

1 **How effective is direct seeding to restore the functional composition of neotropical**
2 **savannas?**

3

4 **Running head:** *Restored neotropical savannas have acquisitive traits*

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20 **Author contributions**

21 IBS, ABS, conceived the restoration practice; ALG, PBC, RSO AA conceived the
22 experimental design; ALG, GW, PBC, AB, LL, LV, MC, AP, MM performed the data
23 sample; ALG; AMD analysed the data; ALG, LR, RSO, MCS, wrote and edited the
24 manuscript; All Authors had substantial contributions do manuscript writing.

25 **Conflict of interest**

26 The authors have no conflict of interest to declare.

27

28 **Abstract**

29 Species loss leads to changes in ecosystem function and services, impacting
30 human well-being. Although biodiversity restoration is pivotal to circumvent this
31 situation, the techniques for restoring old-growth savannas are still limited and the
32 restoration outcomes remain unpredictable. Here, we use a trait-based approach to
33 understand the functional outcomes of ecological restoration via direct seeding in a
34 Brazilian savanna (*cerrado*, hereafter neotropical savanna). We compared the functional
35 composition from woody and non-woody component, total biomass and biomass
36 allocation of a restored relative to a degraded savanna (abandoned pasture) dominated
37 by exotic grasses and a well-preserved old-growth native savanna. We found that the
38 functional composition of restored communities was very similar to those dominated by
39 exotic grasses, both characterized by a greater dominance of species with acquisitive
40 traits, higher above-ground biomass, and lower investment in root biomass. In contrast,
41 the native vegetation exhibited a dominance of conservative traits and higher investment
42 in belowground rather than aboveground biomass. Even though the acquisitive traits in
43 the restored savanna allow a fast aboveground biomass accumulation and soil cover, the
44 lower belowground biomass investment in the restored savanna may limit its resistance
45 and resilience to droughts and fires. Our findings suggest that restoration efforts in
46 neotropical savanna should focus on fostering the establishment of slow-growing
47 species to recover the ecosystem properties provided by the high biodiversity in
48 neotropical savannas.

49 **Key words:** Acquisitive; *Cerrado*; Conservative; Resprouters; Restoration practice;
50 Seeders.

51 **Implications for Practice**

- 52 • Current large-scale techniques for restoring neotropical savannas may not allow
53 for the recovery of the slow-growth component of old-growth savannas.
- 54 • Savanna restoration using fast-growth species may threaten long-term
55 restoration success, through generating low ecosystem resilience.
- 56 • Fast aboveground biomass and soil cover recovery do not fully prevent the risk
57 of exotic invasion.
- 58 • To restore functional diversity from old-growth savanna the direct seeding may
59 need to be combined with other techniques, for example bud banks transplant.

60

61 **Introduction**

62 The process of human occupation in the tropics led to the conversion of hyper-
63 diverse native vegetation into degraded ecosystems (Barlow et al., 2018, IBPES 2019).
64 Especially in this decade, the United Nations will support a “Decade on Ecosystem
65 Restoration” from 2021 to 2030, an attempt to restore lost ecosystem services and stem
66 the rapid decline of biodiversity (UNEP & FAO 2020, Strassburg et al., 2020). Most
67 restoration knowledge is focused on forest successional trajectories, involving mainly
68 woody plants (Silveira et al. 2020; Veldman, Buisson, et al. 2015). However, the old-
69 growth savannas occupy >40% of the land surface (Veldman, Buisson, et al., 2015).
70 These old-growth ecosystems include neotropical savannas with open-canopy where
71 >50% of the ground layer is covered by grasses (Veldman, Buisson, et al., 2015).
72 Although most of the vegetation is composed of grass and herbs, these components of
73 vegetation have been widely neglected for conservation (Veldman, Overbeck, et al.
74 2015; Parr et al. 2014; Bond 2016). Thus, studies seeking to understand how to
75 effectively restore neotropical savannas are imperative. Achieving restoration success in
76 neotropical savannas depends on adequate context-specific knowledge to restore
77 functional diversity, ecosystem functions and resilience (Buisson et al. 2020).

78 In recent decades, the Brazilian savanna (*cerrado*, hereafter neotropical savanna)
79 lost 88 Mha (46%) of its original cover, and only 20% remains well-preserved
80 (Strassburg et al., 2017). The invasion of non-native plant species is among the main
81 causes of species loss and ecosystem degradation (Veldman et al., 2014). These
82 invasions occur by conversion of native vegetation to livestock pasture or agricultural
83 fields that deplete the seed and especially the underground bud bank, trapping the
84 system in a degraded state. Therefore, these areas have slow natural regeneration and
85 requires active restoration practices (Ferreira et al. 2017). Meanwhile, neotropical
86 savanna restoration is still in its infancy relative to forest restoration and the success of
87 most existing techniques remain uncertain at a large scale. The restoration of these
88 ecosystems requires very different approaches than major forest restoration based on
89 tree plantation and successional trajectories (Veldman et al. 2019; Andrade et al. 2015).
90 In fire-prone ecosystems, natural plant populations persist mostly through clonal
91 reproduction (Pausas et al. 2018), and the investment in belowground structures (e.g.,
92 roots and bud banks) is the main mechanism by which plants re-sprout after
93 disturbances, boosting savanna resilience over disturbances (Ott et al. 2019). Even
94 though there is an increasing number of neotropical savanna restoration studies, just a

95 small number of successful models applies to the broad scale (Bustamante et al. 2019;
96 Schmidt et al. 2019). Furthermore, the main challenge in restoration practices of
97 neotropical savannas is the recovery of the belowground component of these
98 communities as a way to ensure higher resilience.

99 Restoration practices that aim to convert abandoned pastures into biodiverse
100 savannas need to deal with the potential invasion from persistent seed- and/or bud-bank
101 of exotic grasses (Gorgone-barbosa et al. 2016; Dantas-Junior et al. 2018). After land
102 clearing and soil liming, alien grasses are often introduced as forage to feed the
103 livestock or disperse from former pastures in the vicinity. Alien grasses frequently
104 outcompete the native species when the soil is disturbed through liming, altering the
105 ecosystem to a degraded state which also limits savannas' restoration success
106 (D'Antonio & Meyerson 2002; Damasceno et al. 2018; Zenni et al. 2019). The potential
107 restoration activity to reduce non-native invasion is to strategically increase the
108 abundance of native species that are functionally similar to the non-native species
109 (D'Antonio & Chambers, 2011; Funk, Cleland, et al. 2008). Invasive grasses are usually
110 fast-growing species and exhibit high aboveground productivity (Milbau & Nijs 2004).
111 Generating fast soil cover by native grasses is a restoration practice which could
112 potentially hamper the invasive potential of exotic grasses (Sampaio et al. 2019).
113 However, invasive plants often generate strong priority effects, self-induced soil
114 modifications that can persist after their removal or death, commonly termed "soil
115 legacies" (Hess et al. 2019, Wolfsdorf et al 2021), and prevent the establishment of
116 native species. Evaluating the functional composition of restored communities may
117 offer insights about restoration success and help to predict vegetation trajectories.

