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Remaining eucalypt trees may hamper woody plant regeneration in a neotropical savanna

Pavel Dodonov[a,b,*], Andreza Lanza Braga[a], Maria José Dias Sales[c], Rafael de Oliveira Xavier[a,d], Dalva Maria da Silva Matos[a]

[a] Ecology and Conservation Lab, Department of Hidrobiology, Federal University of São Carlos, São Carlos, SP, Brazil
[b] Institute of Biology, Federal University of Bahia, Salvador, Bahia, Brazil
[c] Laboratório de Mirmecologia, Centro de Pesquisa do Cacau, CEPLAC, 45600-970, Itabuna, Bahia, Brazil
[d] Universidade de São Paulo – Departamento de Ecologia – Rua do Matão 14, 05508-090, São Paulo, SP, Brazil

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ABSTRACT

When an area previously used for agricultural or sylvicultural purposes is abandoned, it may undergo natural regeneration. However, the outcome of such regeneration depends on a number of factors, including the presence of non-native invasive plants, and, when production forests such as eucalypt plantations are considered, remaining non-native trees may also affect the natural regeneration possibilities. We studied how remaining eucalypt trees affect woody species regeneration and invasive grasses in an abandoned *Eucalyptus grandis* plantation in a regenerating Brazilian savanna site. We sampled the woody vegetation and invasive grasses in 30 8 × 8-m plots and surveyed the eucalypt trees within these plots and in 3 m-wide strips around them. Eucalypts negatively affected the cover of the C4 invasive African grass *Melinis minutiflora* and the total abundance and basal area of native woody plants in general and of two dominant species, suggesting an overall negative effect on native plant regeneration notwithstanding the also negative effects on African grasses. Conversely, they had no effect on species richness, species diversity nor mean height of woody plant communities nor on the abundance of three other dominant native woody species. Interestingly, a low eucalypt abundance had small effects on native woody species but much stronger effects on the cover of *M. minutiflora*, possibly due to shading. Thus, our results indicate that remaining eucalypt trees may hamper the natural regeneration of native woody plants, but also suggest that maintaining a low density of eucalypt trees may be a cost-effective strategy, given the high costs associated with the complete removal of remaining trees and the difficulties in controlling invasions by African grasses.

1. Introduction

Land abandonment following anthropogenic uses is ubiquitous in terrestrial landscapes and may result in highly degraded landscapes dominated by undesirable species (Cramer et al., 2008). Although restoration of these degraded areas may sometimes rely on an area's natural regeneration potential, this potential is often very limited (Holl et al., 2017). The natural regeneration potential may depend on a variety of factors, such as vegetation type, propagule availability, presence of invasive species, and the extent of the legacy of previous land uses (Florentine and Westbrooke, 2004; Lugo and Helmer, 2004; Chazdon, 2019). Specifically in the case of natural regeneration in abandoned plantation forests, natural regeneration may putatively be hampered by remaining non-native trees, for example by shading (Richardson, 1998), Bone et al., (1997). Conversely, if remaining trees provide, for example, perching sites or control of invasive species (which may also occur by shading), they may aid the natural regeneration process (Viani et al., 2010; Castelli et al., 2015). Thus, assessing how remaining plantation forest trees affect regeneration in abandoned areas may aid in restoring native vegetation in such sites.

Although plantation forests often lead to lower biodiversity compared to native forests (Gainsbury and Colli, 2014) and may favor undesirable plant species (Ostertag et al., 2008), a variety of studies have shown that well-managed non-native plantation forests may have an overall positive effect on native species regeneration in severely degraded sites (Chazdon, 2012; Silva et al., 1995; Alencar et al., 2011).

* Corresponding author. Ecology and Conservation Lab, Department of Hidrobiology, Federal University of São Carlos, São Carlos, SP, Brazil
E-mail addresses: pdodonov@gmail.com, pdodonov@ufba.br (P. Dodonov).

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Understanding this process is important for planning the restoration of plantation forests into native vegetation. For instance, a recent study showed that planting eucalypts may help offset ecological restoration costs of tropical forests while having neutral or only slightly negative effects on the native species (Brancallion et al., 2020). Mechanisms by which plantation forests may increase regeneration include the control of light-demanding invasive plants (Viani et al., 2010), decreased competition between native species, increased organic matter availability, and increased presence of seed dispersers in plantations (Modna et al., 2010). For instance, Modna et al. (2010) observed a decrease in grass cover with increasing density of silvicultural trees in a regenerating site in the Brazilian *cerrado*.

The Brazilian *cerrado* is an ecosystem with mostly savanna vegetation (Coutinho, 1979; Ribeiro and Walter, 2008) and considered a biodiversity hotspot of worldwide significance (Myers et al., 2000). Although not the main land use in areas with *cerrado* occurrence, large *cerrado* areas have been converted into plantation forests (especially eucalypt ones) during the second half of the 20th century (Klink and Machado, 2005; Durigan et al., 2007). However, many of these plantations were abandoned starting in the 1990s, when government incentives were discontinued (Bacha, 2007; Gainsbury and Colli, 2014). Thus, understanding how eucalypt trees affect native species regeneration is important for planning the restoration of abandoned plantation forests into native vegetation and for assessing the possibilities of natural regeneration in such activities – a process that may be essential for large-scale landscape restoration and is much cheaper than active restoration (Chazdon and Uriarte, 2016).

