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# Colonization-related functional traits of plants in a 50-hectare plot of secondary tropical forest

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## ABSTRACT

The growth-survival trade-off hypothesis states that functional traits of stem, wood, leaves and fruits govern acquisitive and conservative strategies of plant species that grow/survive differently in forests. We aimed to determine whether heterogeneity during the colonization of a secondary Atlantic Forest fragment causes differences in colonization-related traits and determines taxonomic composition of subplots. A total of 5,078 subplots were censused with leaf and fruit traits and height measurements being determined for each tree of each species, and with averaged-abundance-weighted values calculated for each subplot. A dendrogram was generated from the taxonomic composition of subplots using Sorensen similarity and UPGMA clustering. A total of 74,335 trees of 178 species were recorded. Clustering revealed five main groups of subplots that were tested against each other and found to differ in terms of average leaf width, leaf-width/petiole-width, wood density, mean height, height mode, fruit width and fruit length. Greater leaf averages in subplots were associated with greater fruit averages, and with higher wood densities and greater heights among groups of subplots, revealing that heterogeneity during colonization directed the communities of the 50-ha plot. The averaged values of functional traits detected subplots associated with conditions favorable to colonization, thereby reinforcing the growth-survival trade-off hypothesis.

**Keywords:** colonization, fruit size, LEEP 50-ha plot, leaf functional traits, plant height, wood density, plant functional traits, phytosociology

## Introduction

The Brazilian Atlantic Forest is not only one of the most diverse tropical forests worldwide, but also one of the most threatened, mainly because of intense disturbance leading to habitat loss and fragmentation (Ribeiro *et al*. 2009; Magnago *et al*. 2015). Nonetheless, there still remains high plant diversity, even on the most fragmented Atlantic Forest landscapes, although taxonomic, functional, and phylogenetic diversities are vanishing (Gastauer & Meira-Neto 2013; Matos *et al*. 2017). The future of the Brazilian Atlantic Forest is uncertain and its fragments essentially composed of secondary forests, forecast homogenized landscapes with much lower diversity (Ribeiro *et al*. 2009; Solar *et al*. 2015). The understanding of the composition and functioning of the Brazilian Atlantic Forest is crucial to understand the future of tropical forests in general (Magnago *et al*. 2015; Pyles *et al*. 2018).

Studies of large plots (50 hectares) in tropical forests have generated evidence for some major theoretical and practical advances based in ecology. Barro Colorado Island

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(BCI) in Panama, Central America, was the first 50-ha plot to be studied, which added to the knowledge of tropical forests in an unprecedent way. According to the Scopus database, from 1972 to 1981 an average of 2.2 papers were published per year with 'Barro Colorado Island' as the tag, while from the year of the 50-ha sampling, 1982, to 2017 there was an average of 19.2 published papers per year with the same tag.

The LEEP (Laboratory of Ecology and Evolution of Plants) 50-ha plot is an outstanding example of a fragment of Brazilian Atlantic Forest because it is a 40-year-old patch of secondary growth forest situated within a highly fragmented landscape with exceptionally low possibilities for immigration (Fig. 1) and with predictable neutral drift given the strong dispersal limitation (sensu Hubbell 2001). The plot would be more representative of future tropical forests fragments than of the current situation. Thus, its floristic composition and functional traits may be indicative of features that forecast future characteristics of tropical forests.

Some ecological cornerstones owe their origin to databases from the BCI 50-ha plot, such as neutral theory (Hubbell *et al*. 1990; Hubbell 2001), growth-survival trade-off (Wright *et al*. 2010; Rüger *et al*. 2012; Francis *et al*. 2017), phylogenetic ecology (Kembel and Hubbell 2006), and density dependence effects (Visser *et al*. 2011; Jansen *et al*. 2014). Pasoh Forest Reserve in Malaysia, Korup National Park in Cameroon, and Mudumalai Game Reserve in India also contain 50-ha plots, which together are responsible for more than 200 articles on tropical forest ecology (*e.g.*, Parmentier *et al*. 2014; Verma *et al*. 2017; Shima *et al*. 2018). The LEEP 50-ha plot is the first such large plot on the South American continent, and the first large plot in the Brazilian Atlantic Forest, with its entire area undergoing regeneration after clear-cut during the mid 1970's.

In the LEEP 50-ha plot of secondary tropical forest we aimed to detect and label ecological and functional differences that commonly occur in large plots. In the BCI 50-ha plot, ecological differences were determined by moist soil around the island, by swamps, by slopes, and by regeneration (Condit *et al*. 1995; 1996). Based on the theoretical foundations of growth-survival trade-off, also known as colonization-related trade-offs (Cadotte 2007; Muller-Landau 2008; 2010), ecological heterogeneity of regenerated forests may influence functional traits (Martin *et al*. 2010; Inman-Narahari *et al*. 2014) because colonization-associated trade-offs may influence seed/fruit size (Pérez-Harguindeguy *et al*. 2013; Dombroskie *et al*.

