.s.l.).

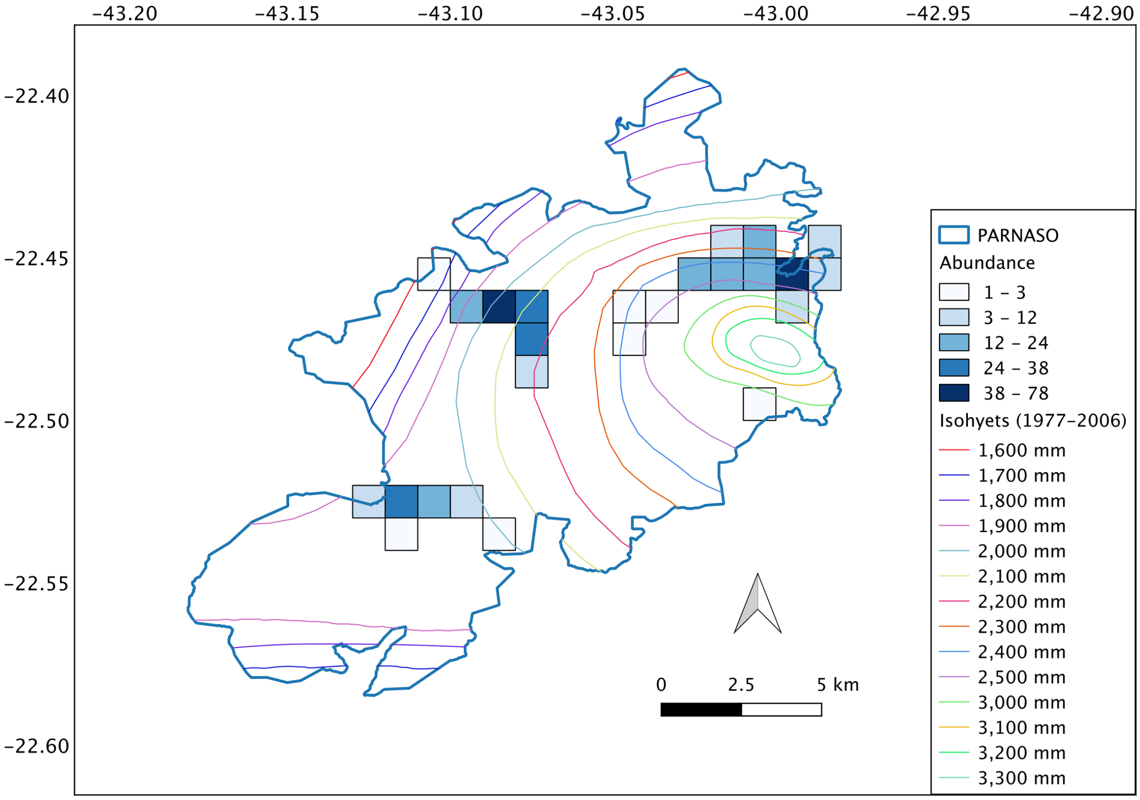

Figure 8 – Occurrence records of *Passiflora* species with rainfall data (between 1977–2006) in Serra dos Órgãos National Park, Rio de Janeiro, Brazil.

Moraes *et al*. (2020) reported similar results in another study undertaken in Serra da Mantiqueira along a gradient from 0–2,500 m.a.s.l., with the greatest richness of Passifloraceae *s.s.* species being observed at 1,000 m.a.s.l., and more than 40 species in a montane ombrophilous forest. There was a significant decline after that peak of richness, with the number of species becoming reduced by half (Moraes *et al*. 2020).

The first specimen of Passifloraceae *s.s.* found in the present study was at an elevation of 346 m.a.s.l., and others followed along the increasing elevational gradient, with the last sample collection occurring at 2,131 m.a.s.l. The intermediate areas between the first and last collections were the richest and most abundant (1,300 and 1,100 m.a.s.l. respectively). It is important to note that Grytnes (2003) found a similar pattern in his study of elevational distributions, demonstrating that the mid-portion of the gradient between the base and summit, regardless of the size of the mountain, showed greater species richness.

The flora of the Ibitipoca State Park in Minas Gerais State (Milward-de-Azevedo 2007) listed *P. campanulata* at an elevation slightly below that found in the present study (1,390 m.a.s.l.), although it was collected in a rupestrian field - which reinforces the specificity of this species to environments with more restricted vegetation types.

Another factor analyzed in this study was the influence of different facing slopes (oceanic *vs*. continental) on Passifloraceae *s.s.* species richness and abundance. The Teresópolis, Guapimirim, and Magé areas are part of the ocean-facing slope, while the Petrópolis area is on the continent-facing slope (ICMBio 2008). The climates are different on different sides of the mountain range, with the slopes facing inland (encompassing the Paraíba River Valley) being drier, while the slopes facing the ocean are much more humid and receive the greatest rainfall - resulting in marked landscape differences (Hueck 1972; ICMBio 2008).