Invasive African grasses are widely considered a major conservation threat in the *cerrado* (Pivello et al., 1999). In addition to dominating extensive areas (Klink and Machado, 2005; Durigan et al., 2007), such grasses may change fire behaviour (Hoffmann et al., 2012; Gorgone--Barbosa et al., 2015) and decrease the survival of native woody seedlings (Hoffmann and Haridasan, 2008), thus further displacing native species (Pivello et al., 1999; Hoffmann and Haridasan, 2008; Damasceno et al., 2018). Understanding the relation between plantation forests, biological invasions, and regeneration may further aid in the development of restoration strategies, and the Brazilian *cerrado* is a well-suited system to address such issues. Brazil is among the largest cellulose, paper and wood producers wordlwide, with over 7.8 million hectares of non-native plantation forests, including 5.7 million hectares of eucalypt plantations (IBÁ, 2017). The nutrient-poor soils which dominate the cerrado (Dantas and Batalha, 2011) are favorable for the plantation of eucalypts (Oliveira et al., 1998), which therefore have been widely planted in this and other environments in Brazil during the 20th century, especially since the 1960s (Ferreira, 2016). Still, eucalypt plantations may have relatively high native species richness and regeneration potential (Sartori et al., 2002; Saporetti et al., 2003; Neri et al., 2005; Dodonov et al., 2014a); in addition, they are expected to provide some shading, which has been shown to limit the abundance of C4 invasive African grasses (Klink et al., 1989; Xavier et al., 2007). Thus, and considering the threat posed by invasive grasses to this environment (Pivello et al., 1999), a better understanding of the regeneration process in these areas may aid restoration activities.

We assessed the relations between remaining eucalypt trees, native woody species, and invasive African grasses in a regenerating *cerrado* area in São Paulo state, South-Eastern Brazil. We aimed to compare between two contrasting hypotheses regarding the relationship between eucalypt and native vegetation: 1) eucalypts would negatively affect native woody plant communities due to competition, allelopathy, or other mechanisms, which would be shown by a monotonic negative relationship; or 2) eucalypts would indirectly favor the native plants at low densities by hampering the establishment of invasive grasses, but would have negative effects at higher densities, thus showing a humped (non-monotonic) relationship. We also aimed to assess whether these effects are determined mostly by the number of remaining eucalypt trees or their basal area, as such information may guide management decisions: if the number of trees is more important, larger individuals whose removal would be harder may be left in place whereas the smallers ones are removed, but the opposite strategy could be better if the determinant variable is basal area.

2. Methods

2.1. Study area

This study was carried out in a *cerrado* site occupying ca. 185 ha in the Federal University of São Carlos, São Paulo State, South-Eastern Brazil (21° 58' - 22° 00′ S and 47° 51′- 47° 52′ W). This area may be classified as typical *cerrado*, a savanna vegetation characterized by a nearly continuous herbaceous cover and by a woody vegetation with an average height of 3–5 m (Ribeiro and Walter, 2008). The study site is located on Red Oxisol (Santos et al., 1999), with distrophic soils and a flat topography (Damascos et al., 2005). Regional climate is mesothermic subtropical with a rainy summer and dry winter (Cwa according to Köppen's classification), with a yearly rainfall of 1315 mm and average yearly temperature of 21.3 °C (Dantas and Batalha, 2011). The study was performed in an area of ca. 47 ha that had been occupied by a eucalypt plantation before 1972; sometime between 1972 and 1988 the eucalypts were removed and the native vegetation was able to recover (Fushita et al., 2017). The area also has a large cover of two invasive African grasses, *Urochloa decumbens* (Stapf) R. Webster and *Melinis minutiflora* Beauv. (Dodonov et al., 2013, 2019).

2.2. Study species

Eucalyptus grandis (Hill) (Myrtaceae) is one of the most widely used eucalypt species in plantations worldwide (Stanturf et al., 2013), with over half a million hectares planted in tropical and subtropical areas, especially in South Africa and Brazil (Burns and Honkala, 1990). It is native to the east coast of Australia, characterized by a humid subtropical climate, with an average rainfall of 1020–1780 mm concentrated in the summer and a monthly precipitation of less than 20 mm in the dry season (Burns and Honkala, 1990). It grows best on wet, well-drained, deep soils (Clemens et al., 1978; Stape et al., 2010; Binkley et al., 2017).

Melinis minutiflora is a C4 perennial grass native from West and South-Eastern Africa, which likely has been present in Brazil at least since the XIX century (Parsons, 1972; Williams and Baruch, 2000). It is widespread in the cerrado and other seasonally dry ecosystems (Pivello et al., 1999; D'Antonio et al., 2001; Martins et al., 2011), in part as a result of its effective seed dispersal (Martins et al., 2009), phenotypic plasticity (Zenni et al., 2018), and high competitive ability (Pivello et al., 1999; Martins et al., 2009). This species occurs throughout our study site, often with high cover (Dodonov et al., 2019).

Urochloa decumbens (Stapf) R. Webster is a perennial grass native from East and Central Africa (Williams and Baruch, 2000). Although it was only introduced in Brazil in the late 1960s (Jank et al., 2014), it has spread rapidly to *cerrado* remnants, where it often becomes dominant to the detriment of native herbaceous species (Pivello et al., 1999). *U. decumbens* typically shows high resource use efficiency and highly effective vegetative reproduction (Stur and Humphreys, 1988), which suport its greater dissemination in the environment (Williams and Baruch, 2000). It also occurs throughout our study site, but with a lower frequency and cover than *M. minutiflora* (Dodonov et al., 2019).

2.3. Sampling

We sampled 30 8 × 8-m plots randomly distributed throughout the study area, at least 50 m distant from the edges and from each other. The plots varied in the number of eucalypts and in invasive grass cover present therein (Fig. 1). Within each plot, we obtained the diameter and height of all native woody individuals that had at least one stem with a

