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### FUNCTIONAL TRAITS PROVIDE EVIDENCE OF LAND USE TRANSFORMATIONS OF TUCUMAN-BOLIVIAN FORESTS AT THE CATCHMENT SCALE

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All content in this magazine is licensed under a Creative Commons Attribution License. Attribution-Non-Commercial-Non-Derivatives 4.0 International (CC BY-NC-ND 4.0). Abstract: Bolivia has one of the highest rates of deforestation in South America and is one of the countries with the highest frequency of forest fires worldwide, leading to a decrease in forest coverage and increased anthropogenic land pressure. The objective of this study was to characterize plant functional traits and determine their relationship with the landscapetransformation of Tucuman-Bolivian Forests. A comparative study was designed by selecting three catchments with well-preserved natural vegetation and three transformed catchments for studying structural (height, diameter at breast height, canopy size, resprouting, and main branches) and foliar (leaf water content, leaf area, specific leaf area, stomatal density, and trichomes density) traits of vegetation, as well as community traits (epiphyte biomass and fine root density). Increased landscape fragmentation, augmented intraspecific trait variability, being more evident in foliar traits and species present in both types of catchments. Yet, structural traits were reduced (except resprouting) due to the replacement of species that arrive after the transformation, along with a decrease in light competition. In contrast, height of herbaceous species increased in transformed catchments, resulting from the anthropic selection of pastures from the Poaceae family for livestock. The vegetation of transformed catchments had lower stomatal density as a possible strategy to reducing water loss through transpiration. Also, lower epiphyte biomass was evidenced due to microclimatic changes devoid of canopy, particularly due to the reduction in air relative humidity and the increase in solar radiation.

**Keywords:** landscape heterogeneity, structural traits, leaf traits, community traits, functional response.

#### INTRODUCTION

In South America, deforestation is mainly caused by fires and the transformation of native forests for agriculture, pasture, and forest plantations (Jones et al., 2016). Bolivia has historically been among the South American countries with the highest rate of forest loss, which has been intensified in the last decades due to population increase, agricultural expansion, and road construction (Bagan et al., 2020; Fernandez et al., 2023). Deforestation rates in Bolivia vary by region and biome, with the Dry Inter-Andean Forests, the Amazon, and the Chiquitano Dry Forest being the eco-regions most affected by human pressure (Bustillo et al., 2021). The latter two regions have shown the largest increase in burned areas, ranking Bolivia as one of the countries with the highest incidence of forest fires in the world (Bustillo et al., 2021).

The objective of this research was to study the interaction between landscape transformation and functional traits. The connections of land use changes and deforestation, which increases forest fragmentation and soil degradation (Tobón et al., 2010; Wilson et al., 2016), leading to changes in the abundance, spatial distribution, composition and structure forest, and assembly of species are widely known (Mayfield et al., 2013; Ma, et al., 2023). However, the impact of landscape transformation on functional traits is less known, due to the complexity of landscapes in terms of habitat loss and fragmentation (Zambrano et al., 2019), differences in species life-history strategies, and biotic interactions (competition and facilitation) among species (Mayfield et al., 2013). Most studies have focused on dispersal traits and resource availability, such as the rapid acquisition of resources (productivity) or conservation of resources (survival), while persistence traits have rarely been studied in the context of landscape transformations (Poorter et al.,

2021; Reich, 2014; Zambrano et al., 2019).

This investigation was carried out in the Natural Integrated Management Area of Río Grande-Valles Cruceños (NIMA, RG-VC) in Santa Cruz, Bolivia (Figure 1). This protected area is part of the Tucuman-Bolivian Forest biome, extending from western Santa Cruz to Tucuman in Argentina between 19° and 29° south latitude (Malizia et al., 2012). It is an important buffer zone and biological corridor, but it is vulnerable due to increasing in deforestation as a product of the expansion of burned areas, agriculture, pasture and grazing activities, and forest plantations (Fernandez et al., 2023; Entrocassi et al., 2020; Bustillo et al., 2021). We used a comparative design involving the selection of three catchments with well conserved vegetation and three transformed ones, as well as tree species that added a relative abundance of 80%, to study the interaction between landscape transformation and functional traits. We analyzed traits associated with the structure and complexity of the forest (Carreño-Rocabado et al., 2012; Poorter et al., 2017), including height, diameter at breast height, canopy size, resprouting, and main branches. Foliar traits such as leaf water content, leaf area, specific leaf area, stomatal density, and trichomes density related with growth and survival were also studied, aiming to explain their distribution across light, water, and nutrient gradients (Reich, 2014). Lastly, we studied community traits such as epiphyte biomass and fine root density susceptible to landscape fragmentation, land use and soil properties (Krömer et al., 2014; van der Sande et al., 2022). We hypothesized that: (1) Structural traits would present higher values in conserved catchments resulting from the accumulation of years of forest biomass and the competition for light capture; (2) Foliar traits would be higher and with increased variability in transformed catchments due to their high

sensitivity to environmental variation and landscape heterogeneity; and (3) Community traits would be higher in conserved catchments due to the microclimate and the supply of organic matter to the soil provided by the forest canopy. Accordingly, the objective of this study was to characterize plant functional traits and determine their relationship with the landscape transformation of Tucuman-Bolivian Forests. It is expected that results here presented improve the understanding of the vegetation composition of the Tucuman-Bolivian Forest, their functional traits and functional responses of plants following landscape transformation, with the aim of fostering projects that promote the conservation and protection of the Natural Integrated Management Area of Río Grande-Valles Cruceños and the Tucuman forests in general.

#### **METHODS**

#### STUDY AREA AND SAMPLING

This study was carried out in the municipalities of Postrervalle (Pv), Pucará (Pc) and Vallegrande (Vg), all parts of the NIMA RG-VC (Figure 1), where three paired catchments (three conserved and three transformed) were selected, which resulted in six catchments across the entire NIMA RG-VC. The landscape is composed of a mosaic of preserved forests dominated by Myrtaceae, Lauraceae and Podocarpaceae (Navarro, 2011) mixed with patches of different land uses, mainly degraded pastures with extensive livestock farming and crops such as corn, potato, peanut, wheat, and small areas with fruit trees. When these patches are abandoned (migratory agriculture), they are colonized by grasses and shrubs of Poaceae and Asteraceae (Carilla & Grau, 2011).

The unimodal precipitation condition of NIMA RG-VC has a rainy season from November to March with a mean rainfall of 1900 mm, and a dry period from April to October when precipitation is less than 500 mm. Selected paired catchments at each municipality are similar in all morphometric parameters and soil types, but with a marked difference in vegetation land cover (Table 1, Supplementary Table S1). Conserved catchments are those that have dense and/or riparian forest dominance, while transformed catchments are dominated by abandoned and clean pastures, and/or secondary vegetation, reflecting land use changes (Table 1).

#### SPECIES SELECTION AND FUNCTIONAL TRAITS

We used cartographic information to determine the degree of conservation or transformation of catchments (Supplementary Table S1). Based on the dominance of coverage, those with forest dominance were grouped in conserved catchments, and those dominated by pastures, secondary vegetation, and crops, were grouped in transformed catchments (Table 1). For the study area we established 60 plots (30 plots of 50 m x 20 m for woody species and 30 plots of 1 m x 1 m for herbaceous species), 10 for each catchment. Based on their relative abundance, adding at least 80% per catchment, we selected 28 woody and 26 herbaceous species, from selected plots. It is important to highlight that species found in two or more catchments were sampled in all catchments where they were found. For each species, we selected six mature and healthy individuals to study their functional traits associated with plant structure (especially in woody species), such as height, diameter at breast height (DBH), canopy size (Cs), resprouting, and number of main branches (Branching). Foliar traits assessed were, the water content in leaves (LWC), leaf area

(LA), specific leaf area (SLA), stomatal density (SD), and trichomes density (TD) using the methodology proposed by Pérez-Harguindeguy et al. (2013). We also measured epiphyte biomass (EB) and fine root density (FRD) to characterize community traits. EB was determined as an index of epiphyte cover and content on trunks and branches, by selecting tree individuals in each catchment with similar characteristics (species, height, DBH and number of branching). Individuals with most of their surface area covered by epiphytes were assigned 100% of coverage, and the others were assigned a relative percentage, according to the fraction of epiphyte cover. Then, the loose pulley methodology (Perry, 1978) was applied to collect all epiphytes from different individuals in each catchment, once their percentage of epiphyte cover was determined. To calculate the biomass of epiphytes, we followed the methodology proposed by Köhler et al. (2007) and additionally, the maximum water storage capacity of epiphyte was calculated. Finally, the relationship between the percentage epiphyte cover and their dry biomass was established, generating an equation (dry biomass as a function of percent cover), which was applied to determine the biomass of epiphytes per individual. For fine root density ( $\leq 2$  mm), we excavated soil pits of 1.0 m x 1.0 m x 1.0 m (seven per catchment) and collected two soil samples every 10 cm to 1.0 m depth using a metal box of 10 cm x 10 cm x 10 cm. Samples were carefully washed, and fine roots were separated and weighed (wet weight), dried, and finally re-weighed (dry weight) to determine the FRD (Tobón et al., 2010).

