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Beyond the "resprout or not resprout" dichotomy: on the prevalence and evolutionary fingerprint of resprouting in tropical dry forest trees

1   **Beyond the "resprout or not resprout" dichotomy: on the prevalence and**
2   **evolutionary fingerprint of resprouting in tropical dry forest trees**
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19 **Abstract**

20 Resprouting is a plant persistence response to disturbance or stressful environmental
21 conditions. Frequent resprouters dominate in stressful environments, with a tendency to
22 phylogenetic structuring of associated traits. Nevertheless, knowledge on resprouting
23 expression in drought-prone, yet fire-free, is poorly understood. Here, we assess the
24 incidence of resprouting in tree communities of tropical dry forests (TDF) subject to
25 substantial seasonal water stress, also seeking to identify its main drivers and the
26 evolutionary history underlying patterns. Based on inventories of 16 TDF fragments
27 (15,642 trees of 321 species), we calculated two resprouting metrics (proportional number
28 of multi-stemmed trees – resprouting frequency; and stems *per* tree), classified taxa
29 according to their resprouting frequency and assessed the prevalence of these groups in
30 the sampled fragments. We investigated the relative importance of environment versus
31 taxonomic and evolutionary identity for resprouting response. Taxa with low and medium
32 resprouting frequencies (17.19 and 40.2 % of resprouting frequency, respectively) are the
33 most prevalent in TDF, compared to non-resprouters and high-frequency resprouters.
34 Resprouting frequency was better explained by taxonomic identity than by environmental

factors. Altogether, resprouting ability appears to be an intrinsic trait that varies in response to environmental conditions but only within a range previously constrained by taxonomic identity. However, we found no phylogenetic signal above the genus level for any resprouting variables. Thus, the variation of resprouting variables in TDF lineages may have been determined by divergence between closely related taxa and convergence between distantly related ones, reflecting the specific restrictive factors to which they have been subjected.

Key-Words: Tillering; persistence niche; sprouting; deciduous forests; phylogenetic signal.

1 INTRODUCTION

Environmental pressures select functional traits and plant responses that increases species fitness (Cadotte & Tucker, 2017; Diaz et al., 1998). One such plant responses, the capacity to resprout, has been shown to increase plant persistence and fitness (Poorter et al., 2010) via the production of new shoots in response to physical or physiological stress (Bellingham & Sparrow, 2000; Pausas et al., 2016, Vesk & Westoby, 2004). The ability to resprout is widespread among ecosystems worldwide in response to several stressors, such as fire, herbivory, floods, hurricanes, water stress and edaphic restrictions (Araujo & Santos, 2019; Bond & Midgley, 2003; Ceccon et al., 2006; Jimenez-Rodriguez et al., 2018; Souza et al., 2019; Zeppel et al. 2015). Resprouting in these different contexts of restriction are associated to a complex set of functional traits, thus not being a simple binary trait, but an ecological syndrome that integrates several functional traits and is inserted in a wide spectrum of ecological variability (Bond & Midgley, 2003; Pausas et al., 2016). Due to role in species maintenance in community, resprouting is normally considered part of a species' "persistence niche", as opposed to the classic "regeneration niche" that comprises traits of sexual reproduction (Bond & Midgley, 2001; Grubb, 1977; Pausas et al., 2016).

During the resprouting plants respond by allocating non-structural resources (carbohydrates) toward the maintenance of buds and to producing a new shoot that become new stems (Moreira et al., 2012, Schwilk & Ackerly, 2005). In a mature organism, new shoots benefit from mature root and leaf systems, which facilitate resource acquisition and resistance to local ecological stressors, since resprouts do not face environmental pressures that are usually experienced by seedlings (Bond & Midgley,

2003; Clarke et al., 2013; Pausas et al., 2016). In addition, some studies point to the existence of resprouting vs sexual trade-offs in the resource allocation, since the issuance of new stems reduces the resources used in reproduction, with consequences for the quality and quantity of seeds produced (Knox & Clarke, 2005; Nzunda & Lawes, 2011; Verdú, 2000). Finally, the adoption of resprouting by trees also reduces the plant species dependence on pollinators and seed disperses, in addition to resprouters not conditioning their permanence in the community to the existence of environmental conditions favorable enough for the reproductive age to be reached (Bond & Midgley, 2001; Bond & Midgley, 2003; Nzunda & Lawes, 2011).

The occurrence of resprouting as strategy by species is thus intrinsically related to gains and losses in individuals' survival and success. Besides the environmental stressors, the variations in the prevalence of resprouting in different ecosystems are thus also a direct response to local productivity and the intensity and frequency of disturbances (Nzunda & Lawes, 2011; Pausas & Keeley, 2014; Vesk & Westoby, 2004). It is expected that the importance of resprouting is greater in ecosystems subject to a regime of frequent and intense disturbances or with continuous restrictive factors, and consequently present lower importance in ecosystems with less stressful characteristics with few disturbances or low intensity disturbances (Bond & Midgley, 2003; Vesk & Westoby, 2004). This variation of the importance of resprouting response to variations in ecological constraints has implications for the ecological patterns of different biomes, conditioning the structure and diversity of their communities and consequently their functioning (Pausas et al., 2016; Vesk & Westoby, 2004; Heineman et al., 2021).