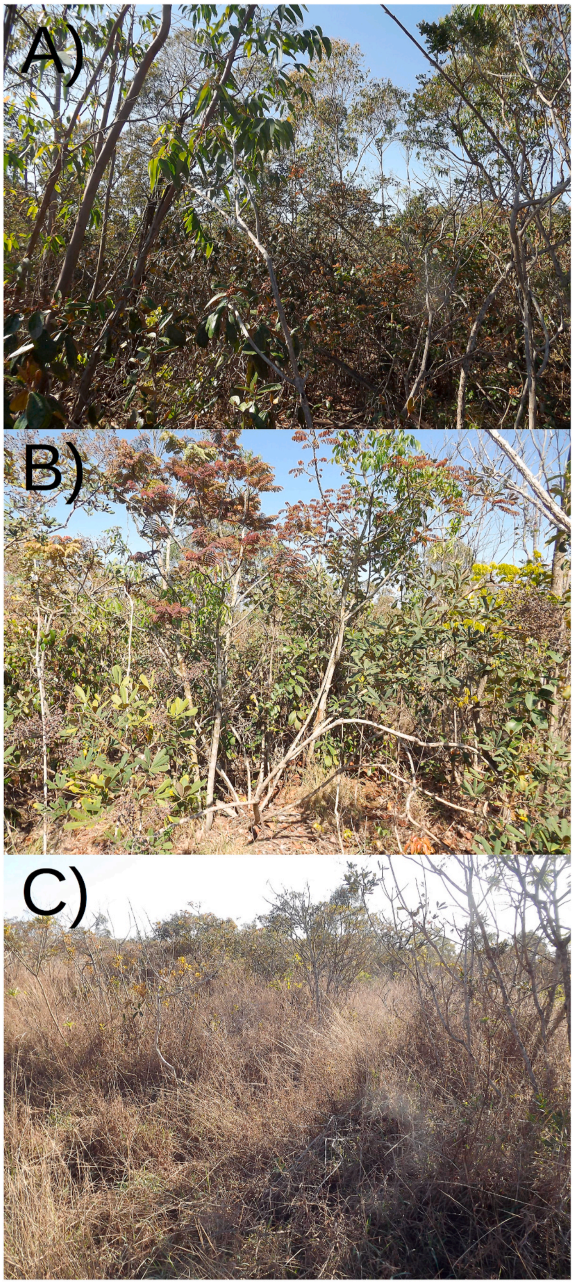

Fig. 1. Images of the study site: a) a plot with eucalypts'and no invasive grasses, b) a plot with both eucalypts and invasive grasses, c) a plot with no eucalypts and fully dominated by *Melinus minutiflora.*

diameter at breast height (DBH - measured at 130 cm above ground) of at least 1.5 cm. We included native plants with multiple stems when at least on stem satisfied the inclusion criterion. In these cases, we measured the DBH of all stems and the height of the tallest ones. We afterwards calculated the total basal area of each native individual by assuming circular stems and summing the areas of each stem to obtain the individual's basal area. Native plants were identified to the most precise taxonomic level possible.

We measured the DBH of all eucalypt stems within the plot and in a 3 m-wide strip around the plots (thus resulting in larger plots of 11 × 11 m). We included this additional strip because it is possible that eucalypts outside the plots affect the vegetation, for example by shading. We then calculated the basal area of each eucalypt stem, following the same procedure as for the native species. We also visually estimated the percent cover of invasive grasses (*M. minutiflora* and *U. decumbens*) in the herbaceous layer of each plot. Although we realize that this method for sampling invasive grasses is rather imprecise considering our plot size, we believe that it may nevertheless provide important information, especially because testing our second hypothesis required a plot-level estimate of invasive grass cover. Given the time constraints for performing this study, we were unable to use more precise estimates of invasive cover and biomass.

2.4. Analysis

We assessed the effects of eucalypts on twelve response variables: four related to vegetation structure (total abundance of native woody plants, total and mean basal area of native woody plants, and mean height of native woody plants), two related to community structure (native woody species richness and Shannon's diversity index), one related to biological invasion (invasive grass cover), and five related to the population structure of individual plant species (abundance of the five most abundant woody species in our study - Table 1) - *Schefflera vinosa* (Cham. & Schltdl.) Frodin & Fiaschi, *Miconia albicans* (Sw.) Triana, *Miconia ligustroides* (DC.) Naudin, *Piptocarpha rotundifolia* (Less.) Bakerand, and *Stryphnodendron obovatum* Benth.). We did not analyze the two invasive grasses separately because *U. decumbens* occurred in only two plots.

As explanatory variables, we used the total number and basal area of eucalypts (including the plot and its surroundings). We removed one plot which had a much larger number of eucalypts than the others (26 eucalypts, whereas the other plots had 0 to 9 eucalypts) from all analyses. In one plot, there were only eucalypt resprouts with a height below 1.3 m; in this one case, we considered that there was one individual in the plot, but attributed a basal area of zero (because basal area is calculated based on the DBH).

For each response variable, we adjusted two generalized additive models (GAMs - Zuur et al., 2009), one with the number of eucalypts as explanatory variable and the other with their basal area. We used GAMs because our second hypotheses predicted a non-linear response but we did not have an *a priori* expectation regarding the precise shape of this response, for which reason we did not use non-linear models that requere a prespecified formula. To avoid overfitting, we limited the maximum non-linearity to three effective degrees of freedom. We used the Poisson distribution with a correction for overdispersion (also known as "quasipoisson") for count variables and the Gamma distribution for the continuous variables (Zuur et al., 2009). The single exception was the cover of invasive grasses, as these species were absent from some plots and hence we could not use the Gamma distribution for this variable; instead, we used a Gaussian distribution for the square-root-arcsin-transformed invasive grass cover.

We used F tests to assess the significance of each GAM and also calculated the proportion of deviance explained by the explanatory variable. We used both of these values to decide which explanatory variable (eucalypt number or their basal area) had stronger effects. Thus, when one explanatory variable had statistically significant ($p < 0.05$) or marginally significant ($p < 0.10$) effects and the other did not, we selected the former variable. When both variables had significant or marginally significant effects ($p < 0.10$), we selected the one which had greater explanation. If the effects of both variables were non-significant ($p > 0.10$), we concluded that neither of them affects the response variable.

To assess whether eucalypts affect species composition, we performed canonical correspondence analyses (CCA) between the species composition and the two explanatory variables (number of eucalypts and their basal area). For this analysis, we removed species that occurred in less than four plots, which left 15 species for the analysis. We performed this analysis separately for native species abundance and presence-absence data and used randomization testes, with 9999 randomizations, to assess significance.

We performed all analyses in R 3.4.4 (R Core Team, 2018), with the

Table 1
Native plant species sampled in the study area, showing their abundance (number of individuals) and rank (from the most abundant to the least abundant).