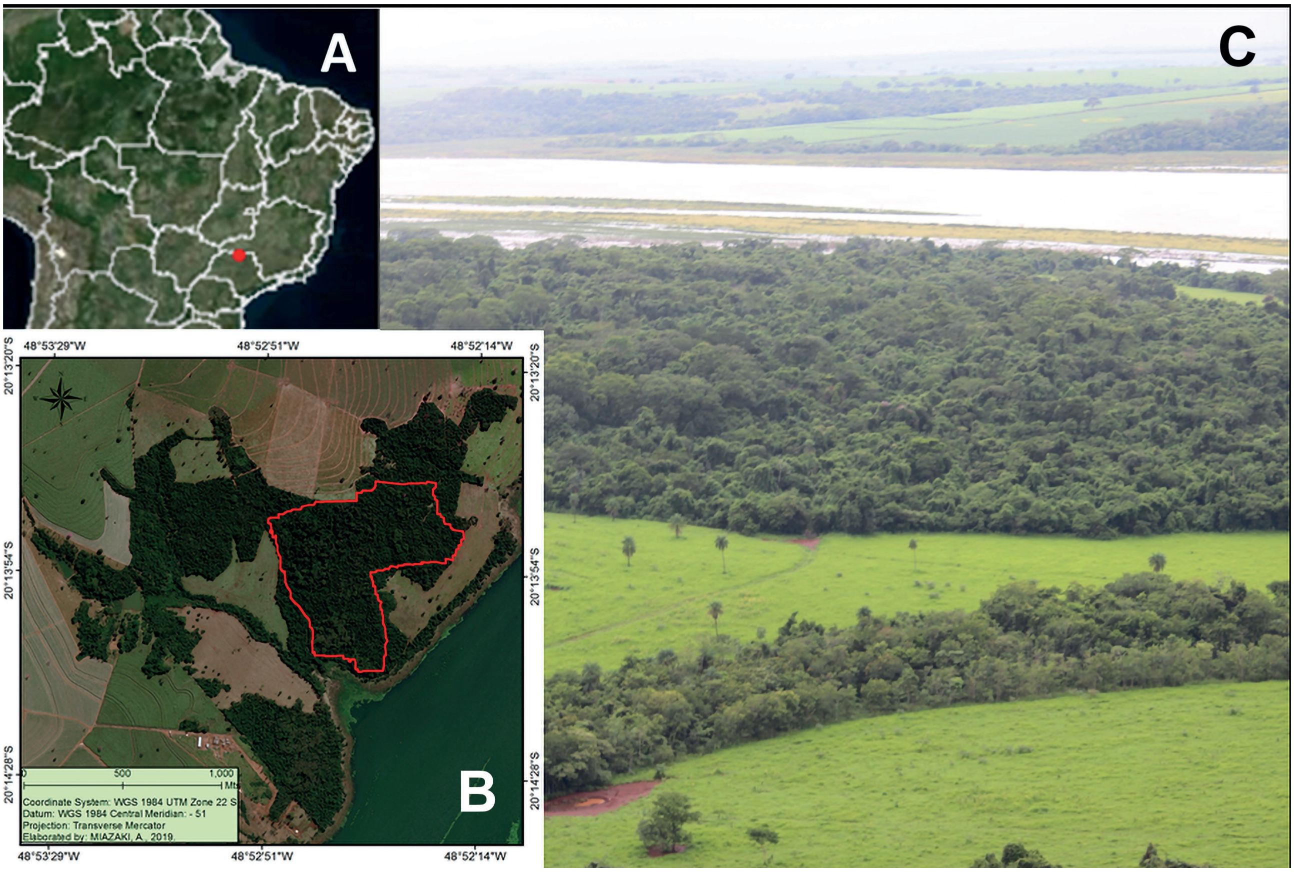

**Figure 1.** The LEEP 50-ha plot in the municipality of Frutal, state of Minas Gerais, Brazil. **A.** The location of the 50-ha plot in South America. **B.** The plot inside a secondary forest fragment near Grande River. **C.** Forest detail evidencing the heterogeneity of the secondary forest.

2016), leaf traits (Sterck *et al*. 2006; 2011; Violle *et al*. 2007; Díaz *et al*. 2016), plant height (Westoby 1998; Moles *et al*. 2009), and wood density (Francis *et al*. 2017; Berenguer *et al*. 2018). Different colonization conditions are also associated with different forest compositions (Petchey & Gaston 2002; Lavorel & Garnier 2002; Vicente-Silva *et al*. 2016). Since we expect forest heterogeneity to influence functional traits and taxonomic similarities in the LEEP 50-ha plot, we hypothesized that heterogeneity of the secondary forest causes differences in measurements of plant functional traits and determines taxonomic composition of subplots. For that, we a) clustered subplots according to their taxonomic composition into groups, b) averaged functional traits from each individual in each subplot, c) tested the averaged traits between each group of subplots.

