Anthropogenic factors, not altitude, shape native and nonnative plant species distributional patterns in a tropical mountain protected area

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Abstract

Biological invasions pose a major threat to biodiversity conservation in protected areas, with roads, tracks, and trails being the main pathways for the spread of non-native species. This study aimed to assess the distribution patterns of non-native and native plant species in relation to elevational gradient, public use intensity, and disturbance by roads and trails in a protected tropical mountain forest in southeastern Brazil. Specifically, we recorded plant species along this gradient and tested whether the richness of native and non-native species differed with elevation. Additionally, we investigated whether the high-altitude non-native species community was a subset of lower-elevation communities and whether non-native species richness was linked to anthropogenic disturbances and public use intensity. Our findings revealed that native and non-native species richness varied along the elevational gradient. Native species exhibited a hump-shaped pattern, with richness peaking at mid-elevations. In contrast, non-native species did not show a clear trend along the altitudinal gradient. Notably, higher non-native species richness was observed in roadside and trailside plots. The non-native species communities at higher altitudes were not simply subsets of those found at lower elevations. Thus, while the richness and composition of native species appeared to be driven by environmental factors along the elevational gradient, the presence of non-native species was more closely associated with anthropogenic disturbances. In summary, our results indicate that non-native plants, although widespread along trails and roads, establish primarily in the most disturbed areas. Therefore, roads, trails, and human and vehicular traffic are key determinants of biological invasions in this mountainous protected area.

Introduction

The spread of invasive non-native species is increasing worldwide and is recognized as a major threat to biodiversity conservation in protected areas (IPBES 2023; Padmanaba et al. 2017). Anthropogenic activities such as human population growth, tourism expansion, and climate change facilitate the establishment and spread of non-native species in these areas, potentially causing drastic changes in the native communities and ecosystems meant to be protected (Dar et al. 2018; Duque et al. 2015; Gottfried et al. 2012; Kueffer et al. 2013). This issue is particularly significant in mountain protected areas, which have seen a rapid increase in non-native species worldwide, with roads identified as one of the main pathways for their spread (Kueffer 2017; Paiaro et al. 2011; Pauchard et al. 2016). Understanding the patterns and drivers of non-native plant invasions in mountain protected areas is essential for management actions aimed at reducing their impact on native communities.

Roads, tracks, and trails are primary pathways for the spread of non-native species in both mountain ecosystems and protected areas (Foxcroft et al. 2019; Pauchard and Alaback 2004; Pickering and Mount 2010). Human-modified habitats provide large-scale (e.g., roads and facilities) and small-scale (e.g., small gaps and informal trails) disturbances that promote non-native species establishment (Lembrechts et al. 2016). The relationship between non-native species establishment and public use is attributed to anthropogenic disturbances such as facilities, trails, and roadsides that enhance water runoff, change soil moisture, composition, and chemistry, and increase light availability and propagule delivery, thus favoring non-native plant occurrences (Daniels et al. 2019; Karr et al. 2018). Consequently, the diversity and number of non-native plant species in mountains are generally higher along roads than in adjacent habitats

(Pauchard et al. 2009). Additionally, human activities are important determinants of non-native species richness, increasing the chances of successful establishment and invasions by boosting propagule pressure to suitable sites (Marini et al. 2013; Seipel et al. 2012). More disturbed areas with higher tourist use intensity are thus expected to harbor more non-native species.

The variations in elevation inherent to mountain ecosystems produce significant environmental changes that greatly affect biodiversity patterns. One of the most noteworthy patterns is species richness along elevational gradients, which can exhibit three main patterns: linear decreases with increasing altitude, hump-shaped patterns with a maximum at mid-elevations, and constant richness from low to mid-elevations followed by declines farther up (Rahbek 1995). However, richness patterns of native and non-native species in mountains may differ due to different ecological processes (Averett et al. 2016). Native species patterns result from long periods of coevolution with the environment, involving various biotic and abiotic interactions and evolutionary changes, leading to distinct native species pools in each ecosystem (Alexander et al. 2011, 2016; Otto et al. 2014). In contrast, non-native species composition in an area is determined by the accumulation of species transported through human agency (Alexander et al. 2011, 2016; Ricciardi 2007). Two main patterns of non-native species richness are expected along environmental gradients: (1) a decline in species richness with increasing elevation, and (2) non-native species at higher altitudes being generalists that also occur at lower altitudes (Alexander et al. 2011; Marini et al. 2013).