Species	Abundance	Rank
Annonaceae		
Xylopia aromatica	3	18
Araliaceae		
Schefflera macrocarpa	1	29
Schefflera vinosa	150	1
Asteraceae		
Baccharis dracunculifolia	4	14
Gochnatia pulchra	4	14
Piptocarpha rotundifolia	28	4
Bignoniaceae		
Memora peregrina	1	29
Caryocaraceae		
Caryocar brasiliense	11	8
Connaraceae		
Connarus suberosus	1	29
Ebenaceae		
Diospyros hispida	7	12
Erythroxylaceae		
Erythroxylum suberosum	1	29
Erythroxylum tortuosum	1	29
Fabaceae		
Acosmium subelegans	13	6
Bauhinia rufa	1	29
Bowdichia virgilioides	1	29
Dalbergia miscolobium	1	29
Dimorphandra mollis	1	29
Stryphnodendron adstringens	3	18
Stryphnodendron obovatum	28	4
Lamiaceae		
Aegiphila lhotzkiana	8	10
Lauraceae		
Ocotea pulchella	4	14
Malpighiaceae		
Banisteriopsis agyrophilum	1	29
Banisteriopsis megaphylla	4	14
Byrsonima coccolobifolia	1	29
Byrsonima intermedia	3	18
Malvaceae		
Eriotheca gracilipes	2	22
Melastomataceae		
Miconia albicans	129	2
Miconia ligustroides	34	3
Miconia rubiginosa	1	29
Pleroma stenocarpum	12	7
Myristicaceae		
Virola sebifera	2	22
Myrtaceae		
Eugenia punicifolia	2	22
Myrcia bella	8	10
Myrcia guianensis	11	8
Ochnaceae		
Ouratea acuminata	1	29
Ouratea spectabilis	2	22
Peraceae		
Pera glabrata	3	18
Primulaceae		
Myrsine coriacea	2	22
Myrsine umbellata	1	29
Proteaceae		
Roupala montana	2	22
Rubiaceae		
Tocoyena formosa	1	29
Rutaceae		
Zanthoxylum rhoifolium	1	29
Salicaceae		
Casearia sylvestris	5	13
Styracaceae		
Styrax ferrugineus	2	22
Vochysiaceae		
Qualea grandiflora	1	29

packages "mgcv" (Wood, 2011) for the additive models and "vegan" (Oksanen et al., 2017) for the canonical correspondence analysis. The data and R codes used are available at <https://github.com/pdodonov/publications>.

3. Results

The number of eucalypts (considering the plots and their surroundings) varied from 0 to 9 individuals, except for one plot with 26 individuals which was removed from the analysis. Most eucalypts had from one to eight stems. The eucalypt stems measured were relatively thin, with a DBH of 0.5–15.4 cm, but were usually resprouts from remaining eucalypt trees, with either one or up to seven stems growing from the same base. We sampled 536 native woody plants belonging to 45 species and 25 families (Table 1). We were not able to identify 33 individuals that did not have leaves at the time of sampling or were juveniles. The most abundant species were *Schefflera vinosa* (Araliaceae) and *Miconia albicans* (Melastomataceae), corresponding to 30% and 26%, respectively, of the identified individuals. Thus, the families with the greatest numbers of individuals were Melastomataceae and Araliaceae, but the family with the greatest number of species was Fabaceae, with seven species, followed by Malpighiaceae and Melastomataceae, with four species each (Table 1). Invasive grasses occurred in 27 of the 30 plots; 25 plots had only *M. minutiflora*, one plot had only *U. decumbens* and one plot had both invasive grasses. Average cover of invasive grasses was of 44.5 ± 36% SD.

Generalized additive models showed that the number of eucalypts had stronger effects than their basal area: of the twelve response variables, six were significantly or marginally significantly ($p < 0.10$) related to the number of eucalypts, but only three to their basal area, and when both explanatory variables had significant effects, the number of eucalypts had consistently greater explanatory power (Table 2, Fig. 2). Thus, the number of eucalypts negatively affected vegetation structure, as plots with more eucalypts had marginally smaller abundance ($p = 0.056$) and significantly smaller basal area (total and mean; $p < 0.007$) of native woody species (Fig. 2a–c). The abundance of two native species, *S. vinosa* and *P. rotundifolia*, decreased with increasing eucalypt abundance ($p = 0.0064$ and 0.075, respectively; Table 2, Fig. 2h,k). Eucalypt abundance explained 16–46% of the variation in these variables. Conversely, eucalypt abundance was not related to mean height, richness, nor diversity of woody plants (Table 2; Fig. 2d–f), nor to the abundance of the three other woody plant species (*M. albicans*, *M. ligustroides* and *S. obovatum*; Table 2, Fig. 2i,j,l). The cover of invasive grasses also decreased with the number of eucalypts ($p = 0.06$), and the highest invasive grass cover was observed in plots with no eucalypts (Table 2, Fig. 2g).

Canonical Correspondence Analysis did not detect any relations between woody species composition and eucalypt abundance or basal area, either for abundance ($p = 0.33$) or presence-absence ($p = 0.41$) data; the two cannical axes cumulatively explained 8.3% of the variation in species abundance and 7.7% of variation in species composition. The biplots can are available as supplementary material 1.

4. Discussion

Our results show that remaining eucalypt trees may have negative effects on Cerrado regeneration in spite of their also negative effects on invasive grasses, thus corroborating our first hypothesis; it must also be emphasized that, as our estimates of invasive grasses were relatively imprecise and as this relationship was only marginally significant, the negative effects of eucalypts on invasive grasses must be considered with caution. Regarding the native woody plants, although their species richness was not related to eucalypt abundance, three aspects of vegetation structure – total abundance and total and mean basal area - were negatively related to it. Our results are in opposition to previous observations of non-native tree species aiding in Cerrado regeneration. For

Table 2
Results for the generalized additive models for each response variable and the two explanatory variables. The effective degrees of freedom (EDF) show how non-linear is the relation between the two variables; linear relations have and EDF o 1.

