Journal of
Plant Ecology

Protection status as determinant of carbon stock drivers in Cerrado *sensu stricto*

Kelly Marianne Guimarães Pereira[1,*,†], Natielle Gomes Cordeiro[2,†], Marcela de Castro Nunes Santos Terra[2], Marcela Venelli Pyles[1], Christian Dias Cabacinha[3], José Márcio de Mello[2] and Eduardo van den Berg[2]

[1]Department of Biology, Federal University of Lavras, Campus Universitário, CEP 37200-000, Lavras, Minas Gerais state, Brazil, [2]Department of Forest Sciences, Federal University of Lavras, Campus Universitário, CEP 37200-000, Lavras, Minas Gerais state, Brazil, [3]Department of Forest Sciences, Institute of Agrarian Sciences, Federal University of Minas Gerais, Campus Regional de Montes Claros, CEP 39.404-547, Montes Claros, Minas Gerais state, Brazil

*Corresponding author. E-mail: kellyguimaraes10@gmail.com
†These authors contributed equally to this work.

Handling Editor: Asko Noormets

Received: 28 September 2019, **Revised:** 18 April 2020, **Accepted:** 19 May 2020**, Advanced Access publication:** 25 May 2020

Citation: Pereira KMG, Cordeiro NG, Terra MCNS, *et al.* (2020) Protection status as determinant of carbon stock drivers in Cerrado *sensu stricto*. *J Plant Ecol* **13**:361–368. https://doi.org/10.1093/jpe/rtaa024

Abstract

Aims Natural vegetation plays an important role in global carbon cycling and storage. Thus, the Cerrado (Brazilian savannah) is considered a carbon sink because of its intrinsic characteristics. Our aim was to evaluate how the aboveground biomass and biodiversity relationship change between three Cerrado remnants with different protection status: a 'control area' (Legal Reserve area), a protected area (PA) and a non-protected area (Non-PA).

Methods All three studied fragments are situated in northern Minas Gerais state, Brazil. We estimated the aboveground carbon stocks based on the forest inventory. We also measured three dimensions of biodiversity metrics for each plot: functional trait dominance, taxonomic diversity and functional diversity. The following functional traits were evaluated for the species: wood density, maximum diameter and seed size. We carried out generalized linear models seeking to evaluate how carbon stocks, community-weighted mean (CWM) trait values, species richness and diversity, and functional diversity indices differ among the remnants.

Important Findings The Cerrado areas without protection status had lower carbon stocks, species richness, species diversity, functional richness and functional dispersion, whereas both PA and Non-PA had lower CWM maximum diameter and seed size compared with the Legal Reserve control area. Generalized linear models showed that carbon stocks, species and functional richness metrics were correlated within and across sites, and thus, species richness could serve as a good proxy for functional richness and carbon stocks. The carbon stocks were positively driven by species richness and CWM maximum diameter, while they were negatively driven by functional dispersion. Functional richness, species diversity and CWM seed size appeared in the set of best models, but with no significant direct effect on carbon stocks. Thus, we concluded that absence of protection in the Cerrado areas decreases both species richness and carbon stocks.

Keywords: functional traits, biodiversity, biomass storage, Brazilian Savanna, human impacts

摘要：天然植被在全球碳循环和碳储存中扮演着重要角色。巴西大草原塞拉多保护区(Cerrado)因自身固有特性被认为是一个碳汇。本研究的目的是评估具有不同保护状况的三个地区，控制区(法定保护区)、保护区(PA)和非保护区(Non-PA)地上生物量与生物多样性关系的变化。这三个被研究的地区都位于巴西米纳斯吉拉斯州(Minas Gerais)北部。根据森林清查资料，该研究对地上碳储量进行了估算，并测量了每个地区生物多样性指标的三个维度：功能性状优势度、分类学多样性和功能多样性。对物种的以下功能性状进行了评价：木材密度、最大直径和种子大小。通过建立广义线性模型，评估了碳储量、群落加权平均值、物种丰富度和多样性以及功能多样性指数在不同地区间的差异。研究结果表明，未受保护的地区碳储量、物种丰富度、物种多样性、功能丰富度和功能分散度均较低，而保护区和非保护区群落加权平均值

最大直径和种子大小均低于法定保护区。广义线性模型结果表明，碳储量与物种和功能丰富度指数在同一地区内和不同地区间存在相关性，因此，物种丰富度可以作为功能丰富度和碳储量的替代指标。物种丰富度和群落加权平均值最大直径对碳储量有正向影响，功能分散度对碳储量有负向影响。功能丰富度、物种多样性和群落加权平均值种子大小出现在最佳模型中，但对碳储量没有显著的直接影响。因此，我们的结论是，在缺乏保护的巴西塞拉多地区会降低物种丰富度和碳储量。

关键词：功能性状，生物多样性，生物量储存，巴西大草原，人类影响

INTRODUCTION

Natural vegetation plays an important role in global carbon cycling and storage since this is one of the most important ecosystem services related to climate change (Locatelli *et al.* 2015; Saatchi *et al.* 2011). Considering the carbon stock relevance, it is fundamental to know the mechanisms which conduct its storage. In this way, most of our knowledge on the relationships between different drivers of biomass storage and productivity in the tropics were conducted in moist and wet forests (Finegan *et al.* 2015). This question is particularly obscure for Cerrado regions (the Brazilian savannah), for which the studies are scarcer in comparison to tropical forests (Nunes *et al.* 2017).

Carbon storage and other ecosystem functions and services have been found to be positively correlated with species, diversity and composition in tropical ecosystems (Díaz *et al.* 2016; Kunstler *et al.* 2016; Silveira *et al.* 2019b; Tilman *et al.* 2014). This assumption is due to the fact that some species have higher carbon stocking than others, being explained by their density, diameter and height (Borah *et al.* 2015). Two main (and somehow self-excluded) hypotheses have been proposed to explain how biodiversity might influence ecosystem functions/services such as carbon storage: (i) the niche complementarity hypothesis, which states that higher levels of biodiversity lead to greater carbon storage due to more efficient resource use; and (ii) the mass ratio hypothesis, which holds that carbon storage is mostly driven by functional trait properties of the dominant species, thus pointing out the importance of species composition and the species relative importance in the communities (Loreau and Hector 2001). Functional diversity metrics have been extensively used to assess this issue (Mensah *et al.* 2016; Wu *et al.* 2017), since functional diversity has been proven to explain primary productivity better than species richness (Ruiz-Benito *et al.* 2014).