To understand the disturbances driving plant species richness patterns along roads and trails in a tropical mountain forest, we examined the distribution of plant species in relation to elevational gradients, public use, and disturbance by roads and trails, and contrasted the results for native and non-native species. We aimed to contribute knowledge on species richness patterns along elevational gradients and the role of anthropogenic disturbances in non-native species invasions. Using field surveys of plant data, we sought to answer the following questions: (1) How are native and non-native species richness affected by altitudinal gradient, public use, and disturbance by roads and trails? (2) Do native and non-native species richness respond similarly to the altitudinal gradient? (3) Are the non-native species communities at higher altitudes a subsample of the lower-altitude non-native species pool?

Materials and Methods

Study Site

The Itatiaia National Park (hereafter Itatiaia Park) is a protected area conserving a remnant of the Atlantic Forest biodiversity hotspot (Myers et al. 2000). The park spans 28,084 ha in southeastern Brazil (22.37°S, 44.63°W). According to the Köppen climate classification, Itatiaia Park experiences a subtropical highland climate (Cwb) at higher elevations (1,600 m above sea level [m asl]) and a warm summer continental climate (Cfb) at lower elevations (ICMBio 2014). Data from the Alto Itatiaia weather station, located at 2,199 m asl, indicate an annual average temperature of 11.5 C, with negative temperatures and frequent hail during the winter months (FBDS 2000; ICMBio 2014). The mean annual precipitation in the municipalities within Itatiaia Park ranges from 1,250 to 2,500 mm, with the driest months from June to August and the wettest months during the Southern Hemisphere summer (ICMBio 2014). The park's phytophysiognomy consists of 62% Montane and Upper Montane Ombrophilous Forests and 17% high-altitude grasslands, with the remaining 21% composed of agricultural areas, urban areas, and rocky outcrops (ICMBio 2014). Itatiaia Park received around 100,000 visitors per year between 2005 and 2017, with annual visitor numbers ranging from 72,703 to 139,616 (ICMBio 2020). The most frequently used mode of transport to visit the park was by car, accounting for 90.5% of all transportation modes (ICMBio 2014).

Fieldwork

Fieldwork was conducted during the rainy season from October 2018 to February 2019 to ensure the collection of fertile individuals for accurate identification. Specimens were identified using vouchers deposited at the ESAL Herbarium at the Federal University of Lavras and the Herbarium of the Rio de Janeiro Botanical Garden. The species' status (native or non-native) to the Atlantic Forest was determined using the Brazilian Flora 2020 (http://floradobrasil.jbrj.gov.br) and the Royal Botanic Gardens Kew website Plants of the World Online (http://www.plantsofthe worldonline.org). Following the criteria of Richardson et al. (2000) and Blackburn et al. (2011), non-native species were defined as those introduced, intentionally or accidentally, to areas beyond their native ranges.

To address our research questions, we selected two roads and two trails representative of all areas of the park for plant surveying. The chosen roads provide the main access to the upper and lower parts of the park, while the trails cross the northern area, meeting at the Serra Negra mountain ridge. The northeast trail is called Santa Clara, and the northwest trail is called Serra Negra (Figure 1A). The study area's elevation ranged from 501 to 2,448 m asl.

