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Vegetation Structure and Composition as Predictors of Small Mammals Assemblages

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ABSTRACT

Whether the diversity and composition of animal communities are determined by vegetation structure or composition has been an ongoing debate. However, due to combined shortcomings of data and methodology, vegetation structure has been prioritised when trying to understand the effects of vegetation upon animal communities. Here, we explored the relative importance of vegetation structure and woody plant species composition on the prediction of small mammal assemblages for an Atlantic Forest landscape. Compositional (small mammals and woody plants) and vegetation structural data were collected in 20 forest sites in the Guapi-Macacu river basin, Rio de Janeiro, Brazil. We used direct ordination techniques (co-correspondence and predictive canonical correspondence analysis) to compare the predictive capacities of vegetation structure and woody plant species composition on small mammal composition. Woody plant species composition explained more variation in small mammal composition than vegetation structure, but more importantly, woody plant species composition and vegetation structure explained different parts of the variation in small mammal composition. Therefore, vegetation structure and woody plant species composition, besides being closely linked, have complementary roles for small mammal assemblages. Among the plant species, *Senefeldera verticillata*, *Myrcia multiflora* and *Guarea guidonia* had the strongest influence on predictive power. Identifying such species is relevant not only statistically, but also for guiding conservation and restoration strategies that aim to sustain small mammal assemblages. We demonstrate that disentangling the role of woody plant species composition on animal community composition might be a complex task; nevertheless, it is a fundamental one to accurately understand the structure, and composition, of animal assemblages.

1 | Introduction

Structurally complex habitats may increase species diversity by providing more niches and diverse ways of exploiting environmental resources (Bazzaz 1975). Plant communities determine the physical structure of most habitats, supporting animal species occurrences and their interactions (review in Lawton 1983; McCoy and Bell 1991). Based on such roles, plant communities are an important vector in ecological studies, serving as a proxy for animal species richness and composition (Tews et al. 2004). However, this role has mostly been attributed to the physical structure of vegetation, while its composition was thought to be less important (e.g., James 1971; Anderson and Shugart 1974; Wiens and Rotenberry 1981).

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Such prioritisation may be related to the fact that vegetation structure is a more easily available variable, without the need for specialised knowledge required by vegetation composition assessments (Wiens and Rotenberry 1981). Besides such characteristics, the lack of adequate analytical methods also contributed to this preference of structure over composition. A new method was proposed to overcome this gap, making it possible to simultaneously integrate two species compositions together at once, and allowing a taxa composition to predict another taxa's composition (ter Braak and Schaffers 2004). However, few studies have used this technique (e.g., Schaffers et al. 2008; Müller et al. 2010; Hanson et al. 2015; Nyafwono et al. 2015; Adams and Matthews 2019; Uboni et al. 2019). Additionally, it may be difficult to draw inferences on tropical systems because many of these studies have focused on temperate regions.

Landscape context is also expected to mediate organismal relationships with vegetation structure (VS, hereafter) and plant species composition (PSC, hereafter), especially within continuous versus fragmented landscapes. In fragmented landscapes, species occurrence and composition are influenced by the regeneration stage of habitat remnants and the degree of fragmentation (Tews et al. 2004; Dunn 2004), creating a diverse range of habitat structure and PSC in these remnants (Aguirre-Jaimes et al. 2021). On the other hand, when disturbances do not occur within large areas of continuous habitat, the successional changes can lead to a reduction or local extinction of generalists and non-forest-restricted species, while forest specialist species may increase (Fonseca and Robinson 1990; Pardini 2004; Pardini et al. 2005; Umetsu and Pardini 2007).

In tropical forest regions, independent of forest physiognomies (e.g., seasonal forest, riparian forest, woodland, savanna), animal composition is influenced by forest structure, with more species coexisting locally in more complex habitats (small mammals: Vieira and Monteiro-Filho 2003; Lambert et al. 2005; Hannibal and Cáceres 2010; primates: Gouveia et al. 2014; amphibians: Ferrante et al. 2017). Such patterns raise questions about the role of PSC, since composition and structure are linked, and the patterns observed in one are influenced by the other (MacNally et al. 2002). When PSC is present as a variable in ecological studies, its use is generally limited to key species, species richness, or as a proxy for nesting sites, shelter, and cover (e.g., Garden et al. 2007; Palmeirim et al. 2014). A set of PSC variables as a predictor of animal communities might provide a more complete picture of how such animal communities are structured in tropical regions.