Although many studies have investigated both vegetation carbon stock and biodiversity for the tropical region, the focus of most previous studies has been on global and continental scales and for tropical rainforests (e.g. Djuikouo *et al.* 2010; Labrière *et al.* 2016; Murray *et al.* 2015). For open-vegetation ecosystems, studies show that total woody plant species diversity seems to increase carbon storage, but the richness of endemic savannah woody plant species seems to reduce carbon storage (Pellegrini *et al.* 2016). Other studies in Cerrado vegetation have indicated that there are positive relationships between plant functional composition, functional diversity and productivity at the plot scale level (Morandi *et al.* 2018). However, more studies are required to better understand the relationship between carbon stock and biodiversity, since tropical savannahs have been increasingly viewed as an opportunity for carbon sequestration (Miranda *et al.* 2014; Ribeiro *et al.* 2011), but insufficient attention has been given to their biodiversity. This is important because, even though many vegetation conservation efforts have been carbon-focused (i.e. 'Reducing Emissions from Deforestation and Forest Degradation, plus the sustainable management of forests' Programme—REDD+; FAO 2018), or biodiversity-focused, it can be mutually beneficial (Silveira *et al.* 2019a). This fact can be inferred because carbon stock and biodiversity generally show a positive correlation (Abreu *et al.* 2017).

In this context, one of the main questions associated with vegetation carbon stock and diversity is how both community features and their relationships are affected by disturbances. For instance, Ferreira *et al.* (2018) found that carbon–biodiversity relationships for rainforest ecosystems (Amazon) strongly depend on disturbance intensity. These authors found that carbon and biodiversity were not statistically associated in forests with higher carbon stock (the most species rich forests), whereas they were strongly and positively related where carbon levels fell below around 100 Mg ha^{-1}. However, this question remains unanswered for open-vegetation ecosystems such as Cerrado.

The Cerrado covers approximately 2 million km^2, forming a mosaic of many physiognomies including grasslands, woodlands, rupestrian grasslands and riparian forests, comprising a complex and heterogeneous landscape (Klink and Machado 2005). The Brazilian Cerrado is the world's richest savannah, harboring 30% of the Brazilian species richness (Lahsen *et al.* 2016), with high levels of endemism, being considered one of the world's biodiversity hotspots (Forzza *et al.* 2010; Myers *et al.* 2000). Cerrado is able to retain large amounts of carbon (Grace *et al.* 2006). For instance, Scolforo *et al.* (2015) estimated an aboveground carbon stock of 21.6 Mg ha^{-1} in central and northern Minas Gerais state, where there is predominance of Cerrado (Terra *et al.* 2017). These numbers are even more expressive if we consider the large belowground carbon stock of the Cerrado (Durigan *et al.* 2012; Fidelis *et al.* 2013).

The Cerrado is currently highly threatened with substantial loss of natural cover every year (Myers *et al.* 2000), mainly associated to the increase of cropland and pastures associated to the flourishing Brazilian agribusiness. Espírito-Santo *et al.* (2016) detected extensive landcover changes from 2000 to 2015 in the Cerrado of northern Minas Gerais state, in Brazil, with a net loss of 9520 km^2. Silveira *et al.* (2019a) found the Cerrado biomass loss between 2007 and 2017 as reaching the amount of 16 549 138 Mg only in MG state, Brazil. The fact that Cerrado legal protection is low compared with Brazilian forest biomes is worsening this scenario even more (Marris 2005).

Therefore, our aim was to evaluate how the aboveground biomass (AGB) and biodiversity relationship change between three Cerrado remnants with different protection statuses: a 'control area' (Legal Reserve area free of impacts), a protected area (PA) and a non-protected area (Non-PA). We address the following questions in our analysis: (i) How does the protection status affect the amount of carbon stocked and the biodiversity metrics (species and functional) of Cerrado? and (ii) How is the relationship between the parameters (tree abundance, species richness, species diversity, functional richness, functional dispersion, community-weighted mean (CWM) maximum diameter, CWM wood density and seed size) and carbon stocks affected by protection status in Cerrado? We expected: (i) the protection of the area to increase taxonomic and functional diversity resulting in larger carbon stocks; and (ii) functional traits have greater influence on the carbon stock than taxonomic attributes.

MATERIALS AND METHODS

Study area and sampling

We conducted this study in three Cerrado *sensu stricto* fragments in northern Minas Gerais state, Brazil (Fig. 1). The region is characterized by a warm and dry tropical semi-arid climate (Aw Megathermic climate of Köppen). The mean annual precipitation is 1060 mm and the mean annual temperature is 24°C. The soil classification is generally Latosols and Cambisol (Alvares *et al.* 2013).

Two of the Cerrado fragments are located within an urban landscape in Montes Claros city, MG. One of them (Non-PA) is located in the Institute of Agrarian Sciences (ICA) of the Federal University of Minas Gerais (UFMG) (−43.862512° Lon; −16.682959° Lat) (Supplementary Fig. S1-A) and the other fragment (PA) is situated in the Lapa Grande State Park (−43.949710° Lon; −16.732959° Lat) (Supplementary Fig. S1-B). Both areas (Non-PA and PA) had farming activities in the past resulting in the presence of exotic plant species such *Brachiaria* spp. Moreover, these remnants had animal circulation such as free-ranging cattle, which impacted the vegetation. Nonetheless, the PA became a strictly PA since 2006, achieving a protection status with no further impacts after 2006 (Minas Gerais 2006). Considering the PA protection status, the vegetation is in advanced regeneration stage. On the other hand, the Non-PA became a designated area for research and studies in the same. Thus, the Non-PA is still suffering impacts, such as walking trails, movement of people and animals, garbage and selective logging. Given the characteristics of the Non-PA area, the vegetation is in an earlier successional stage. Regarding the control area (Control), the data are from the Inventory of Minas Gerais. This area is situated in Itacambira city—MG (−43.2652788° Lon; −16.9164859° Lat) (Supplementary Fig. S1-C), which is configured as a Legal Reserve according to the Forest Brazilian Code (Brazil 2012), and it is classified as non-anthropized vegetation (Scolforo *et al.* 2008). Therefore, the control area is a legal-protected long-term Cerrado fragment which has been free of impacts and holds a great amount of carbon stock.

We sampled 25 plots (20 m × 20 m) totaling 1 ha in the PA, and the same amount in the Non-PA. Furthermore, 22 plots were used to sample the vegetation (10 m × 100 m) in the control area, totaling 2.2 ha. All trees with diameter at 1.30 m above the ground (DBH) ≥5 cm were measured in each area. Total height of these arboreal individuals was also registered at this moment. All sampled trees had botanical material collected, which were identified at the species level according to literature and with the aid of specialists (Silva-Júnior 2012), as well as classified according to the APG IV (APG 2016).

