

Functional assembly of tropical montane tree islands in the Atlantic forest is shaped by stress-tolerance, bamboo-invasion and facilitation

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Abstract

Aims:

Amidst the Campos the Altitude (Highland Grasslands) in the Brazilian Atlantic Forest, woody communities grow either clustered in tree islands or interspersed within the herbaceous matrix. The functional ecology, diversity and biotic processes shaping these communities are largely unstudied. We characterized the functional assembly and diversity of these tropical montane woody communities and investigated how those communities fit within the Grime's CSR (C – competitor, S – stress-tolerant, R – ruderal) scheme, what trade-offs they exhibit and how traits and functional diversity vary in response to bamboo invasion.

Methods:

We sampled five leaf traits and wood density along transects covering the woody communities both inside tree islands and outside (i.e. woody plants in the grasslands community) to characterize the functional ecology of the community. We used Kruskal-Wallis test, t-test and variation partitioning to determine effects of inside vs outside the tree island and bamboo invasion on traits, woody species diversity and functional diversity.

Results:

We found a general SC/S strategy with drought-related functional trade-offs. Woody plants in tree islands had more acquisitive traits, whereas woody plants within the grasslands had more conservative traits. Trait variation was mostly taxonomically driven, and species composition varied between inside and outside tree islands. Leaf thickness, wood density and foliar water uptake were unrelated to CSR-strategies, suggesting independent trait dimensions and multiple drought-coping strategies within the predominant S-strategy. Bamboo-invaded islands showed lower Simpson diversity, lower functional dispersion, lower foliar water uptake and greater leaf thickness than non-invaded tree islands.

Conclusions:

The observed functional assembly in response to bamboo and facilitation have implications for future forest expansion and response of the communities to climate change. Further studies on eco-physiological and establishment traits and the mechanisms behind biotic interactions are needed to better understand the response of these communities to future environmental changes.

1. INTRODUCTION

Tropical montane ecosystems harbour exceptionally high biodiversity, due to a combination of unique abiotic conditions and isolation (Aparecido *et al.* 2018; Safford, 1999). They provide important ecosystem services worldwide (Aparecido *et al.* 2018) but are threatened by global environmental changes (Oliveira *et al.* 2014, Assis and de Mattos, 2016), such as drought caused by reductions in fog exposure (Eller *et al.* 2016). Tropical mountain ecosystems in the Brazilian Atlantic Forest are found above 1500 m asl, where diverse micro-environmental conditions give rise to various vegetation formations from grasslands and shrublands to bogs (Christmann and Oliveras 2020). These ecosystems are called Campos de Altitude and are characterised by grass-dominated mountaintop formations restricted to the highest summits of the south-eastern Brazilian Highlands (Safford, 1999). Abiotic factors such as recurring drought, frost and rainfall seasonality (Safford, 1999b), as well as

temporary disturbances (fire, mechanical damage) shape the physiognomy and composition of the vegetation in the Campos de Altitude (Assis and de Mattos 2016), which shows a large functional and eco-physiological diversity (Scarano et al. 2001; Duarte et al. 2005; Matos et al. 2020).

The grassland communities of the Campos de Altitude have been well characterised (Scarano 2009; Assis and de Mattos 2016; Matos et al. 2020). However, the woody communities, occurring either in tree islands or as interspersed individuals within the grasslands, have been overlooked. Tree islands are ‘clusters of two or more trees surrounded by a dissimilar vegetation type’ and are characteristic features in alpine ecotones (Resler and Stine 2009). In mountain regions tree islands often occur as part of the tree line ecotone where small-scale topographic features improve edapho-climatic conditions for tree growth, while between tree islands seedling mortality limits tree establishment (Harsch and Bader 2011). Trees in islands persist due to positive feedback mechanisms caused by micro-climatic facilitation inside islands that ameliorates and reduces exposure to harsh conditions, even promoting tree infilling and tree island expansion (Resler and Stine 2009; Albertsen et al. 2014). The edges of tree islands can harbour safe sites for grassland species, as reported for tree islands at the forest-tundra ecotone (Albertsen et al. 2014).

The presence of these tree islands in the Campos de Altitude could be explained by two hypotheses. First, tree islands could be remnants from time of fire absence in these areas; an increase in fire frequency in the last centuries might have restricted montane forest expansion, notably in the mountains of Itatiaia National Park (Behling et al. 2020). Second, those islands could be a result of recent woody encroachment of the herbaceous communities of the Campos de Altitude, as observed for tree islands in temperate alpine regions which were shown to provide microclimatic shelter and enable further tree establishment (Resler and Stine 2009).

The assembly of these woody communities can be studied through the lens of community ecology. Abiotic filters and biotic interactions select a subset of species able to survive and coexist in a given environment (reviewed in Cadotte & Tucker, 2017; Kraft et al. 2015). The two main biotic processes acting at the community level are competition and facilitation (see Brooker et al. 2008). Competition

refers to negative interactions between co-occurring plants, and can negatively impact the establishment and growth of the woody community and the tree islands. On the other hand, facilitation is a positive interaction mediated through amelioration in the physical environment and has been described as an important process in high altitude ecosystems, where many species are at their physiological limits of survival (Callaway et al. 2002).

The study of functional traits (*sensu* Violle et al. 2007) has become one of the most promising ways to understand the assembly of plant communities and their response to environmental change (Funk et al. 2017; Lavorel & Garnier, 2002; McGill et al. 2006). Because of developmental, evolutionary and environmental constraints, functional traits exhibit different levels of coordination and trade-offs, leading to sets of traits related to the same function; (Chapin et al. 1993, Delhayé et al. 2020, Wright et al. 2004). At the global scale, the leaf economic spectrum (Wright et al. 2004), the wood economic spectrum (Chave et al. 2009) and the whole plant economics spectrum (Reich 2014) have been widely used to classify species along a continuum from fast growth and high resources acquisition to slow growth and high resource conservation. Another classification of strategies based on those trade-offs is the CSR-strategy (Grime, 1977), which categorizes plants as competitor (C), stress-tolerant (S) or ruderal (R). This can be done based on three easily measurable leaf traits - leaf area (LA), specific leaf area (SLA) and leaf dry matter content (LDMC) – which together allow the determination of individual based CSR percentages (Pierce et al. 2017). CSR-analysis can help predict how species will respond to changes in biogeochemical cycles, climate and land-use variation (Pierce et al. 2017) and has proven successful to investigate many ecological processes in a variety of environments (e.g. Li and Shipley 2017; Pierce et al. 2017; Rosado and de Mattos 2017), including the grassland community of the Campos de Altitude (Matos et al. 2020).