	Number of eucalypts			Eucalypt basal area		
Response variable	EDF	Deviance explained (%)	P-value	EDF	Deviance explained (%)	P-value
Native woody plants						
Abundance	1.0	12.8	0.056	1.0	8.8	0.12
Total basal area	1.0	46.1	0.00060	1.0	27.5	0.032
Mean basal area	1.0	27.5	0.0068	1.4	23.7	0.061
Mean height	1.0	0.2	0.80	1.0	0.2	0.81
Richness of native woody plants	1.0	2.7	0.38	1.0	3.2	0.34
Shannon's diversity index	1.0	0.0	0.95	1.0	0.0	0.94
Invasive African grasses						
Invasive grass cover	1.6	21.3	0.058	1.6	13.6	0.21
Dominant native woody plant species						
Schefflera vinosa	1.0	26.6	0.0064	1.0	25.1	0.013
Miconia albicans	1.0	1.1	0.56	1.8	12.4	0.28
Miconia ligustroides	1.0	0.0	0.99	1.0	0.1	0.89
Piptocarpha rotundifolia	1.0	16.4	0.075	5.8	65.9	0.12
Stryphnodendron obovatum	1.0	6.8	0.19	1.0	2.3	0.48

instance, Modna et al. (2010) observed increasing density of native species with increasing *Pinus* biomass, likely related to the lower invasive grass cover due to shading. Still, another study observed decreasing regeneration with increasing eucalypt biomass (Durigan et al., 2004), and a recent study in the Atlantic forest observed neutral or slightly negative effects of planted eucalypt trees on native species regeneration (Brancalion et al., 2020). Thus, there appears to be much variation in the effects of non-native trees on Cerrado regeneration, likely due to factors such as the non-native tree species, land use history, and management (Viani et al., 2010).

Of the ten response variables related to vegetation structure or composition, four were negatively affected by intermediate to high eucalypt abundance; two of them referred to vegetation structure (abundance and basal area of native woody plants) and two referred to the population structure of dominant species (*S. vinosa* and *P. rotundifolia*); the effects on total plant abundance appeared to be largely due to the effects on these two species. Thus, even if there are no effects on the number of species, eucalypts appear to affect vegetation structure and individual plant populations, similar to what was observed by Durigan et al. (2004). In addition to affecting the abundance of native woody plants, they apparently also affect their growth, thus leading to decreased mean basal area (but not height). Likewise, large negative effects of invasions by non-native trees on native species cover have been observed in other open vegetation types (Holmes and Cowling, 1997), including as a result of plantation forests of non-native species (Richardson, 1998). Possible reasons for such negative effects include competition by exploitation and/or interference with the native vegetation (Begon et al., 2006).

Competition by exploitation may take place when the eucalypts decrease the amount of water and/or nutrients in the soil available for the native plants, whereas competition by interference can take place by shading and/or allelopathic effects (Begon et al., 2006). Cerrado soils are naturally nutrient-poor with low water retention capacity and deep groundwater (Dantas and Batalha, 2011), and the presence of a species with high water demands is likely to have negative effects on the native vegetation. In our study, the eucalypt stems measured were relatively thin, but were resprouts from larger remaining eucalypt trees. Thus, even if the remaining stems were relatively small, they probably had well-developed root systems (du Toit, 2008), which, through competition with the native woody vegetation, may have led to the effects on vegetation structure observed here.

E. grandis also produces a moderately dense crown and hence may lead to high canopy cover when occurring in high abundance (Wilson et al., 1990), which in turn may hamper the establishment and growth of light-demanding cerrado woody species (Durigan and Ratter, 2016). Eucalypt trees in the study site are also relatively tall compared to the cerrado plants, reaching up to 18 m in height, whereas the native plants do not reach over 8 m (P. Dodonov, unpublished data), indicating that eucalypts may also impact the native vegetation by shading. In addition, previous field studies found negative effects of litter and roots of *Eucalyptus* species on the germination and initial establishment of native woody species (Zhang and Fu, 2009; Zhang et al., 2016), so that allopathic effects may contributed to the lower number of woody individuals where there were more eucalypts. Our data do not permit us to assess the relative importance of shading and allelopathy, which could be explored in future studies.

We did not detect effects of eucalypt abundance on either species richness or species composition – thus, they apparently do not provoke differential recruitment at the scale examined here. In addition, high undergrowth species richness had been observed in a nearby site with a much higher eucalypt cover (Dodonov et al., 2014a). Similarly, eucalypts are unlikely to preclude seed dispersal, as they are often used as perching sites by birds and, as such, might even increase seed dispersal (Brockerhoff et al., 2008), although poor habitat quality in plantations may limit bird diversity (Marsden et al., 2001; Barlow et al., 2017). In our study the abundance of certain abundant species was not affected by the abundance of eucalypts, including *M. albicans*, the second most abundant species found in this study, and the functionally similar *M. ligustroides*. Considering that both species are common in cerrado areas with intermediate to dense woody cover (Garcia et al., 2004; Dodonov et al., 2014b), similar responses may putatively be observed for other common species. Still, our results show that positive effects of eucalypts on regeneration are less likely than observed in other studies (Silva et al., 1995; Alem and Woldemariam, 2009).

Eucalypt trees also had negative impacts on invasive grasses, which decreased with increasing eucalypt abundance; still, as our methods focused more on woody species, these results must be interpreted with care. In any case, it appears that the presence of a few remaining eucalypt trees may decrease invasive grass cover. Plantations of *E. grantis* were previously showed to either increase or decrease the productivity of different tropical grasses depending on their tolerance to shading (Wilson et al., 1990; Robinson, 1991). Likewise, a previous study in silvicultural plantations has also found that increasing biomass of *Pinus* decreased the cover of invasive African grasses and hence favoured the abundance of native species (Modna et al., 2010). Considering that both invasive African grasses found in our study are C4 species which perform better under high light availability (Klink and Joly, 1989; Xavier et al., 2017), this negative effect of eucalypt trees is likely related to increasing shading. Although further canopy cover and sunlight availability measurements would be required to test this hypothesis, our findings are consistent with the negative effect of even a small number of eucalypt trees on the cover of exotic grasses, suggesting that even a small