Carbon estimates

We estimated the aboveground carbon stocks (Mg ha^{-1}) through the allometric equation developed for the Brazilian savannah vegetation (Scolforo *et al.* 2008) which was applied to all individual trees present in the plots. The equation considers the diameter at breast height (DBH ≥5 cm) and tree height (m):

$$C:\ e^{(-11.23+2.37\mathrm{Ln(DBH)}+0.67\mathrm{Ln(Ht)})}\quad (R^2:\ 97.08\%\ \ \mathrm{Syx}:\ 39.45\%)$$

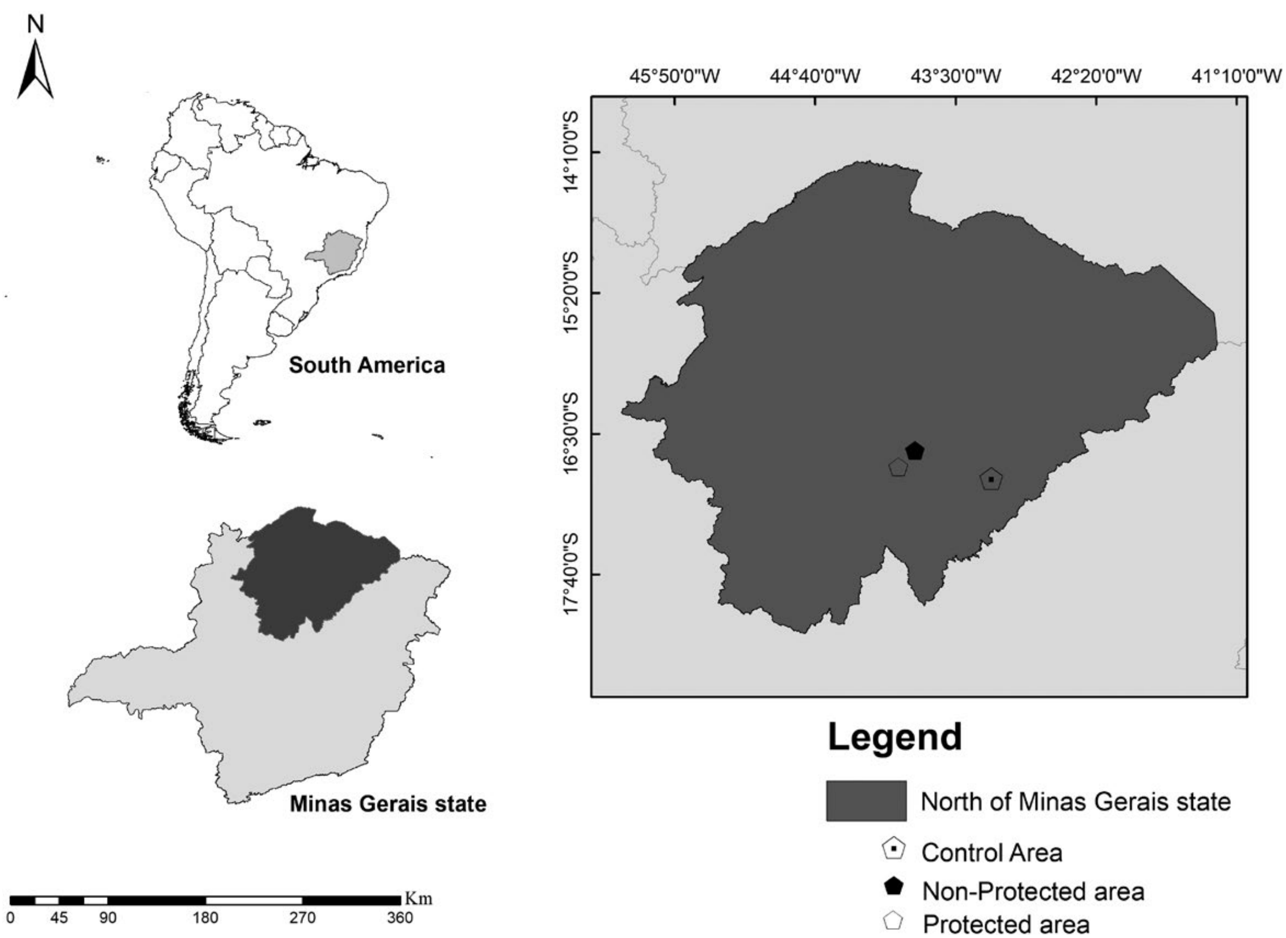

Figure 1: Study areas location into the Cerrado *sensu stricto* in the north of Minas Gerais state, Brazil.

where C = aboveground carbon stock (Mg ha^{-1}); e = base of the natural logarithm; ln = natural logarithm; DBH = diameter measured at 1.30 m above the ground (cm); Ht = total height (m); R^2 = coefficient of determination; Syx = residual standard error.

Biodiversity metrics

We measured three dimensions of biodiversity in each plot: functional trait dominance, taxonomic diversity and functional diversity. Functional traits were chosen based on their relation to the carbon stock potential of the species: wood density, maximum diameter and seed size. Species wood density (WD, g cm^{-3}) was obtained from the Global Wood Density database (filtered by Tropical South America, Zanne *et al.* 2009), while the maximum diameter was calculated as the 95th-percentile diameter of all trees of the species. The seed size is related to the physiological and morphological traits, life history trait and competitive vigor of the seedlings (Kitagima 2007; Osuri and Sankaran 2016; Poorter and Rose 2005; Prado-Júnior *et al.* 2016). Thus, the seed size was obtained from herbarium specimens, which were classified in small seeds species (seed c ≤1.5 cm) and large seeds species (length between ≥1.6 cm), following Tabarelli and Peres (2002) and Santos *et al.* (2008).

We subsequently calculated species richness (S, number of species per plot) and Shannon diversity (H', which incorporates species abundances) (Supplementary Table S3) for the taxonomic diversity analysis. We also calculated functional richness (FRic, a non-abundance-weighted index) and functional dispersion (FDis, an abundance-weighted index) (Petchey and Gaston 2002; Villéger *et al.* 2008) for functional diversity.

Lastly, we calculated the CWM trait values per plot using the 'FD' package (within the R) (Laliberté *et al.* 2015), which is considered the functional composition by the relative abundance of the species for each dynamic period and for each plot.