118 Trait-based approaches have contributed to our understanding of the
119 mechanisms driving community assembly (HilleRisLambers et al. 2012) and have been
120 extended to explain ecosystem functions and processes (Funk et al. 2008). This
121 approach considers the ecological niche as a result of the knowledge of different axes of
122 plant-trait variation. One of the most comprehensive trait variation axes is the fast-slow
123 continuum (Wright et al. 2004). Environments with high resources are characterized by
124 the dominance of plants with traits associated with fast resource acquisition and the
125 maximum allocation of resources to growth (Wright et al. 2004). Conversely, in
126 environments where soil nutrients or climate limits plant growth, we expect dominant
127 species to exhibit traits that reflect the conservation of long-lived tissues (Oliveira et al.
128 2021; Wright et al. 2004; Jardine et al. 2020). Several studies have used a trait-based

129 approach for improving ecological restoration outcomes (Funk et al. 2008; Laughlin
130 2014) and a growing number of empirical studies have linked specific traits to plant
131 establishment, survival, and persistence in restored systems (Larson & Funk 2016;
132 Zirbel & Brudvig 2020). However, trait-based approaches of neotropical savannas
133 restoration practices remain unknown, especially field-based studies with a focus on
134 individual traits (Laughlin 2014). Several studies use traits from literature databases, not
135 taking into account the trait-dependent context (Passaretti et al. 2020; Coutinho et al.
136 2019; Cava et al. 2018).

137 Several savanna species tend to grow slowly and have high tissue construction
138 costs, which allow them to persist in habitats with low nutrient and water availability
139 (Maracahipes et al., 2018; Viani, Rodrigues, Dawson, & Oliveira, 2011). Early stages of
140 forest restoration are known for their trees with acquisitive traits and even old-growth
141 forests have more acquisitive traits than the woody-component of neotropical savannas
142 (Maracahipes et al. 2018). However, savannas and grasslands most likely do not follow
143 successional trajectories because these ecosystems are dominated by resprouters (Pilon
144 et al. 2020; Pausas et al. 2018; Bond & Midgley 2001a). Principally in these fire-prone
145 ecosystems, the fast-slow strategy is also linked to specific reproductive strategies
146 (Enright et al. 2014). Overall, acquisitive species tend to reproduce through seeds, that
147 are usually small and with high germination rates, while rapidly growing aboveground
148 (Power et al. 2011; Verdú 2000). In contrast, conservative species tend to resprout as a
149 main reproductive strategy, they grow more slowly and allocate a greater proportion of
150 their resources belowground (Eller & Oliveira 2017; Power et al. 2011; Verdú 2000). In
151 the neotropical savanna vegetation, the main technique known for large-scale
152 restoration is direct seeding (Schmidt et al. 2019; Pellizzaro et al. 2017; Sampaio et al.
153 2019). By using an expressive number of seeds to quickly cover the soil, this technique
154 is likely to favor mostly seeders/acquisitive species, which may be a problem if the goal
155 is to restore an ecosystem where resprouters/conservative species are prevalent in the
156 community (Pilon et al. 2020).

157 In this study, we used a trait-based approach to understand the functional
158 composition of savanna communities and offer insights into the functional outcome of
159 current restoration practices in the neotropical savanna. We evaluated the functional
160 composition of a 3-years-old restored savanna by direct-seeding when compared to
161 areas dominated by exotic grasses (abandoned pastures) and well-preserved old-growth
162 vegetation. We evaluated multiple leaf traits (see Table 1) of 61 native species, and

163 species from restored and invaded savanna communities. Additionally, we measured
164 exotic cover, bare soil cover and below- and aboveground biomass as biomass
165 allocation has major implications for ecosystems resilience. We addressed the following
166 questions and hypotheses:

- 167 • What is the functional composition of restored savanna vegetation via direct
168 seeding compared to pastures and native savannas? Because direct seeding uses
169 mostly seeders/fast growing plants, we expect the restored vegetation through
170 this technique to be dominated by acquisitive traits, thus occupying the same
171 functional space as abandoned pastures (H1).
- 172 • Does the restored neotropical savanna recover the functional diversity and
173 biomass allocation of an old-growth state? We expect restored savanna to have
174 higher Functional dispersion (FDis) and Functional richness (FR) than
175 abandoned pasture, and exhibit higher soil cover and higher aboveground
176 investment that might avoid invasive grasses. Besides, the higher aboveground
177 biomass allocation in restored communities in comparison to higher
178 belowground allocation in native communities may have implications to
179 resilience to disturbance (H2).

180 **Methods**

181 *Study site*

182 The study was conducted in the Chapada dos Veadeiros National Park
183 (14°07'03" S, 47°38'31" W), located in Central-Western Brazil in the municipality of
184 Alto Paraíso de Goiás – Goiás; mean altitude: 1240 m (Pellizzaro et al. 2017). Mean
185 annual precipitation is 1453 mm, 60% of which occurs between October and May and
186 the mean annual temperature is 21°C (Pellizzaro et al. 2017). We selected three areas
187 with different vegetation states, old-abandoned pasture (hereafter abandoned pasture),
188 native old-growth vegetation (hereafter native), and restored vegetation.

189 The areas that are being restored in the park have generally been used for
190 extensive livestock grazing before the park establishment in 1961 (ICMBIO 2009). In
191 these areas, the soil was ploughed and limed, exotic grasses were sown, and the areas
192 were constantly burned to stimulate grass growth (ICMBIO 2009). These areas were
193 traditionally used for extensive livestock production, but have since been abandoned in
194 two main periods: 1985 and 1995 (ICMBIO 2009). Our sites of abandoned pasture are

195 dominated by the invasive exotic species: *Urochloa eminii* (Stapf) R.D. Webster and
196 *Melinis minutiflora* P. Beauv. (Pellizzaro et al. 2017).

197 In restored areas, the vegetation was restored using direct-seeding of native
198 species applied in 2016. This area was previously dominated by invasive grasses. To
199 reduce the biomass of invasive grasses, these sites were burnt, and then ploughed five
200 times (250 mm deep) followed by inversion tillage (400 mm deep) to reduce the seed
201 bank and regeneration of exotic grasses (Coutinho et al. 2019; Sampaio et al. 2019).
202 Seeds of 75 species of native herbs, shrubs, and trees were collected at undisturbed sites
203 in the surroundings of the restoration plots (Pellizzaro et al. 2017; Coutinho et al. 2019;
204 Sampaio et al. 2019). The restored area in 2016 corresponded to a total of 40 ha. Sixty-
205 two out of the 75 seeded species were established, and the areas presented 60% cover by
206 native species two years after seeding in a previous experiment at the same site
207 (Pellizzaro et al. 2017).

208 Finally, we also selected an undisturbed native area adjacent to the restoration
209 and an abandoned pasture, yet to undergo restoration. We consider this native area as a
210 vegetation target because it is the native area closest to the restored area (<100m) and it
211 is characterized by the dominance of non-woody species with <20% woody species
212 cover (similar proportion achieved by direct-seeding; $78 \pm 6\%$ grass cover; Sampaio et
213 al., 2019). These systems are ancient ecosystems characterized by slow-growth species,
214 high herbaceous species richness, high endemism, and unique species compositions,
215 commonly called old-growth savannas (Veldman, Buisson, et al. 2015). Therefore, the
216 reference ecosystem selected is well preserved and consequently have a representative
217 functional composition to neotropical savanna. While the abandoned pasture is
218 characterized by a degraded state of vegetation with dominance of fast-growth species,
219 which has remained in a similar state for the last 30 years, with livestock production
220 abandoned in 1985.