In the Campos de Altitude abiotic factors such as recurring drought and frost (Safford 1999a) shape the grassland community, pushing species towards stress-tolerant ecological strategies (Matos et al. 2020). However, the species in these communities can differ in relation to eco-physiological integrative traits (such as foliar water uptake) (Matos et al. 2020). Integrative traits reflect the results of the combinations of multiple functional traits and are more responsive to environmental factors

(Rosado and de Mattos 2017). A multivariate analysis of morphological and physiological traits of the grassland community by Matos et al. (2020) showed a first trait dimension of drought resistance (via high LDMC and high stem specific density) vs resilience (via high re-sprout ability and high leaf water potential at turgor loss point). Thereby, stress-tolerant plants (S) showed traits associated with drought-resistance (e.g. high LDMC and high stem specific density) while competitive-ruderal (CR) plants showed more acquisitive traits and drought-escape through resprouting ability and large seed size. The second trait dimension was underlined by a trade-off between water storage (via succulence) vs. water absorption (via foliar water uptake). CR-species showed a tendency towards water absorption, while species with a mixture of stress-tolerance and competitiveness (CS) exhibited water storage traits (Matos et al. 2020). However, the ecological strategies and eco-physiology of woody communities above the tree line and particularly in the tree islands are still unknown.

Regarding the effect of biotic interactions, because of their physiognomy, tree islands could provide shelter through facilitation and favour tree infilling (Resler and Stine 2009; Mendoza-Hernández et al. 2013; Albertsen et al. 2014). On the other hand, strong competitive interactions could be expected from the invasion of tree islands by the dwarf bamboo species *Chusquea pinifolia*, a clear stress-tolerant (S) species (Matos et al. 2020), which is abundant and native in the Campos de Altitude (Safford, 1999a) and occurs both within the grasslands and inside the tree islands. Other species of *Chusquea* have been shown to turn into aggressive colonizers under disturbance, modifying vegetation structure, soil and nutrient properties, and decreasing woody species diversity elsewhere, even within their native ranges (Pagad 2016). Therefore, the presence of *C. pinifolia* could negatively affect the ecology and functional composition of the tree islands.

Here, we characterised the functional composition of 10 tree islands and their neighbouring woody communities, using six traits related to the plant economics spectrum and water use. We evaluate the effect of facilitation and bamboo invasion on the community trait composition. Our overarching hypothesis is that environmental abiotic conditions shape the woody communities by selecting for a set of conservative traits and a stress-tolerant strategy, with bamboo influencing trait assembly and reducing diversity of invaded islands. Specifically, we expect 1) a strong S-selection in the woody

communities, supported by a set of conservative functional trait values (e.g. high LDMC, high wood density, low SLA) and trade-offs due to harsh abiotic conditions; 2) less conservative trait values of woody plants inside tree islands compared to woody plants within the grasslands due to facilitative processes; 3) differences in species composition and traits associated to stress tolerance strategy in bamboo invaded in comparison to non-invaded tree islands. We further expect a decrease in woody taxonomic and functional diversity due to a convergence to a more water conservative strategy due to competitive effects in bamboo invaded islands.

2. MATERIALS AND METHODS

2.1 STUDY AREA

The study was conducted in the Campos de Altitude of the Itatiaia National Park in the Brazilian Atlantic Forest. The Campos de Altitude are found in Rio de Janeiro state (22°22'37"S 44°42'28"W) above the treeline which lies between 1800 and 2300m asl, and are cool-humid, grass-dominated mountaintop formations restricted to the highest summits of the south-eastern Brazilian Highlands (Fig. 1). Soils in the Campos vary locally depending on hydrology and topography, but are generally moderately fertile, with dark-humic upper horizons and argillic-podzolized lower horizons across the altiplano (Safford, 1999a). The climate in Itatiaia has subtropical and temperate influences with a pronounced dry season between May and October (Koeppen-Geiger Cwa). Mean temperature is 14.4 °C and yearly precipitation is between 2,000 and 2,200 mm (Segadas-Vianna and Dau 1961). Frost occurs on average 56 days per year and fog 218 days per year (Safford, 1999a). Fires recur yearly, most of which are anthropogenically caused (Aximoff and de Carvalho Rodrigues 2011).

2.2 DATA COLLECTION

Ten woody communities were assessed through 20m transects covering 10m inside the tree island (hereafter 'inside') and 10m outside of the edge of the island within the grasslands (hereafter 'outside'), all maintaining a South-North aspect (Fig.1b, Supp. Tab.1). Therefore, there were 10 'inside' subcommunities and 10 'outside' subcommunities (Fig. 1a). The edge of the tree island was defined as the last woody species higher than > 2m with a canopy overlap with the trees in the tree

island. Sampling of woody plants was done with a point centred quarter method every 2.5m. The closest rooted individual to the centre point taller than 1m within each 1.25x1.25m quadrant was sampled and tagged. If the closest individual was outside the quadrant it was regarded as empty. Minimum distance between islands was 100m and maximum distance 3.5km. Woody communities inside tree islands were classified binarily as bamboo-invaded or non-bamboo invaded in field observations (Fig. 1b), as they were either overgrown by bamboo or completely non-invaded. We assessed five bamboo-invaded and five non invaded tree island subcommunities (Fig. 1a). Further information on the tree islands are available in Supp. Tab.S1.

We measured leaf dry matter content (LDMC [g/cm^3]), leaf area (LA [cm]), specific leaf area (SLA [cm/g^2]) and leaf thickness (LT [mm]) on five intact fully developed sun leaves. Wood density (WD [g/cm^3]) was measured on one piece of branch wood. All trait measurement followed Pérez-Harguindeguy et al. (2013) (see Supp. Methods 1 for exact measurement procedures).

Foliar water uptake (FWU, [%]) was measured based on the protocol of Limm et al. (2009) on three mature and healthy leaves and calculated as the percentage increment in leaf water content after submersion (see Supp. Methods 2). FWU was then averaged across three leaves for each sampled tree to obtain a mean value.

Since ecosystem functions are largely determined by the abundant and dominant species (see Avolio et al. 2019) for analysis comparing variation of traits or strategy between and within species, we focused on eight dominant species, which comprised 80% of all sampled woody plants.

2.3 DATA ANALYSIS

Data processing was carried out in Microsoft Excel® and data analysis in R (version 4.0.2) using the R studio interface (Version 1.2.1335).

CSR strategy and trade-offs

To test if the woody community exhibits a strong S strategy, CSR values were calculated using the globally calibrated StrateFy tool in Excel (Pierce 2017) which uses a Principal component analysis (PCA) on three leaf functional traits to assign a percentage value for C, S and R strategy to each

sample. Mean and standard errors for the whole woody community, as well as for the eight ‘dominant’ species, were calculated for the traits and CSR percentages.

Traits and CSR-percentages were all non-normally distributed. Hence, to test for trade-offs and coordination between traits Spearman’s rank correlations were used to assess non-linear relationships between all traits and CSR-percentages on all sampled woody plants. We carried out a PCA on all six square-root transformed traits (Supp. Tab S2). However, a broken stick test showed that none of the components were significant and we therefore decided not to use the PCA outputs for further analysis.