## Materials and methods

### *Study site*

The LEEP 50-hectare plot is located in a private area in the municipality of Frutal, state of Minas Gerais, Brazil, near the Marimbondo-dam reservoir of the Grande River built during the early 1970's. The plot, censused during 2013, is inside a fragment of about 150 ha of forest undergoing regeneration, which was initiated in the mid-1970's and has since experienced no clear-cutting. After deforestation, the fragment regenerated within a landscape with minimal possibilities of immigration because its localization on the north-south oriented bank (nearly 30 km long, 10 km wide) surrounded by a large, meandering river system, that was almost completely deforested. The 50-ha plot is inside the largest remaining Atlantic Forest fragment of the river system (20°13'56" S 48°52'38" W, 450 meters above sea level). The town of Frutal is on the landscape to the north, thereby affecting connectivity with other forest fragments, while the Marimbondo-dam reservoir of Grande River limits connectivity to remaining directions. Beyond the barriers formed by the reservoir and the town of Frutal, the surrounding landscapes are extremely fragmented (Fig. 1).

The topography of the plot has minimal variation, with the north part being the highest, while the terrain was influenced by the effect of the river system in the past. The soil is red and influenced by the river, with particles of different textures, from clay and silt to rolled basalt pebbles. Despite its proximity to the Grande River and its reservoir, they do not directly influence the 50-ha plot, even during the largest floods. The flooding limits are clearly outside the plot because the reservoir rules the flooding regime consistently creating a line of woody vegetation just above the flooding limits, distanced from the limits of the 50-ha plot.

A total of 5078 subplots (10 m x 10 m) were surveyed. All trees with diameter at breast height greater than 3 cm were tagged, measured for height (using metric sticks) and identified to the species level. Every tree was then located by x and y coordinates inside each subplot.

### *Functional traits*

For functional analysis, we chose functional proxies for the leaf-height-seed (LHS) strategy of (Westoby 1998), but replacing seed traits with their related fruit traits (Pérez-Harguindeguy *et al*. 2013). The following functional traits were used for each censused species: maximum height (Hmax), average height (Have), mode of height (Hmode), wood density (WD), leaf length (LL), leaf width (LW), petiole length (PL), petiole width (PW), fruit width (FW), fruit length (FL), and leaf-width/petiole-width (LW/PW). Interspecific variation in functional traits is often sufficient to sort species, especially regarding invariant functional traits, such as leaf traits. Such traits are also useful for modeling plants using 'average' trait properties (Price *et al*. 2014). Thus, average trait values were determined for each subplot from species trait values of each individual (abundance-weighted).

Wood density was acquired from the Global Wood Density Database (Zanne *et al*. 2009). Species without data in the database had their wood density estimated as the averaged value of wood density for their respective genera. Leaf, and fruit traits were acquired from the exsiccatae tool of SpeciesLink (CRIA 2017). Plant height measurements (maximum, average, and mode) were calculated from individual height measurements during censusing.

### *Statistical analyses and cluster analysis*

In order to detect taxonomic groups, and determine their composition, among subplots, a hierarchical cluster analysis was performed using the pvclust package by means of the unweighted pair-group method analysis (UPGMA) of a taxonomic (species) similarity matrix (Sörensen index) (Suzuki & Shimodaira 2006). The consistency of the groups was verified by means of 999 bootstrap randomizations. The resulting dendrogram was exported to FigTree software (Rambaut 2007) by means of vegan (Dixon 2003), and ape (Paradis *et al*. 2004) packages. All statistical analyses were performed with R statistical environment (R Development Core Team 2015). Large clusters were grouped by means of the cartoon function of FigTree software (Rambaut 2007).

The significance ($p < 0.05$) of differences in functional traits between groups were assessed by Kruskal-Wallis tests (Dinno 2017) using Dunn tests (dunn.test package) in R statistical environment (R Development Core Team 2015) for multiple pairwise post-hoc comparisons.

## Results

A total of 74,335 trees of 178 species from 48 families were recorded, with most of the species and the trees belonging to Fabaceae, Myrtaceae, Rubiaceae, Bignoniaceae, Malvaceae, Lauraceae, Meliaceae, Annonaceae and Sapindaceae (Tab. S1 in supplementary material). Among the recorded species, 23 represented 70 % of the individuals and 67 % of the basal area: *Astronium fraxinifolium*, *Acacia polyphylla*, *Calyptranthes cuspidata*, *Rhamnidium elaeocarpum*, *Inga uruguensis*, *Anadenanthera peregrina*, *Guazuma ulmifolia*, *Xylosma prockia*, *Aspidosperma subincanum*, *Terminalia brasiliensis*, *Bauhinia longifolia*, *Xylopia aromatica*, *Tabebuia roseoalba*, *Zeyheria tuberculosa*, *Casearia rupestris*, *Unonopsis guatterioides*, *Protium heptaphyllum*, *Machaerium aculeatum*, *Psidium guajava*, *Schefflera morototoni*, *Pterogyne nitens*, *Hymenaea stigonocarpa*, and *Cariniana estrellensis*. Of these species, *Psidium guajava* is not native, and so its position among the most important species is indicative of its level of alteration.