Beyond its prevalence in fire-prone ecosystems, resprouting is a broadly adopted tree strategy under seasonal climates with little to no precipitation during the dry season, in detriment to reseeding, that may be harmed by stressful condition in initial plant life-stages (Ceccon et al., 2006; Zeppel et al., 2015). In these dry ecosystems where a continuous restrictive factor related to water availability is present, the emission of new stems is a strategy to increase the chances of survival of the individuals through a new leaf and hydraulic system without the damages suffered by the main stem (Zeppel et al., 2015). Due to these physiological characteristics, these new stems will have a greater chance of survival in the short term, with greater resistance to water scarcity compared to seedlings in the lower forest strata with leaf and root systems still under development (Ceccon et al., 2004; Souza et al., 2019; Zeppel et al., 2015).

101   However, there are many uncertainties around resprouting strategy in drought-
102   prone, yet fire-free environments, such as their importance in communities, their patterns
103   of variation between taxa, what are their main drivers (the role of environmental
104   restriction) and if there is a structuring phylogenetics of associated variables, with related
105   taxa having similar resprouting. Expectations exist on such issues, however obtained in
106   one-off studies with limited data sets that do not allow large-scale inferences, specially
107   related to phylogenetic issues that only recently had significative advances (Bellingham
108   & Sparrow, 2000; Bond & Midgley, 2003; Vesk & Westoby, 2004; Zeppel et al. 2015;
109   Coelho de Souza et al., 2016). In addition, studies related to resprouting in environments
110   with non-punctual but continuous stresses such as TDF are faced with the difficulty of
111   identifying the association between environmental effects and the emission of new stems,
112   in addition to overlapping the trends of trees changing to shrub forms (Götmark et al.,
113   2016). An alternative especially for studies involving permanent plots is to relate the
114   occurrence of multi-stemmed trees with resprouting events, considering that in
115   environments of continuous stress the emissions of new stems occur as a response to
116   environmental pressures (Dunphy et al., 2000; Souza et al., 2021).

117   Tropical dry forests (TDF) are a particularly relevant and widespread vegetation
118   formation for understanding the links between water stress and resprouting as a
119   regeneration strategy across different taxa and communities (Fernandes et al., 2020;
120   Pennington et al., 2009). TDF undergo seasonal water stress, with average annual rainfall
121   below 1800 mm and 3 to 6 months with less than 100 mm of monthly rainfall
122   (DRYFLOR, 2016; Pennington et al., 2009). Besides this, TDF are also particularly
123   drought-prone in South America, with high inter-annual variability in water availability
124   (Allen et al., 2017; Pennington et al., 2009). In fact, exploring the patterns related to
125   resprouting occurrence in TDF is likely to provide relevant information about the ecology
126   of seasonal communities and help to predict how other vegetation types may respond to
127   predicted scenarios of increasing aridity worldwide (Allen et al., 2017; Bond & Midgley,
128   2003; IPCC, 2014; Pausas et al., 2016). In addition, exploring the ecological patterns of
129   resprouting in an approach that goes beyond the classic approach (i.e., presence vs
130   absence of resprouting) can contribute to understanding their role in ecological patterns
131   and in the functioning of these drought-prone ecosystems, which can be important
132   including to think about the response of other ecosystems to arid increase scenarios
133   (IPCC, 2014; Zeppel et al. 2015).

Here we explored resprouting expression within and across lineages in tropical dry forests (TDF) with no recent (>40 years) anthropic disturbances to understand the importance of this ecological strategy as a means of persistence by species in drought-prone ecosystems. First, we investigated the variability in the frequency of resprouting across species and genera of trees, assessing the existence of taxa groups with similar resprouting frequency and also their ecological representativeness in TDF. Considering the high ecological constraints caused by the limitations of water availability such strong seasonality, low rainfall and drought caused by interannual variations in the TDF (Allen et al., 2017; DRYFLOR, 2016; Pennington et al., 2009), our expectation is that species and genera with high resprouting frequency are the most representative in the communities. Second, we evaluated the influence of taxonomic identity (without phylogenetic information) and environmental factors on two resprouting variables: the frequency of resprouting and the number of stems per tree. We expect environmental factors are the main conditioning factors for the variation of resprouting variables, considering the recognized role of environmental stresses in determining the adoption of resprouting as a regeneration strategy in relation to reseeding (Bellingham & Sparrow, 2000; Bond & Midgley, 2003; Nzunda et al., 2007; Pausas et al., 2016). Finally, we investigated the evolutionary fingerprint on resprouting patterns across TDF genera by quantifying the extent of phylogenetic signal for resprouting characteristics. As it is a crucial strategy for the survival of individuals in the face of restrictive factors, we hope that the resprouting variables are more similar in phylogenetic closer species, with their expression having been passed through the lineages. We rely on forest inventory data in which we consider multi-stemmed trees as a proxy for resprouted trees, considering that in the presence of continuous restrictive factors in the environment (such as water scarcity in the TDF), the largest part of the stems was produced in response to ecological restriction. By studying variation in the number of stems produced by resprouters and in the frequency with which different taxa resprout, we aim to advance knowledge on resprouting expression in tropical trees beyond a traditional binary classification of taxa as resprouters versus non-resprouters.