Comparison between inside and outside tree islands

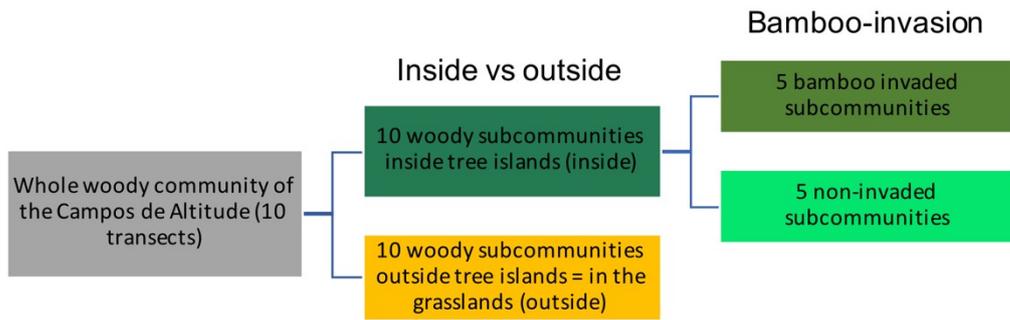
To compare trait assembly inside and outside tree islands, mean values and standard errors for all traits and CSR-percentages were computed across all woody communities inside and across all woody communities outside the tree islands. Differences in traits and vegetation strategy between woody plants growing inside and outside were tested with Mann Whitney test, since response variables were not normally distributed, and no transformation resulted in normality. We further compared community weighted means (CWM) (Supplementary methods 3), woody species richness and Simpson index between communities inside and outside tree islands with Mann Whitney test and calculated Sørensen similarity index (R-package 'vegan', Oksanen et al. 2019) to assess species similarity. We performed variation partitioning (R-package ‘lme4’, Bates et al. 2015) to examine trait variation in response to species-identity, inside vs outside and in response to differences between the 10 woody communities with a linear mixed effect model, similarly to Oliveras et al. (2020) (Supplementary methods 4).

Influence of bamboo on traits and diversity of tree islands

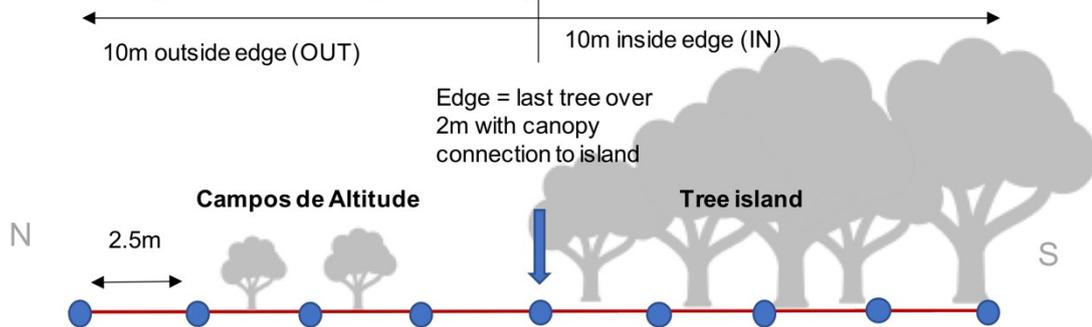
To test the effect of bamboo onto traits and diversity of the tree islands, only samples occurring inside (‘in’) the tree islands were used as response variables (see Fig. 1a). Tree islands were assigned a binary value of ‘b’ for bamboo-invaded or ‘n’ for non-invaded as a predictor variable. Difference in traits and CSR strategies between woody plants occurring in bamboo-invaded and non-invaded tree island were tested with Mann Whitney test. Differences in CWM between bamboo invaded inside-subcommunities and non-invaded inside-subcommunities were tested with Mann Whitney test.

Sørensen similarity index was calculated by comparing species abundances across all bamboo-invaded and all non-invaded tree islands. To assess differences in taxonomic and functional diversity between bamboo and non-invaded tree islands, woody species richness, Simpson index and Functional Dispersion were calculated for inside each tree island subcommunity (10 inside subcommunities, of which 5 bamboo-invaded and 5 non-invaded) as response variables. We calculated the Functional Dispersion index (FDis) with the R-package 'FD' (Laliberté et al. 2015) since it can be computed from any distance or dissimilarity measure, can handle any number and type of traits (including more traits than species, which was the case in some of the tree islands), and is not strongly influenced by outliers (Laliberte and Legendre 2010). The FDis index is by construction unaffected by species richness (Laliberté et al. 2015) which varied from 3-7 species between the tree islands. Functional Dispersion could not be calculated as a response variable to compare CWMs between inside and outside the tree islands (research question 2) because for three of the 'outside' subcommunities less than three species occurred. Since Simpson-index and FDis were not normally distributed, differences between bamboo-invaded and non-invaded tree island subcommunities were tested with Mann Whitney test, while differences in species richness were tested with t-test.

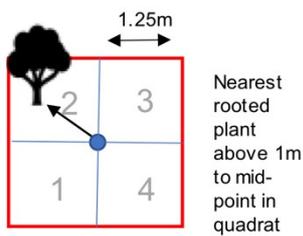
a) Community sampling



b) Transect design in each woody community



c) Bamboo classification



At every center point four 1.25x1.25m quadrats



Figure 1: a) Community sampling design b) Sampling along transects through the tree islands c)

Example of the inside of a bamboo and non-bamboo invaded island

3. RESULTS

3.1 CSR-STRATEGY, FUNCTIONAL ASSEMBLY AND TRADE-OFFS IN THE WOODY COMMUNITY

Across the 10 woody communities, we recorded a total of 24 woody species. Eight of those species (Tab.1) made up exactly 80% of the community and were considered as ‘dominant’ species in further analysis. 13 of all species occurred less than 3 times. Of all samples, 10 (5.6%) could not be identified to the species level, but to morpho-species. *Myrsine gardneriana* was the most abundant species (27%), followed by *Baccharis stylosa* (13.5%), *Myrsine umbellata*, *Pleroma trinervia* and *Archibaccharis serratifolia* (all 8-10%) (Tab.1).

Of the eight ‘dominant’ woody species *A. serratifolia* showed the highest average SLA (23.82 cm²/g) and the highest R-score (7.96%). *M. gardneriana* showed the highest average LA (18.46 cm²) and the highest C-score (31.87%), while *B. uncinella* showed the highest LDMC (0.5g/cm³), the highest FWU (60.36%) and the highest S-score (98.6%). The highest average WD was observed for the morpho-species of the genus *Symplocos* (1.09 g/cm³) (Tab.1).

The average vegetation class of the woody community was stress-tolerant (C: 23.64, S:73.05, R: 3.31), whereby S-strategy showed the highest standard error. CSR strategies differed significantly between the eight dominant species (Fig 2 a). Species predominantly growing mainly outside the tree islands (e.g. *P. trinervia*, *Symplocos sp.*, *B. uncinella*, *Gaultheria serrata*) showed the highest S-percentages and narrow strategy ranges, while species that occurred both inside and outside the tree islands (e.g. *M. gardneriana*, *Baccharis stylosa*, *A. serratifolia* and *M. umbellata*) had higher C-scores and greater ranges in C and S strategy.