According to Hugget (1995), continental and ocean-facing slopes in mountain ranges have

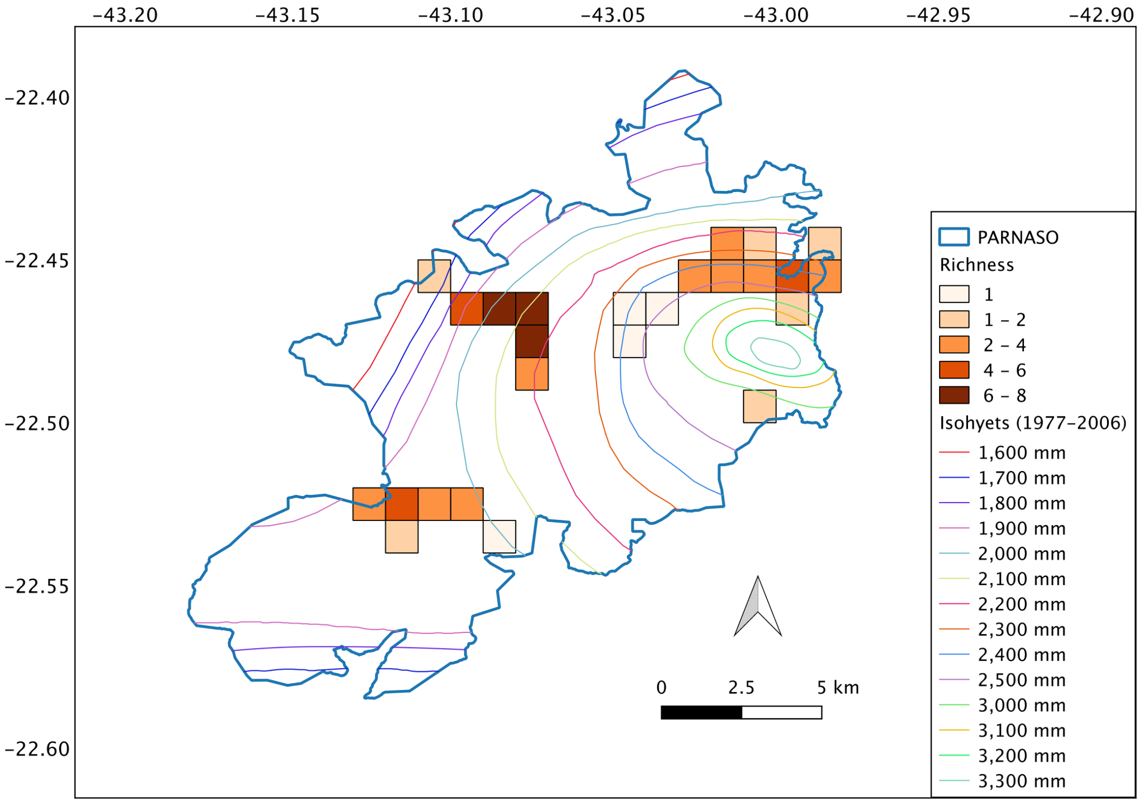

Figure 9 – Species richness of *Passiflora* with rainfall data (between 1977–2006) in Serra dos Órgãos National Park, Rio de Janeiro, Brazil.

important attributes in relation to plant species distributions due to their different precipitation and temperature regimes. The low similarity in terms of species composition seen in this study (28%) reflects the escarpment region of Serra do Mar in PARNASO, as the ocean-facing slopes receive humid oceanic air masses (RBMA 2007).

The greatest species richness in the present study was observed in the northwestern sector - the range facing inland. Cortines *et al.* (2011) inventoried the arboreal vegetation on different slopes in a section of the Serra do Mar Range in the municipality of Nova Friburgo, Rio de Janeiro state, and likewise noted a greater richness on inland-facing slopes, as the abiotic conditions there can influence species compositions at local levels. Additionally, a study by Cortines (2012) in the same locality reported differences in fog interception, and noted that the ocean-facing slopes intercepted more humidity than the inland-facing slopes, even on days without rainfall, which consequently influences the distributions of living organisms.

In a study examining the floristic composition of Maciço de Itatiaia, Pereira *et al*. (2006) similarly encountered greater angiosperm richness on inland-facing slopes, and identified additional determinant factors related to fragment size and local disturbance events. The different orientations of the mountains resulted in differences in environmental conditions that influenced vegetation characteristics. It is worth noting that north-facing slopes in the southern hemisphere tend to be drier and warmer, as they receive higher levels of incident solar radiation. Inland-facing slopes dominate the Petrópolis area of the PARNASO and, in addition to their having different phytophysiognomies and greater exposures to solar radiation than ocean-facing slopes, there are also factors related to land-use and occupation that can directly influence vegetation composition (Cortines *et al*. 2011; Oliveira *et al.* 1995; Hugget 1995; ICMBio 2008).