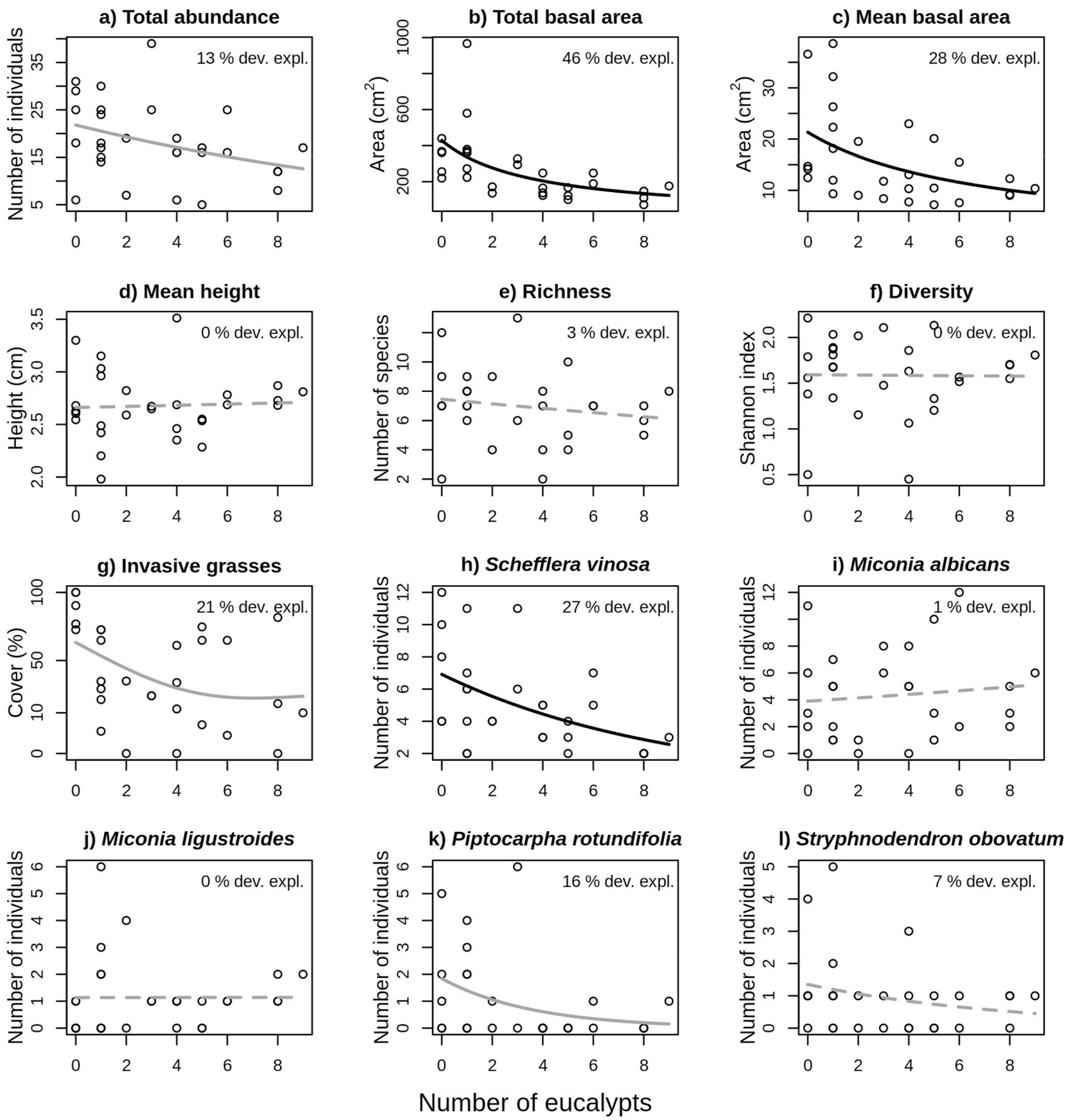

Fig. 2. Relation between the response variables and number of eucalypts in the plots and their surroundings. The response variables were measured in 8×8 m plots and the eucalypts were measured in these plots and in an additional 3 m-wide strip around them. The circles represent the plots. Black lines represent significant ($p < 0.05$) relationships, as shown by generalized additive models; gray solid lines represent marginally significant relationships ($0.05 \leq p < 0.10$); dashed lines represent non-significant relationships ($p \geq 0.10$). All plots also show the amount of deviance explained by the explanatory variable ("% dev. expl.").

increase in canopy closure caused by a few trees may have a large negative effect on the performance of C4 African grasses.

Although these findings suggest that the presence of remaining eucalypts in our study site would have a positive indirect effect on cerrado woody species regeneration, the impacts on invasive grasses were relatively weak, and there were plots with a large number of eucalypts that had over 75% invasive grass cover. Thus, apparently the shade offered by the remaining eucalypts did not provide a strong control of the invasive grasses. Considering that the dominant African grass in our study site (*M. minutiflora*) is a widespread species which often show high phenotypic plasticity (Xavier and D'antonio 2017; Zenni et al., 2019), and highly effective seed dispersal (Martins et al., 2009, Xavier et al. in prep), this species is possibly efficient in occupying microsites suitable for C4 grass establishment even under generally less favorable light conditions, thus contributing to moderately high cover of invasive grasses in eucalypt plantations in our study (although smaller than in plots without eucalypts).