Data analyses

We performed generalized linear models followed by Tukey's *post hoc* test to evaluate how carbon stocks, CWM trait values, species richness and diversity, and functional diversity indices differ among areas (Control, PA and Non-PA). We fitted the generalized linear model (GLM) with Gamma family and 'log' link for carbon stocks, due to its positively skewed distribution. We also used a quasi-Poisson generalized linear model for species richness, and the models were fitted using a Gaussian error distribution with identity link function (normality was tested and confirmed by the Shapiro–Wilk test) for the other variables.

We accessed the relative importance of the different carbon drivers in Cerrado fragments with and without protection status, relating carbon stocks to species and functional diversity metrics (S, H', FRic and FDis) and CWM trait values (CWMdmax, CWMwd and CWMss), by using the following generalized linear model: $Cp,cs \sim \beta 0 + PS^{*} (\beta 1 Ni + \beta 2 S + \beta 3 H' + \beta 4 FRic + \beta 5 FDis + \beta 6 CWM_{Dmax} + \beta 7 CWM_{WD} + \beta 8 CWM_{SS})$, in which Cp,cs is the carbon per plot in areas with or without protection status; $\beta 0$ is the average carbon stocks (model-intercept for all plots); PS is the protection status of vegetation (with or without protection status) with interaction with all other fixed terms; β is the standardized coefficient of each fixed factor; S, H', FRic and FDis are species richness, Shannon diversity index, functional richness and functional dispersion, respectively, and CWMdmax, CWMwd and CWMss (which was calculated according to the size class) are the CWM trait values for species maximum diameter, wood density and seed size, respectively.

We then ranked the best set of models among all possibilities based on Akaike Information Criterion of the Second Order (AICc), considering those with ΔAICc <2 as equally supported (Burnham and Anderson 2002). Next, we used a model-averaging approach to estimate averaged coefficients from these set of candidate models, which represent the sum of the product of the parameter estimates in each model with the weight of the associated model (Vierling *et al.* 2013). The relative importance of each predictor (models fixed factors) was assessed by comparing their standardized coefficients (β). All models are shown in Supplementary Tables S1 and S2.

The analyses were performed using platform R software (R Core Team 2017) and the following packages: multcomp (Hothorn *et al.* 2008), lme4 (Bates *et al.* 2015), lmerTest (Kuznetsoza *et al.* 2017), MuMIn (Barton 2019) and ggplot2 (Wickham 2016).

RESULTS

Effect of protection status on vegetation attributes and carbon stocks

The Cerrado areas (considered as protected and non-protected) presented differences in relation to the vegetation attributes found in the control area. Maximum diameter, seed size, taxonomic richness and diversity and functional richness and dispersion were lower in the non-protected Cerrado area. Only maximum diameter and seed size had lower values than the control area in the PA, while taxonomic richness of species showed a higher value than that found in the control area (Fig. 2).

We did not detect differences between the control and PA regarding carbon stocks. A lower value was conversely found in the Non-PA. The carbon stocks in the control area vegetation were 10.38 ± 1.86 Mg ha^{-1} (average ± standard error) and 11.82 ± 1.98 Mg ha^{-1} in the PA, while they were 2.20 ± 0.353 Mg ha^{-1} in the Non-PA.

Effect of vegetation protection status on vegetation carbon drivers

Generalized linear models indicated that the carbon stock drivers in the Cerrado are not related to previous use or to the protection status of the area. The same vegetation attributes drive carbon stocks in the control area, PA and Non-PA. No interaction between attributes and protected status appeared in the set of best models (Fig. 3). The carbon stocks were positively driven by species richness (standardized regression coefficient β = 0.882, P-value = <0.001) and by CWM maximum diameter (β = 0.544, P-value = <0.001), while they were negatively affected by functional dispersion (β = −0.270, P-value = <0.05). Functional richness, species diversity and CWM seed size appeared in the set of best models, but with no significant direct effect on carbon stocks.

DISCUSSION

We looked at how protection status affects the vegetation attributes and to what extent these attributes drive the carbon stocks of the Cerrado. We showed that protections applied to the reforested PA area seemed to have led to biodiversity and carbon stocks values close to those of the control area and further way from the Non-PA. In contrast, recovery of the non-protected reforested area had very low diversity values and carbon stock. Even under such different conditions, we found that the protection status did not change the main correlates of carbon stocks. Thus, we concluded that protecting Cerrado areas is a very effective way to guarantee of biodiversity and carbon stock return in Cerrado areas, even in short time periods. We also verified that both the niche complementarity (supported by species diversity driver) and the biomass ratio (supported by functional dispersion) simultaneously drive the carbon stocks of the Cerrado.