221 *Vegetation survey*

222 To determine vegetation composition, we installed 10 plots of 4 m² in each
223 vegetation type, 40 m apart from each other. In each plot, we measured all woody and
224 non-woody individuals over 10 cm in height. We separated the sampled species in
225 shrub-tree layer (hereafter woody component) and the herb-layer (hereafter non-woody
226 component), and determined the vegetation cover by species based on the vertical

227 projection of the aerial part of the plant in each plot (Mueller-Dombois; Ellenberg
228 1974). We surveyed the vegetation at the peak of the wet season during the year 2019
229 (Jan/2019).

230 We sampled soils to measure multiple chemical properties, which might drive
231 differences in community functional composition. We took soil samples with 20 cm
232 deep soil core around each plot per vegetation type. We measured the concentration of
233 total soil N, available P, and soil organic matter (SOM), Aluminum concentration, and
234 soil pH, as a proxy of the nutrient pool. The soil N concentration was determined by
235 sulfuric acid digestion followed by Kjeldahl distillation (Bremner 2016); soil P and
236 potassium (K) concentrations were determined following a Mehlich-1 extraction (Raij et
237 al. 2001); and SOM was determined by the Walkley-Black reaction (Nelson 1996).
238 Separately, we assessed soil water holding capacity at the 3 soil samples with 3 depth
239 (surface, 50 cm, 100cm) at plots level in each area to estimate the slope of water-
240 saturation by the Van Genuchten method (Genuchten 1980).

241 We measured biomass during the peak of wet season, and exotic cover and bare
242 soil cover during the peak of the dry season (Jul 2018) and the peak of the wet season
243 (Jul 2018 for the dry and Jan 2019 for the wet season). To measure aboveground
244 biomass production, we clipped all plant material in a 50 x 50 cm plot around each
245 vegetation plot at the peak of the dry season and the peak of the wet season in around
246 each plot. To measure belowground biomass, we took 3 cm² by 10 cm deep soil cores
247 from the corner of each plot at the end of the growing season. We sorted root samples to
248 remove litter and oven-dried them at 65 °C for at least 48 h before weighing. We took
249 10 cm² by 10 cm deep soil cores until 100 cm. All samples were taken from the corner
250 of each plot in the same area where the aboveground biomass sample was collected. We
251 sieved all soil samples (< 2 mm) to collect all roots which were then washed and dried
252 at 65°C for 48 h before weighing. We calculated the root:shoot ratio (Dry weight for
253 roots/dry weight for aboveground biomass) for each plot and for each treatment. To
254 measure exotic cover and bare soil cover we use the grid of 4m² separated into 64
255 subplots of 6.25 cm² and visually estimated the number of subplots covered by exotic
256 species, native species, and bare soil cover.

257

259 To determine plant community functional composition we collected trait data for
260 species that were present during the vegetation survey using standard methods (Pérez-
261 Harguindeguy et al. 2013). We sampled traits of 61 species, 13 in restored, 15 in
262 abandoned pasture, 44 in native savannas, covering 80% of species dominance. We
263 focused on leaf traits – leaf area (cm²) (LA), Specific leaf area (g.cm⁻²) (SLA), leaf
264 thickness (mm) (LT), Leaf dry matter content containing (mg.g⁻¹) (LDMC), leaf
265 nitrogen (LNC), and leaf phosphorus concentration (LPC), and plant maximum height
266 (H_{max}). Vegetative height is related to a species' competitive ability with taller species
267 better adapted to compete for light (Weiher et al. 1999). We chose these traits because
268 in the neotropical savannas community most of the aboveground biomass consists of
269 leaves from non-woody species. Added to that, leaf traits are a good predictor of
270 acquisitive and conservative strategies using the leaf economic spectrum (Poorter,
271 Niinemets, Poorter, Wright, & Villar, 2009; Wright et al., 2004). Acquisitive foliar traits
272 include high SLA, leaf area, small LT and LDMC (Lohbeck et al., 2015; see Table 1).
273 We obtained trait data from 3 individuals at each vegetation site. While we recognize
274 the important role that intraspecific trait variation can play in community assembly
275 (Jung et al. 2010; Laughlin et al. 2012), we could not measure it. These traits represent
276 important facets of the leaf economic spectrum, a known gradient between fast and
277 slow-growing species that can be associated with ecosystem processes, successional
278 trajectories and reproductive strategies after disturbance (Reich 2014; Van Der Sande et
279 al. 2016). Mean values of each trait for each species are available in Table S3 in
280 supplementary information.

281 We measured the Community Weighted Means (CWM) for all functional traits
282 by species dominance through the species cover in each plot per treatment (Laliberté &
283 Legendre 2010). We conducted the CWM analyses considering life forms separately
284 (woody and non-woody components). We considered as woody component, traits from
285 shrubs and trees species and as a non-woody component, traits from grass, graminoids
286 (Cyperaceae) and other herbaceous species. The CWM is suggested as a predictor of the
287 functional composition in the plant community, taking into account the dominant
288 species in a community. We used a functional diversity index, functional richness (FR),
289 that indicated the breadth of the niche based on the variation in a set of traits within a
290 community. This is calculated as the minimum convex hull (minimal intersections of

291 the convex sets containing the trait data) which includes all the species considered; the
292 convex hull volume is then the volume inside this hull (Villéger et al. 2008). In
293 addition, we calculated functional dispersion (FDis) that is the mean distance of
294 individual species to the centroid of all species in the community. This index takes into
295 account species relative abundances weighting distances of individual species by their
296 relative abundances. In this study, we use FDis as an indicator of the niche
297 complementary and as estimate the community functioning in each vegetation type (See
298 (Laliberté & Legendre, 2010, for more details). Vegetations with similar index values
299 probably have similar functioning. All functional diversity indexes were calculated
300 using package “FD” (Laliberté et al. 2010).

301 *Statistical analyses*

302 To evaluate how leaf traits of species were associated, a principal component
303 analysis (PCA) was done with leaf traits, using CWM values in each plot per treatment
304 and then using species (n= 61) as data points. We conducted generalized linear mixed
305 models (GLMM), considering all vegetation types (restored, abandoned pasture, native)
306 as fixed factors and plot as random factors. The GLMM were fitted separately for each
307 CWM traits, using Gamma distribution with the *nlme* or *glmmTMB* R packages (Brooks
308 et al., 2017). In all CWM models we use life form (Woody and non-woody) as an
309 interaction factor in each vegetation type. A one-way ANOVA with multi-comparison
310 and Tukey post hoc comparisons were performed with the *lsmeans* package (Lenth,
311 2016) and estimated marginal means (EMMs) using *emmeans* package. Tukey post-hoc
312 tests was used to evaluate whether leaf traits between species belonging to different
313 vegetation types and life forms. We checked model assumptions graphically by plotting
314 residuals and running likelihood ratio tests. All data was log₁₀-transformed before
315 analysis to smooth the distributions.

316 A correlation analysis was carried out, to test how leaf-traits and vegetation were
317 correlated with soil nutrients. To evaluate differences in above and below-ground
318 between the vegetation types, we developed generalized linear models (GLMM),
319 considering all vegetation types (native, restored, abandoned pasture) as fixed factors
320 and plot as random factors. The GLMM were fitted separately for each response
321 variable, using Poisson and Gaussian distribution.

322 To investigate the relation among soils properties and functional diversity index
323 and functional diversity index and ecosystem functions, we used linear models. We
324 considered the soil PCA axis as the predictor variable and FDis and FR as the response
325 variable. All statistical analyses were carried out using R 3.3.