As natural eucalypt recruitment near plantation sites appears to be a rare process in Brazil (e.g. Brancalion et al., 2020), our data suggest that maintaining a small density of eucalypt trees may have a short-term overall positive effect on cerrado regeneration under conditions similar to the ones studied here, as it may not be detrimental to the presence of most cerrado woody species while decreasing the cover of African grasses. In addition, complete eucalypt removal may not be a feasible strategy (Casselli et al., 2018). *E. grandis* trees typically exhibit high resprouting capacity, as demonstrated by the multiple stems observed in our study: simply removing the standing trees is not sufficient, and continuing management activities and/or the use of glyphosate (Brancalion et al., 2020) may be necessary to preclude them from resprouting for a long enough time for the Cerrado to regenerate. Also, complete removal of the remaining eucalypts may result in increased sunlight availability, favouring the spread of C4 exotic grasses such as *M. minutiflora* and hence indirectly harming the regeneration of native species (Hoffmann and Haridasan, 2008). In addition, the absence of *E. grantis* may favor certain fast-growing light-demanding cerrado woody species and hence led to increased native woody cover, but not necessarily higher local woody species diversity. Therefore, as has been previously shown in other *E. grandis* plantations (Cummings and Reid, 2008), the removal of most, but not all, eucalypts may be a cost-effective management strategy to obtain high local biodiversity value, given that complete removal of the species may depend on large financial resources and cause extensive disturbance (Casselli et al., 2018).

In summary, our results indicate that care should be taken to remove most commercial plantation trees when a silvicultural plantation is abandoned and left to regenerate, as remaining trees may have negative effects on the native vegetation. In our study, although they led to a slight decrease in the cover of invasive grasses, this was not enough to compensate their negative effects on woody plants. However, considering the high financial cost of removing eucalypts and that small abundance of eucalypt trees were detrimental to exotic grasses but did not have large effect in most cerrado woody species, partial removal would be a cost effective strategy. The number of eucalypts had much stronger effects than their basal area, indicating that eucalypt trees of different sizes may have similar effects. Thus, we speculate that the removal of smaller eucalypt trees would be a feasible strategy, as this would reduce the number of eucalypts (and thus their impacts) but would probably be less expensive and have smaller direct impacts on the native vegetation than the removal of larger individuals. As always with single studies, care should be taken when generalizing the results. However, we do believe that our study site is representative of the conditions found in large part of the Cerrado in São Paulo – where it is represented mostly by small fragments subjected to strong anthropic pressures (Durigan et al., 2007) – and possibly elsewhere.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actao.2020.103658.

Author contributions

PD, ALB and DMSM designed the study; ALB and PD collected the data; PD analyzed the data; PD, ROX and MJDS led the writing of the manuscript; all authors contributed critically to the drafts and gave final approval for publication. This study was ALB's undergraduate honors study in Biological Sciences, supervised by DMSM and cosupervised by PD.

References

Alem, S., Woldemariam, T., 2009. A comparative assessment on regeneration status of indigenous woody plants in Eucalyptus grandis plantation and adjacent natural forest. J. For. Res. 20, 31–36.

Alencar, AL de, Marangon, L.C., Feliciano, A.L.P., Ferreira, R.L.C., Teixeira, L. de J., Alencar, AL de, Marangon, L.C., Feliciano, A.L.P., Ferreira, R.L.C., Teixeira, L. de J., 2011. Regeneração natural avançada de espécies arbóreas nativas do sub-bosque de povoamentos de *Eucalyptus saligna* Smith., na Zona da Mata Sul de Pernambuco. Ciência Florest. 21, 183–192. https://doi.org/10.5902/198050983218.

Bacha, C.J.C., 2006. The evolution of reforestation in Brazil. Oxf. Dev. Stud. 34, 243–263. https://doi.org/10.1080/13600810600705189.

Barlow, J, Mestre, L.A.M, Gardner, T.A, Peres, C.A, 2017. The value of primary, secondary and plantation forest for Amazonian birds. Biol. Conserv. 136, 212–231.

Begon, M., Townsend, C.R., Harper, J.L., 2006. Ecology: from Individuals to Ecosystems. Blackwell Publishing, Malden, USA.

Binkley, D., Campoe, O.C., Alvares, C., Carneiro, R.L., Cegatta, Í., Stape, J.L., 2017. The interactions of climate, spacing and genetics on clonal Eucalyptus plantations across Brazil and Uruguay. For. Ecol. Manag. 405, 271–283.

Bone, R., Lawrence, M., Magombo, Z., 1997. The effect of a *Eucalyptus camaldulensis* (Dehn) plantation on native woodland recovery on Ulumba Mountain, southern Malawi. For. Ecol. Manag. 99, 83–99.

Brancalion, P.H.S., Amazonas, N.T., Chazdon, R.L., van Melis, J., Rodrigues, R.R., Silva, C.C., Sorrini, T.B., Holl, K.D., 2020. Exotic eucalypts: from demonized trees to allies of tropical forest restoration. J. Appl. Ecol. 57, 55–66.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodivers. Conserv. 17, 925–951.

Burns, R.M., Honkala, B.H., 1990. In: Silvics of North America: 2. Hardwoods. U.S. Department of Agriculture, Forest Service, Washington. Available at: https://www.srs.fs.usda.gov/pubs/misc/ag_654/table_of_contents.htm.

Casselli, V., Prata, G.A., Seixas, F., 2018. Operating performance and economic viability in the eucalyptus stump harvest in two alternative extraction systems. Sci. Forestalis 46, 97–106.

Castelli KR, Barreto MG, Francesconi W, Valle LD, Mondelli G, Abilio FM, Silva AM 2015 Analysis of effectiveness of three forest interventionist techniques and proposal of a new and integrated model of forest restoration. Environ. Technol. 36: 2712-2723.

Chazdon, R., 2012. Regeneração de florestas tropicais. Bol. Mus. Para. Emílio Goeldi. Cienc. Nat. 7, 195–218.

Chazdon, R.L., 2019. Towards more effective integration of tropical forest restoration and conservation. Biotropica 51, 463–472.

Chazdon, R.L., Uriarte, M., 2016. Natural regeneration in the context of large-scale forest and landscape restoration in the tropics. Biotropica 48, 709–715.

Clemens, J., Kirk, A.M., Mills, P.D., 1978. The resistance to waterlogging of three Eucalyptus species. Oecologia 34, 125–131.

Coutinho, L.M., 1978. O conceito de cerrado. Rev. Bras. Botânica 1, 17–23.

Cramer, V.A., Hobbs, R.J., Standish, R.J., 2008. What's new about old fields? Land abandonment and ecosystem assembly. Trends Ecol. Evol. 23, 104–112.