Sampling points were placed at 500-m intervals along each road and trail. The distances were measured using Google Earth Pro 7.3.2 (free version). We established 24 points in the upper part, 16 in the lower part, 14 in Serra Negra, and 13 in Santa Clara (Figure 1A). At each sampling point, three plots were set up: the first plot at the edge of the road or trail (plot 0 m away), the second plot 5 m away, and the third plot 10 m away. Each plot measured 1 by 10 m and was parallel to the road or trail (Figure 1B). The
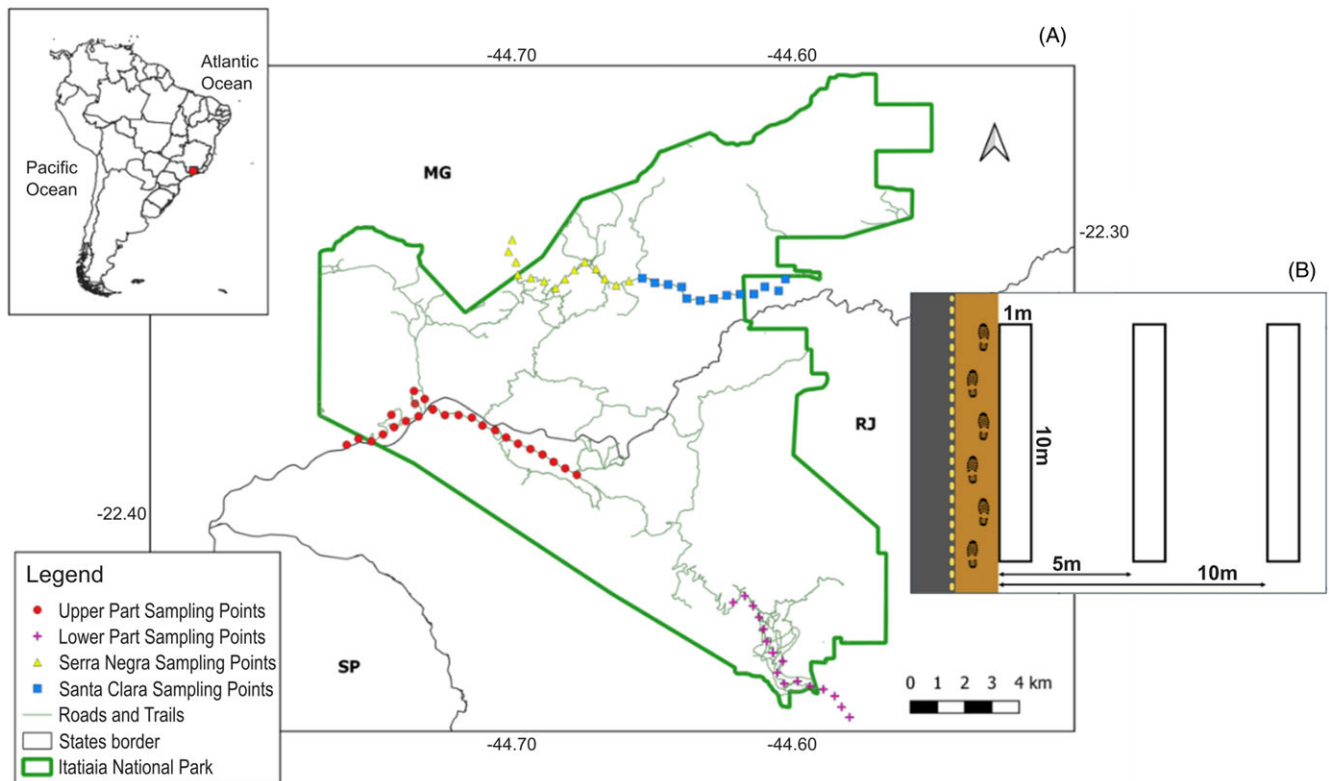
Figure 1. Itatiaia National Park location in Brazil, the distribution of the sampling points in each area of the park (A) and the plot design (B). The sampling points are separated by 500 m in a straight line (A). At each sampling point, three plots of 1 × 10 m were set up, they were parallel to the road or trail and to each other (B).

positions of the plots along the road or trail (left or right) were determined randomly. These plots were established at varying distances to assess the influence of disturbances from roads and trails on native and non-native plant species richness. The 0-m plots experienced the highest levels of anthropogenic disturbance due to road and trail maintenance, traffic, and tourism. The 5-m plots had intermediate disturbance levels, while the 10-m plots had the lowest disturbance levels, representing more natural ecological conditions (Figure 1B). We recorded herbaceous plants, herbs, and grasses in each plot. Altitude was measured at each sampling point using a Garmin 62s GPS.