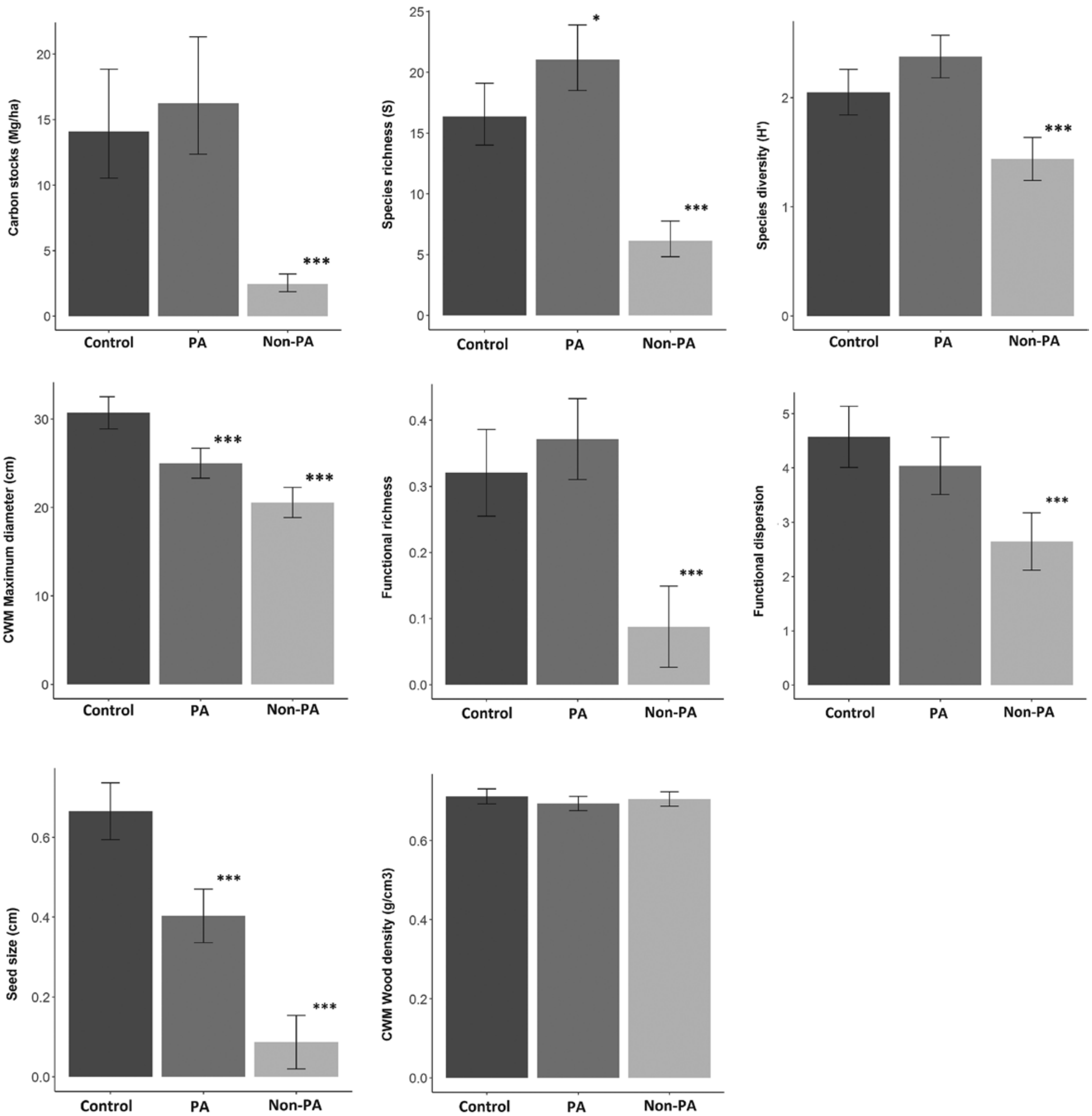

Figure 2: Effect of protection status on the amount of carbon stocked and the biodiversity metrics. Control is the control area. The asterisks are significantly different at $P < 0.01$, as per Tukey's test after GLM. Errors bars represent the 95% of confidence intervals.

Relationship between protection status and biodiversity metrics and carbon stocks

We found similar biodiversity metrics and carbon stock values for the control area and the PA. A significant difference was only found for the species richness, seed size and Dmax. All biodiversity metrics and carbon stocks were significantly lower in the Non-PA than the other two sites, with the exception to wood density.

Higher carbon stocks in PAs are expected. This is explained by the fact that PAs are less susceptible to disturbances such as logging, having a greater density of trees and consequently a higher basal area (Fuller *et al.* 2015; Lohbeck *et al.* 2015). They also have higher resource availability and the ecological processes are more prone to have their equilibrium related to microclimate, soil quality, light intensity and forest dynamics (García-Llorente *et al.* 2018; Pelletier *et al.* 2017).

On the other hand, human disturbances in Non-PAs cause lower biomass and carbon stock, as well as lower species diversity, total height, diameter and functional diversity (Calgaro *et al.* 2015; Diniz *et al.* 2010; Giroldo and Scariot 2015). Both anthropogenic interferences and natural disturbances affect carbon stock (Nunes *et al.* 2017). Human-induced carbon loss leads to a reduction in the potential of providing ecosystem services. For instance, tree carbon in agricultural landscapes, such as in the study region, play an important role in mitigating climate change (Zomer *et al.* 2016) and therefore deforestation of such areas could actually contribute to worsening global warming.

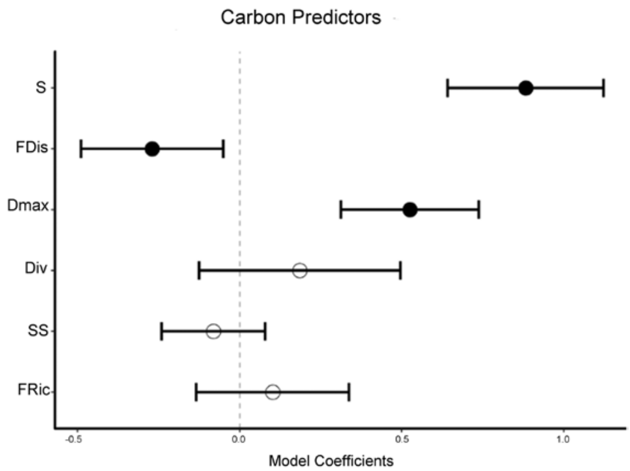

Figure 3: Relationship between biodiversity metrics and carbon stocks. *S* = species richness, FDis = functional dispersion, Dmax = maximum diameter, Div = species diversity, SS = seed size, FRic = functional richness. The full circles are the variables that were significant for the best models and the empty circles are the non-significant variables.

The PA generally showed a higher carbon stock and greater biodiversity metrics when compared with the control area and Non-PA. This is significant considering the short period of area protection (8 years). This relatively fast recovery from past disturbances highlights the resilience of such ecosystems. For instance, in studying Cerrado vegetation in a period of 4 years after a fire event, Gomes *et al.* (2014) detected a higher recruitment than mortality and basal area increment, showing the area to have recovered quickly after the fire event. Nevertheless, in studying 11 Cerrado fragments and their relationship with different disturbance levels, Carmo *et al.* (2011) found that the Cerrado structure is affected by interventions resulting in basal area and biodiversity losses.

The resilience potential of each area certainly depends on the type, magnitude and frequency of disturbances, as well as the ecosystem characteristics prior to the disturbances (Buma and Wessman 2011; Murphy and Romanuk 2014; Souza *et al.* 2011); however, the present PA seemed to have recovered its attributes very quickly.

Carbon stock drivers

We found the same carbon drivers in the study areas, independently of their protection status. This result corroborates previous studies of Cerrado (Loiola *et al.* 2015; Prado-Júnior *et al.* 2016) and also for other types of vegetation (Cavanaugh *et al.* 2014; Finegan *et al.* 2015; Pyles *et al.* 2018; Ziter *et al.* 2013). Species richness and Dmax positively drove the carbon stock in the study areas. Considering forest environment the relation between species richness and carbon stocks has generally been shown as positive, meaning that the greater the species richness the greater carbon stock (Cavanaugh *et al.* 2014; Shirima *et al.* 2015; Strassburg *et al.* 2010; Sullivan *et al.* 2017). Regarding Cerrado vegetation, some studies found an opposite relationship, which means that lower richness implies in a greater carbon stock (Abreu *et al.* 2017; Morandi *et al.* 2018). It is noted that this relation can vary in some cases according to the area size (Pellegrini *et al.* 2016). Furthermore, a decrease in plant and ant biodiversity was observed with a carbon increase (Abreu *et al.* 2017; Honda and Durigan 2016). On the other hand, some studies have shown the same relationship found in our study (Poulain *et al.* 2010). A positive relationship between diversity and carbon stock can be explained by the niche complementarity effect, meaning that a higher niche occupation linked to a higher number of present species (Rodríguez-Alarcón *et al.* 2018) make better use of the resources, resulting in a greater carbon stock (Lohbeck *et al.* 2015, 2016).