326

327 **Results**

328 *Functional composition*

329 The CWM leaf area (LA) in the restored area was similar the abandoned pasture
330 and 36.4 % lower than in the native area (GLMM see Table S1). The high LA values in
331 the native area are driven by the greater woody vegetation component and were 70.5%
332 higher than in the restored area, which remained similar to the abandoned pasture (Fig.
333 2 a). The CWM SLA in the restored area was similar to the abandoned pasture and on
334 average 44.3% higher than in the native area (GLMM Table S1). For both life forms,
335 the SLA in the restored area was higher than in the native area. This was however more
336 evident for the woody vegetation component in restored area, which was 57.8% higher
337 than abandoned pasture and 37.7% higher than native area (Fig. 2 b). The LT was
338 similar among vegetation types. However when considering life forms separately, the
339 LT from woody component in the restored area was lower than the abandoned pasture
340 and native area (Fig. 2c). The non-woody component in the restored area had 37.9%
341 greater LT than abandoned pasture and similar values to the native area (Fig. 2 c). The
342 leaf dry mass content (LDMC), was 28.8% greater in the restored area relative to the
343 abandoned pasture area and 26.2% higher than in the native vegetation, which has
344 similar values to the abandoned pasture. The high LDMC values in restored area are
345 driven by variations in the woody component, driving LT values which were 42%
346 higher than abandoned pasture and 48.8% higher than the native area (Fig. 2 d). Leaf P
347 concentration (LPC) in the restored area was similar to the abandoned pasture and on
348 average 8.4% greater than in the native area. Leaf N concentration (LNC) was similar
349 among vegetation types with interaction between vegetation and life forms (Table S1).
350 The LNC from Woody component in restored area was similar to the abandoned pasture
351 and 8% higher than native area (Fig. 2 f).

352 The lower LT, higher LNC and LPC from woody component, and principally
353 higher SLA in both life forms in the restored area compared to native area, indicate that
354 the functional outcome of direct seeding is a community with acquisitive strategies,

355 contrasting with the conservative native (All average statistical values are showed in
356 Table 2 and Fig. 2 a-f).

357 Associations amongst the 6 leaf traits and maximum height were analyzed with a
358 PCA (Fig. 3). The first axis explained 46.5% of the variation, and was positively related
359 to SLA, LDMC, and P concentration in leaves and negatively related to leaf area. The
360 second axis explained 25% of the variation and was positively related to N
361 concentration and negatively related to leaf thickness. The three vegetation types
362 (native, restored, pasture) were grouped in this multivariate trait space according to their
363 trait community weighted means in each plot per community. Acquisitive strategies
364 were related to the abandoned pasture and restored area, with high SLA, LPC, and H_{max} .
365 Conservative strategies were related to the native area, with high LA and LT.

366 In the restored area 78.3% was covered by non-woody species and 21% by
367 woody species. In contrast, the abandoned pasture had 90% cover of non-woody
368 component with 70% dominated by *U. eminii* and 11% by *M. minutiflora*; whereas,
369 native areas was dominated by non-woody species (55% cover) and by woody species
370 (31% cover) (Table S3). The shrub *Lepidaploa aurea* was the most dominant species
371 (15.2%) in the restored area, followed by the grasses *Schizachyrium* (10.3%), *Axonopus*
372 *pressus* (8.9%) and *Axonopus chrysoblepharis* (6.1%), but also by the exotic *Melinis*
373 *minutiflora* (6.1%) and *Urochloa eminii* (5.9%).

374 In restored areas, the high values of LA and SLA were strongly influenced by
375 two invasive grasses, *U. decumbens* and *M. minutiflora* and the native species *Axonopus*
376 *pressus*. The high values of SLA were mostly associated with species of the genus
377 *Schizachyrium*. The shrubs *L. aurea* and *Mimosa clausenii*, and grasses from the genus
378 *Axonopus* showed higher LDMC values (Table S3). The restored area showed overlap
379 of dominant species with the abandoned pasture (*U. decumbens* and *M. minutiflora*).
380 Both exotic species have acquisitive traits, with high SLA values and lower LT, and
381 together covered more than 12% of restored community. In contrast, the species
382 overlapping with natives was the grass *Axonopus pressus* and the shrub *Mimosa*
383 *clausenii*, both exhibiting conservative foliar traits. The grass species *Trachypogon*
384 *spicatus* was the only species that had more conservative traits among grasses in the
385 restored area, covering less than 4% of the plots. Overall, dominant species in the native
386 area have lower values of SLA, and high values of LDMC and LT. In contrast, the
387 species in the abandoned pasture have with higher SLA and lower LT (Table S3).

389 The Functional Richness index (FR) in the restored area was similar to the
390 abandoned pasture and lower than the native area ($F_{(2,27)}=7.76$, $p=0.001$, Fig 4 a). When
391 the species abundances are taken into account, the Functional Dispersion index (FDis)
392 in the restored area was higher in relation to the abandoned pasture (Tukey test, $p<0.01$)
393 and similar to that of the native area (Tukey test, $p=0.084$) ($F_{(2,27)}=5.16$, $p<0.001$, Fig 4
394 b). That means, the multivariate space filled by traits are more similar between native
395 and restored areas than to abandoned pasture.

396 Restoration practices resulted in higher aboveground biomass (ABG) in the
397 restored area (6254.56 ± 2368.63 kg ha⁻¹) than in the abandoned pasture ($3774.2 \pm$
398 1585.13 kg ha⁻¹) than in the native areas (4710.64 ± 3068.31 kg ha⁻¹) ($F_{(2,27)}= 2.684$,
399 $p<0.005$, Fig 4 c). However, the restored area (25.6 ± 6.4 kg ha⁻¹) showed lower
400 belowground biomass (BLG) when compared to the abandoned pasture (11.6 ± 5.6 kg
401 ha⁻¹) and the native area (50 ± 35.2 kg ha⁻¹). Yet, the BLG from the abandoned pasture
402 was lowest than native areas ($F_{(2,27)}=5.93$, $p=0.01$; Fig 4 d). The root: shoot ratio in the
403 restored area was lower when compared abandoned pasture and native ($F_{(2,27)}=4.63$,
404 $p=0.02$; Fig S2). The mean bare soil cover in the wet season was 21.5% in the restored
405 area, 24.2% in the abandoned pasture and 13.2% in the native area. In the dry season,
406 the bare soil cover was 33.75% in the restored area, 21.51% in the abandoned pasture
407 and 29.37% in the native area. When compared among seasons, the restoration practice
408 provided a decrease of 65% in bare soil cover from dry to wet season. These values
409 were similar to native areas that decreased 55.3% the bare soil cover from the dry to the
410 wet season (GLMM see table S2). In contrast, the abandoned pasture remained
411 unaltered among seasons (GLMM see table S2). However, when we compare the exotic
412 cover among seasons, we find an increase in 56.7% of exotic cover in the restored area
413 from dry to the wet season, while abandoned pasture and native areas remained
414 unaltered (GLMM see table S2).

415 Associations amongst the soil nutrients were analyzed with a PCA (Fig. S1). The
416 first axis explained 41.5% of the variation and was used to correlate with traits and
417 functional diversity. The first axis of soil PCA was positively correlated with N, organic
418 matter, K, and silt, separating native area to abandoned pasture and restored. These
419 areas were in another group positively correlated with % of sand, P, and Al soil content
420 (negative values of PCA). The correlation between the PCA axes from soil nutrients

421 with vegetation showed the decoupling of restored vegetation with the soil properties.
422 None of the leaf traits were correlated with the soil PCA axis (Table S4). Yet, when we
423 fit the values only for native and abandoned pasture areas the PCA1 axis showed a good
424 predictor of functional richness and functional dispersion to both communities (Table
425 S4; Fig S3). This relationship disappears when restored areas are included.