To measure public use intensity, we calculated the distance of each sampling point from tourist facilities and attractions. For each transect, we assigned a value of 0 to the farthest sampling point from any tourist facilities or attractions. We then measured the distance of consecutive sampling points along the road or trail using the Ruler Tool in Google Earth Pro 7.3.2 (free version). To avoid disproportionate influence from absolute distances, we standardized each sampling point's value in proportion to the total distance of the corresponding transect, resulting in values ranging from 0 to 1. Sampling points closer to tourist facilities or attractions had higher proportional values (closer to 1), indicating higher public use intensity.

Data Analyses

To account for spatial autocorrelation between plots at each sampling site, we used principal coordinates of neighbor matrices (PCNMs) as spatial explanatory variables (Borcard et al. 2011; Dray et al. 2006). The PCNM eigenvectors are orthogonal spatial variables representing the spatial structure of the data at different

spatial scales, with the first axes representing broad scales that become progressively finer as the axes increase (Borcard et al. 2011).

Next, we created three generalized linear models containing explanatory variables related to space against the absolute native and non-native species richness and relative non-native species richness. We applied backward selection using the *drop1* function to progressively remove nonsignificant variables with smaller *F*-values (R package STATS; R Core Team 2022). The residuals of the three final models related to each response variable were used as measures of richness without the influence of spatial distances.

Following this, we used a generalized mixed model to test whether altitudinal gradient, public use intensity, disturbance level by roads and trails, and type of access (i.e., roads or trails) affected absolute native and non-native species richness and relative non-native richness. The residuals from the previously mentioned models were used as response variables. We created the linear mixed-effects models using *lmer* from the package LME4 (Bates et al. 2015) and included area as a random effect in the models to remove bias caused by the nested sampling. Considering the potential unimodal patterns of species richness along the elevational gradient, we created a model with predictor variables including a second-order polynomial of elevation using the *poly* function in R (R Core Team 2022), which uses QR factorization to generate monic orthogonal polynomials.

To compare the models, we ranked them according to the corrected Akaike's information criterion (AICc) using the *model.sel* function in the MuMIn package (Barton 2019). The model with the lowest ΔAICc was considered the best-fit model (Akaike 1974; Sugiura 1978). Models were considered significantly better when they presented 2 ΔAIC units lower than another. The

coefficient of determination was obtained for the models with the $r2$ function from the SJSTATS package (Lüdecke 2022).

We checked residual distributions, impacts of outliers on results, and dispersion using diagnostic tests implemented in the DHARMA package v. 0.4.6 (Hartig 2022). We tested for under-dispersion in the residuals of the models using the *testDispersion* function, which tests the quantiles of scaled simulated residuals against a uniform distribution (Hartig 2022). The fit of the models was validated using the *simulateResiduals* function (Hartig 2022; Supplementary Figures S1–S4).

Finally, to determine whether the non-native species community composition of the sampling points at higher altitudes was nested within sampling points from lower altitudes, we used the functions *nestednodf* and *oecosimu* from the VEGAN package v. 2.6-4 (Almeida-Neto et al. 2008; Almeida-Neto and Ulrich 2011; Oksanen et al., 2022). We used the nestedness metric based on overlap and decreasing fill (NODF), because this measure is less dependent on the size and shape of the interaction matrix than other measures of nestedness, providing an unbiased estimate of the degree of nestedness (Almeida-Neto et al. 2008). The *nestednodf* calculated nestedness was compared with a null model using *oecosimu* with default settings, except for the Methods parameter, where we used "r0" to maintain the site (row) frequencies and fill presences anywhere on the row with no respect to species (column) frequencies. The *nestednodf* output gives a statistic for nestedness of rows (sites), where 0 indicates no nesting and 100 indicates perfect nesting. This analysis requires two basic properties for a matrix to have the maximum degree of nestedness: (1) complete overlap of 1s from right to left columns and from down to up rows and (2) decreasing marginal totals between all pairs of columns and all pairs of rows (Almeida-Neto et al. 2008). The nestedness statistic is evaluated separately for columns (*N* columns) and for rows (*N* rows) and combined for the whole matrix (NODF). We set order = FALSE so the statistic evaluates with the current matrix ordering, in our case, the altitude values. The weighted argument, when TRUE, finds the weighted version of the index, but instead, we used weighted = FALSE, considering our matrix as presence/absence data (Almeida-Neto et al. 2008; Almeida-Neto and Ulrich 2011).