2 MATERIAL AND METHODS

2.1 Study areas

We used data from 16 fragments (hereafter plots) of tropical dry forests (TDF) located in the Brazilian states of Minas Gerais and Bahia, distributed in the southern

168 portion of the Caatinga biome and in patches within the Cerrado biome (Fig. 1; Table S1).

169 The regional climate is classified as Köppen As/Aw (tropical with dry winters), with

170 average monthly temperature in the sampled sites ranging from 22 to 24.6 ° C, and total

171 annual rainfall ranging from 754 to 1060 mm, concentrated between November and

172 March. Flatlands predominate in the region, although relief may vary in areas near

173 watercourses or adjacent to limestone outcrops. Arboreal Caatinga, a tall upright

174 deciduous forest vegetation, predominates in the region (Santos et al., 2012), with

175 occasional variations in vegetation physiognomy, floristics and structure driven by

176 microenvironmental factors such as the presence of rocky outcrops and floodplain

177 sandbanks (Aguiar-Campos et al., 2020; Apgaua et al., 2015; Paula et al., 2018; Souza et

178 al., 2019). The sites sampled are considered old-growth forests, with no large-scale

179 disturbances in the last 40 years, according to information collected from residents of the

180 region and satellite image observations.

181

182 **2.2 Vegetation data collection**

183 From 2006 to 2017, we established 313 permanent sample units or subplots, each

184 of 400 m², in the dimensions of 20 x 20 m or 10 x 40 m, depending on terrain

185 characteristics (see Fig. S1), totaling 12.52 ha of sampled area. Sampling intensity at each

186 plot ranged from 5 to 51 subplots, depending on environmental heterogeneity, fragment

187 size and data collection goals (see references in Table S1). In each subplot we included

188 all woody individuals (excluding lianas) with diameter at breast height (DBH, 1.30 m

189 above the ground) $\geq$3 cm. An individual with multiple stems was included in the sample

190 when its equivalent diameter was $\geq$ 3 cm, that is obtained by the square-root of the sum

191 of squares of the stems' DBH (only stems with DBH $\geq$ 1cm are included due to measure

192 limitation). That is, a multi-stemmed individual may be sampled even when no individual

193 stem surpassed 3 cm, but the stems joint may correspond to a tree with an equivalent

194 diameter that reach the minimum size. Thus, we sample all the variety of behaviors related

195 to multi-stemmed individuals, including since single stem individuals to multiple stems

196 individuals. It is also important to highlight that many of the woody individuals included

197 in the sample correspond to shrub/arboreal or shrub life forms according to traditional

198 classifications REFLORA (2020), but which perform ecological functions like trees in

199 the community due to vegetational characteristics. In other words, in a forest with a

200 canopy at a height of 10 - 12 m, individuals with shrub forms measuring 2.5 or 3 m are

201 an important part of the lower forest strata.

202   The use of equivalent diameter as measure we adopted for the decision of
203   sampling or not a tree was proposed by Souza et al. (2021), which called this practice as
204   the inclusion method "by tree". The use of this method is a common practice in tropical
205   forest in which multi-stemmed trees are very frequent, since it allows to consider the tree
206   size as a whole by the contribution of all stems and allow to sample tree species in shrub
207   form due to environmental conditions (Araújo & Santos, 2019; Paula et al., 2018; Souza
208   et al. 2019; Souza et al., 2021). We identified all individuals to the species level and
209   measured each stem diameter that met the inclusion criterion (achieving breast height, or
210   1.30 m above the ground). Plant identification was carried out by experts in the field or
211   in herbaria and followed taxonomic nomenclature of the Angiosperm Phylogeny Group
212   (APG IV, 2016). Name standardization followed REFLORA (2020), through the *flora*
213   package (Carvalho, 2016), implemented in the software R v. 4.0.3 (R Core Team, 2020).
214   Forest inventory data for the 16 sites are stored in the ForestPlots.net database
215   (https://www.forestplots.net/) (see plot codes in Table S1).   Our total sample thus
216   comprises 16 TDF fragments (12.52 ha of total area sampled), with 15,642 trees of 321
217   species.