Finally, to extrapolate data from the different species to catchment scale, we used information from the 10 study plots per catchment, by using the relative abundance of the species. We also assigned them a percentage of the landscape in function of the land coverage to which they belonged (dense forest, secondary vegetation, and pastures); all the parameters were related to the weighted average of each trait by modifying the equation of Garnier et al. (2004) and Pérez-Harguindeguy et al. (2013) (Supplementary 2).

#### STATISTICAL ANALYSES

Data were analyzed by comparing the mean and standard deviation of each trait by studied species and catchments, then the traits were grouped into conserved (three conserved catchments) and transformed catchments (three transformed catchments). A principal component analysis (PCA) was subsequently carried out to evaluate the relationship and distribution of structural, foliar, and community traits between catchments. Lastly, we made a non-parametric test of multiple comparisons of Dunn's and Mann-Whitney to determine the differences in functional traits between catchments. The statistical analyses were done in R-Studio version 3.5.1.

#### RESULTS

The average values and their standard deviation for studied traits are presented in Table 2. The height of woody species was 58% lower in transformed catchments than in conserved ones, while herbaceous species in transformed catchments were 74% higher than those herbaceous species in conserved ones (Table 2, Figure 2a). Average DBH was 19  $\pm$  10.5 cm and Cs showed a high intraspecific variability with an average of  $24 \pm 16.3 \text{ m}^2$ ; both traits for woody species were 30% higher in conserved catchments than in transformed ones (Table 2, Figures 2b-c). Resprouting reported a high standard deviation in most woody species, but no significant differences were found ( $p \ge 0.05$ ), even though this trait was 63% higher in woody species of transformed catchments (Table 2, Figure 2d). Branching showed an average of 8  $\pm$ 3.9 and it was slightly higher (7%) in woody species of conserved catchments than in transformed ones (Table 2, Figure 2e). These trends were maximized by applying the equation (Supplementary 2, eq. 1) showing that height, DBH, Cs and main branching were higher in conserved catchments than in transformed ones, which showed higher resprouting. All structural traits had a high dispersion between catchment types (Figures 3a-e). Significant differences were found in structural traits ( $p \le 0.05$ ) (except resprouting among species), especially in species that appear in both, conserved and transformed catchments (Table 2). Moreover, there were significant differences ( $p \le 0.05$ ) between catchment types and structural traits, except in resprouting (Figures 3a-e).

LWC showed high interspecific variability in woody species with an average of  $4.1 \pm 5.6$ mg., with a 78% higher LWC in transformed catchments than in conserved ones, while herbaceous species had an average of 1.2  $\pm$ 0.9 mg., being slightly higher (6%) in the herbaceous species of transformed catchments (Table 2, Figure 2f). The LA of woody species had an average of  $29.3 \pm 33.9 \text{ cm}^2$  with high interspecific variability, and it was 54% higher in woody species of transformed catchments than in conserved ones, and an average of 16.5  $\pm$  12.1 cm<sup>2</sup> with high intraspecific variability for herbaceous species, which was 11% higher in herbaceous species of transformed catchments, as compared with conserved ones (Table 2, Figure 2g). SLA presented high variability in woody species, with an average of 26.3  $\pm$  50.8 cm<sup>2</sup>/mg that was 38% higher in woody species of transformed catchments than in conserved ones, while herbaceous species had an SLA average of  $112.5 \pm 104.7 \text{ cm}^2/\text{mg}$ and it was 41% higher in herbaceous species of conserved catchments than in transformed ones (Table 2, Figure 2h). SD was highly variable among woody species with an average of 2858.6 ± 1762.2 #/mm<sup>2</sup> and 38% higher in woody species of conserved catchments, while the average value for herbaceous species was  $1246.3 \pm 775.8 \ \#/mm^2$  and 34%higher in herbaceous species of transformed catchments than in conserved ones (Table 2, Figure 2i). Trichomes were present in 62% of herbaceous species and in 36% of woody species with an average of 249.2  $\pm$  645.3 #/ mm<sup>2</sup> and 36% higher in woody species of transformed catchments. Herbaceous species had an average of 448.4  $\pm$  424.3 #/mm<sup>2</sup> and it was slightly higher (7%) in herbaceous species of transformed catchments than in conserved ones (Table 2, Figure 2j). Statistical differences were found ( $p \le 0.05$ ) for all leaf traits among species (woody and herbaceous), including concurrent species in both catchment types (Table 2). In conserved catchments, foliar traits were characterized by a high standard deviation, particularly the SLA (Figures 3fj). However, significant differences were only found for SD among catchment types ( $p \le$ 0.05), while LWC, LA, SLA and TD were higher in transformed catchments, whereas SD was larger in conserved ones (Figures 3fj).

All woody species had epiphytes with high intraspecific variability with an average of 947.4 ± 1299 g. of dry mass per individual, woody species of conserved catchments had 59% more EB in comparison to transformed ones (Table 2, Figure 2k). Significant differences were found ( $p \le 0.05$ ), particularly in species that appear in both conserved and transformed catchments. By using the equation (Supplementary 2, eq. 1), tendency was maximized and was 2.9 times higher in conserved than in transformed catchments (p  $\leq$  0.05) (Figure 3k). Lastly, FRD was higher in transformed catchments, while conserved catchments had higher dispersion but with no significant differences ( $p \ge 0.05$ ) (Figure 3l).

PCA 1 explained 40.8% of the variance and was determined by structural traits such as height, DBH, Cs, and main branches at the negative end, and by SLA and FRD at the positive end of the axis (Figure 4a). This led to catchment segregation: conserved catchments were at the negative end with high values in structural traits (except resprouting), epiphyte biomass, and SD (Figures 4a-b), while transformed catchments were at the positive end with high SLA and FRD values. The second axis, with 30.1% variability, exhibited an intermediate state in the Vg\_t catchment with high regrowth, LA, LWC, and TD (Figures 4a-b).

#### DISCUSSION

We present the first description of 54 species of the Tucuman-Bolivian forests in the region of Santa Cruz, Bolivia, spanning 11 traits for woody and 6 for herbaceous species. This plant trait characterization is very valuable per se, and it the context of providing a framework to advance our understanding on the impact of land use changes on the structure and functioning of plant communities of these type of ecosystems.

Landscape transformation had a less perceptible effect on vegetation composition, since all catchments had one or more species in common, including species from native families. This is in line with Wilson et al. (2016), because transformed catchments had an important reduction in dense forest coverage, but not its total disappearance (Supplementary Table S1). Contrary, to that found in other studies of the Tucuman-Bolivian Forest, such as Villarroel & Ruíz (2009), and Zenteno-Ruiz & López (2010), we observed a diversification in vegetation composition, but not in the structure of woody species, because the vertical structure of the Tucuman-Bolivian Forest had a more representative development in the middlestratum. Nevertheless, our data showed that the height of woody species in transformed catchments decreased due to the presence of the Baccharis genus, given its colonization and dominance in the Tucuman-Bolivian Forest after disturbance (Carilla & Grau, 2011). Conserved catchments showed higher values in structural traits, except resprouting, due to the larger aboveground biomass and the state of forest conservation (Lutz et al., 2018). The high variability in structural traits was also in line with studies by Mayfield et al. (2013), Wilson et al. (2016), and Zambrano et al. (2019) since fragmentation and land use generated differential gradients in biotic interactions. As suggested by others (Poorter et al., 2018; Yin et al., 2019), our results showed that there was greater competition for light in conserved catchments, leading individuals to increase their vertical and horizontal area to augment light capture capacity, especially in Pv\_c and Vg\_c, catchments with the highest area of dense forest cover (Figure 4; Supplementary Table S1). Resprouting also had a high standard deviation and the highest values in transformed catchments; however, with no significant differences among catchment type, possibly due to landscape heterogeneity in these catchments. Contrary to findings by Barchuk (2019) and Clarke et al. (2015), resprouting in our study area was highest in sites with disturbance, loss of aerial biomass, and decreased soil nutrients, probably because resprouting provides individual advantages of greater carbon gain and more efficient reproduction, being a common response of woody species to ensure their survival (Clarke et al., 2015). On the other hand, the height of herbaceous species increased in transformed catchments, as a result of the dominance of the Poaceae family. Local farmers prefer species such as U. brizantha due to their high growth rate and leaf palatability (Azurduy et al., 2016). In turn, J. ichu is a common pasture that increases its frequency by colonizing disturbed sites (Soliz, 2014).