426 **Discussion**

427 To our knowledge, this is the first study evaluating the recovery of functional
428 composition following direct-seeding restoration in Neotropical savanna communities.
429 We evaluated how a neotropical savanna restored area varied in its community-
430 weighted mean (CWM) trait composition, and whether total biomass and biomass
431 allocation changed when compared to the degraded state (abandoned pasture) and well
432 preserved old-growth savannas (native). Multivariate CWM trait composition differed
433 strongly between native, restored and abandoned pasture areas. The restored
434 communities and abandoned pasture showed a greater dominance of species with more
435 acquisitive traits while the native vegetation presented conservative traits. Hence, the
436 functional composition of a restored neotropical savanna via direct seeding is more
437 similar to an abandoned pasture than old-growth reference area. Our results showed that
438 the species pool used in direct-seeding is an effective technique to establish a large
439 number of acquisitive native species with high aboveground biomass investment and
440 provides a fast gain in soil cover. Nevertheless, this fast aboveground recovery did not
441 guarantee resistance to invasion. In contrast, the restored neotropical savanna
442 maintained lower belowground investment compared to the reference system, which
443 implies in a lower vegetation resilience against common local disturbance such as fires
444 (Ott et al. 2019; Pausas et al. 2018b).

445 *Functional composition*

446 For the majority of the analyzed traits, the restored area was functionally similar
447 to the abandoned pasture, both harboring a great dominance of acquisitive species
448 whereas the native vegetation harbored conservative species. The exception was LDMC
449 which had greater values in the restored area, relative to the pasture area, due to
450 presence of a particular woody species. Savanna woody species usually have slow
451 growth and higher leaf carbon investments compared to grass species (Maracahipes et
452 al., 2018; Rossatto et al., 2015). *Mimosa clausenii*, a slow-growing shrub, frequent in

453 the restored site, has a LDMC of 4.44 g.g⁻¹ which can explain the higher LDMC
454 following restoration. In contrast, the restoration showed a similar distribution of
455 LDMC from non-woody species among areas. Surely, in our study LDMC had a lower
456 contribution to discriminate vegetation along the PCA axis, thus may not reflect the
457 filtering processes among the studied plant communities. In addition, the SLA often
458 discriminates between communities better than LDMC, because SLA is influenced by
459 both light and soil fertility, whereas LDMC largely reflects soil fertility (Hodgson et al.
460 2011). The restored area showed higher SLA values to woody component and higher
461 than the native area to non-woody component. The dominant grasses and shrubs in the
462 restored area have inexpensive short-lived leaves, which leads to the high CWM values
463 of LPC and high SLA. These traits facilitate greater photosynthetic capacity, faster
464 resources use, and high above-ground biomass investment to dominant species (Osnas
465 et al. 2013). These patterns also were also present to non-woody component in the
466 abandoned pasture area, suggesting similar ecosystem functioning and consequently
467 low gain in terms of functionality when compared to the degraded state.

468 These fast-growing species in the restored area are associated with a high
469 density of individuals, which can cover the soil and supposedly compete with invasive
470 grasses (Hulvey & Zavaleta 2012). In fact, the fast soil cover and high aboveground
471 biomass suppresses the exotic-grass spread in the first year of restoration. The use of a
472 fast-growing shrub (*Lepidaploa aurea* – Asteraceae) also assisted in avoiding exotic-
473 grass invasion in the first year (Sampaio et al. 2019; Lopes et al. 2018). However, the
474 effect of this fast soil cover restricting the invasion of exotic grasses is short-lived as we
475 observed an increase in exotic cover from the dry to the following wet season. This
476 suggests that only the high aboveground investment and soil cover in the area does not
477 prevent the invasion. Furthermore, the use of species with supposedly allelopathic
478 potential (e.g. *Lepidaploa aurea*) demonstrates success only in the first years, because
479 *L. aurea* is an opportunistic species and has a short life cycle (2- years) and its death
480 offers a window of opportunity for exotic invasive grasses to spread, especially in the
481 site that is close to sources of propagules.

482 The high SLA, associated with a fast-growth strategy are characteristics that
483 define seeders which tend to produce high numbers of smaller seeds (Power et al. 2011;
484 Verdú 2000). Seeders are a dominant strategy in highly productive habitats with some
485 form of disturbance, e.g. fire (Fynn et al. 2011). However, the neotropical savanna is an
486 ecosystem with low nutrient availability and, in general, species associated with low-

487 fertility soils have comparatively low SLA and slow growth (Jager et al. 2015;
488 Maracahipes et al. 2018; Pinho et al. 2019). Slow-growth strategies tend to have the
489 resprouting reproductive strategy and allocate a greater proportion of their resources
490 belowground (Eller & Oliveira 2017; Power et al. 2011; Verdú 2000). Indeed,
491 neotropical savanna native plant communities have a higher dominance of resprouter
492 species (Pilon et al. 2020) differently from what was observed in restored community
493 where the high dominance of seeders/acquisitive species implied in a low investment in
494 belowground biomass and high accumulation of aboveground biomass strongly
495 associated to ecosystem resilience after disturbance.

496 *Functional composition, Biomass investment and implications for resilience*

497 Overall, the conservative traits of resprouter species observed in the native area
498 underpins slow aboveground growth (Pellizzaro et al. 2017; Silva et al. 2015) and high
499 investment in belowground tissues (De Castro & Kauffman 1998; Hoffmann et al.
500 2003). In contrast, most acquisitive seeders savannas species often have a high specific
501 leaf area, a low root-tissue density, and thin roots (Lachaise et al. 2020), which explain
502 the low belowground biomass investment and low root:shoot biomass in the restored
503 area. However, in neotropical savannas, about 40% to 70% of the total biomass and
504 carbon stocks are located belowground, mostly in roots (Fidelis et al. 2013; De Castro
505 & Kauffman 1998; Ribeiro et al. 2011; Loiola et al. 2015). These are composed of roots
506 and rhizomes, important components of resprouting after disturbances, especially fires
507 (Fidelis et al. 2014; Ott et al. 2019). Several studies show that the most capacity of
508 resilience after fires are in resprouting from underground organs (Bond & Midgley
509 2001b; Bardgett et al. 2014; Pausas et al. 2018; Ott et al. 2019). Rhizomes, lignotubers,
510 and belowground stems can allow plants to resprout and survive disturbances, such as
511 fire, and promote regrowth after unfavorable seasons (Ottaviani et al. 2020). Given that
512 the recruitment of resprouter species occur mostly from belowground organs, we need
513 to consider including vegetative reproductive tissues (e.g. bud banks) and not only seeds
514 to quickly achieve greater resilience in neotropical savanna under restoration.