218   We also obtained edaphic and climatic variables for each subplot. The edaphic
219   variables were collected in the field in the superficial layer (0-15 cm depth) of each
220   subplot (313 samples) and latter send to specialized laboratories to extract the measures
221   of interest according to EMBRAPA reference manual (EMBRAPA, 2017). The variables
222   measure were pH in water, available phosphorus content (P – mg/cm³); aluminum (Al –
223   cml/cm³), soil organic matter (SOM – dag/kg), sum of basis (SB – cmolc/cm³) and
224   proportion of sand (%). The climatic variables of each subplot were obtained using the
225   WorldClim Global Climate Data repository based on their spatial coordinate, with 30 arc-
226   seconds resolution (1-km² spatial resolution) (Fick & Hijmans 2017). From the available
227   variables, we selected 6 that have a recognized influence on vegetation patterns: BIO 1,
228   the mean annual temperature (MAT - ° C x 10); BIO 4, the temperature seasonality
229   (MAT_{SZ} - ° C x 100); BIO 5, the max temperature of warmest month (MTW - °C x 10);
230   BIO 12, the mean annual precipitation (MAP - mm); BIO 15, the precipitation seasonality
231   (MAP_{SZ}, %); and BIO 17, the precipitation of driest quarter (MAP_{DQ}, mm). The variable
232   MAT-SZ corresponds to standard deviation of temperature × 100, while MAP-SZ
233   corresponds to the coefficient of variation of precipitation between months.

234

235

2.3 Analyses of resprouting

For general patterns of resprouting across taxa, we calculated two measures for each species and genus across our dataset: the average number of stems per tree and the proportion of individuals that are multi-stemmed (hereafter, resprouting frequency). We are considering that the presence of two or more stems in a tree is a sign of an ecological response to some restrictive factor, that may be a punctual disturbance or a continuous stress that may be part of the environment itself. That is, we assume that the additional stems to the main one (here considered as the one with the greatest DBH) were produced in response to some stress, at some point in the individual's life history. Although there are theoretical controversies regarding the equivalence between resprouted trees and multi-stemmed trees, we consider that this approach is appropriate in environments such as TDF where stressors have a continuous effect. The point of split of stems varies a lot between trees and could be observed below-ground, at the ground-level and above-ground.

To classify species and genera into groups based on resprouting frequency, we used the k-means algorithm (Jain, 2010). To ensure sufficient sampling to quantify resprouting patterns, we set a threshold of including taxa (species or genus) with a minimum abundance of 10 individuals sampled in the entire dataset (167 species and 114 genera). We tested a number of k-values ranging from two to seven and selected the optimal number of groups (i.e., optimal k-value) based on within-group sum of squares through the elbow method (Kodinariya & Makwana, 2013). Aside from the non-resprouting taxa (not included in this partitioning), the analyses indicated the existence of three groups (optimal k-value = 3), which we term low-frequency (center value of 16.4 %), medium-frequency (center value of 42.01 %) and high-frequency (center value of 76.2 %) resprouters. We quantified the proportion of species and genera in our dataset that fell into each category, and also the proportion of each group in the total number of trees, total number of stems and total aboveground woody biomass, the latter obtained using allometric equations at the tree-level from Chave et al. (2014) (see supplementary information for more details).

In order to compare the relative influence of site-specific environmental factors versus taxonomic identity on resprouting variables, we used generalized linear mixed effects models and variance partitioning. For understanding variation in number of stems per individual, we modelled the observed stem count for each individual as a Poisson distributed variable in function of edaphic and climatic variables (as fixed variables) and

270 with two sets of nested random effects as explanatory variables: the site factors, using the

271 subplot and plot within which the individual to control the dependence between trees

272 located in the same subplot and plot; and taxonomic identity, using the species, genus and

273 family of each individual. For understanding variance in frequency of resprouting, we

274 calculated the number of individuals that had resprouts for each species in each plot

275 versus the number of individuals in the plots that did not have resprouts. We modelled

276 this as a binomial response ('successes' and 'failures' to resprout) with the same edaphic

277 and climatic variables as fixed variables and with same two sets of nested random effects.

278 For modelling we used the *glmer* function of the *lme4* package (Bates et al., 2010). The

279 global model obtained for the two resprouting variables followed the mold of equation

280 (1).

281

282 **Equation (1)**

283 $Resprouting\ variable \sim MAT + MAT_{SZ} + MAP + MTW + MAP_{SZ} + MAP_{SZ} +$

284 $pH + P + Al + SOM + SB + Sand + (1|Plot:Subplot) +$

285 $(1|Family:Genus:Species)$

286

287 From the models' results, first we quantified the marginal (referring to the fixed

288 effects) and conditional (referring to the fixed plus random effects) coefficient of

289 determination (R^2) using the *r.squaredGLMM* function of the *MuMin* package (Bartón

290 2009; Nakagawa & Schielzeth, 2013), with subsequent quantification of the R^2 of the

291 random effects by subtracting the previous two. With this we can quantify how much of

292 the variation is associated with environmental effects (fixed variables) and how much is

293 associated with taxonomic and sampling factors (random effects). Then, we performed a

294 variance partitioning analysis to assess variance explanation by random effects (Fyllas et

295 al., 2009; Oliveras et al., 2020). This aimed to quantify inside the random effects the

296 contribution of taxonomic factors (family, genus and species identity) and sample factors

297 (plot and subplot) on resprouting expression. We also compared the effect of each factor

298 (Fixed vs Sampling vs Taxonomic) using the Akaike Information Criterion corrected for

299 small sample size (AICc), to assess the importance of variables for the model fitting. For

300 this, we compared the AICc of the global model with options without each one of the

301 factors, in order to evaluate which has a great impact on the AICc value. We stress that

302 this approach does not include relatedness between species, genera or families, so that the

303 results related to the taxonomic component comes down to how much species' identity
304 influences the variation in resprouting expression.