Small mammals are frequently studied regarding the effects of VS on species composition, and occasionally also the effects of PSC (e.g., Garden et al. 2007). Tropical small mammals are a diverse group of animals that often serve as important seed predators and dispersers (e.g., Bricker et al. 2010; Grenha et al. 2010) and a food source for predator populations (e.g., Wang 2002; Bianchi et al. 2010). Therefore, tropical small mammals are important for evaluating potential cascading effects of forest structural and compositional shifts under environmental change (Pardini et al. 2010). Small mammal composition has been shown to be more influenced by VS (Garden et al. 2007). Yet, these results were based on univariate indices of plant species richness or diversity rather than PSC. Such simplification, however, could mask the relationships between these groups. The goal of this study is to compare the predictive power of VS versus PSC for tropical small mammal assemblages in a fragmented landscape of the Atlantic Forest, a tropical biodiversity hotspot. Based on previous studies, we expected that (i) plant species composition would be a stronger predictor of small mammal assemblages than vegetation structure, given the potential for species-specific plant-mammal associations, and (ii) vegetation structure and composition would explain complementary portions of the variation in small mammal composition. Clarifying these expectations in a highly diverse tropical system is important because most previous studies have focused on temperate regions, where plant diversity is lower, and because disentangling the relative roles of vegetation structure and composition has implications for both ecological theory and the management of fragmented forests.

2 | Materials and Methods

2.1 | Study Area

We sampled 20 study sites comprised of one continuous forest and 19 forest fragments located in the Guapi-Macacu river basin, in the municipalities of Cachoeiras de Macacu (22°28′ S 42°39′ W) and Guapimirim (22°2′ S 42°59′ W), Rio de Janeiro State, Brazil (Figure 1). The region has a long history of human settlement and is currently comprised of small forest fragments (< 200 ha) with different fragmentation histories and disturbances (e.g., fire, wood extraction, cattle ranging; Vieira et al. 2009; Finotti et al. 2012). The matrix includes variable intensity urbanisation and agriculture (e.g., plantations and pastures). The climate is mild-humid-mesothermic (Nimer 1994). All sample sites were located below 200 m.a.s.l., ranging between 15 and 243 ha in size for the fragments; the continuous site has more than 10 000 ha (Supporting Information S1).

2.2 | Vegetation Structure Data Sets

At each site, four 280 m long transects were established from the centre to the edge of forest fragments or from the interior to the edge of the continuous site. Transects were oriented at different cardinal directions and included 15 sampling stations arranged 20 m apart along each transect. Each sampling station included a 3-m radius plot where five VS variables were measured: 1—vines; 2—logs; 3—predominant size of trees; 4—degree of openness of the canopy; and 5—degree of openness of the understory. Variables 1 and 2, were measured as present or absent. For variable 3, all standing trees ≥ 5 cm diameter at breast height (DBH) within the 3 m radius plots were measured and assigned to classes: small size refers to trees with a circumference at breast height (CBH) < 30 cm, medium between 31 and 70 cm CBH and large CBH > 71 cm. Vines were recorded as present if climbing plants were rooted within the plot. Logs were recorded if woody trunks > 5 cm diameter were present on the ground. Variable 4 was measured as the vegetation density immediately above the sampling station, with the observer looking through a vertical axis of forest structure and including both canopy cover and understory vegetation density. Our last VS variable, the degree