The cluster analysis split the subplots into five main groups (Fig. 2). The five groups differed regarding tree density, species richness and number of tree species (Tab. 1). The plots of groups 1 and 5 dominated the northwestern to northern portions of the LEEP 50-ha plot, whereas the eastern to southern portions were dominated by groups 3 and 4; Group 2 dominated the central portion of the plot (Fig. 3).

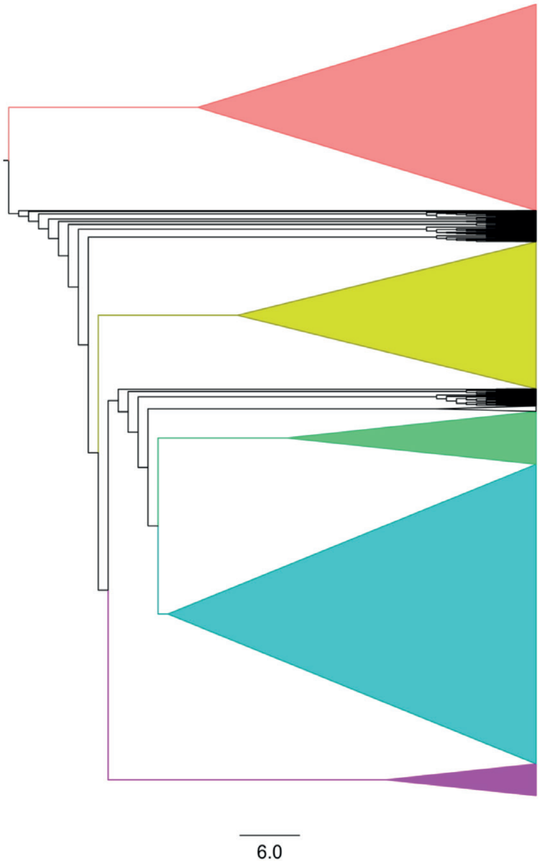

**Figure 2.** Cluster analysis of the taxonomic composition of the 10 m x 10 m subplots of the LEEP 50-hectare plot. Clusters were grouped based on similarity in composition (Sörensen index) using the UPGMA algorithm. Group 1 (coral pink), Group 2 (lemon yellow), Group 3 (green), Group 4 (blue), and Group 5 (fluorescent pink). Less than 1 % of the subplots did not fall inside a group (47 subplots represented by the black branches of the tree).

**Table 1.** Information on identified clusters (cluster): size (in hectares-ha, each subplot = 0.01 ha), number of censused trees per group (individuals), tree density per hectare (density) and tree species richness (richness).

| Cluster | Size (ha) | Individuals | Density | Richness |
|---|---|---|---|---|
| Group 1 | 13.01 | 18,451 | 1,418 | 157 |
| Group 2 | 9.33 | 12,319 | 1,320 | 138 |
| Group 3 | 3.28 | 4,837 | 1,474 | 116 |
| Group 4 | 18.70 | 30,054 | 1,607 | 148 |
| Group 5 | 1.81 | 2,651 | 1,464 | 111 |

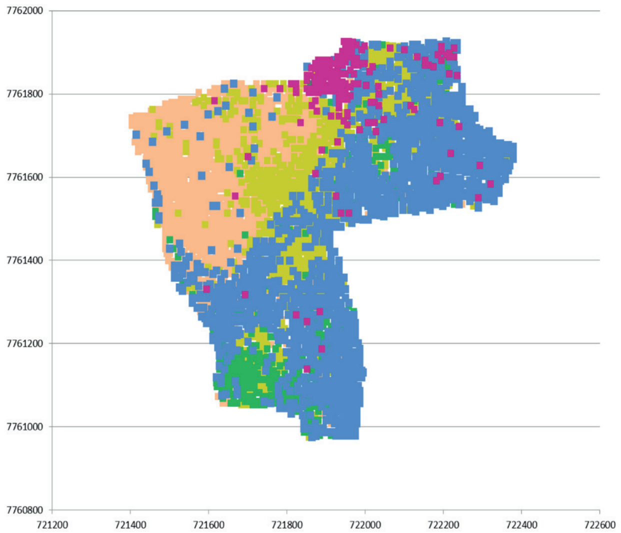

**Figure 3.** Spatial dominance of groups of subplots: Group 1 (coral pink), Group 2 (lemon yellow), Group 3 (green), Group 4 (blue), and Group 5 (fluorescent pink).