Regarding Dmax, Cavanaugh *et al.* (2014) found a positive relationship between the carbon stock amount and trees with greater diameters. It is expected that trees with greater diameter and total height have larger biomass and consequently a greater quantity of carbon (Ali and Yan 2017; Prado-Júnior *et al.* 2016). Therefore, protection can enable trees to reach larger dimensions, and hence stock more carbon when compared with disturbed areas, where the trees are younger and smaller. Thus, old growth vegetation remnants which have lower disturbance incidence have the capacity to stock a greater amount of carbon (Arasa-Gisbert *et al.* 2018).

Functional dispersion is defined as the mean distance of each taxon to the centroid of all taxon from the community when considering the relative abundance (Laliberté and Legendre 2010). This metric had a negative effect on carbon stocks in our study, showing that the greater the functional similarity among the most abundant species, the greater the carbon stocks in the community. Thus, the dominance of species with traits related to stand biomass volume should be more important than the functional differentiation between species (Conti and Díaz 2013; Pyles *et al.* 2018). Conversely, the higher the functional dispersion, the higher the presence of trees with characteristics which do not contribute to carbon stocking will be (Ribeiro *et al.* 2017; Ziter *et al.* 2013).

CONCLUSIONS

We showed that protection status correlated with species richness, functional richness and carbon stocks in Brazilian Cerrado. The metrics were correlated with one another across locations, suggesting a mechanistic relationship, and that species richness could serve as a good proxy for quick carbon stock assessment. However, given that this study was unreplicated, the representativeness of the findings should be evaluated more broadly.

Carbon stock was found most strongly related to functional dispersion and maximum diameter. These parameters allow to infer about the niche complementarity which indicates that the arboreal community has a significant number of species with different function at the ecosystem. Our results point out that conservation strategies which reduce human impact and stimulate biodiversity gain and tree growth, especially protecting survival of large individuals, are the best choices for maintaining regional carbon stock.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Table S1: Generalized linear models for the relationship between study areas, AGB (aboveground biomass) and forests attributes.

Table S2: The standardized effect of variables included in each of the top twenty models (M1–M20) for estimating aboveground carbon stock.

Table S3: Taxonomic diversity metrics from the Cerrado *sensu stricto* fragments in the northern Minas Gerais state, Brazil.

Figure S1: Limits of the studied fragments in the northern Minas Gerais state, Brazil.

Funding

This study was partly financed by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brasil (CAPES)—Finance Code 001.

Acknowledgements

We express our gratitude to the Institute of Agrarian Sciences, Federal University of Minas Gerais (UFMG), the State Forest Institute (IEF Minas Gerais) and the Federal University of Lavras (UFLA) for the support and infrastructure to develop of the study.

Conflict of interest statement. The authors declare no conflicts of interest.

REFERENCES

Abreu RCR, Hoffmann WA, Vasconcelos HL, *et al.* (2017) The biodiversity cost of carbon sequestration in tropical savanna. *Sci Adv* **3**:e1701284.

Ali A, Yan E (2017) Functional identity of overstorey tree height and understorey conservative traits drive aboveground biomass in a subtropical forest. *Ecol Indic* **83**:158–68.

Alvares CA, Stape JL, Sentelhas PC, *et al.* (2013) Köppen's climate classification map for Brazil. *Meteorol Z* **22**:711–28.

APG (2016) An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APG IV. *Bot J Linn Soc* **181**:1–20.

Arasa-Gisbert R, Vayreda J, Román-Cuesta RM, *et al.* (2018) Forest diversity plays a key role in determining the stand carbon stocks of Mexican forests. *For Ecol Manage* **415–416**:160–71.

Barton K (2019) *MuMIn: Multi-Model Inference*. https://cran.r-project.org/package=MuMIn (2 January 2019, date last accessed).

Bates D, Mächler M, Bolker BM, *et al.* (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* **67**:1–48.

Borah M, Das D, Kalita J, *et al.* (2015) Tree species composition, biomass and carbon stocks in two tropical forest of Assam. *Biomass Bioenerg* **78**:25–35.

Buma B, Wessman CA (2011) Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere* **2**:1–13.

Burnhan KP, Anderson DR (2002) *Model Selection and Multimodel Inference.* 2nd edn. New York, NY: Springer-Verlag.

Calgaro HF, Buzetti S, Silva LR, *et al.* (2015) Distribuição natural de espécies arbóreas em áreas com diferentes níveis de antropização e relação com os atributos químicos do solo. *Rev Árvore* **39**:233–43.

Carmo AB, Vasconcelos HL, Araújo GM (2011) Estrutura da comunidade de plantas lenhosas em fragmentos de cerrado: relação com o tamanho do fragmento e seu nível de perturbação. *Rev Bras Bot* **34**:31–8.

Cavanaugh KC, Gosnell JS, Davis SL, *et al.* (2014) Carbon storage in tropical forests correlates with taxonomic diversity and functional dominance on a global scale. *Glob Ecol Biogeogr* **23**:563–73.

Conti G, Díaz S (2013) Plant functional diversity and carbon storage—an empirical test in semi-arid forest ecosystems. *J Ecol* **101**:18–28.

Díaz S, Kattge J, Cornelissen JH, *et al.* (2016) The global spectrum of plant form and function. *Nature* **529**:167–71.

Diniz S, Prado PI, Lewinsohn TM (2010) Species richness in natural and disturbed habitats: Asteraceae and Flower-head insects (Tephritidae: Diptera). *Neotrop Entomol* **39**:163–71.

Djuikouo MNK, Doucet J, Nguembou CK, *et al.* (2010) Diversity and aboveground biomass in three tropical forest types in the Dja Biosphere Reserve, Cameroon. *Afr J Ecol* **48**:1053–63.

Durigan G, Melo ACG, Brewer JS (2012) The root to shoot ratio of trees from open- and closed-canopy cerrado in south-eastern Brazil. *Plant Ecol Divers* **5**:333–43.

Espírito-Santo MM, Leite ME, Silva JO, *et al.* (2016) Understanding patterns of land-cover change in the Brazilian cerrado from 2000 to 2015. *Philos Trans R Soc B Biol* **371**:20150435.