305

306 **2.6 Evolutionary fingerprint on resprouting expression**

307   To explore the evolutionary fingerprint on resprouting characteristics (average
308 number of stems per tree and resprouting frequency) in TDF, that is, the phylogenetic
309 structure of resprouting variables, we used data from genera with a minimum of 10
310 individuals in the sampled region. This threshold aimed to avoid potential errors in
311 quantifications for undersampled genera. As a phylogenetic tree, we used the genus-level
312 phylogenetic hypothesis for lowland tropical tree genera in South America from Neves et
313 al. (2020) due to its recognized quality in comparison to other available options, specially
314 related to the occurrence of polytomies.

315   To evaluate the evolutionary fingerprint, we measured the extent of phylogenetic
316 signal for each resprouting variable using Pagel's λ (Freckleton et al., 2002; Pagel, 1999),
317 which is a more robust parameter for incomplete phylogenies (Molina-Venegas &
318 Rodríguez, 2017). To estimate whether phylogenetic signal was greater than expected by
319 chance, we shuffled genera randomly in the phylogeny and calculated the proportion of
320 1000 randomizations that have λ greater than the observed. λ quantifies similarities
321 between sister lineages and usually ranges from 0 to 1. If $\lambda = 0$, there is a lack of
322 phylogenetic signal and no correlation between resprouting values and relatedness of
323 taxa; if $\lambda = 1$, the distribution of trait values across the phylogeny reflects the evolutionary
324 relatedness among taxa and fits the expectation under a null Brownian motion model of
325 evolution (Freckleton et al., 2002); if $0 < \lambda < 1$, trait values are similar between closely
326 related taxa, but influenced by evolutionary processes other than BM (Crisp & Cook,
327 2012).

328   To account for the uncertainty of the phylogenetic hypothesis used herein, we
329 repeated our analyses with 100 trees from the posterior distribution (also available in
330 Neves et al., 2020). From the 100 trees, we calculated the confidence interval and p-value
331 significance for Pagel's λ values obtained with each tree for each of the resprouting
332 variables. We also performed phylogenetic signal analyses for the resprouting categories
333 (low-, medium- and high-frequency resprouters) using two different approaches: the *D*
334 measure for binary comparisons between categories (Fritz & Purvis, 2005), and the δ
335 measure by Borges et al. (2019) for discrete categories. We conducted all phylogenetic
336 analyses using functions from the *phytools* (Revell, 2012), *ape* (Paradis et al., 2004),

337 *geiger* (Harmon et al., 2008) and *caper* (Orme et al., 2020) packages in the R Statistical
338 Software v.4.0.3 (R Team, 2020).

339

340 **3 RESULTS**

341 **3.1 Resprouting occurrence and prevalence in TDF**

342   The total sample consists of 15,642 individual trees and 25,720 stems, belonging
343 to 321 species (239 with multi-stemmed trees), 171 genera (134 with multi-stemmed
344 trees) and 51 plant families (49 with multi-stemmed trees; Tables S2 and S3). The average
345 number of stems *per* tree and resprouting frequency varied widely across genera (Figs 2
346 and 3; Table S2; S3 and S4). Across all monitored individuals, 32.5% (5084 individuals)
347 had multiple stems, with an average of 1.64 stems *per* tree. When considering just trees
348 with resprouts, the average increases to 2.98 stems per tree.

349   Most genera and species fit the categories of low- and medium-frequency
350 resprouters (Figs 2 and 3). Only a small proportion of the pool of genera and species in
351 the studied TDF was classified as non-resprouters (i.e., with resprouting never observed)
352 or as high-frequency resprouters (i.e., 70% of resprouting frequency) (Fig. 2 and 3). Most
353 genera and species had an average number of stems *per* tree between 1 and 2 (low- and
354 medium-frequency resprouters). Only a small proportion of the pool of genera and species
355 never resprouted or had an average of more than three stems *per* tree (Fig. 2). In general,
356 most genera and species recorded are considered facultative resprouters (intermediate
357 categories), meaning that individuals belonging to these taxa may or may not adopt the
358 resprouting strategy.