In general, foliar traits had huge variability, considering that standard deviations were highest than the mean values in transformed and conserved catchments. This can be explained by the heterogeneity in vegetation cover and the different fragments that compose the landscape of each catchment (Supplementary Table S1). These factors tend to augment the edge effect, increased stressors such as wind velocity, solar radiation, and temperature, and reduced nutrients and water content in the soil (Maza-Villalobos et al., 2022). Since foliar traits are highly sensitive to environmental variation (Salgado, 2016), these conditions generated different responses from foliar traits as observed in the high variability and dispersion of the data (Table 2; Figures 3f-j). It is necessary to underline that we found significant differences in foliar traits among species (Figures 2f-j), especially in those species present in both catchment types. These differences indicated a speciesspecific functional response to environmental conditions in each catchment (Mayfield et al., 2013). However, significant differences at the catchment level were only found in SD, as a response trait of stressful environmental conditions to which species were subject to in transformed catchments, where anthropic activity was higher due to cattle raising, the generation of big and discontinuous exposed areas where temperature and solar radiation were elevated, caused large water loss from the soil through direct evaporation (Potts et al., 2010). This likely resulted in a lower SD in vegetation of transformed catchments, as a mechanism to control transpiration and thus, promote more efficient water use (Delian, 2020; Maza-Villalobos et al., 2022).

The presence of epiphytes in all the woody species from both catchment types can be explained by the environmental conditions of the Tucuman-Bolivian Forest, which is characterized by a high annual average relative humidity (Table 1), mainly during the rainy season and given the altitudinal gradient (Navarro, 2011). The lower biomass of epiphytes in transformed catchments was probably a response to environmental physical conditions, due to their high sensitivity to forest fragmentation and grazing (Krömer et al., 2014). Microclimatic conditions under such conditions are expected to change, particularly in terms of relative humidity, temperature, light availability, and nutrient depletion (Li et al., 2017). This resulted in a higher epiphyte biomass in the Vg\_c catchment which has the largest area of dense forest, while the lowest epiphyte biomass was found in the Pv\_t catchment, with the highest levels of livestock activity (Table 2, Figure 4).

Fine root density is a trait generally associated to hydrophysical and chemical conditions of the soil. Activities such as grazing intensify soil degradation, soil compaction, and bulk density (Poca et al., 2018; Tobón et al., 2010). During land preparation for crops, or in cattle areas, soil crusting is a common feature, impeding root growth (Cai et al., 2019). However, no significant differences were found due to the fragmentation of catchments that could have promoted a variety of responses in FRD as a result of the physical conditions of the soil surface, soil water and resource availability. Fort & Freschet (2020) that different environmental discussed parameters can influence the variation of fine root traits, for example soil structure and resource availability may vary at small scales, making it difficult to distinguish the response of species to environmental gradients. This variation was evident in our results as shown by the data dispersion and the PCA that was located in the same ordination area as the FDR and transformed catchments, which had the largest number of patches (Figure 4, Supplementary Table S1).

#### CONCLUSIONS

Our results support only partially the hypotheses that we originally proposed since landscape transformation diversifies functional traits of Tucuman-Bolivian Forest, as the specific conditions of each fragment increase the variability of all functional traits. First, structural traits (except for resprouting) were larger in conserved catchments, probably as a result of light capture competition and the replacement of species with less structural complexity after landscape transformation. Second, foliar traits showed higher variability in both types of catchments. Only significant differences were found in SD, which was lower in transformed catchments, suggesting as a response mechanism for efficient water use efficiency and water loss reduction through evapotranspiration. Third, epiphyte biomass was greater in conserved than in transformed catchments most probably due to microclimatic changes in transformed catchments, such as reduction in air relative humidity and the increase in solar radiation, all known as restrictive factors for epiphyte establishment. Nevertheless, no defined pattern nor significant differences in FRD were found. In general, the functional response of vegetation was more noticeable in species found in both catchments. For example, foliar traits showed significant differences when compared to the weighted averages of each species, but not at the catchment level, which underlines the high variability of foliar responses to the physical conditions of each catchment. Our results provide evidence that functional traits are useful tools to demonstrate the impact of land use changes at catchment levels. Likewise, these results allowed us to move forward in future studies, specifically in determining whether changes in functional traits in the studied catchments translate into changes in ecosystem functioning, such as water fluxes.

#### AUTHOR CONTRIBUTIONS

**Yurani M-Rengifo:** Conceptualization, Methodology, Data curation, Formal analysis (species level), Investigation, Writing original draft, Writing – review and editing (equal).

**María Poca:** Formal analysis (scaling up), Writing – review and editing (equal).

**Conrado Tobón:** Funding acquisition, Supervision, Investigation, Writing – review and editing (equal).

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Municipalities	Precipitation (mm/yr)	Average temperature (°C)	Average humidity (%)	Conserved catchment (dominant land use)	Transformed catchment (dominant land use)
Postrervalle	1067.3	16.6	80.6	Dense forest 62.8%	Abandoned and clean pastures 62.1%
Pucará	1122.7	15.3	79.6	Dense forest and riparian forest 45.8%	Abandoned and clean pastures 54.3%
Vallegrande	2003	16.2	83.9	Dense forest 75.0%	Secondary vegetation and pastures 69.0%

 Table 1. Locations and main characteristics of study catchments in the Natural Integrated Management

 Area of Río Grande-Valles Cruceños.