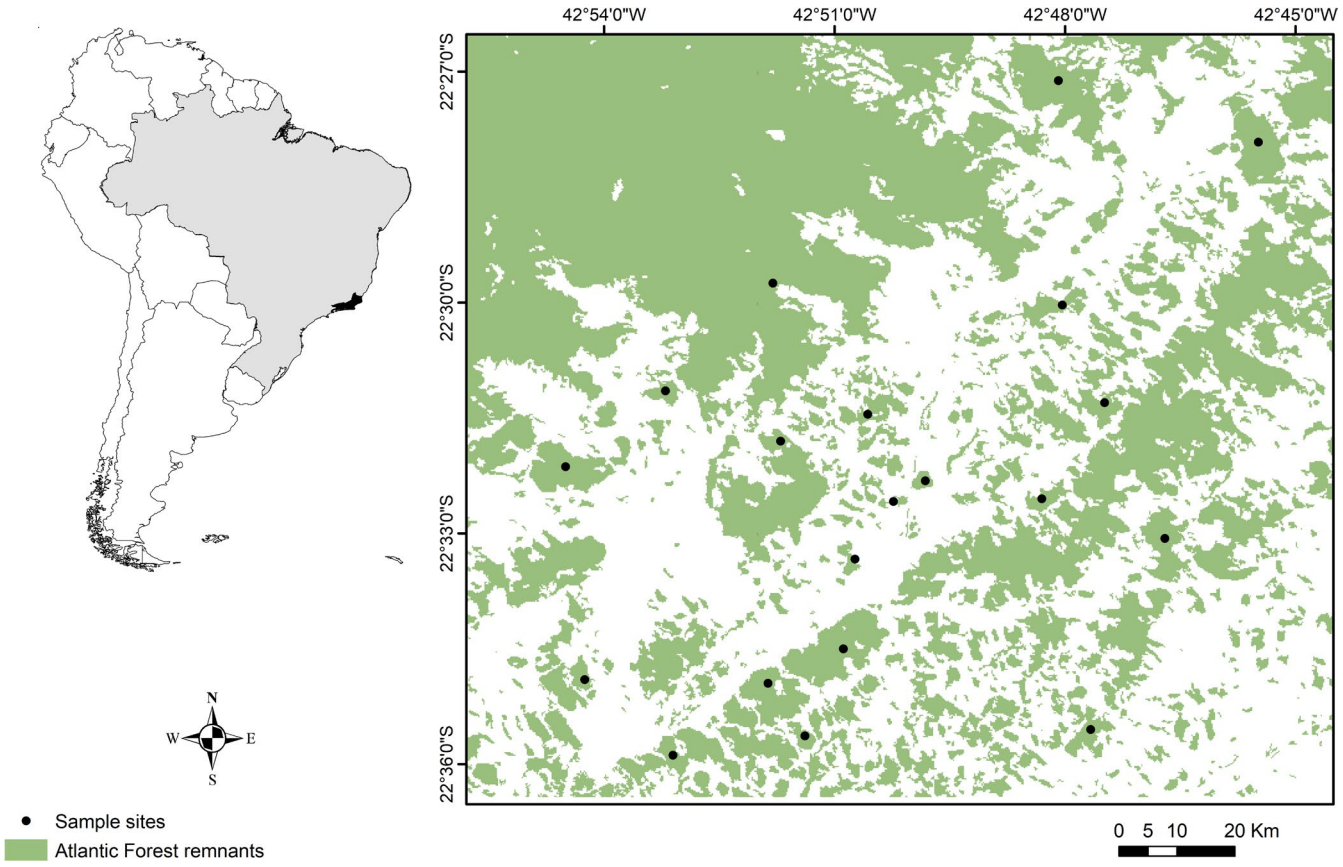


FIGURE 1 | Study site locations (black dots) within Atlantic Forest remnants (green) at Guapi-Macacu river basin, Rio de Janeiro estate (inset map in black), Brazil (grey).

of openness of the understory, was measured as the vegetation density around the trap station, with the observer looking through a horizontal axis of forest structure. Variables 4 and 5 were classified into three categories: 1—open, 2—semi-open and 3—closed. Measurements of the variables in the field were standardised, and bias was minimised by reducing the number of observers and training the observers in the same protocols. This minimised inter-observer bias in data collection. Values for all sampling stations of the same site were added, generating an aggregated score for each variable per site, that was used in the analysis (for more details, see Delciellos et al. 2016; Delciellos et al. 2018).

2.3 | Woody Plant Compositional Data Sets

Woody plant species composition (PSC) was sampled at three sampling units of 50 × 5 m each, located at least 65 m from the forest edge to minimise direct edge effects, totaling 750 m^2 of sample area per site. The sampling units were oriented parallel to the forest edge and placed 10 m apart from each other, both laterally and longitudinally, in a staggered arrangement resembling steps of a ladder. All standing woody plants ≥ 5 cm diameter at breast height (DBH) were identified to species within each sample unit; thus, PSC here refers specifically to woody vegetation, and does not include ground-layer forbs, grasses, ferns, or shrubs below this threshold. Some sites were originally sampled with a distinct effort (10000 m^2, the five sites sampled by Finotti et al. 2012; Supporting Information S1). To make sampling in these five sites comparable to the other sites, individuals were resampled up to the mean number of individuals sampled in all other 15 sites ($N = 177$) using the *sample* function from the *base* package in R environment (R Core Team 2022).

2.4 | Small Mammal Compositional Data Sets

Small mammals were surveyed during two discrete sampling periods: 1999–2001 and 2005–2009. Eight sites were sampled between 1999 and 2001, and the remaining 12 sites between 2005 and 2009. The first set of sites (1999–2001) was surveyed in both rainy and dry seasons, but because no difference in species composition was detected between seasons (Vieira et al. 2009), only the first survey from each site was retained for analysis. The later set of sites (2005–2009) was surveyed once each. A detailed account of the year in which small mammal, vegetation structure, and woody plant composition data were collected for each fragment is provided in Supporting Information S1.

A constant sampling effort of 600 trap-nights per forest fragment was applied. Each sampling station (the same described in the 'Vegetation structure data sets' section) had two live traps: one Sherman (model XLK, 7.6 × 9.5 × 30.5 cm; H.B. Sherman Trap Company, Tallahassee, USA) and one Tomahawk (model 201, 40.6 × 12.7 × 12.7 cm; Tomahawk Live Trap Company, Tomahawk, USA). In six sampling stations per transect, one trap was set 1–2 m above the ground, alternating the trap type (Sherman or Tomahawk) between stations. Traps were checked

early in the morning and rebaited if necessary with a mixture of peanut-based butter, banana, oats and bacon.