FAO (2018) From reference levels to results reporting: REDD+ under the UNFCCC 2018 update. Rome, Italy: Food and Agriculture Organization of the United Nations (FAO), p. 38.

Ferreira J, Lennox GD, Gardner TA, *et al.* (2018) Carbon-focused conservation may fail to protect the most biodiverse tropical forests. *Nat Clim Change* **8**:744–9.

Fidelis A, Lyra MFS, Pivello VR (2013) Above- and below-ground biomass and carbon dynamics in Brazilian Cerrado wet grasslands. *J Veg Sci* **24**:356–64.

Finegan B, Peña-Claros M, Oliveira A, *et al.* (2015) Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. *J Ecol* **103**:191–201.

Forzza RC, Baumgratz JFA, Bicudo CEM, *et al.* (2010) Síntese da Diversidade Brasileira. In Forzza RC, Leitman PM, Costa A, *et al.* (eds). *Catálogo de Plantas e Fungos Do Brasil.* Rio de Janeiro, Brazil: Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, 21–43.

Fuller MR, Doyle MW, Strayer DL (2015) Causes and consequences of habitat fragmentation in river networks. *Ann N Y Acad Sci* **1355**:31–51.

García-Llorente M, Harrison PA, Berry P, *et al.* (2018) What can conservation strategies learn from the ecosystem services approach? Insights from ecosystem assessments in two Spanish protected areas. *Biodivers Conserv* **27**:1575–97.

Giroldo AB, Scariot A (2015) Land use and management affects the demography and conservation of an intensively harvested Cerrado fruit tree species. *Biol Conserv* **191**:150–8.

Gomes L, Maracahipes L, Marimon BS, *et al.* (2014) Post-fire recovery of savanna vegetation from rocky outcrops. *Flora* **209**:201–8.

Grace J, José JS, Meir P, *et al.* (2006) Productivity and carbon fluxes of tropical savannas. *J Biogeogr* **33**:387–400.

Honda EA, Durigan D (2016) Woody encroachment and its consequences on hydrological processes in the Savannah. *Philos Trans R Soc B Biol* **371**:1–9.

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biom J* **50**:346–63.

Kitagima K (2007) Seed and seedling ecology. In Pugnaire FI, Valladares F (eds). *Functional Plant Ecology.* 2nd edn. New York, NY: CRC Press, 549–80.

Klink CA, Machado RB (2005) A Conservação do Cerrado Brasileiro. *Megadiversidade* **1**:147–55.

Kunstler G, Falster D, Coomes DA, *et al.* (2016) Plant functional traits have globally consistent effects on competition. *Nature* **529**:204–7.

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) LmerTest package: tests in linear mixed effects models. *J Stat Softw* **82**:1–26.

Labrière N, Locatelli B, Vieilledent G, *et al.* (2016) Spatial congruence between carbon and biodiversity across forest landscapes of Northern Borneo. *Glob Ecol Conserv* **6**:105–20.

Lahsen M, Bustamante MMC, Dalla-Nora EL (2016) Undervaluing and over-exploiting the Brazilian Cerrado at our peril. *Environ: Sci Policy Sustain Dev* **58**:4–15.

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**:299–305.

Laliberté E, Legendre P, Shipley B (2015) *Measuring Functional Diversity (FD) From Multiple Traits, and Other Tools for Functional Ecology*. https://cran.r-project.org/web/packages/FD/FD.pdf (2 January 2019, date last accessed) .

Locatelli B, Catterall CP, Imbach P, *et al.* (2015) Tropical reforestation and climate change: beyond carbon. *Restor Ecol* **23**:337–43.

Lohbeck M, Bongers F, Martinez-Ramos M, *et al.* (2016) The importance of biodiversity and dominance for multiple ecosystem functions in a human-modified tropical landscape. *Ecology* **97**:2772–9.

Lohbeck M, Poorter L, Martínez-Ramos M, *et al.* (2015) Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. *Ecology* **96**:1242–52.

Loiola PP, Scherer-Lorenzen M, Batalha MA (2015) The role of environmental filters and functional traits in predicting the root biomass and productivity in savannas and tropical seasonal forests. *For Ecol Manage* **342**:49–55.

Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**:72–6.

Marris E (2005) The forgotten ecosystem. *Nature* **437**:944–5.

Mensah S, Veldtman R, Assogbadjo AE, *et al.* (2016) Tree species diversity promotes aboveground carbon storage through functional diversity and functional dominance. *Ecol Evol* **6**:7546–57.

Minas Gerais (Estado) (2006) *Decreto nº 44.204, de 10 de janeiro de 2006. Cria o Parque Estadual da Lapa Grande, no Município de Montes Claros.* Minas Gerais: Diário do Executivo.

Miranda SC, Bustamante M, Palace M, *et al.* (2014) Regional variations in biomass distribution in Brazilian Savanna woodland. *Biotropica* **46**:125–38.

Morandi PS, Marimon BS, Marimon-Junior BH, *et al.* (2018) Tree diversity and above-ground biomass in the South America Cerrado biome and their conservation implications. *Biodivers Conserv* **5**:1–18.

Murphy GEP, Romanuk TN (2014) A meta-analysis of declines in local species richness from human disturbances. *Ecol Evol* **4**:91–103.

Murray JP, Grenyer R, Wunder S, *et al.* (2015) Spatial patterns of carbon, biodiversity, deforestation threat, and REDD+ projects in Indonesia. *Conserv Biol* **29**:1434–45.

Myers N, Mittermeier RA, Mittermeier CG, *et al.* (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**:853–8.

Nunes MH, Terra MCNS, Oliveira IRC, *et al.* (2017) The influence of disturbance on driving carbon stocks and tree dynamics of Riparian Forests in Cerrado. *J Plant Ecol* **11**:401–10.

Osuri AM, Sankaran M (2016) Seed size predicts community composition and carbon storage potential of tree communities in rain forest fragments in India's Western Ghats. *J Appl Ecol* **53**:837–45.

Pellegrini AF, Socolar JB, Elsen PR, *et al.* (2016) Trade-offs between savanna woody plant diversity and carbon storage in the Brazilian Cerrado. *Glob Change Biol* **22**:3373–82.

Pelletier F, Pigeon G, Bergeron P, *et al.* (2017) Eco-evolutionary dynamics in a contemporary human population. *Nat Commun* **8**:15947.

Petchey OL, Gaston KJ (2002) Functional diversity (FD), species richness and community composition. *Ecol Lett* **5**:402–11.