Pv_c	Vg_c	Pv_t	Pv_c	Pv_t	Vg_t	Pc_c	Vg_c	Pv_t	Pc_c	Vg_t	Pc_t	Pv_t	Pv_t	Pv_c	Pc_t	Pv_t	Vg_t	Catchment
Myrcia multiflora	Ilex argentina	Ilex Argentina	Ilex argentina	Dodonaea viscosa	Dendrophorbium cabrerae	Crinodendron tucumanum	Clethra scabra	Clethra scabra	Blepharocalyx salicifolius	Baccharis latifolia	Baccharis dracunculifolia	Baccharis dracunculifolia	Athyana weinmanniifolia	Athyana weinmanniifolia	Alnus acuminata	Alnus acuminata	Alchornea glandulosa	Species
$7.7 \pm 2.2$	11.0 ± 2.5**	4.5 ± 0.8***	$11.7 \pm 1.0^{**}$	$3.9 \pm 1.1$	$3.9\pm0.6$	$7.9 \pm 2.3$	$6.0 \pm 1.9$	$5.3 \pm 1.6$	$11.7 \pm 4.9^{*}$	$3.9\pm0.6$	$3.3 \pm 1.0$	$3.7\pm1.3$	3.9 ± 0.8***	$13.7 \pm 1.5^{*}$	13.5 ± 2.9**	$7.2 \pm 1.9^{**}$	12.3 ± 2.9**	Height (m)
$9.1 \pm 5.2$	21.9 ± 5.9*	$9.1 \pm 2.0^{*}$	41.9 ± 13.9**	$14.0\pm22.1$	3.4 ± 0.6***	$19.8\pm6.9$	$9.6 \pm 3.2$	$10.2 \pm 2.6$	$22.8 \pm 16.3$	4.3 ± 1.8**	4.4 ± 2.0**	$5.7 \pm 4.1^{*}$	$6.1 \pm 1.4^*$	$30.1 \pm 9.3^{*}$	36.2 ± 13.8*	$19.5\pm19.1$	$35.5 \pm 9.6^{*}$	DBH (cm)
$11.8\pm8.5$	22.3 ± 15.1*	18.3 ± 11.5*	59.0 ± 43.9*	$6.3 \pm 4.2^{*}$	$10.7\pm5.6$	$23.0\pm10.5$	$23.5 \pm 29.8$	6.8 ± 2.9*	$17.5 \pm 21.4$	$13 \pm 7.5$	$4.8 \pm 1.8^{**}$	$10.3 \pm 6.0$	9.7 ± 3.7*	35.5 ± 24.6*	50.3 ± 20.6**	16.0 ± 4.1**	27.3 ± 9.7	Cs (m <sup>2</sup> )
$0.2 \pm 0.4$	$0.2 \pm 0.4$	$0.5 \pm 0.5$	$0.0 \pm 0.0$	$0.2 \pm 0.4$	$1.0 \pm 0.0$	$1.0 \pm 0.4$	$0.0 \pm 0.0$	$0.5 \pm 0.5$	$0.0 \pm 0.0$	$1.0 \pm 0.0$	$0.8 \pm 0.4$	$0.7\pm0.5$	$1.0 \pm 0.0$	$0.5\pm0.5$	$0.0 \pm 0.0$	$0.5\pm0.5$	$0.2 \pm 0.4$	Resprouting
$6.0 \pm 2.5$	3.3 ± 0.8**	16.3 ± 11.5**	17.5 ± 8.5**	5.7 ± 3.7*	$10.2 \pm 4.8$	$13.2 \pm 5.8^{*}$	2.3 ± 0.5***	8.7 ± 4.1**	$5.2 \pm 3.7$	12 ± 5.9	4.5 ± 2.3***	13.0 ± 3.2**	16.2 ± 3.1***	$12.2 \pm 6.9$	$7.2 \pm 3.5$	$12.0 \pm 6.5$	$6.2 \pm 1.9$	Branching
$0.7\pm0.2$	$2.7 \pm 0.4$	$2.5\pm0.3$	$2.6 \pm 0.4$	$1.5\pm0.5$	15.9 ± 2.9***	$1.8\pm0.4$	$2.8\pm0.9$	$4.0 \pm 0.9^{*}$	$0.7\pm0.4$	$4.1 \pm 0.5^{*}$	0.2 ± 0.0***	$0.1 \pm 0.0$ ***	$2.9 \pm 0.7$	$3.7 \pm 0.9^{*}$	$4.3 \pm 1.2^{*}$	$7.0 \pm 1.3^{*}$	19.8 ± 3.0***	LWC (mg)
$8.6 \pm 1.1$	$14.6 \pm 4.1$	$14.5 \pm 1.6$	$49.1 \pm 87.9$	$12.8 \pm 4.9$	83.1 ± 27.1***	$8.7 \pm 1.6$	36.3 ±6.9***	$24.5 \pm 7.0$	$8.1 \pm 1.8$	$28.7 \pm 1.4*$	$1.0 \pm 0.1^{***}$	0.7 ± 0.3***	$16.3 \pm 2.2$	$18.9 \pm 4.9$	49.2 ± 8.2**	57.4 ± 4.5***	142.4 ± 35.6***	LA (cm <sup>2</sup> )
$20.5 \pm 5.2$	$8.6 \pm 1.2^{*}$	9.1 ± 1.2**	23.5 ± 39.2**	$17.8 \pm 2.0$	$45.8 \pm 20.3$	$43.4\pm74.1$	$14.9\pm1.7$	9.5 ± 1.3**	$17.3 \pm 11.3$	18.9 ± 2.8	$20.0 \pm 5.3$	$27.7 \pm 16.5$	$17.1 \pm 12.0$	$30.8 \pm 14.2$	9.8 ± 1.0**	$10.1 \pm 0.9^{**}$	346.7 ± 520.6	SLA(cm <sup>2</sup> / mg)
$2509.0 \pm 448.5$	4626.1 ± 417.4**	2980.5 ± 448.4*	2876.9 ±344.8*	$1869.4 \pm 277.5$	1106.6 ± 315.7*	$1555.6 \pm 335.6$	4241.7 ± 633.1**	1126.1 ± 195.1*	8867.9 ± 2271.7**	2848.3 ± 248.4*	2567.6 ±280.5**	2066.1 ± 266.3**	2609.6 ± 298.9	$2464.0 \pm 610.2$	$1465.5 \pm 250.5^{*}$	1138.1 ± 209.8*	920.4 ± 257.2**	SD (#/mm <sup>2</sup> )
$0.0\pm0.0^{*}$	$318.3 \pm 155.6$	$0.0\pm0.0^{*}$	$0.0 \pm 0.0^{*}$	2277.8 ± 375.0*	$361.9\pm99.2$	$0.0\pm0.0^{*}$	$0.0 \pm 0.0^{*}$	$0.0\pm0.0^{*}$	$7.5\pm18.4$	$0.0 \pm 0.0^{*}$	$0.0 \pm 0.0^{*}$	1138.1 ± 107.3	$0.0\pm0.0^{*}$	$0.0 \pm 0.0^{*}$	1677.2 ± 425.9*	$0.0\pm0.0^{*}$	$261.3 \pm 29.1$	TD (#/mm <sup>2</sup> )
$64.9 \pm 158.9^{*}$	508.9 ± 461.4***	$3.0 \pm 6.5^{**}$	713.7 ±517.5***	5.7 ± 9.7*	122.9 ± 161.8	2844.6 ± 1853.6**	$250.8 \pm 197.3$	$146.1 \pm 327.2$	894.5 ± 937.3	$298.9 \pm 302.4$	$226.1 \pm 329.1$	$0.0 \pm 0.0$ **	2.0 ± 2.2**	$376.3 \pm 585.1^{*}$	741.8 ± 547.3*	$78.1 \pm 161.4^{*}$	$2329.0 \pm 4266.3$	EB (g)