Animals were not individually marked, as the study focused on assemblage composition rather than population estimates, and our design aimed to minimise recaptures. From 1999 to 2001, captures were euthanized and deposited in the Museu Nacional – Universidade Federal do Rio de Janeiro, as part of the PROBIO Project (MMA/GEF). From 2005 to 2009, all individuals identified to species were housed in plastic cages, provided food and water *ad libitum*, and released at their original capture sites at the end of each trapping session; only individuals that could not be identified in the field were euthanized. Captures were relocated at least 100 m away into similar forest habitat during sampling sessions, following IBAMA/MMA permit conditions (authorizations number 87/05-RJ, 009-06-RJ, 13861-1, 13861-2, 16703). Trapping and handling procedures conformed to the guidelines of the American Society of Mammologists (Sikes et al. 2011). See Vieira et al. (2009), Delciellos et al. (2016) and Delciellos et al. (2018) for additional details on small mammal sampling protocols.

2.5 | Data Analysis

We used predictive versions of canonical correspondence analysis (partial least squares extension, CCA-PLS) to predict small mammal composition using VS, and co-correspondence analysis (CoCA) to predict small mammal composition using PSC (ter Braak and Schaffers 2004; Schaffers et al. 2008). All analyses were conducted using abundance data for both small mammals and woody plant species. Model fit was evaluated using a leave-one-out cross-validatory procedure, in which models were tuned each time withholding a site to serve as the test data until all sites were used in validation. Prediction accuracy was assessed with the cross-validatory fit (%), calculated as:

$$cross-validatory\ fit = 100\left(\frac{1-ssp_n}{ssp_0}\right)$$

with ssp_n as the sum of square prediction errors using n axes, and ssp_0 as the sum of the square prediction errors under the null model of no relationship. Cross-validatory fit (CVfit) values are notably lower compared to values customary in explanatory methods, but do not imply weak relationships (ter Braak and Schaffers 2004; Schaffers et al. 2008). Rather, a CVfit greater than zero indicates that the model prediction is better than expected by chance. We used simple randomisation tests (999 permutations; van der Voet 1994) to compare whether the prediction accuracies between VS and PSC were statistical different. We chose the number of ordination axes for final interpretation according to the predictive fit (Schaffers et al. 2008), only maintaining axes with CVfit above zero. We also evaluated the effect of rare species on the results by excluding species that were only present once in the data set (singletons). As anticipated, this adjustment affected the predictability of the datasets, but did not yield statistically significant changes. The results presented here include the removal of singleton species.

Additionally, to understand the role of each plant species in the prediction of small mammal composition, the analysis was repeated, this time withholding one plant species at a time (Müller et al. 2011). If the removal of a plant species caused a drop in the CVfit value, that plant species is an important species for the prediction of small mammal composition. The same approach was done for the VS variables. All analyses were conducted in the R environment (R Core Team 2022). We used the *cocorresp* package (Simpson 2009) for CoCA analysis, whereas canonical correspondence analysis was implemented by adapting functions in *cocorresp* and scripts available in the supporting information of ter Braak and Schaffers (2004).

3 | Results

Our final data set comprised 12 small mammal species and 213 plant species. Mean richness was 3 (±1.61 SD) small mammal species and 41.5 (±15.36 SD) plant species per study site. For small mammals, the most abundant species was *Philander frenatus* ($N=243$), followed by *Marmosa paraguayana* ($N=36$). The most abundant plants were *Astrocaryum aculeatissimum* ($N=237$) and *Miconia prasina* ($N=151$). The two predictive data sets, based on VS and PSC, showed cross-validatory fit above zero, rejecting the null hypothesis of no relationship with the small mammal species composition (Figure 2). Final models included one and two axes for VS and PSC, respectively (Table 1). Plant species composition (2.92%) explained slightly more variation in small mammal composition than VS (1.73%). However, this difference was statistically insignificant according to the randomisation tests ($p=0.87$).

Plant species composition biplot shows a complex relationship with small mammal composition, with a gradient based on forest fragment size (Figure 3 and Figure 5). Regarding VS, a regular CCA biplot shows logs ($p=0.017$) and the size of trees ($p=0.063$) as the most important variables to explain small mammal composition (Figures 4 and 5).