359

360 **3.2 Resprouting across forest plots: site and taxonomic effects**

361   Variation in resprouting variables was determined to a greater degree by
362 taxonomic identity (species, genus and family) than by the plot or site in which
363 individuals occurred (i.e., greater variance explained by all taxonomic levels together;
364 Fig. 4). The environmental effects (fixed variables) had an R^2 of 1.30 and 2.76% for
365 average stems per tree and resprouting frequency, respectively, while the random effects
366 corresponded to 23.68 and 42.21% for the same variables (Fig 4 - a), accounting for the
367 largest part of the variation of the global model. The unexplained part of the variation
368 evaluated corresponded to 75.02 % and 45.03 % for stems per tree and resprouting
369 frequency, respectively. Within the random effects, taxonomic effects explained 12.46 %
370 and 27.68 % of total variance in the average number of stems *per* tree and resprouting

371 frequency respectively, whereas sampling effects explained only 2.14 % and 15.73 % of
372 the variation for the same variables (Fig. 4; Table S5). Within taxonomic levels, for both
373 resprouting frequency and average number of stems *per* tree, genus identity was the most
374 important taxonomic component, followed by species and family identity (Fig. 4; Table
375 S5). The large majority of the variation in these measures of resprouting remained
376 unexplained, 85.41 % for average stems *per* tree and 56.59 % for resprouting frequency.
377 Greater importance of taxonomic effects is also confirmed by examining the AICc values
378 of different models: removing taxonomic effects generated a greater increase in AICc
379 compared to removing environmental variables and sampling factors (Table 1).
380
381 **3.3 Resprouting across lineages: phylogenetic signal**
382   We found no significant phylogenetic signal for resprouting according to
383 estimates for Pagel's Lambda across 100 phylogenetics genus-trees (mean of $\lambda = 0.15$
384 and mean p = 0.19 for average number of stems per tree and mean $\lambda = 0.16$ and mean p
385 = 0.19 for frequency, both using the values 100 phylogenetics genus-trees) (Figs. 5 and
386 6; Table S6). Phylogenetic signal results for resprouting frequency categories through D
387 (Fritz and Purvis, 2005) and δ (Borges et al., 2019) corroborate this result: an absence of
388 phylogenetic signal for resprouting expression (see supplementary information and Fig.
389 S2). That is, resprouting variables are not phylogenetically structured so that related taxa
390 have more similar values and less related taxa have more distinct values.
391
392 **4 DISCUSSION**
393   Our results show that diverse resprouting strategies exist in tropical dry forests
394 (TDF), in which low- and medium-frequency (10-50 % of frequency) were the most
395 prevalent resprouting groups, in contrast with our expectations of high prevalence of
396 high-frequency resprouters. Contrary to our expectation, we also found that resprouting
397 patterns across TDF species are determined more by taxonomic identity (with no
398 relatedness considered yet) than environmental factors. That is, both resprouting
399 frequency and average number of stems *per* tree are intrinsic taxonomic characteristics,
400 significantly explained by taxonomic information, mainly genus and species identity.
401 Additionally, although it is a crucial strategy for survival in these environments, there is
402 no phylogenetic signal for resprouting strategies above the genus level. These results
403 suggest that resprouting strategies are phylogenetically labile, in which sister lineages can
404 show contrasting resprouting patterns in these highly threatened, yet poorly understood

405 dry ecosystems. These findings suggest that resprouting ability may have evolved
406 repeatedly and independently over the phylogeny, rather than constrained to certain
407 clustered clades.

408

409 **4.1 General resprouting patterns and environmental vs taxonomic effects**

410 We expected that the high-frequency resprouter species were the most
411 representative, however we found that within TDF most species are low- and medium-
412 frequency resprouters, with values of representativity of multi-stemmed trees lower than
413 previous reported in other works in tropical dry forests (Dunphy et al., 2000). These
414 species of resprouting frequency between 10 and 50 % in average are the most part of
415 species, trees, stems and biomass, thus been consequently related to the TDF ecosystem
416 functioning. Although water stress is a continuous restrictive factor that we expect to
417 promote broad resprouting (Pausas et al., 2016; Vesk & Westoby, 2004), these species of
418 moderate and low resprouting tend to dominate in these dry environments. This finding
419 agrees with the expected variation of occurrence of resprouting due to their consequences
420 to population growth capacity and individual fitness (Bond & Midgley, 2003; Ceccon et
421 al., 2006; Clarke et al., 2013; Pausas & Keeley, 2014). In a context of not restrictive
422 conditions, species would naturally tend to "opt" for seedling strategy, which is associated
423 with greater growth capacity and, among other factors, increased genetic diversity
424 (Bellingham & Sparrow, 2000; Nzunda & Lawes, 2011; Pausas et al., 2016). However,
425 due to strong environmental filters in TDF, particularly strong seasonal water stress, some
426 individuals of these species could resprout to ensure their survival by emitting a new leaf
427 and hydraulic system to obtain resources. The prevalence of low and medium-frequency
428 resprouters, even in relation to non-resprouters, corroborates with this strategy: high-
429 frequency species can guarantee their local survival, but may not ensure broad ecological
430 success within TDF communities due to the resprouting negative consequences for
431 individual fitness.

432 Resprouting is adopted by tree species to endure the hydric stress in TDF, which
433 is caused by the long dry season (that may last for up to 8 months), by the large year-to-
434 year variation in the timing of wet season start and in the intensity of precipitation
435 (Pennington et al., 2009). In these stress situations, especially due to the delay in the start
436 of water availability or precipitation reduction, the resprouting is being adopted as an
437 immediate response to water deficit and to the water stress physiological challenge that
438 threatens individual survival (Ceccon et al., 2006; Pausas et al., 2016; Zeppel et al., 2015).