Group 1 was dominated by *Calyptranthes cuspidata* (Myrtaceae) with 4420 trees (Tab. S2 in supplementary material). *Acacia polyphylla* (Fabaceae, 2851 trees), *Anadenanthera peregrina* (Fabaceae, 1117 trees), and *Astronium fraxinifolium* (Anacardiaceae, 1012 trees) (Tab. S3 in supplementary material) were most abundant tree species in Group 2. Group 3 was characterized by dominance of *A. peregrina* (Fabaceae, 711 trees), *Tabebuia roseoalba* (Bignoniaceae, 760 trees), and *A. fraxinifolium* with 655 individuals (Tab. S4 in supplementary material), while Group 4 was dominated by *Rhamnidium elaeocarpum* (Rhamnaceae) with 4330 trees, and *A. fraxinifolium* with 4159 trees (Tab. S5 in supplementary material). Most abundant trees in Group 5 were *Xylopia aromatica* (Annonaceae) with 315 trees, *A. fraxinifolium* with 271 trees, and *A. polyphylla* with 248 trees (Tab. S6 in supplementary material). The five groups presented different profiles of functional measurements. Although maximum height differed among groups, average height and height mode exhibited clearer trends. Groups 3, and 4 had higher height averages and modes than groups 1, 2, and 5 (Fig. 4).

Group 3 had the greatest leaf width, the lowest petiole width and, consequently, the highest LW/PW. Group 1 polarized with Group 3 with the lowest leaf width and the lowest LW/PW and the highest leaf width and the highest LW/PW, respectively (Fig. 5). Group 3 had the highest wood density, while Group 4 had the lowest. Groups 3 and 4 were the most similar in composition (Fig. 2), although they differed significantly in wood density (Fig. 6). Group 2 had the greatest average fruit length and width, while Group 5 had the lowest average fruit length and Group 1 the lowest average fruit width (Fig. 6).

Data indicate that Groups 1 and 5 presented similar functional profiles, meanwhile groups 2, 3 and 4 were similar among them (Tab. 2). Furthermore, Groups 1 and 5 were the groups with more acquisitive strategy than conservative strategy among plants regarding leaf, fruit, height and wood traits, while Groups 2, 3 and 4 represent more conservative strategy than acquisitive strategy among plants regarding leaf, fruit, height and wood traits.

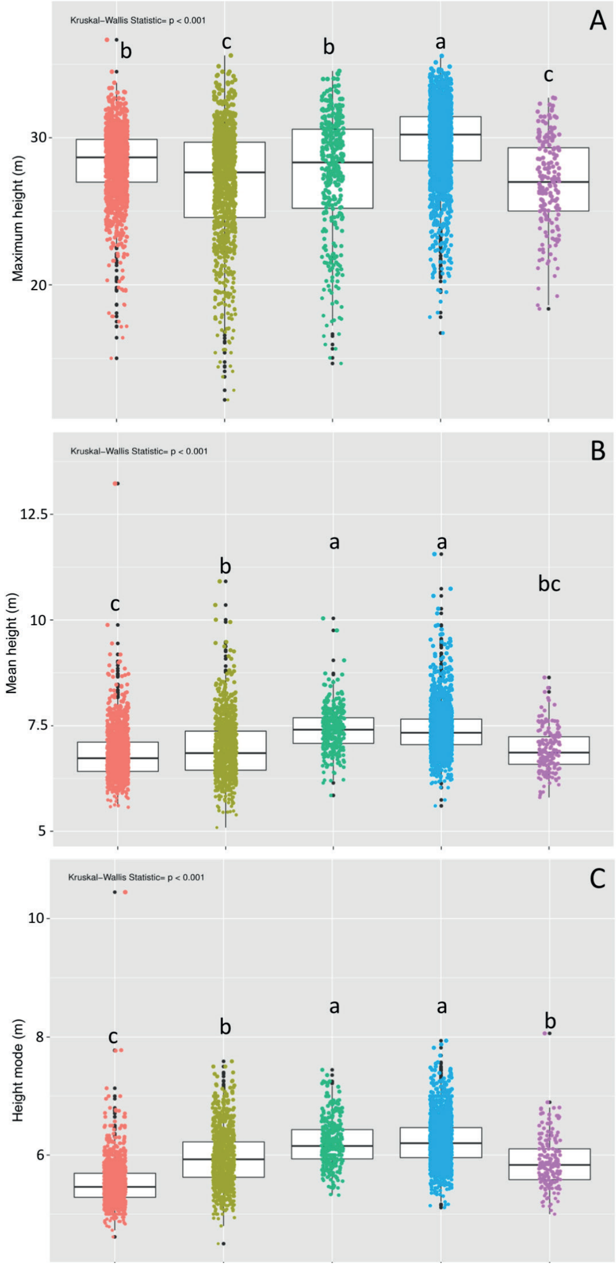

**Figure 4.** Group 1 (coral pink), Group 2 (lemon yellow), Group 3 (green), Group 4 (blue), and Group 5 (fluorescent pink). Groups differed significantly according to Kruskal-Wallis statistic $p<0.001$. A, B and C are groups' maximum height, mean height and height mode, respectively. Different minuscule letters in boxplots mean difference between groups - Kruskal-Wallis post hoc Dunn test.