The removal of one plant species at a time showed that *Senefeldera verticillata* was the species that, when removed, caused the most drop in CVfit value (new CVfit at 0.5636 for the first axis), followed by *Myrcia multiflora* (2.4007) and *Guarea guidonia* (2.4205) (Figure 6). The removal of vegetation structure

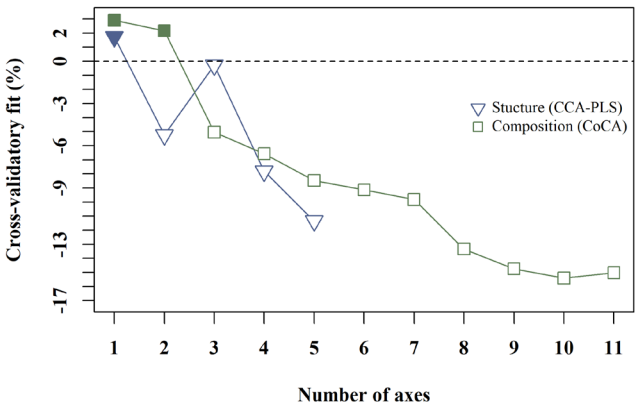


FIGURE 2 | Prediction levels (% cross validatory fit) of small mammals' composition by the structural and compositional data sets, and methods (CCA-PLS = canonical correspondence analysis-partial least squares; CoCA = co-correspondence analysis). Filled symbols represent selected axes for each model.

variables caused a drop in CVfit values in all cases (Figure 7). Understory and the size of trees were the variables that caused the most drop in CVfit values (Figure 7).

4 | Discussion

In this study, we compared the predictive power between VS and PSC for small mammal communities in a fragmented landscape in the Atlantic Forest biome. We showed that VS and PSC present complementary effects on small mammal species composition. Our findings go against previous studies that found a stronger effect of either PSC (e.g., Uboni et al. 2019; Adams and Matthews 2019) or VS (Müller et al. 2010). However, this result is in hand with other studies evaluating the effects of VS and PSC on small mammal communities (Garden et al. 2007).

TABLE 1 | Prediction levels (% cross validatory fit) of the final models for the composition of small mammals and plant communities constrained by vegetation structure or composition.

	Dependent matrix	
Independent matrix (model)	**Plant composition**	**Small mammal composition**
Structure (CCA-PLS)	−2.24	1.73
Composition (CoCA)	—	2.92

Abbreviations: CCA-PLS, canonical correspondence analysis-partial least squares extension; CoCA, co-correspondence analysis.

Such low explanatory fit difference between VS and PSC may be related to the greater species richness of plants found in the study area. Until now, most of the published papers using such analysis were done in temperate regions, with a much lower plant species richness than the one presented here (e.g., Müller et al. 2010; Nyafwono et al. 2015; Adams and Matthews 2019). Another factor that could be affecting our results is the ecological scale of the analysis. For example, VS is thought to be most important at broad spatial scales and floristics at more local scales (Rotenberry 1985; Wiens et al. 1987).

Typically, there is a higher number of animal and plant species, as well as interactions, in landscapes with greater vegetation coverage (Hanski et al. 2013; Marjakangas et al. 2021). The predictive power demonstrated by PSC may be a direct result of species-specific relationships between communities. Examples of such interactions for small mammal communities are not as common as for other animal groups (e.g., Gabbe et al. 2002; Bakermans and Rodewald 2009; Wood et al. 2012). For small mammals, there is more information regarding the effect on seedling communities and seed banks (e.g., Dybzinski and Tilman 2012; Culot et al. 2017; Guiden et al. 2019). Studies addressing the feeding habits of small mammal species often demonstrate the consumption of seeds from certain species or genera particularly by rodent or marsupial species (e.g., Carvalho et al. 1999; Casella and Cáceres 2006; Lessa and Costa 2010).