515 Another possible explanation for low belowground and high aboveground
516 biomass allocation is the early-stage of the vegetation establishment (4 years after
517 seeding) (Wilson 2011). In forest ecosystems, early successional stages have a high
518 abundance of acquisitive species, followed by conservative species in the later stages
519 (Lohbeck et al., 2015, 2013; Poorter et al., 2019). However, succession characterized by

520 a high species turn-over through time is most likely improbable in the neotropical
521 savanna given that most species in surrounding native patches are resprouters (Silveira
522 et al. 2020). The pioneer, secondary, or late-successional species are far from adequate
523 to categorize plant species colonizing, covering the ground, and persisting in savanna
524 vegetation (Dayrell et al. 2018). Fire-prone vegetation are characterized by the
525 coexistence of conservative and acquisitive species, with low recruitment from seed
526 banks (Pilon et al. 2020). The source of seeds for direct seeding restoration in this
527 ecosystem is most likely biased towards seeder species because only seeds are easily
528 collected in the field (Schmidt et al. 2019). The seeder species most used and also most
529 favoured by the technique of direct seeding that provides seeds with high germination
530 rates (Pellizzaro et al. 2017; Sampaio et al. 2019), leading to an acquisitive community
531 in the restored area. The main problem of promoting restoration with acquisitive species
532 relies on the possibility of trapping the restored area in an ecosystem state composed of
533 acquisitive species, which is likely more vulnerable to invasion and less resilient to fire.
534 Because conservative species tend to reproduce vegetatively, the probability of arrival
535 and establishment of resprouter/conservative species is very low because they have low
536 investment in seed production. In addition, the legacy effect mediated by the presence
537 of invasive grasses in the restored area will potentially increase the exotic dominance in
538 the restored area (Hess et al. 2019; Wolfsdorf et al 2021). Therefore, to provide a more
539 stable system to exotic invasion, we need to incorporate vegetative reproduction organs
540 such as underground buds in restoration efforts (Pilon et al. 2019) and also manage the
541 soil towards low nutrient availability, to favor the dominance of slow-growing plants.
542 The use of direct seeding with a high abundance of seeders species increases the risk of
543 creating unstable ecosystems, with a low resistance to invasion and low resilience to
544 fires.

545 Overall, restoration using direct seeding was effective at limiting exotic invasion
546 in the first few years post-restoration, alongside being effective at recovering soil cover
547 and aboveground biomass using fast-growing native plants. These outcomes were
548 facilitated by frequent ploughing prior to seeding, followed by inversion tillage to
549 remove exotic grasses from the seed bank and prevent their regeneration (Coutinho et
550 al. 2019; Sampaio et al. 2019). However, these ploughing and tilling practices probably
551 destroyed native belowground organs. This "trade-off" between avoiding invasion and
552 maintaining the underground organs of resprouter species promotes low investment in
553 belowground biomass and high accumulation of aboveground biomass, from the planted

554 acquisitive native species. In addition, the high accumulation of aboveground biomass
555 can also increase the risk of severe fires, especially in dry season (as occurred in 2020 in
556 the restored site) (Rissi et al. 2017; Santos et al. 2021; De Moraes et al. 2016; Gomes et
557 al. 2020; Schmidt et al. 2017). Principally, in areas with high invasion potential, as in
558 the case of our restored area, fire disturbance might favour the return of exotic species
559 through promoting additional nutrient input into the soil (Damasceno & Fidelis 2020;
560 Eller & Oliveira 2017; Lannes et al. 2016). Clearly, we must investigate solutions to
561 avoid catastrophic fires and exotic invasion, however, longer-term fire exclusion is
562 probably not an ideal strategy to restore fire prone-ecosystem (Pausas et al. 2018c;
563 Charles-Dominique et al. 2015; Buisson et al. 2019). Therefore, the low chances of
564 recovery of native species by sprouting and high potential to recovery exotic grasses
565 invasion creates a low resilience restoration system. Future efforts may therefore need
566 to use a combination of direct seeding and other restoration techniques, such as bud
567 bank transplantation, or soil and litter transplantation, which may improve neotropical
568 savanna restoration outcomes.

569 *Restoration and soil uncoupling*

570 The coupling among soil and vegetation provides high resistance and resilience
571 to disturbance mediate by feedbacks plant-soil (Mack et al. 2019). The results of
572 uncoupling among functional index's and soil properties from the restored area suggest
573 that the first years of neotropical savanna restoration have low resilience. The
574 dominance of only acquisitive/seeders strategies may lead the system to be sensitive to
575 any disturbance. Obviously, the short time since sowing might influence these results.
576 However, the direct seeding practice eliminates the dispersion filters and change soil
577 characteristics responsible for neotropical savanna community assembly. Clearly, the
578 species pool favoured by direct-seeding not includes the range of species pool found in
579 old-growth savanna communities that were built with different environmental filters
580 than those proposed by direct seeding. The coexistence of conservative and acquisitive
581 strategies represented by species pool found in neotropical savannas may increase the
582 resilience improving restoration outcomes. However, to achieve this we need to foster
583 the coupling and feedbacks between soil and vegetation typical of a slow functional
584 state. To target this, future restoration research should focus on the use of more slow-
585 growing species and adjustments of soil conditions towards the nutrient-poor state to
586 support the development of conservative species.

587

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597

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862

863 **Figures and tables**

864 **Table 1.** Traits included in the study, the trait category the functional strategy that high
 865 values of this trait refer to (A = acquisitive, C = conservative) description of the
 866 ecological significance, units and abbreviations list of measured traits, abbreviations,
 867 and units used (Adapted from Lohbeck et al., 2013)

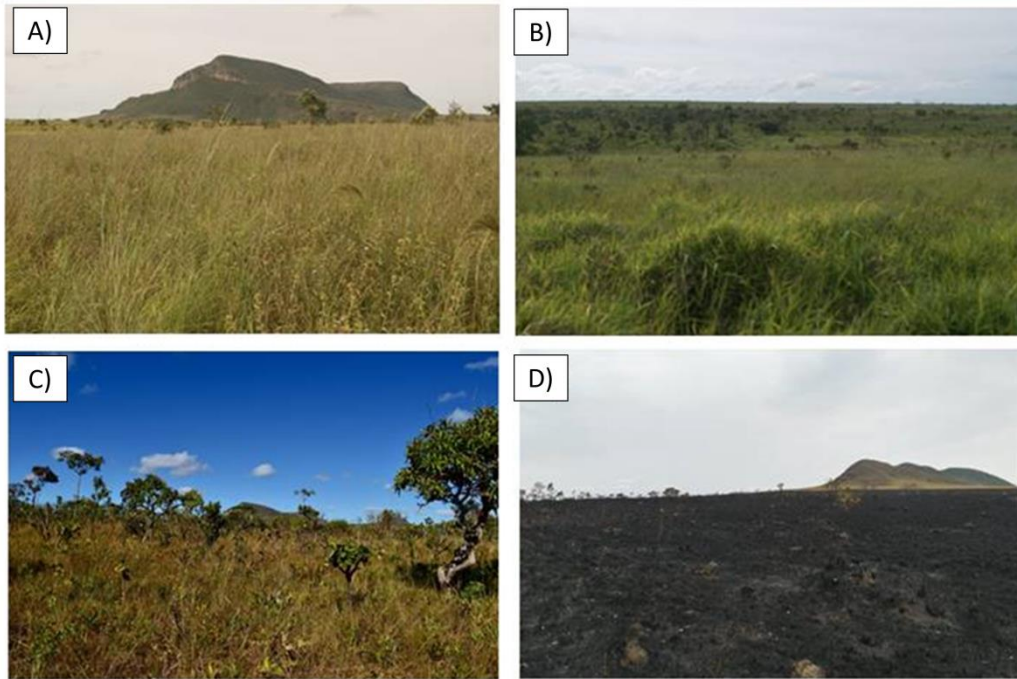
Code	Trait	Ecological significance	Strategy
SLA	Specific leaf area (cm ² g ⁻¹)	Resource use, maximum photosynthetic rate, and the related environment disturbance	A
LA	Leaf area (cm ²)	Light intercepting area, dry matter production, respiration, leaf cooling, gas exchange	A
LT	Leaf thickness (mm)	Resistance to lower water availability, nutrient-poor soil	C
H _{max}	Maximum height (cm)	Access to light and competitive ability	A
LNC	Leaf nitrogen (N) concentration (g/kg)	Response to soil nutrient availability, photosynthetic capacity	A
LPC	Leaf phosphorous (P) concentration (g/kg)	Photosynthetic capacity , plant development and growth	A
LDMC	Leaf dry-matter content (g g ⁻¹)	Relative growth;, leaf lifespan , construction costs, nutrient retention	C

869 **Table 2.** List of measured community weighted means (CWM) traits, showing estimated mean from the fit model (GLMM) and confidence
870 intervals, by life forms (woody and non-woody) for each vegetation type. (See results test details in table S1). UCI= Upper confidence intervals;
871 LCI= Lower confidence intervals.