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Pc_t	Pv_c	Vg_t	Vg_c	Pv_t	Vg_c	Pc_t	Pc_c	Pv_t	Pv_c	Vg_c	Vg_t	Vg_t	Vg_c	$Pv_t$	Pc_c	Pv_c	Pc_t	Pc_t
Prunus tucumanensis	Prunus tucumanensis	Prunus oleifolia	Prunus oleifolia	Prunus oleifolia	Prumnopitys exigua	Podocarpus parlatorei	Podocarpus parlatorei	Podocarpus parlatorei	Podocarpus parlatorei	Ocotea puberula	Ocotea porphyria	Nectandra longifolia	Nectandra laurel	Myrsine laetevirens	Myrcianthes pseudomato	Myrcianthes pseudomato	Myrcianthes osteomeloides	Myrcianthes mato
$8.3 \pm 0.7^{*}$	10.9 ± 2.7**	10.6 ± 2.7**	$14.2 \pm 2.0^{**}$	$7.7\pm1.4^{\star}$	$12.5 \pm 1.8^{**}$	10.4 ± 3.0**	11.8 ± 4.3**	$9.2 \pm 2.6$	12.0 ± 3.2**	$6.3 \pm 1.5$	$10.9 \pm 4.8^{*}$	11.3 ± 2.6**	$11.1 \pm 5.1^{*}$	$6.3 \pm 1.5$	$9.2\pm3.5$	$8.1 \pm 2.4$	$6.7\pm1.9$	$7.9 \pm 2.0$
17.8 ± 5.9	$24.8\pm9.7$	21.0 ± 6.2**	31.0 ± 12.0*	13.8 ± 2.5**	35.9 ± 8.1**	$31.8 \pm 5.3^{*}$	$21.4 \pm 3.4$	$19.3 \pm 4.5$	44.3 ± 23.2**	$11.7 \pm 4.0$	$19.8 \pm 12.1$	$22.7 \pm 3.2$	27.8 ± 19.7	$11.9\pm3.2$	$14.5 \pm 3.9$	$10.5 \pm 3.0$	$12.4 \pm 3.7$	$16.2 \pm 5.6$
21.8 ± 10.7	$21.7 \pm 17.6$	30.7 ± 15.5*	53.7 ± 29.7*	19.0 ± 13.4*	61.3 ± 11.4***	46.0 ± 36.4***	12.3 ± 4.5***	17.5 ± 5.5***	69.5 ± 43.7**	$8.0 \pm 3.8^{*}$	$36.8 \pm 23.4$	$27.3 \pm 6.3$	$36.6 \pm 44.1$	$4.9 \pm 1.7^{**}$	$17.2 \pm 10.8$	$19.8\pm8.0$	$18 \pm 9.5$	$32.3\pm20.5$
$0.7\pm0.5$	$0.2 \pm 0.4$	$0.3 \pm 0.5$	$0.0 \pm 0.0$	$0.5\pm0.5$	$0.0 \pm 0.0$	$0.2 \pm 0.4$	$0.5\pm0.5$	$0.5 \pm 0.5$	$0.0 \pm 0.0$	$0.3 \pm 0.5$	$0.7\pm0.5$	$0.2 \pm 0.4$	$0.2 \pm 0.4$	$0.0 \pm 0.0$	$0.0 \pm 0.0$	$0.8 \pm 0.4$	$0.3 \pm 0.5$	$0.5\pm0.5$
4.8 ± 2.6**	10.8 ± 3.8**	$6.5 \pm 1.5$	$5.7 \pm 2.2$	9.8 ± 8.3	$5.5 \pm 2.7$	$5.5 \pm 2.2^{*}$	$6.5 \pm 2.7^{*}$	$8.8\pm4.6^{*}$	13.2 ± 3.9**	$3.2\pm1.6^*$	$9.0 \pm 3.6$	$4.5 \pm 1.4$	$4.7 \pm 2.0$	$5.7\pm2.3$	4.2 ± 0.8***	$11.8 \pm 3.5^{*}$	$4.3 \pm 0.8$	$6.8 \pm 2.6$
$3.2 \pm 0.6^{*}$	$2.9 \pm 0.7$	$5.5 \pm 1.0^{*}$	$4.6 \pm 1.5^{*}$	$5.2 \pm 0.6^{*}$	0.1 ± 0.02***	$0.3 \pm 0.0^{**}$	$0.3 \pm 0.1^{**}$	$0.3 \pm 0.1^{**}$	$0.3 \pm 0.0^{**}$	$3.5 \pm 0.8^{*}$	$1.8\pm0.4$	22.4 ± 4.6***	5.3 ± 2.3*	$2.4 \pm 0.5$	$2.0 \pm 0.4^{**}$	$1.2 \pm 0.3^{**}$	0.04 ± 0.01***	$3.0 \pm 3.5$
24.6 ± 4.5	76.8 ± 136.3*	43.4 ± 4.5**	38.4 ± 7.4*	42.7 ± 7.1**	$0.5 \pm 0.1^{***}$	1.7 ± 0.2***	$1.4 \pm 0.3^{***}$	$1.9 \pm 0.4^{***}$	$1.4 \pm 0.2^{***}$	$32.4 \pm 6.0*$	$16.3 \pm 3.3$	120.6 ± 25.8***	44.7 ± 5.4**	$11.7\pm2.2$	$14.7 \pm 1.2$	$10.3 \pm 1.4$	0.2 ± 0.04***	$12.1 \pm 2.8$
$13.1 \pm 1.2$	$63.5 \pm 121.4$	$23.5\pm11.6$	$15.7 \pm 4.5$	$16.6 \pm 2.4$	$34.8 \pm 15.5$	$8.4\pm0.8^{*}$	$8.5\pm1.6^*$	9.2 ± 2.6**	$9.0 \pm 1.6^*$	$15.1 \pm 5.6$	$15.1 \pm 3.2$	$30.6 \pm 12.9$	$12.3\pm2.2$	$10.1 \pm 1.7^{*}$	$10.5 \pm 1.6^{*}$	$8.5 \pm 1.4^{**}$	$17.1 \pm 5.6$	$10.6 \pm 1.0^{**}$
3522.5 ± 494.3*	2635.1 ± 259.5**	2222.2 ±278.4	$2644.1 \pm 608.8$	$2060.1 \pm 217.1$	3650.2 ± 1019.6*	2932.4 ± 218.1*	1948.9 ±252.0***	1681.7 ±292.3***	1306.3± 176.4***	5346.8 ± 561.9*	3527.0 ± 373.9*	$2130.6 \pm 198.6$	3439.9 ± 735.1*	$2270.3 \pm 822.1$	4873.9 ± 2189.2*	4456.5 ± 489.4*	4542.0 ± 1637.0*	3211.7 ± 1685.0
$0.0 \pm 0.0^*$	$0.0\pm0.0^*$	$0.0\pm0.0^*$	$0.0\pm0.0^{*}$	$0.0\pm0.0^{*}$	$0.0\pm0.0^{*}$	$0.0\pm0.0^*$	$0.0\pm0.0^{*}$	$0.0\pm0.0^*$	$0.0\pm0.0^*$	187.7 ± 89.3*	$0.0\pm0.0^*$	1435.4 ± 558.9	2973.0 ± 1783.4*	$0.0\pm0.0^{*}$	327.3 ±114.8	$0.0\pm0.0^*$	$0.0\pm0.0^*$	$0.0\pm0.0^*$