All statistical analyses were performed using the software RStudio v. 4.3.1 (R Core Team 2022).

Results and Discussion

We identified a total of 112 species encompassing 34 botanical families. Among these, 82 species (73%) belonging to 24 families were native, and 30 species (27%) belonging to 16 families were non-native (Supplementary Table S1). Most native species belonged to the families Poaceae and Asteraceae, while most non-native species were in the families Poaceae, Asteraceae, Zingiberaceae, and Fabaceae. The number of native species was higher than the number of non-native species in all areas of Itatiaia Park. Despite this, Itatiaia Park is listed among the protected areas with the highest occurrence of non-native invasive species in Brazil (Sampaio and Schmidt 2013). Non-native species can promote biotic homogenization (e.g., Winter et al. 2009) and impact native species (e.g., Heringer et al. 2019), potentially becoming invasive and spreading from points of introduction to other areas of the park.

The quadratic models presented the smallest ΔAIC in the three sets of models for non-native, native, and proportion of non-native species (Table 1). Non-native species richness was affected by the disturbance level caused by roads and trails, with richness decreasing progressively with distance from these features (Table 1). The quadratic model's total explanatory power was conditional $R^2 = 0.34$, and the part related to the fixed effects alone was marginal $R^2 = 0.30$. This was close to the linear models, which had a conditional $R^2 = 0.32$ and marginal $R^2 = 0.30$. The best model representing relative non-native species richness showed a similar result, with disturbance caused by roads and trails negatively affecting the proportion of non-native species (Table 1). However, the explanatory power for the quadratic model (conditional $R^2 = 0.19$ and marginal $R^2 = 0.15$) and the linear model (conditional $R^2 = 0.16$ and marginal $R^2 = 0.15$) was smaller.

We did not find that non-native plant species were concentrated at lower altitudes in montane areas, although a decreasing richness pattern for non-native species has been often observed in previous studies (Chytrý et al. 2005, 2009; Dar et al. 2018; McDougall et al. 2005; Pauchard and Alaback 2004; Pauchard et al. 2009; Zhang et al. 2015). In our study, the positive effect of roads and trails on the spread of non-native species likely favors their distribution regardless of the altitudinal gradient and public use intensity. Thus, non-native species may exhibit an even distribution across the altitudinal public use intensity gradients if they are closer to roads and trails.

The high proportion of non-native species close to roads and trails supports the idea that disturbances caused by these networks play a key role in the introduction of species to mountain systems, being a main driver of non-native species introduction and establishment (Alexander et al. 2016; Padilha et al. 2015). The decline in non-native species could be due to decreased human disturbance intensity, lower propagule pressure, or greater resistance to invasion of more natural communities away from frequently disturbed sites (Seipel et al. 2012). Proximity to roads and trails may represent a more favorable, high-light environment for non-native species occurrence (Dar et al. 2018; Dawson et al. 2015). Seeds from various plants can be unintentionally dispersed to protected areas on clothing, potentially traveling many kilometers (Ansong and Pickering 2014). The high number of visitors could mean higher propagule pressure in these areas, facilitating the introduction and establishment of non-native species, mainly in roadside and trailside plots, similar to previous records from other mountain ecosystems (Khuroo et al. 2011; Lembrechts et al. 2017; Liedtke et al. 2020; Pauchard et al. 2009). Although it might be expected that public use would affect the richness of non-native species, we did not find any such effect.