439   In the absence of water stress, or in life stages where individuals have greater resistance

440   to ecological filters, resprouting would probably become an obsolete strategy and

441   therefore, may not be adopted (Bond & Midgley, 2001; Pausas & Keeley, 2014). This

442   non-continuous need of resprouting may explain the generally low resprouting frequency

443   and low average number of stems *per* tree we found here, in addition to other possible

444   relations with physiological responses at deeper levels, such as in anatomical structures

445   relevant to the water use by plants (Pausas et al., 2016). In the rainy season, the water

446   availability enables reproduction, dispersal and germination of seeds produced by

447   resprouting individuals, however with a compromised success due to the previous use of

448   non-structural resources in new shoots emission (Ceccon et al., 2006; Clarke et al., 2013;

449   Moreira et al., 2012; Pausas et al., 2016).

450   Resprouting is an important persistence strategy that increases plant fitness

451   (Poorter et al., 2010), therefore, it should be expected that its manifestation is mainly

452   determined by environmental conditions (i.e., high resprouting frequency and number of

453   stems *per* tree in response to stronger environmental filter). In contrast, our results show

454   that resprouting expression is mainly determined by species identity (taxonomic

455   information), whilst environmental conditions (climatic and soil variables) seem to play

456   a minor role. Thus, resprouting variables considered seems to be intrinsic traits that varies

457   in response to environmental conditions but within a limited range of variation previously

458   determined by taxonomic identity, mainly to genus and species identity. That is, the

459   values presented by the species for the resprouting variables considered vary within a

460   limit established by their taxonomic identity. It is important to state that current abiotic

461   variables may be correlated with a plant response that occurred previously, what can be

462   explain the low exploratory power of the site variables. We also recognized that a large

463   proportion of the variation remains unexplained. The residual variation may be associated

464   with communities' structure and dynamics (dominance, diversity relationships and long-

465   term trends), population age structure, canopy dynamics, biotic interactions, functional

466   traits not correlated to the phylogenetic patterns, intra-specific variability and other

467   factors we did not explore here. We also must consider the limitation of our work related

468   to considering the stems present in multi-stemmed trees as a result of the resprouting

469   process, in response to restrictive factors of continuous action. In this sense, a greater

470   control of the effects of disturbances in the identification of resprouting can help to reduce

471   the residual variation. In addition, studies on larger spatial scales that comprises longer

environmental gradients may find greater importance of environmental factors such as climate and soil on resprouting variation.

Prevalence of low and medium resprouters in TDF rather than high-frequency resprouter as we expected could also reflect the absence of large herbivorous mammals in South America and consequently of their disturbance effects related by herbivory and physical injuries. For African savannas, there is clear evidence that large animals drive woody plant functional patterns, selecting traits such as i) higher wood density that confers greater mechanical resistance to stem breakage) and ii) higher number of spines and iii) lower frequency of resprouting related to the absence of fire due to higher removing of biomass (fuel) by herbivores (Dantas and Pausas., 2020). However, in South America, these large herbivorous mammals went extinct around 10,000 years ago (Doughty et al., 2017), therefore, Cerrado plant functional traits are mainly determined by the presence of fire, in these fire-driven ecosystems (Dantas & Pausas, 2020). In the absence of these large animals, resprouter species may resprout in response to water scarcity, but not often as under the previous disturbance regime in which the higher herbivory may have promoted resprouting, thus adopt the reseeding as strategy of regeneration. In fact, if large herbivores had not been extinct, they would occur in the south, east and southeast South America regions, which overlaps our study region (Doughty et al., 2016). In comparison to the thicker leaves in Cerrado species, TDF species leaves may be more attractive to herbivores due to their high nutritional content (related to TDF richer soils), in addition to be thinner and less tough. Based on current knowledge, this discussion is still incipient, but our results, together with the recent evidence cited, draw attention to possible relationships between the past occupancy patterns of large herbivores mammals and the vegetation patterns in South America as well, especially in the Tropical Dry Forests. More studies are need to better clarify the questions related.

4.2 Resprouting within and across lineages: phylogenetic signal

Contrary to what we expected, we found there is no phylogenetic signal for resprouting variables above the genus-level: evolutionary relationships of lineages do not imply an ecological similarity in terms of resprouting strategies and sister lineages can have contrasting resprouting expression (e.g., the euphorbiaceae genera *Jatropha* and *Croton*). Resprouting ability is likely a result of the different local restrictive factors (e.g., fire, water stress, flood) to which individuals of these genera and their constituent species

have undergone throughout their evolutionary history (Bond & Midgley, 2003; Nzunda et al., 2007; Pausas & Keeley, 2014; Vesk & Westoby, 2004). Although heritability can be an important driver of intrinsic trait values (Coelho de Souza et al. 2016; Fyllas et al. 2009), it would appear that closely related genera may have experienced different selective pressures throughout their evolutionary history, to which they responded with different resprouting patterns. For example, some genera also occur in the Cerrado savannas, in Atlantic semideciduous forests and in the different vegetation types within the Caatinga domain, all of which have different environmental filters (Aguiar-Campos et al., 2020; Moro et al., 2014; Santos et al., 2012; Souza et al., 2019). In contrast, distantly related lineages may have experienced similar selective pressures and converged to similar resprouting patterns. In addition, because resprouting is controlled by a linked set of complex traits and physiological processes (such as a dispersal syndrome), variations in resprouting expression must involve a number of evolutionarily integrated changes and also be influenced by other traits related to reseeding, which is the direct ecological alternative strategy (Bond & Midgley, 2003; Lamont et al., 2011; Pausas & Keeley, 2014; Pausas et al., 2016).