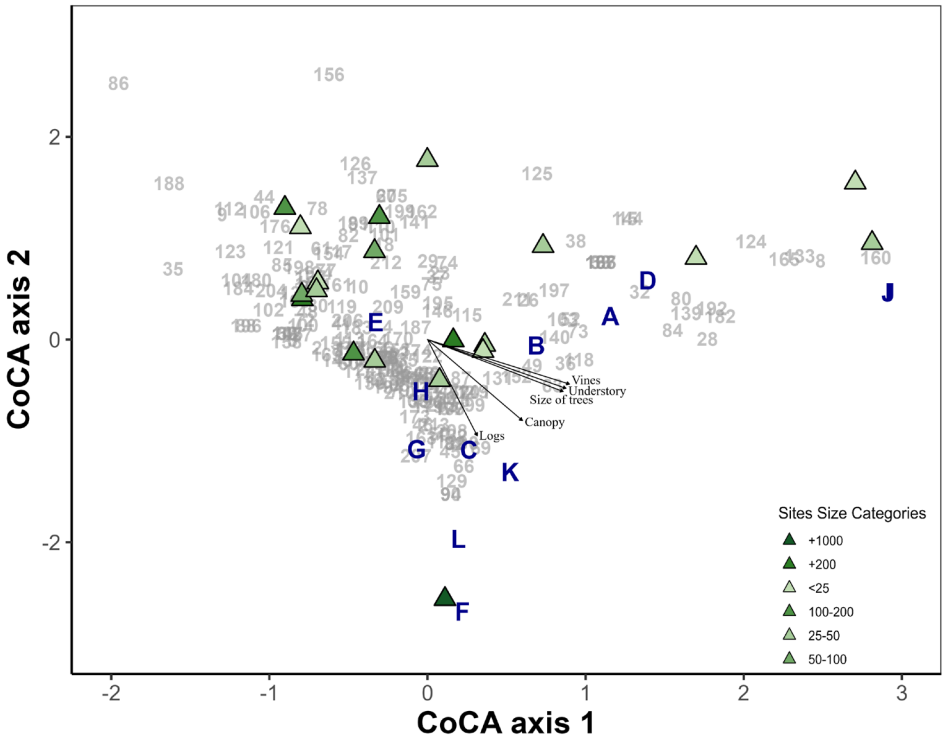


FIGURE 3 | Predictive co-correspondence analysis ordination diagram of small mammals' species composition constrained by plant species composition. Small mammal species are positioned by normalised values of sampled sites, derived from the plant species composition. Vegetation structure vectors (not used in the ordination) were added for interpretation purposes. Triangles represent sampled sites, numbers represent plant species composition, while letters represent small mammal species composition; see Figure 5 for identification. (CoCA = co-correspondence analysis).

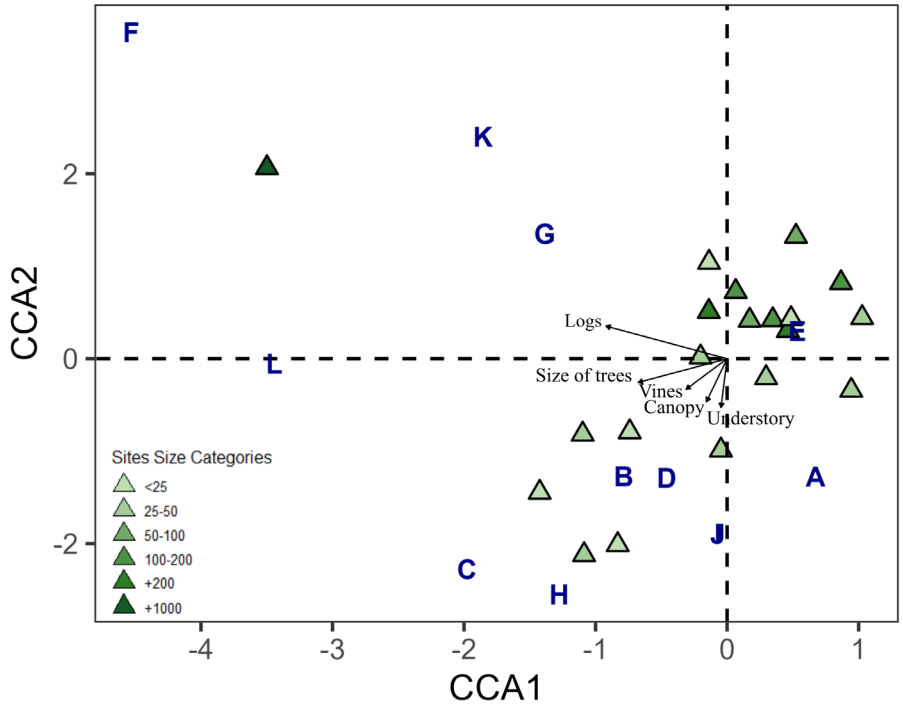


FIGURE 4 | Regular canonical correspondence analysis ordination diagram of small mammal's species composition by vegetation structure predictor set. Triangles represent sampled sites, letters represent small mammal's species composition, see Figure 5 for identification. (CCA = canonical correspondence analysis).

The outcome presented by PSC may not solely be a direct floristic effect, as the composition itself encapsulates other factors that might be responsible for determining use by fauna, in addition to species-specific preferences. This is because plants themselves respond to environmental conditions and contribute to defining and modifying the environment through their growth (as interpreted by Schaffers et al. 2008). Consequently, the correspondence could result from shared responses to the same set of conditions, whether these are shared with small mammal communities or not.

In our ordination, it was only possible to determine a partial segregation among the sampled sites based on site size. Although our intention was not to compare the effects of such environmental variables, their combination with VS variables could reveal other patterns. This may be an effect of the number of sampled sites or the sizes of these sites. Even though our sites show a wide variation in size (Supporting Information S1), the lack of more sites with larger areas might also be what prevented such segregation. Previous studies that demonstrated a greater influence of VS used data from sites spread over a large geographic range, while those reporting a greater influence of PSC used data from a smaller number of sites and less diverse locations (MacNally 1990).