The spearman correlation (Tab. 2) showed that SLA was negatively correlated to both LDMC ($\rho = -0.66$, $p < 0.01$) and LT ($\rho = -0.59$, $p < 0.01$). FWU was weakly negatively correlated to LT ($\rho = -0.32$, $p = 0.038$), yet uncorrelated to all other traits, as well as to CSR-percentages. CSR percentages were further uncorrelated to the three traits that did not feed into the CSR analysis: LT, WD and FWU.

Table 1: Mean and standard error for dominant species and whole community

Species	SLA [cm ² /g]	LA [cm ²]	LDMC [g/cm ³]	LT [mm]	WD [g/cm ³]	FWU [%]	C [%]	S [%]	R [%]	abundance [%]	Present inside or outside tree islands?
<i>Baccharis stylosa</i>	16.21 ±0.80 1	10.59 ±1.22	0.41 ±0.024	0.27 ±0.01 8	0.95 ±0.107	13.14 ±1.68	23.73 ±1.69	75.64 ±1.77	0.64 ±0.317	13.53	both
<i>Baccharis uncinella</i>	14.45 ±0.58 9	0.41 ±0.0198	0.50 ±0.042 7	0.29 ±0.01 6	0.61 ±0.072	60.36 ±11.1	1.40 ±0.203	98.60 ±0.20 3	0.00 ±0	4.12	out
<i>Archibaccharis serratifolia</i>	23.82 ±1.3	9.98 ±1.05	0.34 ±0.010	0.22 ±0.01 8	0.57 ±0.068	20.86 ±2.06	25.92 ±1.36	66.12 ±2.74	7.96 ±2.07	8.82	both
<i>Symplocos (morpho-species)</i>	14.68 ±0.95 2	3.73 ±0.819	0.40 ±0.010	0.30 ±0.02 8	1.09 ±0.2	10.66 ±3.77	14.24 ±2.19	85.76 ±2.2	0.00 ±0	4.71	both
<i>Gaultheria serrata</i>	13.47 ±0.72 2	9.09 ±0.613	0.45 ±0.046	0.39 ±0.05 9	0.80 ±0.109	9.52 ±0.835	21.87 ±1.15	78.13 ±1.15	0.00 ±0	5.29	out
<i>Myrsine gadneriana</i>	15.82 ±0.82 2	18.46 ±1.24	0.39 ±0.013	0.35 ±0.01 4	0.92 ±0.059	12.01 ±1.45	31.87 ±1.02	66.38 ±1.45	1.75 ±0.848	27.06	both
<i>Myrsine umbellata</i>	20.12 ±1.17 2	13.15 ±1.8	0.33 ±0.009	0.30 ±0.02 9	0.89 ±0.079	4.56 ±0.711	31.67 ±1.72	63.97 ±2.83	4.36 ±1.62	8.24	both
<i>Pleroma trinervia</i>	19.92 ±0.81 4	2.63 ±0.597	0.34 ±0.029	0.24 ±0.01 7	0.62 ±0.045	25.14 ±2.95	10.37 ±1.67	86.61 ±2.07	3.02 ±1.11	8.24	both
Mean whole woody community	18.56 ±0.51 2	11.50 ±0.723	0.38 ±0.007	0.30 ±0.00 9	0.87 ±0.037	17.54 ±1.26	23.64 ±0.885	73.05 ±1.08 2	3.31 ±0.505	total species number: 24	

Table 2: Spearman correlation table, asterisks indicate significant combinations

	SLA	LA	LDMC	LT	WD	FWU	C	S	R
SLA									
LA	-0.02								
LDMC	-0.66**	-0.26							
LT	-0.59**	0.11	0.18						
WD	-0.31	0.13	0.11	0.22					
FWU	0.25	-0.3	0.07	-0.32*	-0.14				
C	0.08	0.94**	-0.47*	0.12	0.11	-0.32			
S	-0.32	-0.85**	0.61**	0.03	-0.05	0.19	-0.93***		
R	0.84**	0.01	-0.53**	-0.51**	-0.25	0.21	0.05	-0.33	

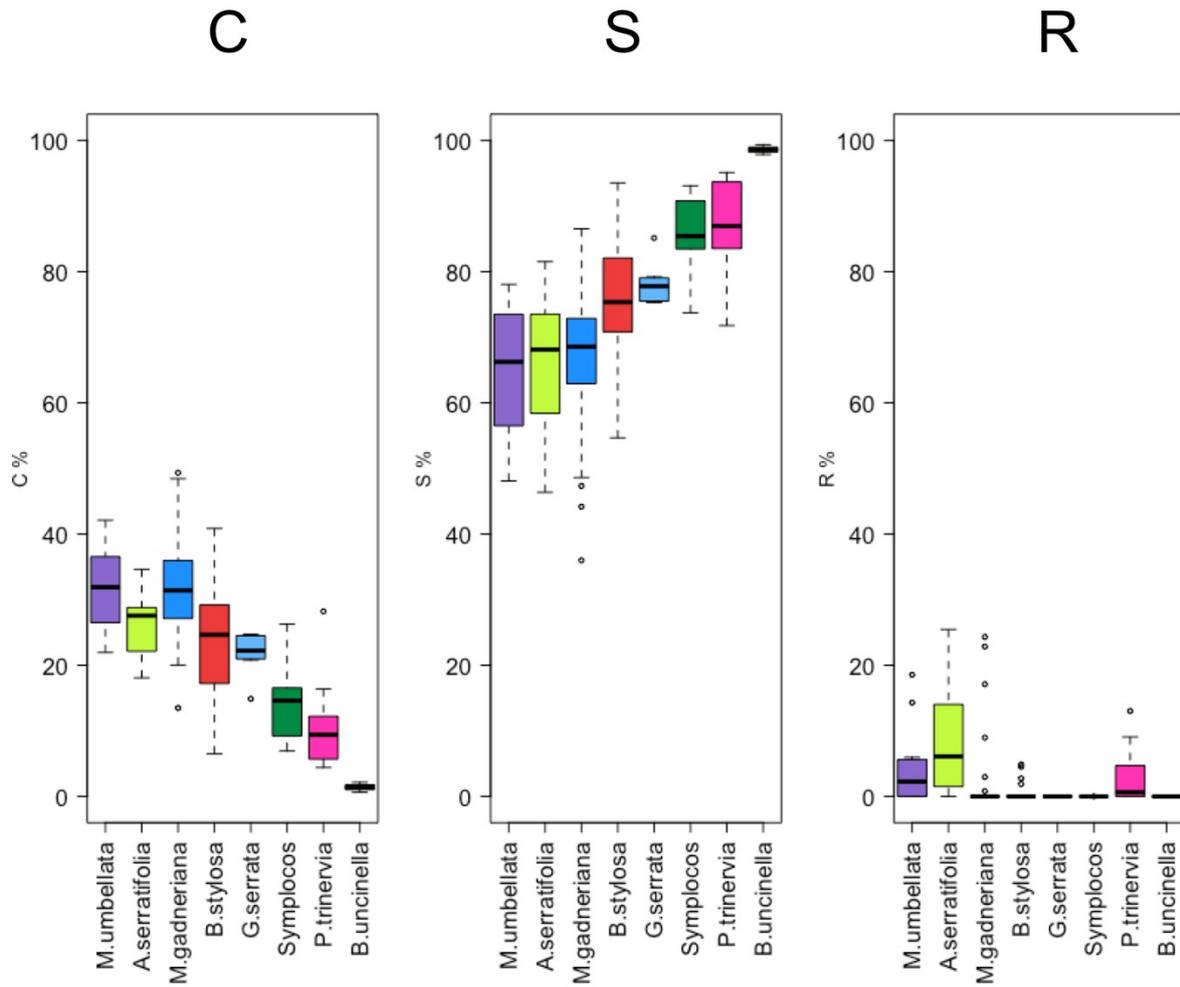


Figure 2: CSR strategy for the eight 'dominant' species, sorted after medians in S-strategy (n=136)