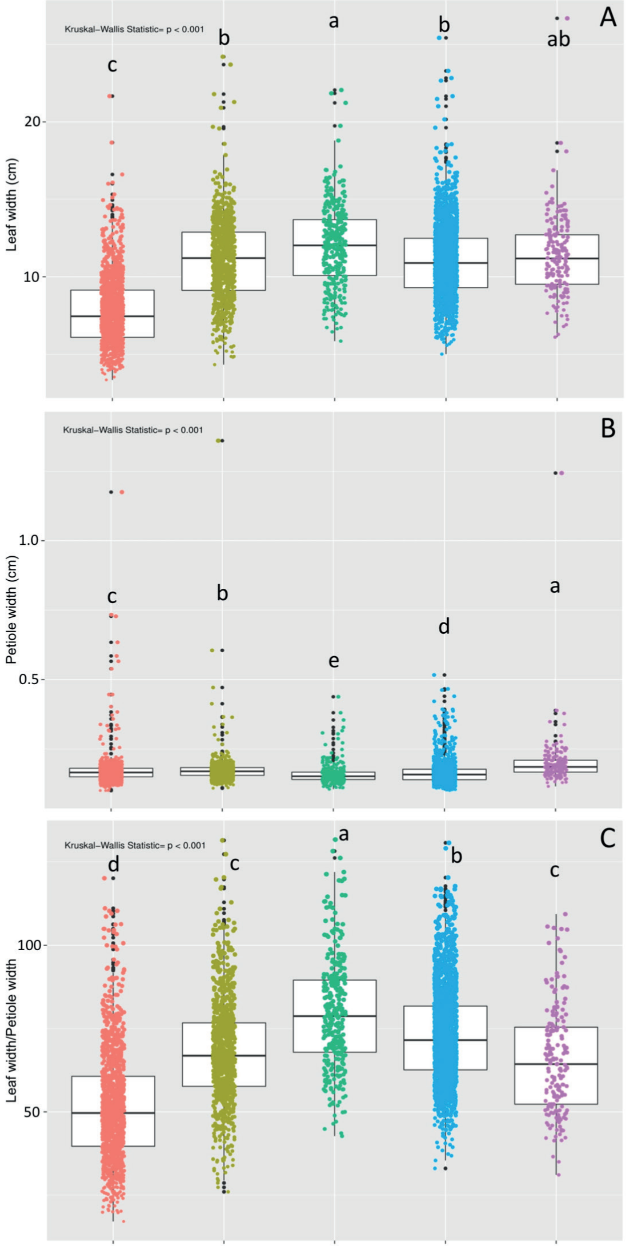

**Figure 5.** Group 1 (coral pink), Group 2 (lemon yellow), Group 3 (green), Group 4 (blue), and Group 5 (fluorescent pink). Groups differed significantly according to Kruskal-Wallis statistic $p<0.001$. Different minuscule letters in boxplots mean difference between groups - Kruskal-Wallis post hoc Dunn test.