Trait	Vegetation type																	
	Restored						Abandoned pasture						Native					
	Woody			Non-Woody			Woody			Non-Woody			Woody			Non-Woody		
	Mean estimate d	UCI	LCI	Mean estimate d	UCI	LCI	Mean estimate d	UCI	LCI	Mean estimate d	UCI	LCI	Mean estimate d	UCI	LCI	Mean estimate d	UCI	LCI
LA (cm ²)	11.30	18.6 0	0.80 8	11.11	18.3 0	7.94	11.80	21.1 1	8.19	21.2	35.1 0	15.2 3	38.3	63.3	27.4	12.5	20.6	8.94
SLA (cm ² .g ⁻¹)	103.5	125. 0	87.8	79.9	95.0	68.9	43.6	51.0	38.1	118.4	145. 1	100. 0	64.9	76.3	56.4	63.4	74.2	55.4
LT (mm)	0.263	0.31 8	0.22 3	0.216	0.25 4	0.18 8	0.360	0.48 5	0.28 6	0.134	0.15 2	0.12 0	0.353	0.46 4	0.28 5	0.216	0.25 8	0.18 6
LDM C (g.g ⁻¹)	5.26	6.28	4.53	3.01	3.39	2.71	3.05	3.45	2.74	2.95	3.29	2.67	2.69	2.98	2.45	2.83	3.14	2.57
LPC (mg.g ⁻¹)	0.084	0.09 1	0.07 8	0.052	0.05 6	0.04 9	0.078	0.08 5	0.07 2	0.048	0.05 1	0.04 6	0.067	0.07 2	0.06 3	0.048	0.05 1	0.04 6

LNC	1.66	1.81	1.54	0.87	0.92	0.82	1.56	1.7	1.44	0.97	1.04	0.92	1.47	1.59	1.37	0.95	1.01	0.90
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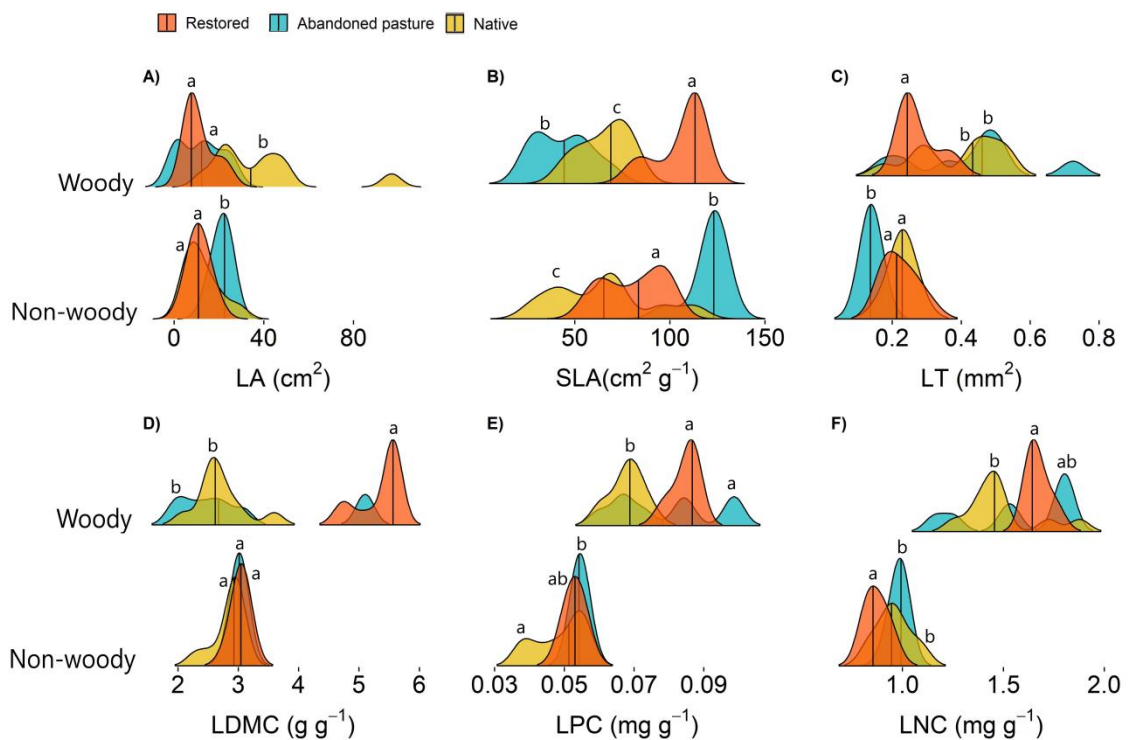
(mg.g⁻¹)



872

873 **Figure 1.** Vegetation types from Chapada dos veadeiros National Park, Brazil. A)
 874 Restored area by direct seeding of native species; B) degraded vegetation dominated by
 875 exotic grasses (abandoned pasture); C) well-preserved old-growth vegetation (Native
 876 area); D) After light-fire (2020) in Restored area.