3.2 COMPARISON OF THE FUNCTIONAL COMPOSITION INSIDE AND OUTSIDE THE TREE ISLANDS

A total of 18 woody species occurred inside tree islands (i.e. in the ‘inside’ subcommunities), while 15 species occurred outside, and 8 species were shared between inside and outside (Sørensen index = 0.55). Six of the ‘dominant’ species occurred inside and outside, while the ‘dominant’ species *G.serrata* and *B.uncinella* occurred exclusively outside the tree islands. The average subcommunity inside a tree island had more woody species than the average subcommunity outside (5.4 vs 4.1), however the difference was below the significance level (Fig.3 b).

S -percentages were significantly higher, and C-percentages were lower for woody plants within the grasslands in comparison to inside the tree islands (Fig. 3 a). CSR-strategy showed mean values of C 25.4: S 70.9: R 3.7 for inside tree islands and C 20.1: S 77.4 : R 2.5 outside tree islands (Supp. Tab.S3). Accordingly, SLA and LA were both higher in trees inside the tree islands (i.e. more acquisitive resource use), while LDMC was higher in trees growing in the grasslands (i.e. more conservative resource use) (Fig.3 c). There was no difference in any of the other traits between woody plants growing inside and outside the tree islands. CWMs differences between the subcommunities inside and outside the tree islands (Supp. Fig. S1) were only significant for LA, which had higher mean values inside the tree islands than outside (11.76 cm² vs 7.19 cm², p= 0.041). The variation partitioning showed that species explained 50-80% of variation for all traits except LDMC and WD, which showed larger residual variation. The effect of inside vs outside was negligible for all traits. Differences between plots (i.e. the 10 woody communities) explained a larger proportion of variation in all traits and CSR-percentages than differences between inside and outside in all traits except LA (Fig. 3 d). Particularly, 30% of the variance in WD was explained by differences between plots (i.e. the 10 transects).

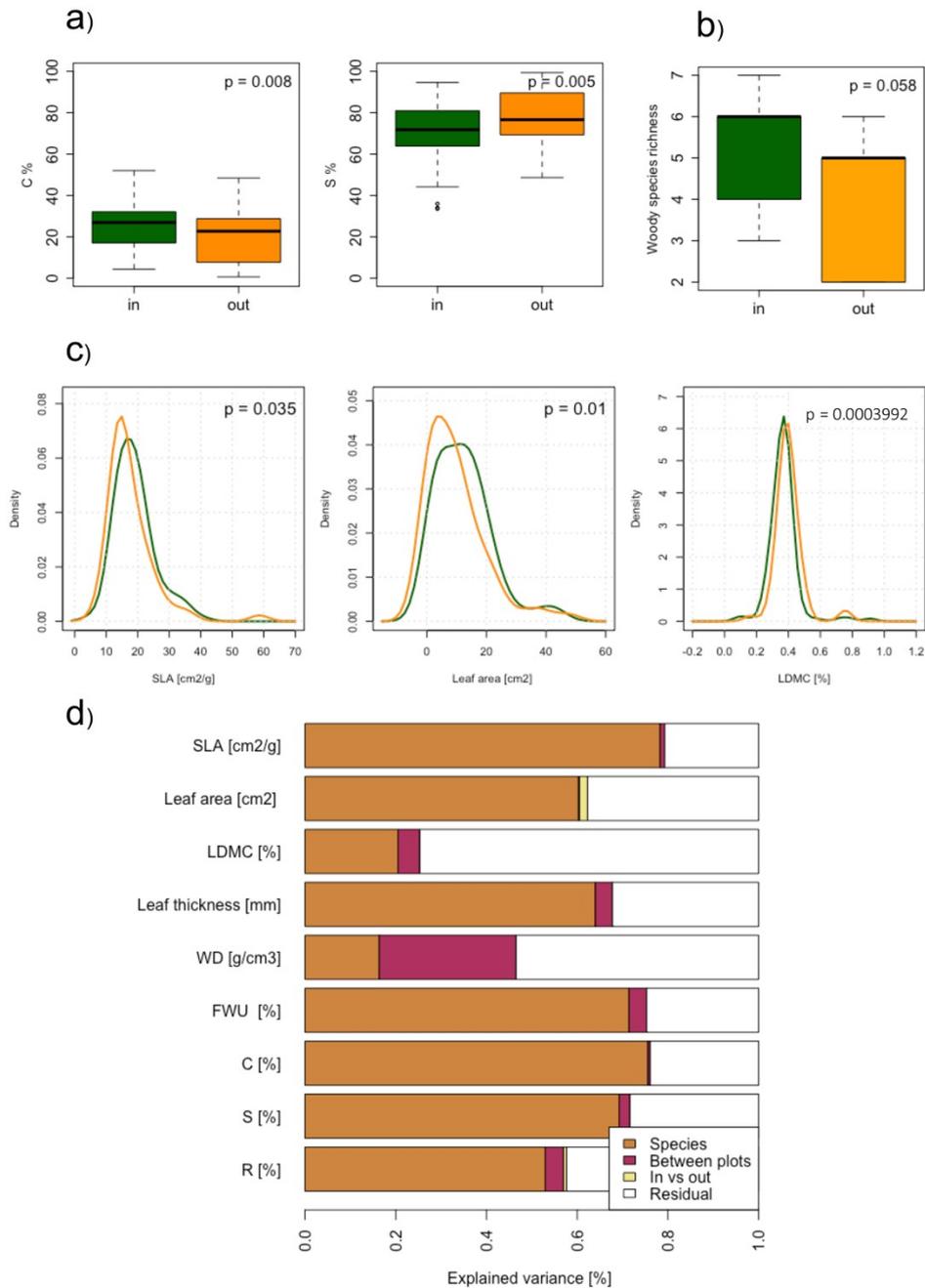


Figure 3: a) Boxplot of variation for C and S strategy between woody plants inside and outside tree islands (n=172), b) Variation in woody species richness between 10 subcommunities inside and the 10 subcommunities outside the tree islands (n=20). c) Density plots for significant variation in traits between woody plants inside (dark green) and outside (orange) the tree islands (SLA n=178, LDMC n=175, LA n=178) d) Variation partitioning for variation between species, plots, and between inside vs outside (n=178).