Poorter L, Rose SA (2005) Light-dependent changes in the relationship between seed mass and seedling traits: a meta-analysis for rain forest tree species. *Oecologia* **142**:378–87.

Poulain M, Peña M, Schmidt A, *et al*. (2010) Relationships between forest variables and remote sensing data in a Nothofagus Pumilio forest. *Geocarto Int* **25**:25–43.

Prado-Junior JA, Schiavini I, Vale VS, *et al*. (2016) Conservative species drive biomass productivity in tropical dry forests. *J Ecol* **104**:817–27.

Pyles MV, Prado-Junior JA, Magnago LFS, *et al*. (2018) Loss of biodiversity and shifts in aboveground biomass drivers in tropical rainforests with different disturbance histories. *Biodivers Conserv* **27**:3215–31.

R Core Team (2017) *R: A Language and Environment for Statistical Computing.* Vienna, Austria: R Foundation for Statistical Computing. doi:10.1007/978-3-540-74686-7.

Ribeiro SC, Fehrmann L, Soares CPB, *et al*. (2011) Above- and belowground biomass in a Brazilian Cerrado. *For Ecol Manage* **262**:491–9.

Ribeiro SC, Jacovine LAG, Torres CMME, *et al*. (2017) Influence of interspecific variation on tree carbon stock of a Brazilian Cerrado. *Rev Arvore* **41**:e410506.

Rodríguez-Alarcón S, Rodríguez-Eraso N, Pineda-Rincón I, *et al*. (2018) Effects of fragmentation on functional diversity associated with aboveground biomass in a high Andean Forest in Colombia. *Landsc Ecol* **33**:1851–64.

Ruiz-Benito P, Gómez-Aparicio L, Paquette A, *et al*. (2014) Diversity increases carbon storage and tree productivity in Spanish forests. *Glob Ecol Biogeogr* **23**:311–22.

Saatchi SS, Harris NL, Brown S, *et al*. (2011) Benchmark map of forest carbon stocks in tropical regions across three continents. *Proc Natl Acad Sci U S A* **108**:9899–904.

Santos BA, Peres CA, Oliveira MA, *et al*. (2008) Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. *Biol Conserv* **141**:249–60.

Scolforo JRS, Mello JM, Oliveira AD, *et al*. (2008) *Inventário Florestal de Minas Gerais: Cerrado: Florística, Estrutura, Diversidade, Similaridade, Distribuição Diamética e de Altura, Volumetria, Tendências de Crescimento e Áreas Aptas Para Manejo Florestal.* 1st edn. Lavras, Brazil: Editora UFLA.

Scolforo JR, Oliveira AD, Acerbi Júnior, FW (2008) *Inventário Florestal de Minas Gerais: Equações de Volume, Peso de Máteria Seca e Carbono Para Diferentes Fisionomias Da Flora Nativa.* 1st edn. Lavras, Brazil: Editora UFLA.

Scolforo HF, Scolforo JR, Mello CR, *et al*. (2015) Spatial distribution of aboveground carbon stock of the arboreal vegetation in Brazilian biomes of Savanna, Atlantic forest and Semi-Arid Woodland. *PLoS One* **10**:e0128781.

Shirima DD, Totland O, Munishi PKT, *et al*. (2015) Relationships between tree species richness, evenness and aboveground carbon storage in Montane forests and Miombo Woodlands of Tanzania. *Basic Appl Ecol* **16**:239–49.

Silva-Júnior CM (2012) *100 Árvores Do Cerrado Sentido Restrito,* 1st edn. Brasília, Brazil: Rede de Sementes do Cerrado.

Silveira EMO, Terra MCNS, Acerbi-Júnior FW, *et al*. (2019a) Estimating aboveground biomass loss from deforestation in the Savanna and Semi-Arid biomes of Brazil between 2007 and 2017. In Silveira EMO, Terra MCNS, Acerbi-Júnior FW, *et al*. (eds). *Tropical Forests in Transition: The Role of Deforestation and Impacts from Community Composition to Regional Climate Change.* London, UK: Intechopen, 1–17.

Silveira EMO, Terra MCNS, ter Steegec H, *et al*. (2019b) Carbon-diversity hotspots and their owners in Brazilian Southeastern Savanna, Atlantic Forest and Semi-Arid Woodland domains. *For Ecol Manage* **452**:117575.

Souza FN, Scolforo JRS, Santos RM, *et al*. (2011) Assessment of different management systems in an area of Cerrado Sensu Stricto. *Cerne* **17**:85–93.

Strassburg BBN, Kelly A, Balmford A, *et al*. (2010) Global congruence of carbon storage and biodiversity in terrestrial ecosystems. *Conserv Lett* **3**:98–105.

Sullivan FB, Ducey MJ, Orwig DA, *et al*. (2017) Comparison of lidar- and allometry-derived canopy height models in an eastern deciduous forest. *For Ecol Manage* **406**:83–94.

Tabarelli M, Peres CA (2002) Abiotic and vertebrate seed dispersal in the Brazilian Atlantic forest: implications for forest regeneration. *Biol Conserv* **106**:165–76.

Terra MCNS, Santos RM, Fontes MAL, *et al*. (2017) Tree dominance and diversity in Minas Gerais, Brazil. *Biodivers Conserv* **26**:2133–53.

Tilman D, Isbell F, Cowles JM (2014) Biodiversity and ecosystem functioning. *Annu Rev Ecol Evol Syst* **45**:471–93.

Vierling LA, Vierling KT, Adam P, *et al*. (2013) Using satellite and airborne LiDAR to model woodpecker habitat occupancy at the landscape scale. *PLoS One* **8**:e80988.

Villéger S, Mason NW, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**:2290–301.

Wickham H (2016) *Ggplot2:Elegant Graphics for Data Analysis*. New York, NY: Springer-Verlag.

Wu H, Xiang W, Fang X, *et al*. (2017) Tree functional types simplify forest carbon stock estimates induced by carbon concentration variations among species in a subtropical area. *Sci Rep* **7**:1–11.

Zanne AE, Lopez-Gonzalez G, Coomes DA, *et al*. (2009) Data from: towards a worldwide wood economics spectrum, v2, Dryad, Dataset, DOI:10.5061/dryad.234

Ziter C, Bennett EM, Gonzalez A (2013) Functional diversity and management mediate aboveground carbon stocks in small forest fragments. *Ecosphere* **4**:1–21.

Zomer RJ, Neufeldt H, Xu J, *et al*. (2016) Global tree cover and biomass carbon on agricultural land: the contribution of agroforestry to global and national carbon budgets. *Sci Rep* **6**:29987.