According to a regular CCA, logs and the size of trees were the most important variables for small mammals' composition (Figure 4). Logs can represent patches of food for small mammals, offering fungi and invertebrates, besides their use as shelter, and as straight and quick locomotion venues inside forests (Bowman et al. 2001; Bellows et al. 2001; Dewalt et al. 2003). They can also help to promote the structural complexity of the forest and may also contribute to the enhancement of community diversity (Bowman and Facelli 2013).

However, it is important to highlight that the VS was not a good predictor of PSC for our study area (Table 1). Such a result could be related to the variables we used to determine the VS. However, the chosen variables are commonly used in other studies that have investigated VS as a determining factor for small mammal communities (e.g., Püttker et al. 2008; Delciellos et al. 2016). Furthermore, something relevant to mention is the possibility of effects obscured by functional redundancy. Our PSC data included several species belonging to the same genus, as well as species with similar characteristics. This factor could have influenced the overall effect presented by the plant community.

Delciellos et al. (2016) compared the influence of local habitat quality (vegetation structure variables such as shrub density, canopy openness and litter cover) and landscape attributes (e.g., patch size, connectivity and forest cover) on small mammal assemblages in the same Atlantic Forest fragments that we studied here. They found that habitat quality explained small mammal composition as much as, or even more than, landscape metrics. In our study, we found that PSC was at least as important as VS for small mammals, which suggests that plant species composition may have an even stronger effect on assemblages than landscape context alone. This highlights the need for future studies to consider both floristic composition and structural or landscape factors when investigating animal community assembly.

The local communities of small mammals in the Guapi-Macacu Basin have been the focus of several studies aimed at assessing the determining factors of their composition



FIGURE 5 | Identification of species used in Figures 3 and 4. Numbers represent plant species, and letters represent small mammal species.

and structure (e.g., Vieira et al. 2009; Delciellos et al. 2016; Delciellos et al. 2018). However, for the first time, it was possible to associate species of small mammals with the group of plants. Since VS is directly related to disturbances and the degree of forest structuring, it is likely that PSC is also partly associated with past disturbances, as well as plant–animal relationships for the species involved. Thus, PSC may have greater predictive capacity than VS, already demonstrated as an important factor in other studies. Future work aiming to understand the role played by VS and PSC may consider data from a broader geographic range, with diverse size classes among fragments, and if possible, fragments in different successional stages. Moreover, testing the effects for different taxonomic groups may also be considered.

Beyond vegetation structure and composition, other unmeasured factors such as soil type, moisture, predator presence, and recent climatic events may also shape mammal assemblages. Although we lacked comparable data across sites to incorporate these variables into our models, we acknowledge that they may contribute to unexplained variation in our results. It is also important to note that PSC in our study was restricted to woody plants ≥ 5 cm DBH. Excluding ground and shrub strata may underestimate the influence of lower vegetation layers on small mammal assemblages, which provide food and cover for many species. This limitation should be considered when interpreting our results and comparing them with studies that assessed whole-plant community composition.

Overall, our findings demonstrate that woody vegetation composition and structure play complementary roles in shaping small mammal assemblages. Recognising this complementarity has important implications for both research and conservation. From a theoretical perspective, it highlights the need to integrate