3.3 INFLUENCE OF BAMBOO ON TRAITS AND DIVERSITY OF TREE ISLANDS

A total of 18 species occurred across all the five bamboo invaded islands, compared to 16 species in non-invaded islands, and 10 species were shared between both (Sørensen similarity index of 0.59). A bamboo invaded tree islands had on average less species than a non-invaded island however the difference was just below the significance level (mean of 4.6 vs 6.2 species, $p=0.053$) (Fig. 4b). Bamboo-invaded islands had a significantly lower Simpson index than non-invaded islands (0.57 vs 0.74, $p=0.016$). Woody species richness and FDis were uncorrelated (Spearman $\rho=-0.14$), showing that FDis was independent of species numbers and thus a good metric to compare functional diversity between islands. FDis was significantly lower in bamboo-invaded tree islands (1.57 vs 2, $p=0.047$) than in non-invaded islands.

CSR-strategies did not differ significantly between woody plants growing in bamboo invaded and non-invaded islands (Supp. Tab S3), accordingly neither SLA, LA nor LDMC differed significantly. However, woody plants occurring in bamboo-invaded islands showed lower FWU (12.37 vs 19.94, $p=0.008$) and higher LT (0.32 vs 0.28, $p=0.005$) than in non-invaded islands (Fig. 4 a, Supp. Tab. S3).

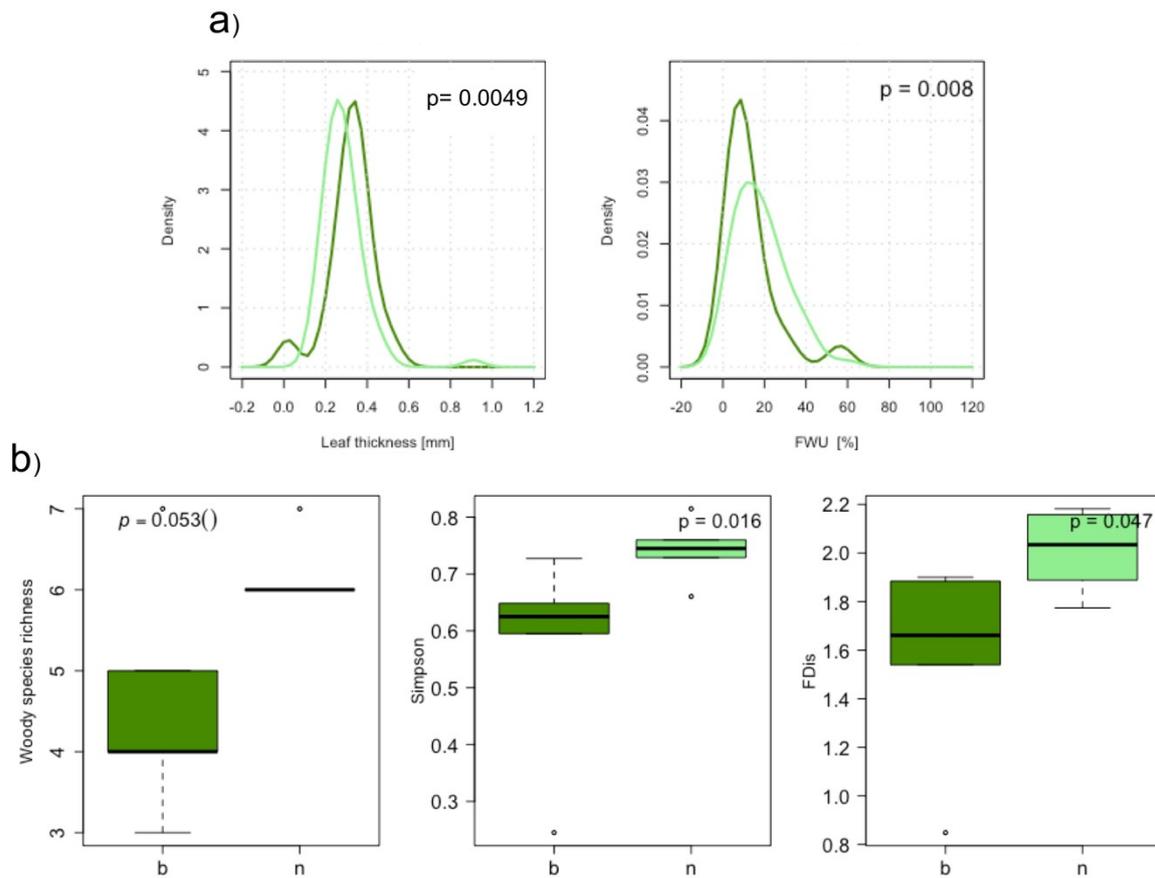


Figure 4: a) Density plots for significant variation in traits between woody plants in bamboo invaded (dark green) and non-invaded (light green) tree islands (LT n=121, FWU n=105) b) Boxplots for variation in diversity metrics (woody species richness, Simpson diversity and Functional Dispersion) in bamboo-invaded and non-invaded tree island subcommunities (n=10).

4. DISCUSSION

The key findings of this study are a selection of the woody communities towards stress-tolerance (S/CS), and trade-offs between traits related to acquisitive and conservative resource use strategies. Woody plants inside tree islands showed more acquisitive leaf traits and a dominant CS strategy, while plants outside were more conservative in resource use, exhibiting a dominant S strategy. Bamboo invasion reduces taxonomic and functional richness of woody communities and woody plants co-occurring with bamboo showed thicker leaves and lower foliar water uptake. We discuss these findings in connection to concepts of biotic and abiotic filtering, facilitation and the conservation implications for the tree island ecosystems under climate change.

4.1 CSR-STRATEGY, FUNCTIONAL ASSEMBLY AND TRADE-OFFS IN THE WOODY COMMUNITY

The hypothesized strong S-selection in the woody communities along with conservative functional trait values and trade-offs was verified. Overall the woody communities showed a similar CSR-strategy to the tussock grasses and shrubs on the Campos de Altitude assessed by Matos et al. (2020). With the prevalent SC/S-strategy the woody communities are strategically equipped to cope with strong environmental filters, such as the seasonally recurring droughts and frost in Itatiaia (Safford, 1999b).

Despite the convergence towards a stress-tolerant strategy in the woody communities, traits not feeding into the CSR analysis (i.e. foliar water uptake, wood density and leaf thickness) were independent from CSR-strategies (i.e. unrelated in the correlation analysis). The uncoupling of leaf thickness and wood density, as well as foliar water uptake from the CSR-strategies is in line with findings by Rosado & de Mattos (2017) and the twin filter model (Grime and Pierce, 2012). According to this model, co-occurring species sharing the same overall CSR-strategy can diverge in eco-physiological traits. While Matos et al. (2020) found three eco-physiological strategies in the grasses and shrubs of the Campos de Altitude, we here found two main eco-physiological strategies for woody plants: S-species with a conservative resource strategy and high foliar water uptake occurring predominantly within the grasslands (*Baccharis uncinella*, *Pleroma trinervia*) and CS-

species with both competitor and stress-tolerance traits and variable levels of foliar water uptake occurring predominantly, but not exclusively inside the tree islands (*Myrsine gardneriana*, *Myrsine umbellata*, *Archibaccharis serratifolia*).