For native species, the quadratic model best represented the richness pattern. We observed a unimodal pattern of altitude with a negative effect of second-degree altitude (Table 1; Figure 2). In other words, native species richness reaches a maximum at an intermediate altitude around 1,750 m. Disturbances caused by roads and trails also affected native species richness, with middle and interior plots having progressively fewer species than plots closer to roads. The quadratic model's total explanatory power was substantial, with conditional $R^2 = 0.50$ and the part related to the fixed effects alone being marginal $R^2 = 0.42$, very close to the linear model's (conditional $R^2 = 0.49$ and marginal $R^2 = 0.40$).

Our findings on native plant species richness along an altitudinal gradient align with those of other studies on plant species richness in temperate forests in Mexico (Sánchez-González and López-Mata 2005) and Korea (Lee and Chun 2016), bryophyte species (Ah-Peng et al. 2012; Marline et al. 2020), and global

Table 1. Results from the analysis for comparisons between models: model parameter results of linear and quadratic models for absolute and relative native and non-native species richness.

	Absolute native species richness			
Models	Linear model		Quadratic model	
Parameters[a]	Estimate	P	Estimate	P
Intercept	1.042	0.106	1.248	0.061
Altitude	0.040	0.815	2.285	0.357
Altitude^2	—	—	−4.117	0.01*
Public use intensity	−0.412	7.2×10^{-5}*	−0.397	9.85×10^{-5}*
Type of access	−0.159	0.786	−0.592	0.36
5 m away plot	−1.797	2×10^{-16}*	−1.797	2×10^{-16}*
10 m away plot	−2.012	2×10^{-16}*	−2.012	2×10^{-16}*
AICc	619.6		606.4	
Weight	0.001		0.999	
	Absolute non-native species richness			
Models	Linear model		Quadratic model	
Parameters	Estimate	P	Estimate	P
Intercept	0.588	0.065	0.506	0.164
Altitude	−0.027	0.812	−0.961	0.608
Altitude^2	—	—	1.718	0.184
Public use intensity	−0.093	0.288	−0.099	0.262
Type of access	−0.038	0.888	0.139	0.704
5 m away plot	−1.239	5.22×10^{-12}*	−1.239	4.62×10^{-12}*
10 m away plot	−1.404	1.41×10^{-14}*	−1.404	1.22×10^{-14}*
AIC	564.3		557.2	
Weight	0.028		0.972	
	Relative non-native species richness			
Models	Linear model		Quadratic model	
Parameters	Estimate	P	Estimate	P
Intercept	0.157	0.190	0.123	0.439
Altitude	0.017	0.746	−0.119	0.898
Altitude^2	—	—	0.60	0.343
Public use intensity	−0.026	0.538	−0.026	0.537
Type of access	−0.058	0.642	0.011	0.950
5 m away plot	−0.360	2.10×10^{-5}*	−0.360	2.06×10^{-5}*
10 m away plot	−0.459	9.01×10^{-8}*	−0.459	8.75×10^{-8}*
AIC	294.9		290.2	
Weight	0.086		0.914	

[a]AIC, Akaike's information criterion.
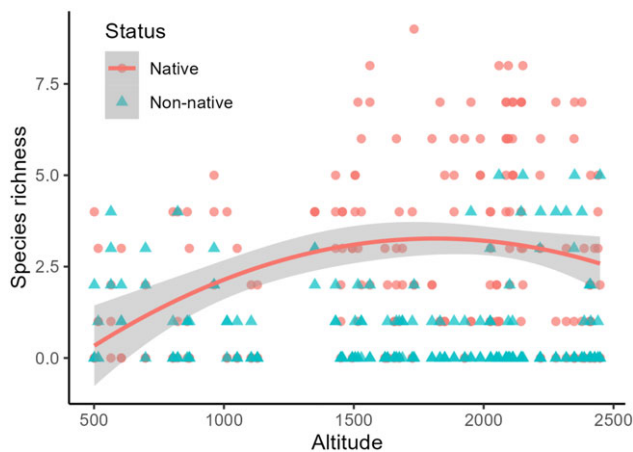*Statistically significant values at alpha < 0.05.