Our conclusions require a note of caution due to an incomplete phylogeny; many genera in our study have relatives that occur outside our study region and were not included. We emphasize that we only considered the final expression of resprouting by the presence of multi-stemmed trees, which could stem from different sets of traits according to different environmental restrictions endured by the individuals that display it (Bond & Midgley, 2003; Pausas & Keeley, 2014). Therefore, these interpretations cannot be directly extended to other resprouting-related traits, given that the final expression of this strategy may owe to several functional patterns (Bond & Midgley, 2003; Pausas et al., 2016).

4.3 General implications

The response of tropical dry forests to observed and predicted climate change scenarios of increased aridity, consecutive years of prolonged droughts and variation in annual precipitation (Allen et al., 2017; IPCC, 2014) are and will be complex. Resprouting is an important immediate strategy to avoid mortality, but carries a cost of mobilizing stored resources to grow new shoots, which could jeopardize other vital functions related to growth and reproduction (Moreira et al., 2012; Schwilk & Ackerly, 2005). However, as resprouting is repeatedly used as a persistence strategy, stored

540 resources may become scarce and the possibility of emitting new shoots and the
541 individual's capacity to endure water stress may be compromised (Pausas et al., 2016).
542   Our study begins to address the need to build knowledge on ecological resprouting
543 patterns in fire-free environments, especially those subject to extreme dry periods.
544 Resprouting is currently an important strategy in these drought-prone plant communities
545 and may have been more in the past. Investigating how it manifests in communities
546 contributes to a better understanding of present-day ecosystem function and future
547 responses to ongoing climate change. In scenarios of climate changes, resprouting may
548 become a more common strategy in communities subjected to extreme or long-term
549 droughts and be an important part of ecosystems ecological responses.
550

557 **CONFLICT OF INTEREST**
558 The author declares that there is no conflict of interest.
559

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870   **Tables**

871

872   **Table 1:** Results for GLMM models for each resprouting variable evaluated: average

873   stems per tree and resprouting frequency. The results are for the global model (1), global

874   model not including fixed variables (2), global model not including sampling effects (3)

875   and global model not including taxonomic effects (4). Delta AICc (Δ AICc) refers to the

876   comparison between the global models and for the options accounting for relative

877   influence of each factor considered.

Model	Average stems per tree		Resprouting frequency	
	AICc	Δ AICc	AICc	Δ AICc
(1) Global model (GM)	44206.3	-	47333	-
(2) GM - fixed effects	44200.5	5.8	47358.9	-25.9
(3) GM - sampling effects	44417.9	-211.6	47374.2	-41.2
(4) GM - taxonomic effects	45746.5	-1540.2	48098.5	-765.5

878

879

880 **Figures legend**

881

882 **Figure 1:** Location of 16 tropical dry forests (TDF) plots in the states of Minas Gerais

883 (MG) and Bahia (BA), Brazil. Position of the sites relative to South America and

884 Brazilian biogeographic regions (official boundaries) are also shown.

885

886 **Figure 2**: Distribution curves of resprouting frequency values and average stems per tree

887 for species and genera evaluated in 16 tropical dry forests, with taxa colored according to

888 our k-means partitioning of resprouting frequency classes.

889

890 **Figure 3:** Proportion of resprouting frequency categories in the total number of taxa,

891 trees, stems and aboveground woody biomass (AGWB) in 16 fragments of tropical dry

892 forests, calculated for when genera are categorized (left-hand panel) or when species are

893 categorized (right-hand panel). The term "taxa" refers to species or genus taxonomic

894 levels, presenting the number of species or genus in each category.

895

896 **Figure 4:** Coefficient of determination (R^2`) of fixed and random effects in the global

897 model (a); and variance partitioning analysis of sampling (plot and subplot) and taxonomy

898 (family, genus and species) effects within the random effects (b) for number of stems *per*

899 tree and resprouting frequency recorded in 16 fragments of tropical dry forests.

900

901 **Figure 5:** Phylogeny of 111 tropical dry forest tree genera with branches colored

902 according to number of stems *per* tree. Note that the number of genera represented here

903 is lower than the total number used in classification, since 3 genera were not present in

904 the phylogenetic tree.

905

906 **Figure 6** Phylogeny of 111 tropical dry forest tree genera with branches colored

907 according to resprouting frequency. Note that the number of genera represented here is

908 lower than the total number used in classification, since 3 genera were not present in the

909 phylogenetic tree.