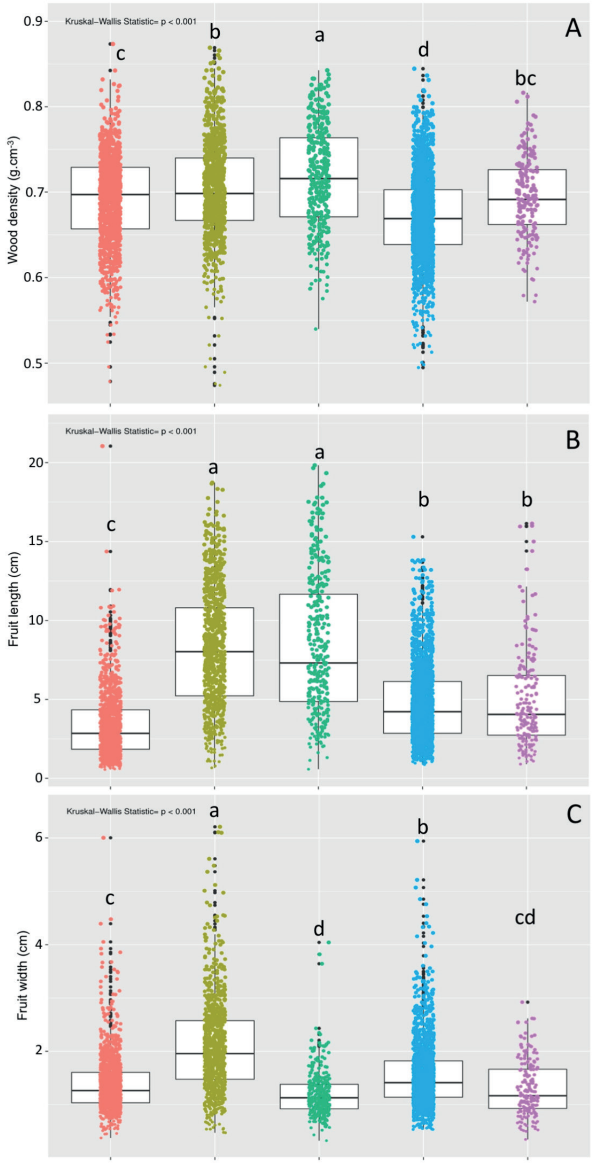

**Figure 6.** Group 1 (coral pink), Group 2 (lemon yellow), Group 3 (green), Group 4 (blue), and Group 5 (fluorescent pink). Groups differed significantly according to Kruskal-Wallis statistic p<0.001. Different minuscule letters in boxplots mean difference between groups - Kruskal-Wallis post hoc Dunn test.

# Discussion

Our results reinforce the growth-survival trade-off hypothesis in secondary forests (*sensu* Venable 1992; Cadotte 2007; Muller-Landau 2008; Inman-Narahari *et al*. 2014). The cluster analysis based on similarities of species composition grouped subplots into five clusters with different functional profiles of colonization-related traits. The clusters were distinguished more evidently by average functional leaf traits. Results of average height (Haver), height mode (Hmode), wood density (WD), and fruit traits, referred as colonization-related traits (Cadotte 2007; Muller-Landau 2008; 2010), were congruent with the results of leaf traits. Therefore, since variation in the topography of the LEEP 50-ha plot is minimal and habitat variations such as swamps, rocky outcrops or inundated areas do not occur, colonization heterogeneity should cause differences in colonization-related traits. Our results also suggest that the groups 1 and 5 of subplots had traits more related to acquisitive strategies compared to the other groups. The groups 2, 3 and 4 of subplots had traits more related to conservative strategies compared to groups 1 and 5.

The five clusters are rather representative of differences in colonization after the clear-cut. Group 1 had the lowest values for leaf width and leaf-width/petiole-width ratio, the lowest average height, the lowest height mode and the shortest fruit length. These results suggest that the functional traits of Group 1 were associated with young colonization, since low leaf width, low leaf-width/petiole-width ratio and small fruits (proxy of small seeds) are associated with shade intolerance (Valladares & Niinemets 2008). Therefore, Group 1 is rather dominated by light-demanding species with small seeds (low seed mass and without reserves), congruently with the acquisition strategy during young colonization (Muller-Landau 2010; Inman-Narahari *et al.* 2014). Group 5 had average traits similar to those of Group 1, suggesting that this acquisition strategy dominates both groups of subplots. This strategy maximizes carbon gain under favorable conditions, and favors rapid growth despite high mortality caused by intolerance to stressful conditions (Valladares & Niinemets 2008; Wright *et al*. 2010). The spatial location of both Group 1 and Group 5 reinforce the association of these groups of subplots with young colonization, since the northwestern to northern portion of the LEEP 50-ha plot is the most vulnerable portion because it is closer to potential origins of disturbances (*i.e.*, croplands and pastures), and opposite to the reservoir.

Groups 2, 3, and 4 of subplots had the greatest average height, height mode, leaf width, and leaf-width/petiole-width ratio. Thus, these three groups of subplots rather represent older colonization than those of groups 1 and 5. Furthermore, the spatial locations of groups 2, 3, and 4 are more protected by the reservoir and less vulnerable to disturbances from croplands and pastures. Groups 2 and 3 also had the greatest wood density and the longest fruits, while Group 2 also had the greatest fruit width and the lowest density of trees per hectare, as expected for old colonization sites (Westoby 1984). Therefore, the functional traits of Groups 2 and 3 suggest an association with the oldest colonization in the LEEP 50-ha plot, since large leaves are associated with larger fruits and with higher average tree height. These results are congruent with the association of leaves' size-to-area ratio and wood density with shade tolerance (Valladares & Niinemets 2008).