1050.0 ±770.9	1297.7 ±1295.1	280.6 ± 219.4	5310.7 ± 2375.0***	$5.4 \pm 4.9^{*}$	$2582.2 \pm 2044.8^{*}$	$3450.8 \pm 5270.6$	2540.4 ±3029.7*	$13.6 \pm 6.6^{*}$	$739.7 \pm 531.5$	$1580.6 \pm 990.3^{*}$	$267.7 \pm 254.4$	$375.9 \pm 210.0$	$2495.3 \pm 1599.5^*$	$10.9\pm10.5^{\ast}$	64.9 ± 121.8*	$19.5 \pm 32.6^{*}$	302.3 ± 133.8	2880.7 ± 4343.6*

Pc_t	$Pv_t$	Vg_t	Pc_c	Pv_t	Pv_c	Vg_t	Pv_t	Pv_t	Pv_c	Pc_t	Pc_t	Pc_t	Pc_t	Vg_t		Vg_c	Pc_t	Pv_t	Pv_c	Pv_c	Vg_c	Vg_t
Jarava ichu	Jarava ichu	Galinsoga quadriradiata	Desmodium affine	Desmodium adscendens	Chaptalia nutans	Centrosema sp.	Cantinoa mutabilis.	Campovassouria cruciata	Brunfelsia plowmaniana	Bidens sp.	Baccharis sp.	Baccharis genistelloides	Asteraceae sp.	Ageratum conyzoides	Herbaceous	Viburnum seemenii	Viburnum seemenii	Viburnum seemenii	Viburnum seemenii	Symplocos neei	Siphoneugena occidentalis	Sapium glandulosum
$0.9\pm0.1$	$1.0 \pm 0.2$	$0.08 \pm 0.02^{**}$	$0.08 \pm 0.02^{**}$	$0.07 \pm 0.02^{**}$	$0.05 \pm 0.01^{**}$	$0.2 \pm 0.1$	$0.1 \pm 0.06^*$	$0.5\pm0.2$	$0.2\pm0.03^{\star}$	0.2 ± 3.3 x 10 <sup>-9</sup>	$0.1\pm0.04^{*}$	$0.4\pm0.05$	0.4 ± 6.7 x 10 <sup>-9</sup>	$0.2 \pm 0.1^{*}$		$6.5\pm1.4$	$5.8\pm0.8$	$4.3\pm0.8$	$6.7\pm1.6$	$10.8\pm2.5^{\star}$	$9.5 \pm 2.5^{*}$	12.0 ± 4.1**
																$8.5 \pm 2.0^{*}$	$12.1 \pm 2.9^{*}$	$6.0\pm1.8^{*}$	$12.1 \pm 6.0^*$	$29.8 \pm 9.5^{*}$	$17.4 \pm 6.4$	$21.3 \pm 7.2$
																$9.1 \pm 5.2$	$10.8\pm3.4$	$7.9 \pm 6.3^{*}$	$12.0\pm5.2$	$41.8\pm22.7$	$20.5\pm8.9$	$18.5 \pm 11.7$
																$0.3\pm0.5$	$0.2\pm0.4$	$0.7\pm0.5$	$0.7\pm0.5$	$0.2\pm0.4$	$0.0\pm0.0$	$0.0\pm0.0$
																$3.0 \pm 1.5^{**}$	$4.0 \pm 0.9^{**}$	9.2 ± 7.9**	6.8 ± 2.5**	$12.5 \pm 6.7^{*}$	$4.2 \pm 1.5$	$4.7 \pm 2.3$
$0.3 \pm 0.2^{**}$	$0.2 \pm 0.2^{***}$	$1.8\pm0.9$	$0.1 \pm 0.1 ***$	$0.4 \pm 0.2^{*}$	$1.9\pm0.7$	$1.0 \pm 0.3$	$0.6 \pm 0.1$	$0.3 \pm 0.1^{**}$	$1.9\pm0.6$	$1.1 \pm 0.3$	$0.1 \pm 0.01 ***$	$2.6\pm1.7$	$0.70\pm0.1$	$2.0 \pm 0.7$		$2.3 \pm 0.3^*$	$2.2 \pm 0.8^*$	$2.1\pm0.4^{*}$	$2.5 \pm 0.4^*$	$2.7\pm0.8$	$1.3 \pm 0.2$	24.0 ± 11.6***
$6.1 \pm 4.0^*$	$13.4 \pm 18.6$	$14.1 \pm 6.4$	$7.5 \pm 2.1$	$10.4 \pm 4.4$	$18.6\pm7.5$	$11.9 \pm 3.0$	29.4 ± 47.2	$2.1 \pm 0.5^{**}$	$15.2 \pm 4.3$	$8.8 \pm 1.7$	$0.5 \pm 0.1^{***}$	$32.9 \pm 7.1*$	$12.2 \pm 17.2$	$15.8 \pm 4.9$		$15.3\pm3.1$	$14.6\pm3.5$	$13.3\pm1.8$	$17.6\pm5.4$	$18.7\pm4.8$	$11.8 \pm 2.1$	128.0 ± 74.5***
$88.4 \pm 46.2^{*}$	$192.6 \pm 405.5$	160.6 ± 63.7**	320.9 ± 200.7**	$81.6 \pm 51.2^{*}$	$65.5 \pm 15.4^{*}$	$31.9 \pm 13.1$	294.8 ± 540.4*	$21.7 \pm 11.3$	$21.6\pm3.7$	$28.6 \pm 8.0$	$19.4 \pm 5.7$	$11.4 \pm 3.2^*$	$41.4 \pm 62.3$	$52.1 \pm 3.4$		$15.7\pm1.9$	$15.9\pm3.7$	$14.7\pm3.3$	$14.7\pm2.7$	$14.6\pm2.4$	$13.0 \pm 2.2$	$43.1\pm32.5$
		$2522.5 \pm 401.8$	882.9 ± 366.6**	708.7 ± 84.8***	$1525.5 \pm 244.9$	953.5 ± 169.1**	659.2 ± 65.8***	759.8 ± 111.0***	$1567.6 \pm 119.4$	717.7 ± 153.1***	841.6 ± 120.8**	$1319.5\pm75.0$	$3291.3 \pm 1453.1^*$	2824.3 ± 270.3*		$2186.2 \pm 364.3$	$2229.7 \pm 534.5$	$1786.8 \pm 147.9$	$1560.1 \pm 260.1$	$1843.8 \pm 142.4$	9211.7 ± 1416.2**	719.2 ± 80.1***
		$400.9\pm67.4$	384.4 ± 104.2	752.3 ± 164.6	$0.0\pm0.0^{*}$	$771.8\pm98.0$	$771.8\pm86.9$	$0.0\pm0.0^*$	$0.0\pm0.0^{\star}$	1009.0 ± 726.7	$0.0\pm0.0^*$	$0.0\pm0.0^{*}$	$1148.6 \pm 671.1$	$334.8\pm91.9$		$0.0\pm0.0^{\star}$	$0.0\pm0.0^{*}$	$0.0\pm0.0^{*}$	$0.0\pm0.0^{*}$	$0.0\pm0.0^{*}$	$0.0 \pm 0.0^{*}$	$0.0\pm0.0^{*}$
																$354.0 \pm 185.7^{**}$	$487.9 \pm 473.6^{**}$	$2.0 \pm 3.4^{**}$	$175.2 \pm 80.7^{**}$	$648.9 \pm 455.1$	4573.1 ± 2198.0**	$568.5 \pm 832.7$