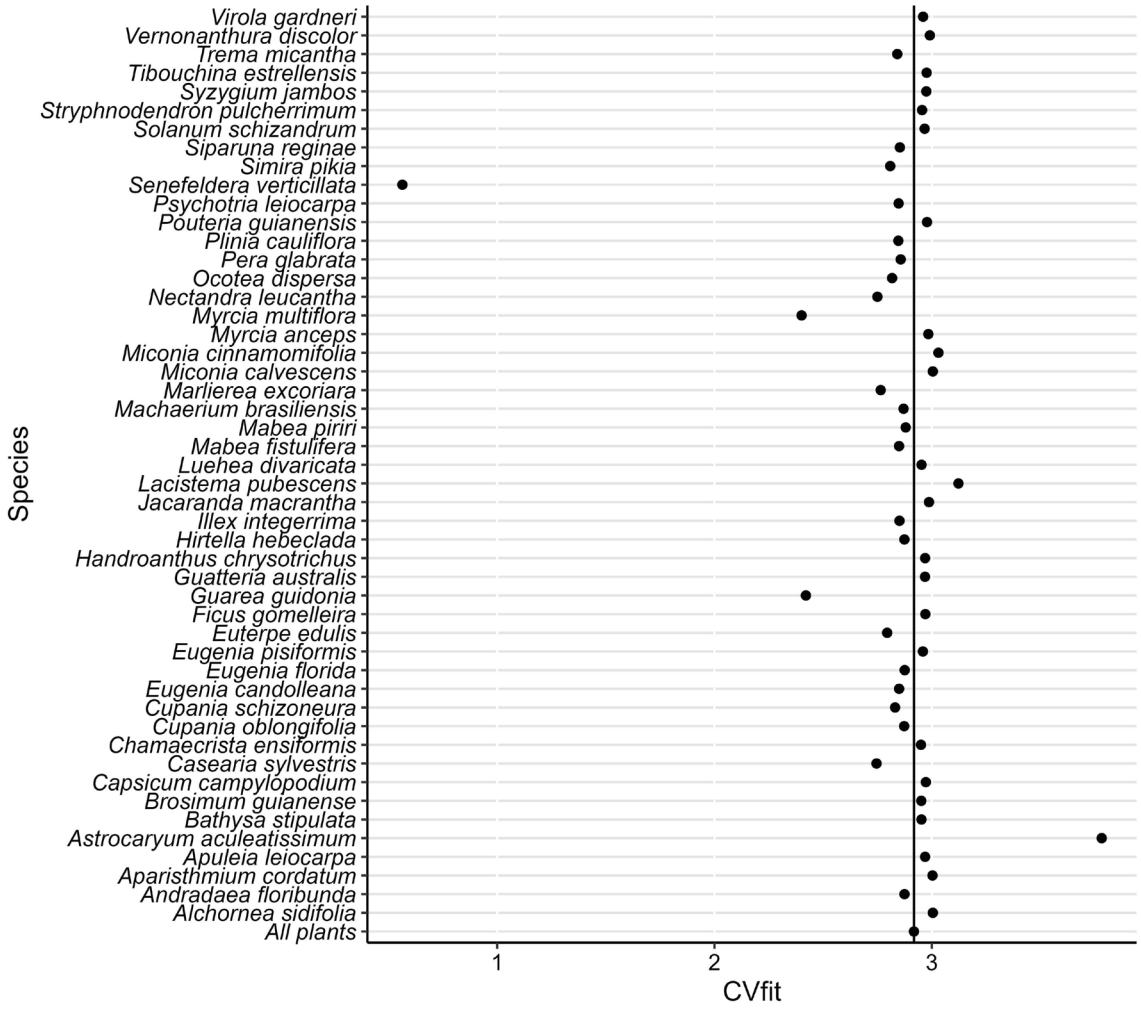


FIGURE 6 | Plotting of CVfit changes when removing one plant species at a time. Plotting only shows the difference in CVfit from the 49 plant species that caused the greater differences in CVfit values.

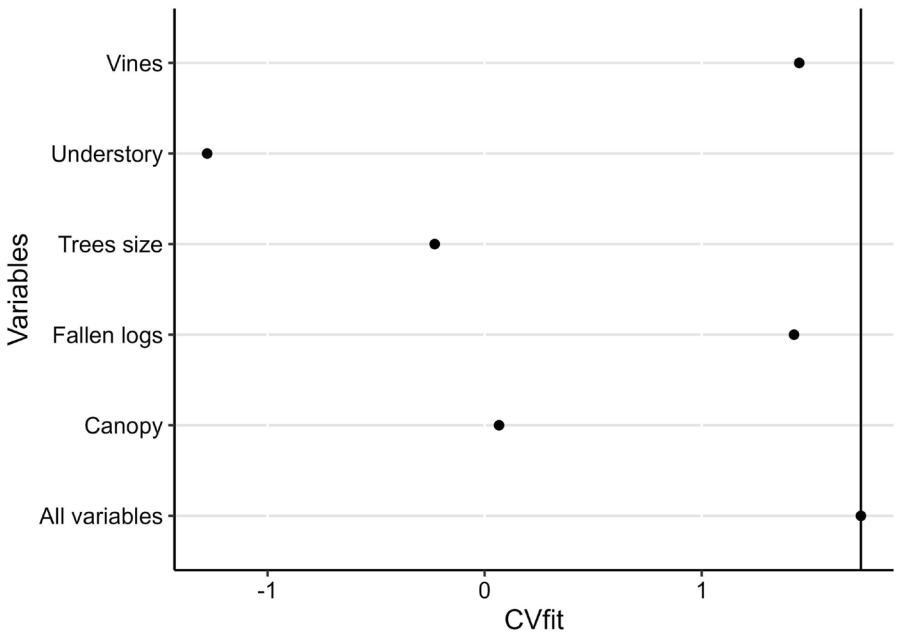


FIGURE 7 | Plotting of CVfit changes when removing one vegetation structure variable at a time.

structural and floristic components of vegetation in studies of animal community assembly. From a management perspective, our results suggest that maintaining or restoring woody plant diversity, alongside structural heterogeneity, may enhance the capacity of fragmented tropical landscapes to sustain diverse small mammal communities. This is particularly relevant in the Atlantic Forest, where conservation strategies often emphasise structural metrics (e.g., canopy cover, patch size), but may overlook the contribution of floristic composition to biodiversity persistence.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data used in the current study is available from the corresponding author on reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** aec70142-sup-0001-supinfo.docx.