Concerning strategies of plant species, larger leaves and larger fruits are associated with shading as well as higher

**Table 2.** Results of probabilities adjustements (P.adj) from the Kruskal-Wallis post hoc test between multiple comparisons (Comp) between groups for maximum height (Max. H.), mean height (Mean H.), height mode (H. mode), wood density (WD), petiole width (PW), fruit length (FL), fruit width (FW), leaf length (LL), leaf width (LW), leaf-width/petiole-width (LW/PW). Bold values mean significant differences.

| Comp | Max. H. | Mean H. | H mode | WD | PW | FL | FW | LL | LW | LW/PW |
|---|---|---|---|---|---|---|---|---|---|---|
| Group 1 - 2 | **8.74E-09** | **3.92E-07** | **1.10E-97** | **5.39E-03** | **4.46E-06** | **2.93E-245** | **1.53E-109** | **6.19E-95** | **1.34E-163** | **2.29E-91** |
| Group 1 - 3 | 1.00E+00 | **2.01E-65** | **4.22E-127** | **3.13E-08** | **2.19E-13** | **3.95E-111** | **4.62E-07** | **1.89E-47** | **2.85E-125** | **1.84E-131** |
| Group 2 - 3 | **2.96E-03** | **1.25E-36** | **9.08E-18** | **8.15E-03** | **1.96E-22** | 1.00E+00 | **1.69E-91** | 1.00E+00 | **9.23E-05** | **2.55E-21** |
| Group 1 - 4 | **1.58E-59** | **6.45E-159** | 0.00E+00 | **1.29E-30** | **9.32E-12** | **5.70E-51** | **1.80E-14** | **1.16E-149** | **1.56E-217** | **8.88E-233** |
| Group 2 - 4 | **5.98E-100** | **2.04E-74** | **5.90E-52** | **5.83E-45** | **2.89E-26** | **3.66E-108** | **7.16E-62** | 1.00E+00 | 1.00E+00 | **3.45E-13** |
| Group 3- 4 | **1.92E-25** | 1.00E+00 | 1.00E+00 | **2.55E-39** | **1.48E-03** | **3.51E-43** | **6.79E-25** | 1.00E+00 | **9.19E-07** | **1.30E-06** |
| Group 1 - 5 | **4.99E-05** | 3.20E-01 | **2.05E-21** | 1.00E+00 | **9.71E-18** | **1.33E-11** | 1.00E+00 | **5.29E-56** | **7.23E-54** | **2.54E-19** |
| Group 2 - 5 | 1.00E+00 | 1.00E+00 | 1.00E+00 | 8.13E-01 | **1.61E-10** | **3.89E-26** | **1.03E-38** | **5.28E-05** | 1.00E+00 | 7.94E-01 |
| Group 3 - 5 | **3.61E-03** | **1.39E-20** | **4.98E-13** | **1.21E-03** | **8.19E-35** | **1.73E-17** | 1.65E-01 | **5.24E-04** | 1.82E-01 | **1.73E-15** |
| Group 4 - 5 | **1.35E-33** | **5.74E-24** | **7.91E-21** | **3.42E-07** | **2.48E-34** | 1.00E+00 | **2.87E-06** | **4.49E-04** | 1.00E+00 | **9.56E-08** |

stems and higher wood densities are associated with tall vegetation, and all of them are associated with conservative strategy of plant growth (Valladares & Niinemets 2008; Martin *et al*. 2010; Inman-Narahari *et al*. 2014). Thus, our study reinforces that different colonization conditions are associated with different plant strategies as well as with different forest compositions (Petchey & Gaston 2002; Lavorel & Garnier 2002; Vicente-Silva *et al*. 2016). According to our results, groups 1 and 5 of subplots might be named as newer colonization subplots whereas groups 2, 3 and 4 of subplots might be named as older colonization subplots.

There are some differences among the groups that might be explained by factors other than colonization. The restricted areas of occurrence for groups 3 and 5, the smallest groups with regard to the number of subplots, is suggestive of different soil conditions. Such potential differences should be further assessed with a focus on soil habitats, since meandering river systems may generate different deposition patterns of sediments (Lecce 1997; Dijk *et al*. 2013).

In addition to soil, dispersion limitation may also explain differences among groups. Group 1 of subplots had the most dominating species among all groups; *Calyptranthes cuspidata*, with 4420 trees or 24 % of all individuals in the group. Such a dominance is unusual in the Brazilian Atlantic Forest, but severe dispersal limitations may explain the trend towards dominance by one species, especially if a high-disturbance regime is associated with dispersal limitation in an isolated community (Hubbell 2001). These results make sense if subplots of newer colonization are associated with increased disturbance in the northwestern portion of the LEEP 50-ha plot. If the dominance of *Calyptranthes cuspidata* in Group 1 of subplots is an effect of dispersal limitation in the highly isolated landscape inside the meandering river system, and under a high-disturbance regime, it would seem likely to represent a common phenomenon of future Brazilian Atlantic Forest landscapes. However, further studies should test the predicted effects of neutral dispersal limitation in the LEEP 50-ha plot. Additional studies should also investigate the differences between the two groups of subplots of newer colonization, as well as differences among the three groups of subplots of older colonization.

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