Wood density, a trait related to hydraulic safety (Eller et al. 2018; van der Sande et al. 2019) showed variation due to differences in plots. This might point towards the existence of different eco-physiological wood-strategies related to xylem water transport between communities. Low wood density is associated with high transport efficiency but low hydraulic safety, while high wood density is connected to low transport abilities but higher hydraulic safety and lower vulnerability to embolism (Chave et al. 2009). This is in line with finding that multiple drought survival strategies often coexist (Pivovarovoff et al. 2016; Rosado & de Mattos, 2017; Rosado et al. 2013).

In the spearman analysis we found a trade-off between leaf thickness and foliar water uptake. This aligns with findings by Gotsch et al. (2015) who found lower foliar water uptake in species with thicker leaves and greater water storage capacity, while thin leaves enable higher foliar water uptake. This trade-off was particularly visible in two of the dominant species outside the tree islands; *Baccharis uncinella* showed the highest levels of mean foliar water uptake (60%) and relatively thin leaves while *Gaultheria serrata* showed the highest mean thickness coupled with lowest foliar water uptake. This underlines two main types of drought response: Thicker leaves could be associated with either a drought avoidance strategy in succulent species, where water is stored in leaf tissue (Ogburn and Edwards 2010), or to a drought tolerance strategy in sclerophyllous species (Gullo and Salleo 1988; Rhizopoulou and Psaras 2003). This study shows that both drought-coping mechanisms co-exist in the woody community.

4.2 COMPARISON OF THE FUNCTIONAL COMPOSITION INSIDE AND OUTSIDE THE TREE ISLAND

We find higher competitiveness and lower stress-tolerance inside tree islands compared to outside. This is further confirmed by more acquisitive single traits (higher specific leaf area, lower leaf dry matter content) inside the tree islands compared to outside. This could be either due to a) higher need for competitive traits when co-occurring with trees sharing similar requirements inside the tree islands

or b) due to facilitative processes decreasing environmental stress, through microclimatic shelter as previously observed in montane tree islands (Albertsen et al. 2014), subsequently enabling allocation of resources towards more competitiveness and less to stress tolerance.

Facilitation has been found to be stronger in resource-limited or relatively ‘extreme’ environments, such as deserts and alpine tundra, in high and exposed places at the physiological and altitudinal limits of a species and in intermediate to high levels of climate stress and disturbance, where it allows species to expand into harsher conditions (Brooker et al. 2008). It could in the first place enable the woody species in tree islands (some of which prominent cloud forest species like *Myrsine gardneriana*) to exist far above the treeline. Many of the assessed species might benefit, but also promote facilitation; in forest-grassland transitions in Southern Brazil. *M.umbellata* for instance has been shown to promote seedling abundance and seedling species richness under its crown, making it a facilitator species (Mendoza-Hernández et al. 2013). We found comparatively low levels of foliar water uptake inside the tree island ecosystem (mean FWU of 16%) compared to measurements of grass and shrub species in the Campos de Altitude (mean FWU of 73.6%) by Matos et al. (2020). On the one hand, this could be associated with differences in rooting depths, as species with shallow roots (like many grasses and shrubs) show higher capacity for FWU than species with deep roots which have better all-year around water access (Cavallaro et al. 2020). On the other hand, this could be another proof of facilitation, since in the tree islands drought buffering due to sheltering effects could be at play, resulting in a lower need of alternative mechanisms of water acquisition.

Five limiting mechanisms have been hypothesized to operate in woody communities of alpine tree line ecotones: stress, disturbance, reproduction limitation, growth limitation and carbon balance (Körner 1998). Based on the observed functional assembly of stress tolerance, but differences in stress-tolerance between inside and outside tree islands it is likely that the ‘stress hypothesis’ primarily applies to these communities. While prevailing drought and frost shapes the vegetation of the Campos de Altitude (Safford 1999b), the tree islands offer sites of reduced drought and frost through facilitation, hence allowing woody communities to exist above the tree line.

The ‘reproduction limitation hypothesis’ could apply too, with the surrounding dense grasslands acting as an impenetrable barrier to seedling establishment, and reducing seedling survival through frost induced seedling mortality as previously observed for a forest-grassland matrix in the Western Indian Ghats (Joshi et al. 2019), while in tree islands seedling establishment is promoted through facilitation. Frost occurs in Itatiaia on average 56 days per year at elevations of 2200m (Safford 1999b), an elevation that coincides with the location of the ten assessed tree islands. While in temperate and boreal altitudes many tree islands and tree line outskirts consist of ‘Krummholz’ (stunted, deformed woody vegetation) due to growth limitation (Harsch and Bader 2011) most trees observed in this study were erect and architecturally intact and thus likely less impacted by growth limitation.

4.3 INFLUENCE OF BAMBOO ON TRAITS AND DIVERSITY OF TREE ISLANDS

In line with our hypothesis, we found significantly reduced functional dispersion and reduced Simpson-diversity in response to bamboo. Even though we did not find significant differences in woody species richness the difference in Simpson-diversity, which accounts for abundance and richness, indicates that bamboo-invaded communities have a less even and less rich species community. Further we found differences in species assembly between invaded and non-invaded islands, as indicated by the Sørensen index. These differences in diversity and species composition could be due to prevalent disturbances, such as recurring fires (Aximoff and de Carvalho Rodrigues 2011), promoting bamboo establishment and impacting co-existing plants through competition and high flammability, consequently reducing species diversity (Pagad 2016). Such processes were observed by Tomimatsu et al. (2011) for fragmented disturbed forests, which provide opportunities for establishment and domination of the dwarf bamboo species *Sasa chartacea* and subsequently reduced understorey communities. Many of the sampled trees between 1m and 1.5m in our study are part of the understory and could be subjected to this process.

Differences in functional and taxonomic diversity between tree islands in response to bamboo-invasion might result in variable levels of tree island resilience to environmental change. Even though no study yet quantified the relationship between tree island resilience and functional diversity, studies

of the adjacent Campos de Altitude (Matos et al. 2020) and of tropical forests (Schmitt et al. 2019) have highlighted that higher functional diversity of a given community may result in higher resilience to environmental change. Bamboo invasion might compromise some of this resilience. In the Campos de Altitude the bamboo *Chusquea pinifolia* shows high resprouting ability after fire (Safford 2001), and could thus be promoted by future increases in the frequency of fires, resulting in changes of abundance and composition of co-occurring woody communities towards poorer and uneven woody communities, if the pattern we find in the tree islands is generalizable. Woody communities which get encroached by *C. pinifolia* could then likely be dominated by *M. gardneriana* and *M. umbellata*, as these species were the most abundant in the bamboo-invaded islands.