Figure 2. The hump-shaped pattern of native species (red circles) in Itatiaia National Park, with species peaking around 1,750 m asl, and the non-native species (blue triangles). Only the curve for the significant relationship was plotted.

mountain plant richness (Haider et al. 2018). Species richness may be highest in middle elevations due to intermediate temperature and rainfall, which provide optimal conditions and higher species richness, while lower humidity at lower altitudes and lower temperature at higher elevations constrain species diversity (Kluge et al. 2006). Additionally, middle-elevation regions often see overlapping plant communities, making these regions highly diverse (Haider et al. 2018). In Itatiaia Park, middle elevations may be considered a transitional region where montane forest habitat (500 to 2,000 m asl) meets high-altitude grassland (above 2,000 m asl), forming an ecotone (Aximoff et al. 2014; Safford 1999). These phytophysiognomic encounters likely explain the unimodal native species richness observed in our study area.

Regarding anthropogenic disturbances, we found a clear effect of roads and trails on the richness of both non-native and native species. The similar response of native and non-native species richness we observed, complementary to the widely accepted notion that frequently disturbed communities are more vulnerable to invasions (Pauchard et al. 2009; Sandoya et al. 2017), suggests
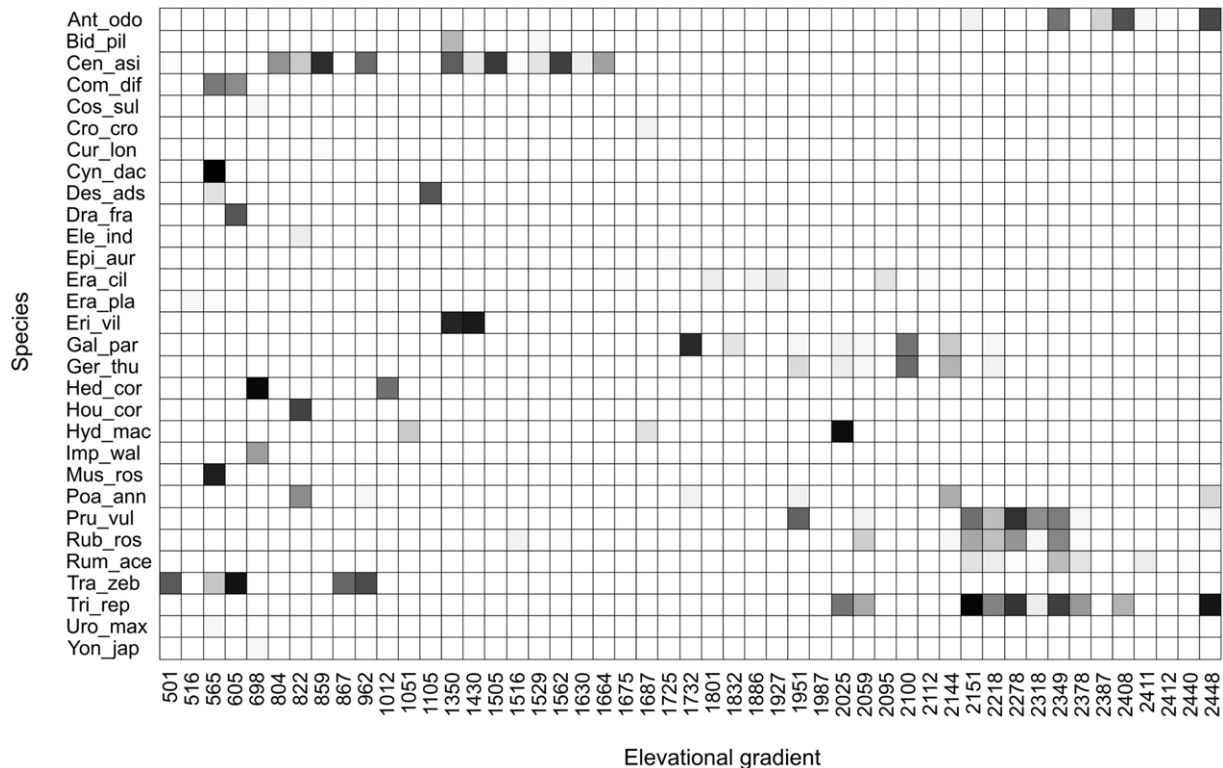
Figure 3. The *nestednodf* analyses plot of non-native plant species ordered in relation to altitude. The species names are abbreviated with the three first letters of its genus and the specific epithet (see Supplementary Table S1). The analyses showed that there is no non-native species nesting from lower to higher altitudes. The non-native species communities of higher altitudes are not formed by the non-native species pool from lower sites.