Marisia sp. $0.3 \pm 0.2$ $1.3 \pm 0.4^{\circ}$ $0.1 \pm 60.1^{\circ}$ $0.1 \pm 0.0^{\circ\circ}$ $0.0 \pm 0.0^{\circ\circ}$ Plana inder provide $0.1 \pm 0.0^{\circ\circ}$ Plana inder provide $0.1 \pm 0.0^{\circ\circ}$ Plana inder provide $0.1 \pm 0.0^{\circ\circ}$ $0.0$	Vg_t	Pv_t	Pv_t	Vg_c	Vg_t	Pc_t	Vg_t	Pc_t	Vg_c	Pv_t	Vg_c	Pc_c	Pc_c	Pv_c
$13 \pm 0.4^{2}$ $10.1 \pm 0.1^{2}$ $40.1 \pm 0.1^{2}$ $40.1 \pm 0.1^{2}$ $16.7 \pm 49.3^{2}$ $16.7 \pm 49.3^{2}$ $16.7 \pm 49.3^{2}$ $10.2 \pm 8.1^{2}$ $0.1 \pm 0.02^{2*}$ $0.1 \pm 0.02^{2*}$ $0.1 \pm 0.02^{2*}$ $12.2 \pm 0.2^{2*}$ $84.6 \pm 28.3^{2}$ $1173.0 \pm 2172.2^{2*}$ $1144.1 \pm 329.4$ $0.5 \pm 0.2$ $0.1 \pm 0.01^{2*}$ $5.4 \pm 1.9^{2}$ $499.2 \pm 24.1^{2*}$ $397.9 \pm 111.4^{2}$ $648.6 \pm 293.9$ $0.5 \pm 0.2$ $0.2 \pm 0.2^{2*}$ $5.4 \pm 1.9^{2}$ $499.2 \pm 24.1^{2*}$ $397.9 \pm 111.4^{2}$ $648.6 \pm 293.9$ $0.1 \pm 0.02^{2*}$ $2.7 \pm 0.6$ $34.7 \pm 9.1^{2}$ $51.3 \pm 7.0$ $1480.5 \pm 23.6$ $250.8 \pm 7.08$ $0.1 \pm 0.02^{2*}$ $1.4 \pm 0.2^{2*}$ $4.7 \pm 0.6^{2*}$ $51.3 \pm 7.0$ $1480.5 \pm 23.6$ $250.8 \pm 7.08$ $0.1 \pm 0.02^{2*}$ $1.0 \pm 0.2$ $10.3 \pm 1.5$ $6.9 \pm 7.8^{2}$ $689.2 \pm 38.3 \pm 15.8^{2}$ $318.3 \pm 53.3$ $0.1 \pm 0.02^{2*}$ $1.0 \pm 0.2$ $10.3 \pm 1.5$ $6.9 \pm 7.8^{2}$ $109.1 \pm 52.7^{2}$ $325.3 \pm 57.9^{2}$ $0.1 \pm 0.02^{2*}$ $0.1 \pm 0.02^{2*}$ $0.3 \pm 1.1^{2*}$ $56.5 \pm 4.3^{2*}$ $0.0 \pm 0.0^{2*}$ $0.1 \pm 0.02^{2*}$ $0.3 \pm 0.1$ $52.5 \pm 9.4^{2*}$ $52.5 \pm 9.4^{2*}$ $0.0 \pm 0.0^{2*}$ $0.3 \pm 0.1$ $0.3 \pm 0.1$ $52.5 \pm 9.4^{2*}$ $52.5 \pm 9.4^{2*}$ $00.24.0^{2*}$ $0.3 \pm 0.1$ $0.3 \pm 0.1$ $52.5 \pm 9.4^{2*}$ $0.0 \pm 0.0^{2*}$ $0.1 \pm 0.05^{2*}$ $0.7 \pm 0.1$ $9.4 \pm 1.4$ $78.5 \pm 7.2^{2*}$ $80.3 \pm 7.06$ $0.1 \pm 0.05^{2*}$ $0.2 \pm 0.2^{2*}$ $52.8 \pm 1.4^{2*}$ $8$	Urochloa brizantha	Tibouchina herzogii	Tibouchina sp.	Solanum turneroides	Solanum sp.	Ruellia sp.	Pseudelephantopus spiralis	Pilea rusbyi	Peperomia blanda	Peperomia blanda	Palicourea guianensis	Oxalis triangularis	Mutisia sp.	Mutisia sp.
$1.3 \pm 0.4^*$ $40.1 \pm 61.4$ $\pm 457.2^*$ $166.7 \pm 49.3^*$ $701.2 \pm 82.1$ $0.1 \pm 0.02^{***}$ $1.2 \pm 0.2^{***}$ $84.6 \pm 28.3^*$ $\frac{1373.0 \pm}{217.2^{***}}$ $1144.1 \pm 329.4$ $0.1 \pm 0.05^{***}$ $5.4 \pm 1.9^*$ $\frac{409.2 \pm}{246.1^{**}}$ $397.9 \pm 111.4^*$ $648.6 \pm 293.9$ $2.7 \pm 0.6$ $34.7 \pm 9.1^*$ $37.1 \pm 7.6$ $1178.7 \pm 103.5$ $0.0 \pm 0.0^*$ $2.6 \pm 0.8^{**}$ $36.6 \pm 12.0^*$ $51.3 \pm 7.0$ $1480.5 \pm 236.0$ $250.8 \pm 70.8$ $1.4 \pm 0.2^{**}$ $4.7 \pm 0.6^{**}$ $51.3 \pm 7.0$ $1480.5 \pm 236.0$ $250.8 \pm 70.8$ $1.0 \pm 0.2$ $10.3 \pm 1.5$ $60.9 \pm 7.8^*$ $689.2 \pm 10.9 \pm 111.4^*$ $0.0 \pm 0.0^*$ $1.1 \pm 0.2$ $39.4 \pm 36.4$ $204.9 \pm 170.8^*$ $109.1^{***}$ $0.0 \pm 0.0^*$ $2.0 \pm 0.5$ $3.7 \pm 1.3^{**}$ $96.2 \pm 16.9^*$ $2397.1 \pm 257.2$ $532.3 \pm 57.9$ $0.7 \pm 0.1$ $9.4 \pm 1.4$ $78.5 \pm 72^*$ $950.5 \pm 94.3^{**}$ $0.0 \pm 0.0^*$ $3.5 \pm 0.9^*$ $19.1 \pm 3.2$ $\frac{247.0 \pm 295.95 \pm 2}{223.8^{**}}$ $800.3 \pm 70.6$ $0.5 \pm 0.2^*$ $20.7 \pm 38.7$ $80.9 \pm 114.1$ $1800.3 \pm 319.1$ $1084.1 \pm 158.0$ $2.1 \pm 0.3$ $28.8 \pm 12.4^*$ $25.8 \pm 14.4$ $0.0 \pm 0.0^*$	1.8 ± 2.7 x 10 - <sup>8</sup>	$0.1 \pm 0.05^{**}$	$0.3\pm0.1$	$0.3 \pm 0.1$	$0.4 \pm 0.2$	$0.1 \pm 0.02^{**}$	$0.1 \pm 0.02^{**}$	$0.2 \pm 0.02$	$0.1 \pm 0.02^{**}$	0.1 ± 8.3 x 10 -10**	$0.5 \pm 0.2$	$0.1 \pm 0.01^{**}$	$0.1 \pm 0.02^{**}$	$0.3 \pm 0.2$
$40.1 \pm 61.4$ $167.2 \times 166.7 \pm 49.3 \times 701.2 \pm 82.1$ $1.2 \pm 0.2 \times 8$ $84.6 \pm 28.3 \times 1373.0 \pm 1172.2 \times 5.4 \pm 1.9 \times 246.1 \times 397.9 \pm 111.4 \times 648.6 \pm 293.9$ $34.7 \pm 9.1 \times 246.1 \times 246.1 \times 397.9 \pm 111.4 \times 648.6 \pm 293.9$ $36.6 \pm 12.0 \times 51.3 \pm 7.0$ $1480.5 \pm 236.0 \times 250.8 \pm 70.8 \times 147.6 \pm 58.4 \times 58.4 \times 58.4 \times 103.5 \pm 10.3 \pm 15.8 \times 109.1 $	$2.1 \pm 0.3$	$0.5\pm0.2^{*}$	$3.5 \pm 0.9^{*}$	$0.7\pm0.1$	$2.0 \pm 0.5$	$0.3 \pm 0.1$ **	$1.1 \pm 0.2$	$1.0 \pm 0.2$	$1.4 \pm 0.2^{**}$	$2.6 \pm 0.8^{**}$	$2.7\pm0.6$	$0.1 \pm 0.05^{***}$	$0.1 \pm 0.02^{**}$	$1.3 \pm 0.4^{*}$
$\pm 457.2^{*}$ 166.7 \pm 49.3^{*}701.2 \pm 82.1 $84.6 \pm 28.3^{*}$ $1373.0 \pm \\ 217.2^{***}$ $1144.1 \pm 329.4$ $409.2 \pm \\ 246.1^{**}$ $397.9 \pm 111.4^{*}$ $648.6 \pm 293.9$ $37.1 \pm 7.6$ $1178.7 \pm 103.5$ $0.0 \pm 0.0^{*}$ $51.3 \pm 7.0$ $1480.5 \pm 236.0$ $250.8 \pm 70.8$ $147.6 \pm \\ 58.4^{**}$ $348.3 \pm 15.8^{*}$ $318.3 \pm 53.3$ $60.9 \pm 7.8^{*}$ $689.2 \pm \\ 109.1^{***}$ $0.0 \pm 0.0^{*}$ $204.9 \pm \\ 170.8^{*}$ $2397.1 \pm 257.2$ $532.3 \pm 57.9$ $96.2 \pm 16.9^{*}$ $950.5 \pm 94.3^{**}$ $0.0 \pm 0.0^{*}$ $57.4 \pm 16.4$ $1226.7 \pm 158.9$ $1052.6 \pm 206.7$ $78.5 \pm 7.2^{*}$ $959.5 \pm \\ 223.8^{**}$ $800.3 \pm 70.6$ $247.0 \pm \\ 69.8^{**}$ $861.9 \pm 72.7^{**}$ $0.0 \pm 0.0^{*}$ $80.9 \pm 1114.1$ $1800.3 \pm 319.1$ $1084.1 \pm 158.0$ $25.8 \pm 14.4$ $\ldots$ $0.0 \pm 0.0^{*}$	$28.8 \pm 12.4^{*}$	$20.7\pm38.7$	$19.1 \pm 3.2$	$9.4 \pm 1.4$	$26.5 \pm 5.4*$	$3.7 \pm 1.3^{**}$	$39.4 \pm 36.4$	$10.3 \pm 1.5$	$4.7 \pm 0.6^{**}$	$36.6 \pm 12.0^{*}$	$34.7\pm9.1*$	$5.4 \pm 1.9^{*}$	$1.2 \pm 0.2^{***}$	$40.1\pm61.4$
$166.7 \pm 49.3^{*}$ $701.2 \pm 82.1$ $1373.0 \pm$ $1144.1 \pm 329.4$ $217.2^{***}$ $1144.1 \pm 329.4$ $397.9 \pm 111.4^{*}$ $648.6 \pm 293.9$ $1178.7 \pm 103.5$ $0.0 \pm 0.0^{*}$ $1480.5 \pm 236.0$ $250.8 \pm 70.8$ $348.3 \pm 15.8^{*}$ $318.3 \pm 53.3$ $689.2 \pm$ $0.0 \pm 0.0^{*}$ $109.1^{***}$ $0.0 \pm 0.0^{*}$ $2397.1 \pm 257.2$ $532.3 \pm 57.9$ $950.5 \pm 94.3^{**}$ $0.0 \pm 0.0^{*}$ $1226.7 \pm 158.9$ $1052.6 \pm 206.7$ $959.5 \pm$ $200.3 \pm 70.6$ $861.9 \pm 72.7^{**}$ $0.0 \pm 0.0^{*}$ $1800.3 \pm 319.1$ $1084.1 \pm 158.0$ $0.0 \pm 0.0^{*}$ $0.0 \pm 0.0^{*}$	$25.8 \pm 14.4$	$80.9 \pm 114.1$	247.0 ± 69.8**	78.5 ± 7.2*	$57.4 \pm 16.4$	$96.2 \pm 16.9^{*}$	204.9 ± 170.8*	$60.9 \pm 7.8^{*}$	147.6 ± 58.4**	$51.3 \pm 7.0$	$37.1\pm7.6$	409.2 ± 246.1**	84.6 ± 28.3*	248.1 ±457.2*
701.2 $\pm$ 82.1 11144.1 $\pm$ 329.4 648.6 $\pm$ 293.9 0.0 $\pm$ 0.0* 250.8 $\pm$ 70.8 318.3 $\pm$ 53.3 0.0 $\pm$ 0.0* 532.3 $\pm$ 57.9 0.0 $\pm$ 0.0* 1052.6 $\pm$ 206.7 800.3 $\pm$ 70.6 0.0 $\pm$ 0.0* 1084.1 $\pm$ 158.0 0.0 $\pm$ 0.0*		$1800.3 \pm 319.1$	861.9 ± 72.7**	959.5 ± 223.8**	$1226.7 \pm 158.9$	$950.5 \pm 94.3^{**}$	$2397.1 \pm 257.2$	689.2 ± 109.1***	348.3 ± 15.8*	$1480.5 \pm 236.0$	$1178.7 \pm 103.5$	$397.9 \pm 111.4^{*}$	1373.0± 217.2***	166.7 ±49.3*
	$0.0\pm0.0^{*}$	$1084.1 \pm 158.0$	$0.0\pm0.0^{*}$	$800.3 \pm 70.6$	$1052.6 \pm 206.7$	$0.0\pm0.0^*$	$532.3 \pm 57.9$	$0.0\pm0.0^*$	$318.3\pm53.3$	$250.8 \pm 70.8$	$0.0\pm0.0^*$	$648.6 \pm 293.9$	1144.1 ±329.4	$701.2 \pm 82.1$