Bamboos can further impact co-occurring plants by modifying the local hydrology (Pagad 2016). For example, species of the genus *Sasa* have been shown to decrease soil water potential, and to limit water availability for co-occurring trees (Takahashi et al. 2003). While we did not find any differences in CSR strategy, we found thicker leaves and associated lower FWU in woody plants in bamboo-invaded islands. This convergence in water-use related trait could drive the reduced functional diversity we found in bamboo-invaded subcommunities. Thicker leaves and lower FWU in response to bamboo invasion could be evidence for competition for water and/or light caused by the presence of bamboos. Thicker leaves have been associated with higher photosynthetic rates (McMillen and McClendon 1983) and with higher leaf water storage (Vendramini et al. 2002) and could thus be synergistic when coping with coupled water and light competition imposed by bamboo. An alternative explanation for lower FWU in woody plants in bamboo-invaded islands could be that bamboos promote micro-climatic sheltering and drought buffering for co-occurring plants in a tree islands, hence minimizing water losses through transpiration and reducing the need for alternative water acquisition through FWU. Interestingly, bamboos have been shown to provide facilitative interactions in montane context: Caccia et al. 2009 showed that the presence of bamboo might increase the survival of some species, such as *Nothofagus sp.* but prevents the growth of other species (*Austrocedrus sp.*), which suggest that the effect of bamboo might be species specific. Furthermore, facilitation by bamboo might be more likely at early life stages, while bamboo tends to impose

competitive effects on co-occurring woody species at later life stages, suggesting life-stage specific impacts (Takahashi et al. 2003). This life-stage effect could lead to the decreased taxonomic and functional diversity found on the mostly adult trees in this study.

Despite the trend of species richness decreasing in response to bamboo presence, our study cannot draw conclusions on the pathways of competitive interactions and potential facilitation between bamboo and the woody species. An experimental study, including bamboo traits, establishment and recruitment traits as well as environmental variables will be needed to elucidate on mechanisms underlying the facilitative and competitive interactions.

4.4 IMPLICATIONS FOR BIODIVERSITY

Tropical montane ecosystems in the Atlantic Forest are subject to habitat reduction, compositional shifts, population decline, and modifications in biotic interactions and phenology (Scarano et al. 2016).

A paleo-botanical sediment-analysis of the summit region in Itatiaia showed that before 4500y BP montane forest covered the altiplano and multiple local fire events in the last centuries coupled with increased fires in recent years limited montane forest expansion (Behling et al. 2020). The tree islands, which share many species with the montane cloud forest, are therefore likely remnants of this forest and enable future forest establishment above the tree line by providing a source of seeds for woody species dispersal and sheltered sites due to facilitation. Isolated woody plants occurring in forest-grasslands ecotones in Southern-Brazil have been shown to promote tree seedlings from the forest, hence favouring forest expansion into grasslands (Mendoza-Hernández et al. 2013). On the other hand, grassland species could find safe sites at the tree islands edge, as previously shown for tree islands in forest-tundra-ecotones (Albertsen et al. 2014). However, the current trend of increased anthropogenic fire frequency (Aximoff & de Carvalho Rodrigues, 2011; Medina et al. 2016) might keep suppressing forest and tree island expansion, and instead promote grass and shrub species with rapid vegetative regeneration (Safford 2001).

While much of the conservation action focuses on protecting large landscapes, protecting and managing small tree islands is crucial for woody community persistence (Tulloch et al. 2016). In the Campos de Altitude any conservation measure involving woody communities needs to be scientifically evaluated to avoid negative consequences for grasslands biodiversity and functioning, as recently highlighted in a study thematizing the role and potential negative impacts of trees for tropical grassland restoration management (Silveira et al. 2020). Further study on dispersal, early life stage traits and fire-related traits could elucidate mechanisms of tree island expansion/retreat and evaluate the consequences for the grassland ecosystem and its biodiversity.

The Campos de Altitude are particularly vulnerable to climate change due to their disjoint geographical distribution, restricted altitudinal range, high levels of endemism and vegetation susceptibility to fires (Assis and de Mattos 2016). Intensification of droughts and reduction of fog occurrence (Scarano et al. 2016) will particularly affect CS-species because of water depletion and their high dependence upon water storage and uptake, as well as causing loss of S-species and community originality if future droughts patterns exceed the tolerance limits of S-tolerant species (Matos et al. 2020). Most species found in the tree islands fall in the first category with limited foliar water uptake (*M. gardneriana*, *M. umbellata*, *B. stylosa*) and S-selected species in the grasslands (e.g. *B. uncinella* and *Pleroma trinervia*) could be lost, causing compositional and functional changes in the woody communities. The woody communities show more conservative water use and lower foliar water uptake than most grasses and shrubs in the Campos de Altitude (Matos et al. 2020). Hence future droughts and less fog occurrence might exceed water acquisition and storage mechanisms and push the woody communities to their hydraulic limits, especially for species with low foliar water uptake, low wood density and associated low resistance to cavitation (such as *A. serratifolia*).

While facilitation might counteract some of the potential vulnerability to climate change, interactions between plants are predicted to shift from positive to negative as environments warm (Brooker et al. 2008). Changing spatio-temporal combinations of drought, frost and fire could subsequently reduce woody species diversity in tree islands and promote bamboo establishment. Beyond that, alpine communities have been shown to respond to long-term drought through species turnover (Jung et al.

2014). With a large part of trait variation found in our study driven by taxonomy, changes in woody community composition are likely, which might irreversibly change the future community and functional assembly of the Campos de Altitude ecosystem.

An assessment of drought survival mechanisms like drought deciduousness, photosynthetic stems, tolerance of low water potentials and xylem vulnerability to cavitation will be needed to give a more complete picture of eco-physiological drought resilience in the woody communities.

5. CONCLUSION

With a lack of research of mountain biodiversity in Brazil (Martinelli 2007), this study provides knowledge about the critically understudied montane tree islands. The prevalence of a woody community increases overall species and functional diversity of the Campos de Altitude ecosystem. The tree islands are eco-physiologically, structurally and compositionally different from the Campos de Altitude, yet show similarities in their competitive-stress tolerant strategy.

Our results point towards large-scale environmental abiotic filtering shaping community strategy, and small-scale biotic interactions, such as facilitation, to drive differences in CSR-strategies between woody community inside and outside the tree islands. Biotic processes such as bamboo invasion result modified eco-physiology and drought-resistance, as well as in reduced diversity.

The ecosystem deserves a closer investigation of facilitative interactions, as a potential mechanism promoting woody community persistence at these high altitudes. Experimental introduction of species inside and outside the tree islands, could help elucidate the effect of facilitation onto woody plant establishment and trait selection to predict expansion or retreat of the islands into the grasslands. Experimental studies with bamboo, fire and herbivory treatments are needed to characterize tree island resilience to biotic disturbance, as well as studies on eco-physiological traits related to drought tolerance to model woody community response to drought intensification. While this study provides descriptive insights into the functional ecology of the woody communities, further trait-based studies will be needed to elucidate management consequences allowing for synergies between the Campos de Altitude and the woody communities.

6. DATA AVAILABILITY STATEMENT

Upon acceptance all primary data files and R-scripts will be made publicly accessible via Dryad.

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