A study by Oliveira *et al.* (1995) focusing on slope-orientation at Tijuca Peak, encountered significant differences between continental and oceanic slopes, largely related to questions of temperature, humidity, and floristic composition. Different from the present study, however, the greatest species richness reported by that group

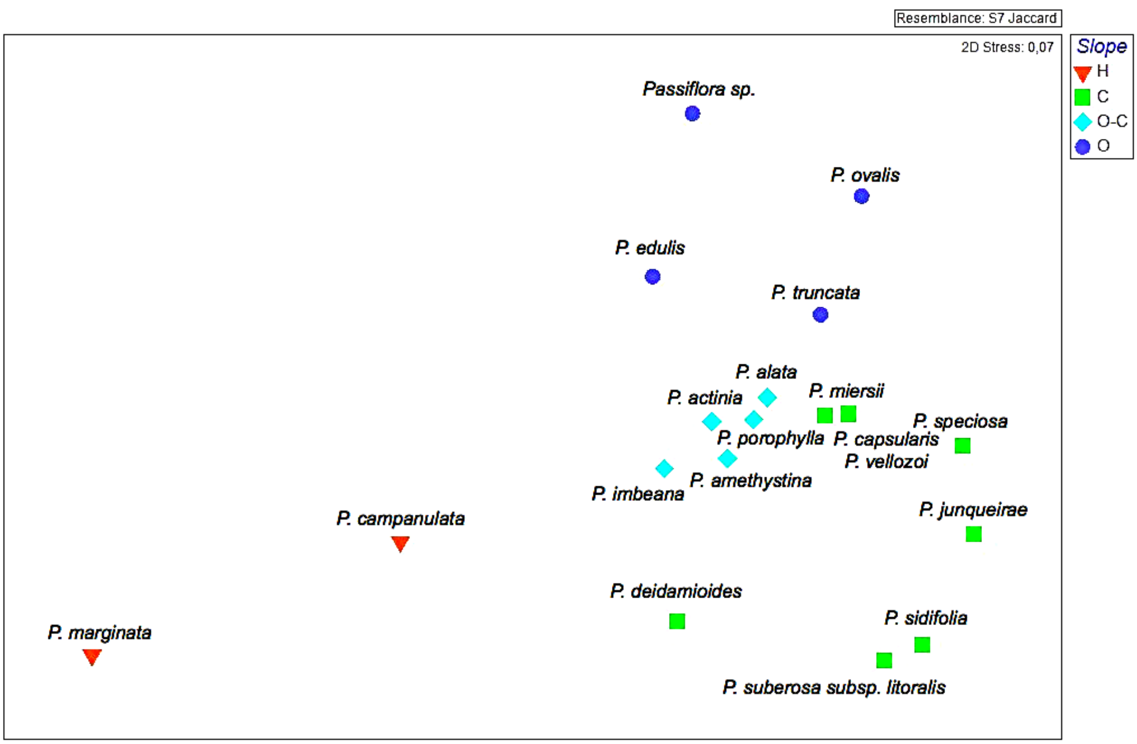

Figure 10 – Non-metric multidimensional scaling (NMDS) ordination through Jaccard similarity index on the continental and oceanic slopes in Serra dos Órgãos National Park, Rio de Janeiro, Brazil. Legends: O = Oceanic; C = Continental; H = Highland Fields; O-C = Oceanic and Continental.

was found on ocean-facing slopes, although it is important to note that the inland-facing slopes there, as reported by Oliveira *et al.* (1995), have large areas of significantly degraded vegetation - which will obviously influence species composition. Oliveira *et al.* (1995) e Cortines (2012) reported similarity values of 49.57% and 40% respectively. Among the studies cited here, our results demonstrated significantly low similarity (28%), indicating an even greater differentiation of species richness between the oceanic and inland-facing slopes in the PARNASO, which apparently reflects the presence of species that are better adapted to those different environments. Likewise, the species common to both sides may represent those with more generalist strategies, capable of occupying both environments. It is important to note that the continental slope, which occurs in the municipality of Petrópolis, has a distinct phytophysiognomy, due to orographic rains and its history of anthropic land use and occupation (ICMBio 2008).

We presented ten new records of *Passiflora* species for PARNASO, including many that were absent from the park's original management plan. The patterns of species distributions within the elevational gradient of the park corroborate the mid-domain effect with Passifloraceae *s.s.*, with higher species richness and abundance at intermediate elevations. The different continental and oceanic slopes also demonstrated differences in *Passiflora* species distributions, with higher species richness on continental slopes and a general preference for habitats with greater insolation and less humidity. A highly significant part of the Passifloraceae *s.s.* diversity described for Rio de Janeiro state and for the dense ombrophilous forest in the Atlantic Domain can be found in the PARNASO, reinforcing its importance to the conservation of the Atlantic Forest global biodiversity hotspot.

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