that native species are also favored and may be expanding their local ranges (Lembrechts et al. 2017). It is frequently observed that road and trail edge vegetation harbors a higher number of both native and non-native species compared with interior areas (Ullmann et al. 1995). Possibly, ruderal native species are favored by the anthropogenic environmental conditions near roads and trails, but this question requires further investigation.

Nestedness analysis, evaluating whether the species community composition of sampling points at higher altitudes was nested within those from lower altitudes, indicated that non-native and native species communities were not nested within the lower-altitude species pool (NODF = 3.34, matrix fill = 0.079, turnover = 0.9705, nestedness = 0.0119; and NODF = 8.29, matrix fill = 0.071, turnover = 0.9752, nestedness = 0.009, respectively) (Figure 3). Thus, both non-native and native species compositions at high altitudes were composed of different assemblages. This result may be explained by the evolutionary development of native plant species in relation to edaphoclimatic variances to altitude. Differences in community composition along the altitudinal gradient highlight that distinct environmental gradients affect species composition, likely due to local and fine-scale factors (Gastauer et al. 2020; Pinto-Junior et al. 2020).

We suggest that each area of Itatiaia Park favors a particular assemblage of non-native species along trailsides and roadsides due to different climates. Previous studies have shown that non-native species communities in high-elevation areas are linked to the alien species pool from the surrounding lowlands, where only broadly climate-tolerant species and species pre-adapted to harsher climatic conditions can spread and sustain populations at higher elevations (Fernández-Palacios and de Nicolás 1995; Kueffer 2017; Pauchard et al. 2016). In our study, however, there was no nesting

from lower to higher altitudes. Although environmental filters in high-altitude environments constrain the establishment of non-native species not adapted to extreme conditions, our results suggest that other non-native species adapted to harsher climates reach higher-altitude environments via roads and trails.

Our findings provide evidence that anthropogenic disturbances associated with roads and trails (i.e., gap openings, propagule pressure) increase non-native plant species introduction, facilitating their arrival and establishment. In Itatiaia Park, this impact occurs evenly along roads and trails, as tourists must traverse these paths to access park attractions. Practical actions to reduce the spread of non-native species include raising awareness among visitors about the risks of introducing species into protected areas, implementing prevention measures at park entrances (e.g., cleaning vehicles), and initiating early detection and rapid response close to frequently used roads and trails.

In conclusion, our study contributes new insights into the distributional patterns of non-native species richness along altitudinal gradients, highlighting the significant role of anthropogenic disturbances. Anthropogenic disturbances associated with roads and trails influence the richness of non-native species along the altitudinal gradient. In contrast, for native species, environmental and edaphoclimatic factors also play crucial roles in driving richness patterns. Moreover, our findings indicate that the non-native species community at higher altitudes does not merely represent a subset of the community found at lower altitudes, contrary to previous observations. This diverse community of non-native species at higher elevations suggests their association with public visitation and the park environment. Therefore, the increasing tourist activities in conservation areas may heighten the threats posed by non-native species to native and endemic

species, given the concurrent rise in disturbances and propagule pressure. Managers of protected areas such as Itatiaia National Park should thus prioritize efforts to prevent the introduction of new non-native species into high-altitude environments due to the ecological significance and vulnerability of these areas.

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