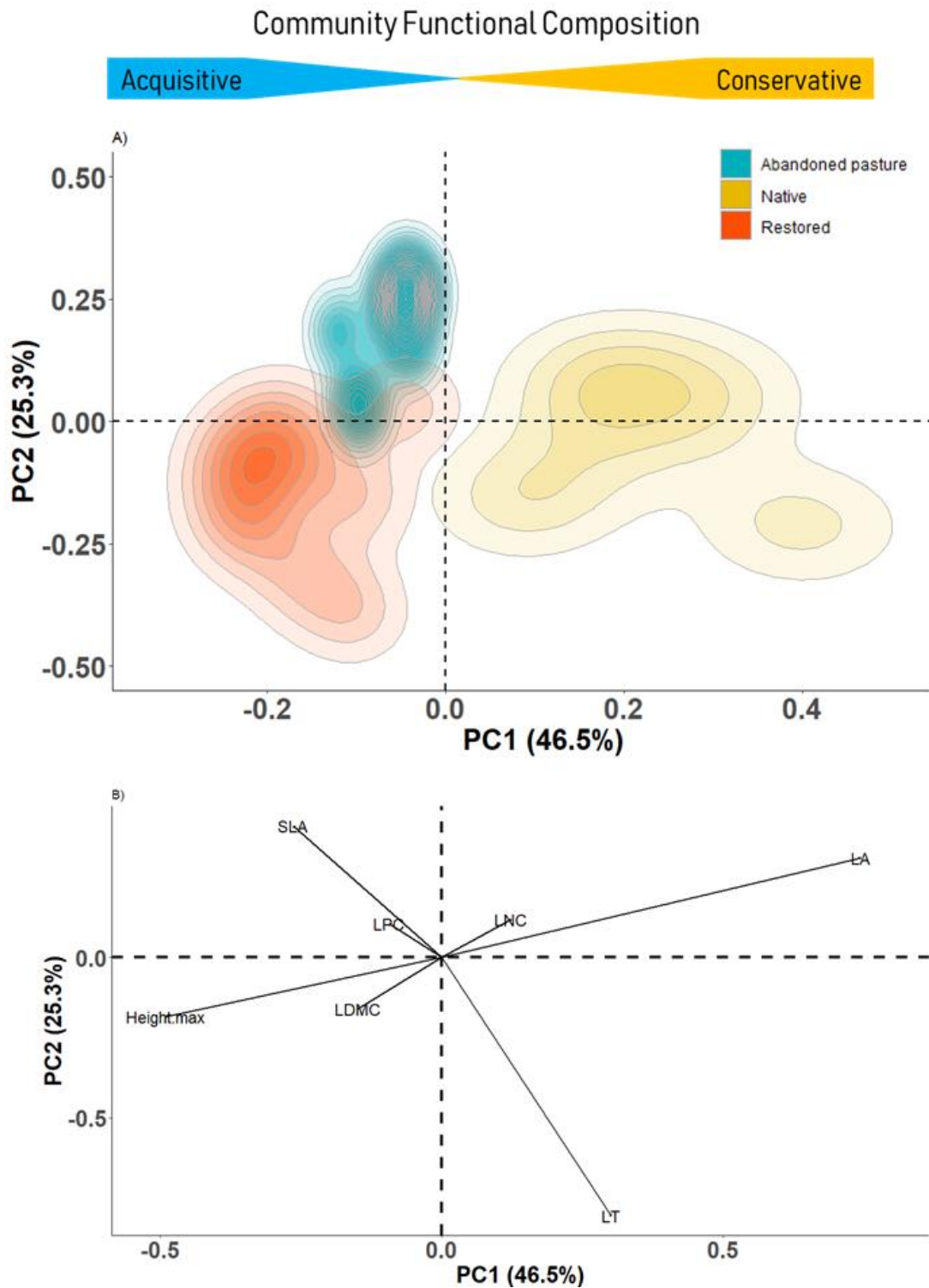
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879 **Figure 2** Distribution from CWM by Leaf traits values per life forms (Woody and
 880 Non-woody) for each vegetation type (restored; abandoned pasture, native vegetation)

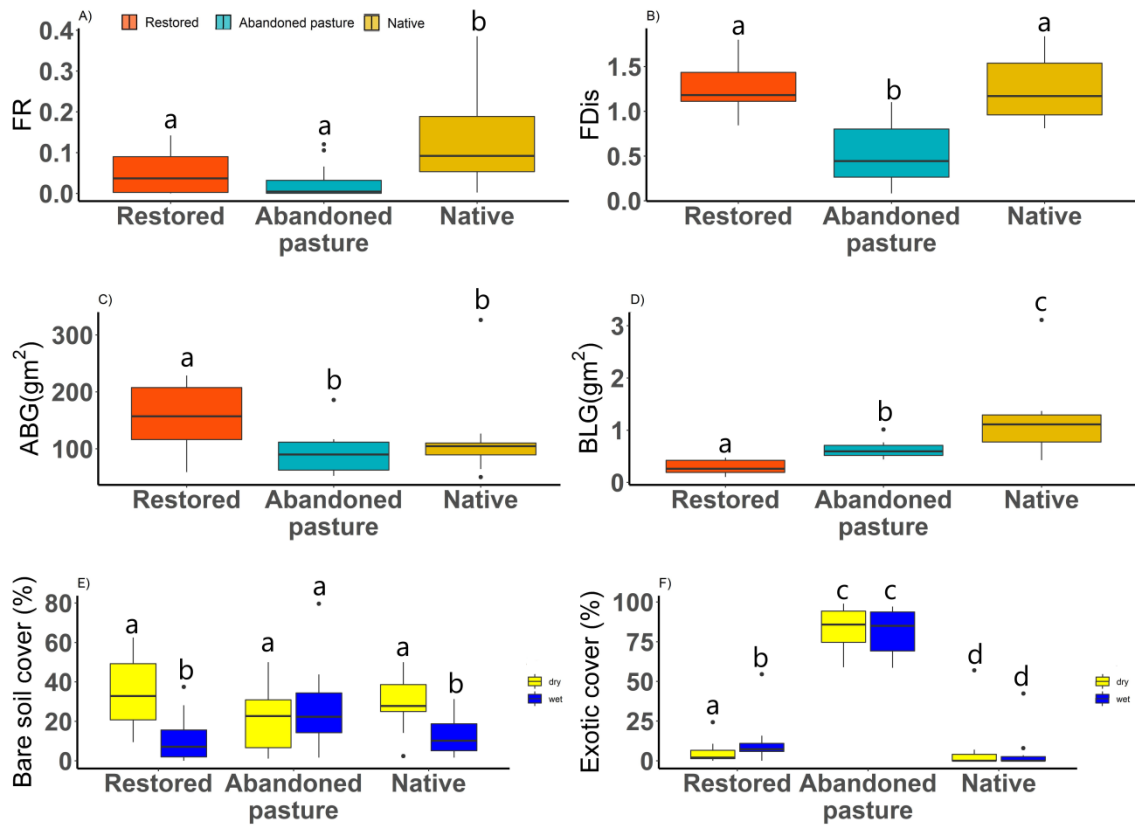
881 in wet season a) Leaf area;) (b) Specific leaf area (SLA); (c) Leaf thickness (LT), (d)
882 Leaf dry mass content (LDMC). (e) Leaf P concentration (LPC); (f) Leaf N
883 concentration (LNC). The colours from distributions represent each vegetation type
884 analyzed. The vertical lines represents median. Different letters represents significance
885 difference from pos-hoc test ($P < 0.01$, see details Table S1).
886



887

888 **Figure 3.** Principal component analysis of 6 leaf traits and maximum height max of the
 889 restored, native, and abandoned pasture community. A) PCA using leaf traits from each
 890 vegetation type , the filled contour bands represent density points estimation and
 891 countours represents the limits of points density. The filled contour bands represent
 892 density estimation from points distribution in 2d space (Traits by species), the density
 893 estimated are represented by colour gradient, following the centre with high-density and

894 strong colours to edge bands with weak colours. The colours from density distributions
 895 represent each vegetation type analyzed B) PCA using leaf traits from each vegetation
 896 type showing leaf traits used in PCA analyses. The traits included are: leaf area (LA);
 897 leaf thickness (LT); specific leaf area (SLA); leaf dry matter content (LDMC); leaf
 898 nitrogen concentration; (LNC); leaf phosphorus concentration(LNC) and Height
 899 maximum (Height.max). The arrows size represents the contribution of PCA axis.
 900



901
 902 **Figure 4.** Functional diversity index, biomass investment and soil cover by vegetation
 903 areas. A) Functional Richness (FR); B) Functional Dispersion (FDIs); C) Bare soil
 904 cover; D) exotic cover; E) Above-ground biomass; F) Belowground biomass. The blue
 905 represents the wet season, yellow represents the dry season. The central lines represent
 906 the medians . The colours from the box from figure (A) to D) represent each vegetation
 907 type analyzed and The colours from the box from figure E) and F represent season
 908 (Wet and Dry season). Different letters represents significance difference from pos-hoc
 909 test (P<0.01, see details Table S2).