# \* $p \le 0.05$ , \*\* $p \le 0.01$ , \*\*\* $p \le 0.001$

number of main branches (branching), leaf water content (LWC), leaf area (LA), specific leaf area (SLA), stomata density (SD), trichomes density (TD) and Table 2. Average values and standard deviation of the functional traits of vegetation: height, diameter at breast height (DBH), canopy size (Cs), resprouting, epiphytes biomass (EB). Per catchments study, Postrervalle, Pucará and Vallegrande, c and t, significant conserved catchments or transformed catchments.

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**Figure 1:** Catchments locations in the region of Santa Cruz, Bolivia. Postrervalle conserved (Pv\_c), Postrervalle transformed (Pv\_t), Pucará conserved (Pc\_c), Pucará transformed (Pc\_t), Vallegrande conserved (Vg\_c), and Vallegrande transformed (Vg\_t).



**Figure 2.** Distribution of structural, foliar, and community traits of dominant woody and herbaceous species according to the catchment type.



**Figure 3:** Scaling up at the catchment level, of structural, foliar and community traits. \* indicates significant differences and NS: No significant differences. C stands for conserved and T for transformed. For details on scaling up procedure see Supplementary Material 2.

 $**p \le 0.01, ***p \le 0.001.$ 



**Figure 4:** (a). Functional traits at catchment level (Supplementary 2, eq. 1), height, diameter at breast height (DBH), canopy size (Cs), resprouting, main branches (branching), leaf water content (LWC), leaf area (LA), specific leaf area (SLA), stomata density (SD), trichomes density (TD), epiphyte biomass (EB), and root density fine (FRD). (b). Distribution of catchments.

Catchments	Main characteristics	Land cover	Pi (%)	NP	MPS (m <sup>2</sup> )	MNN (m)
	Locations: 63°52'17.56" S	High dense forest	62.8	1	2859580	0
	18°27'53.30" W	Clean pastures	12.8	15	38971.9	123.5
	Altitude (m.a.s.l): 2331	High secondary vegetation	11.1	3	29649.6	52.5
Pv_c	Total area: 4.6 km <sup>2</sup>	Low secondary vegetation	6.3	22	13097.9	67.5
	Slope: slightly steep	Abandoned pastures	4.4	21	9432.2	109
	Level catchment: 2	Fragmented forest with secondary vegetation	2.3	3	35469.8	415.2
	Soils: sandy clay loam	Roads network and associated land	0.3	2	7554.6	300
	Leastione: 62950'49.07" 6	Abandoned pastures	31.9	24	41290.2	21.5
	<u>Locations:</u> 65 50 48.07 S 18°30'33.74" W	Clean pastures	23.1	17	42254.0	43.5
	<u>Altitude (m.a.s.l):</u> 2036	Riparian forest	22.7	8	88261.8	29.5
Dry f	Total area: 3.1 km <sup>2</sup>	Low secondary vegetation	12.3	33	11596.2	56.4
rv_t	Slope: slightly steep	Other transient crops	4.1	3	42443.6	130.3
	Level catchment: 2	High secondary vegetation	3.0	7	13220.9	184.1
	Soils: sandy loam	Bare soils and degraded lands	1.5	5	9504.7	163.4
	<u>Sons.</u> Sandy Ioann	Low dense forest	1.3	2	20571.4	1030.0
		Riparian forest	38.2	1	621085.0	0.0
	Locations: 64°7'39.45"S	Clean pastures	17.3	29	9676.0	27.8
	18º41'0.7" W	High secondary vegetation	14.9	30	8098.0	26.8
	Altitude (m.a.s.l): 2776	Abandoned pastures	10.4	18	9373.,5	36.5
Pc_c	Total area: 1.6 km <sup>2</sup>	Low secondary vegetation	9.4	10	15345.0	146.7
	Slope: slightly steep	High dense forest	5.2	2	41961.3	69.9
	Level catchment: 2	Low dense forest	2.5	2	20147.6	198.8
	Soils: sandy clay loam	Other transient crops	1.5	7	3458.6	10.8
		Roads network and associated land	0.7	4	2951.8	33.6
		Clean pastures	49.8	19	36374.5	14.6
		Riparian forest	33.5	1	464752.0	0.0
	Locations: 64°7'51.50" S	Abandoned pastures	4.5	9	6985.6	48.9
	18°42 45.9 W	High secondary vegetation	3.1	11	3877.4	113.5
	Altitude (m.a.s.l): 2/3/	High dense forest	2.2	3	9992.6	28.0
Pc_t	<u>Total area:</u> 1.4 km <sup>2</sup>	Other transient crops	1.9	6	4392.4	75,1
	Slope: slightly steep	Roads network and associated land	1.6	2	11203.9	322.0
	Level catchment: 2	Fragmented forest with secondary vegetation	1.3	1	17922.0	0.0
	Soils: sandy clay loam	Low secondary vegetation	1.1	6	2431.4	156.7
		Low dense forest	0.8	2	5546.0	790.0
		Bare soils and degraded lands	0.2	2	1650.3	321.6
	Locations: 63°54'36.14" S	High dense forest	75.0	1	250586.0	0.0
	10°41 41.11 W	Clean pastures	7.5	4	6288.9	145.5
	Altitude (m.a.s.l): 2358	High secondary vegetation	6.7	4	5621.3	116.7
Vg_c	<u>Iotal area:</u> 0.3 km <sup>2</sup>	Low secondary vegetation	5.9	3	6552.4	161.4
	Slope: moderately steep	Abandoned pastures	3.7	2	6111.7	485.0
	Level catchment: 2	Roads network and associated land	1.2	1	4006.5	0.0
	Soils: sandy clay loam					

		High secondary vegetation	30.5	10	10404.3	34.7
	Locations: 63°52'45.82" S	Clean pastures	14.5	8	6166.3	18.0
	18°46′53.85″ W	High dense forest	13.3	7	6498.8	24.2
Vg_t	<u>Altitude (m.a.s.l):</u> 1710	Low secondary vegetation	12.9	6	7348.0	69.9
	Total area: 0.3 km <sup>2</sup>	Abandoned pastures	11.2	5	7651.9	66.6
	Slope: slightly steep	Riparian forest	10.9	3	12414.7	36.4
	Level catchment: 2	Low dense forest	3.3	1	11366.4	0.0
	Soils: sandy clay loam	Roads network and associated land	2.3	1	7705.3	0.0
		Permanent arboreal crops	1.1	1	3879.0	0.0

Table 1. Locations and values of main characteristics of study catchments and landscape metrics of percentage of landscape (%Pi), number of patches (NP), mean patch size (MPS) and mean nearest neighbor distance (MNN) in the Postrervalle conserved (Pv\_c), Postrervalle transformed (Pv\_t), Pucará conserved (Pc\_c), Pucará transformed (Pc\_t), Vallegrande conserved (Vg\_c) and Vallegrande transformed (Vg\_t) catchments. Metrics were obtained with the Fragstats program version 4.2.1.

#### **SUPPLEMENTARY 2**

For upscaling data to a catchment level, we assigned a percentage of the landscape (landscape metrics %Pi, item 1 of the supplementary material) to each catchment. Then, the relative abundances of each species were obtained for each plot in studied catchments. All the parameters were related to the weighted average of each trait by modifying the equation of Garnier et al. (2004) and Pérez-Harguindeguy et al. (2013) as follows:

Equation 1:

Weighted average of each trait at the catchment  $|evel_j| = \sum_{i=1}^{n} p_i * I_i * trait_i$ 

i = 1

Where  $p_i$  is the average relative abundance of species *i* of all plots in catchment *j*; n is the number of the most abundant species on average in plots of catchment *j*;  $l_j$  is the relative coverage of species *i* in the corresponding landscape unit within catchment *j*; and trait<sub>*i*</sub> is the average value of the functional trait of species *i* in the plots of catchment *j*. For fine root density, the data for each depth was averaged by soil pit and by catchment.