Cummings, J., Reid, N., 2008. Stand-level management of plantations to improve biodiversity values. Biodivers. Conserv. 17, 1187–1211.

Damasceno, G., Souza, L., Pivello, V.R., Gorgone-Barbosa, E., Giroldo, P.Z., Fidelis, A., 2018. Impact of invasive grasses on Cerrado under natural regeneration. Biol. Invasions 20, 3621–3629.

Damascos, M.A., Prado, C.H.B.A., Ronquim, C.C., 2005. Bud composition, branching patterns and leaf phenology in cerrado woody species. Ann. Bot. 96, 1075–1084.

Dantas, V.L., Batalha, M.A., 2011. Vegetation structure: fine scale relationships with soil in a cerrado site. Flora 206, 341–346.

Dodonov, P., Harper, K.A., Silva-Matos, D.M., 2013. The role of edge contrast and forest structure in edge influence: vegetation and microclimate at edges in the Brazilian cerrado. Plant Ecol. 214, 1345–1359.

Dodonov, P, Silva, DM, Rosatti, NB, 2014a. Understorey vegetation gradient in a Eucalyptus grandis plantation between a savanna and a semideciduous forest. N. Z. J. For. Sci. 44, 10.

Dodonov, P., Xavier, R.O., Tiberio, F.C.S., Lucena, I.C., Zanelli, C.B., Silva-Matos, D.M., 2014b. Driving factors of small-scale variability in a savanna plant population after a fire. Acta Oecol. 56, 47–55.

Dodonov, P., Harper, K.A., Xavier, R.O., Silva-Matos, D.M., 2019. Spatial pattern of invasive and native graminoids in the Brazilian cerrado. Plant Ecol. 220, 741–756.

du Toit, B., 2008. Effects of site management on growth, biomass partitioning and light use efficiency in a young stand of *Eucalyptus grandis* in South Africa. For. Ecol. Manag. 255, 2324–2336.

Durigan, G., Ratter, J.A., 2016. The need for a consistent fire policy for Cerrado conservation. J. Appl. Ecol. 53, 11–15. https://doi.org/10.1111/1365-2664.12559.

Durigan, G., Melo, A.C.G., Contieri, W.A., Nakata, H., 2004. Regeneração natural da vegetação de cerrado sob florestas plantadas com espécies nativas e exóticas. In:

Vilas Boas, O., Durigan, G., Org (Eds.), Pesquisas em conservação e recuperação ambiental no oeste paulista: resultados da cooperação Brasil/Japão. São Paulo: Secretaria do Meio Ambiente/IF/JICA.
Durigan, G., Siqueira, M.F., Franco, G.A.D.C., 2007. Threats to the cerrado remnants of the state of São Paulo, Brazil. Sci. Agric. 64, 355–363.
D'Antonio, C.M., Hughes, R.F., Vitousek, P.M., 2001. Factors influencing dynamics of two invasive C4 grasses in seasonally dry Hawaiian woodlands. Ecology 82, 89–104.
Ferreira, M., 2016. A aventura dos Eucaliptos. In: Schumacher, Mauro Valdir, VIERA, Márcio (Eds.), Silvicultura Do Eucalipto No Brasil. Santa Maria. da UFSM, pp. 11–46.
Florentine, S.K., Westbrooke, M.E., 2004. Evaluation of alternative approaches to rainforest restoration on abandoned pasturelands in tropical North Queensland, Australia. Land Degrad. Dev. 15, 1–13.
Fushita AT, Santos JE, Rocha YT, Zanin EM 2017 Historical land use/cover changes and the hemeroby levels of a biocultural landscape: past, present and future. J. Geogr. Inf. Syst. 9:576–590.
Gainsbury, A.M., Colli, G.R., 2014. Effects of abandoned Eucalyptus plantations on lizard communities in the Brazilian Cerrado. Biodivers. Conserv. 23, 3155–3170.
Garcia, M.I.T.J., Barbosa, A.R.A., Valiengo, S.V., Ribeiro, R.R., 2004. Florística e fitossociologia de área de cerrado ss no município de Patrocínio Paulista, nordeste do Estado de São Paulo. Bragantia 63, 1–11.
Gorgone-Barbosa, E., Pivello, V.R., Bautista, S., Zupo, T., Rissi, M.N., Fidelis, A., 2015. How can an invasive grass affect fire behavior in a tropical savanna? A community and individual plant level approach. Biol. Invasions 17, 423–431. https://doi.org/10.1007/s10530-014-0740-z.
Hoffmann, W.A., Haridasan, M., 2008. The invasive grass, Melinis minutiflora, inhibits tree regeneration in a Neotropical savanna. Austral Ecol. 33, 29–36.
Hoffmann, W.A., Jaconis, S.Y., McKinley, K.L., Geiger, E.L., Gotsch, S.G., Franco, A.C., 2012. Fuels or microclimate: understanding the drivers of fire feedbacks at savanna-forest boundaries. Austral Ecol. 37, 634–643.
Holl, K.D., Reid, J.L., Chaves-Fallas, J.M., Oviedo-Brenes, F., Zahawi, R.A., 2017. Local tropical forest restoration strategies affect tree recruitment more strongly than does landscape forest cover. J. Appl. Ecol. 54, 1091–1099.
Holmes, P.M., Cowling, R.M., 1997. The effects of invasion by Acacia saligna on the guild structure and regeneration capabilities of South African fynbos shrublands. J. Appl. Ecol. 34, 317–332. https://doi.org/10.2307/2404879.
IBÁ - Industria Brasileira de Árvores, 2017. Relatório 2017, 80 pp.
Jank, L, Barrios, S.C, Valle, C.B, Simeão, R.M, Alves, G.F, 2014. The value of improved pastures to Brazilian beef production. Crop Pasture Sci 65, 1132–1137.
Klink, C.A., Joly, C.A., 1989. Identification e distribution of C3 e C4 grasses in open and shaded habitats in São Paulo state, Brazil. Biotropica 21, 30–34.
Klink, C.A., Machado, R.B., 2005. Conservation of the Brazilian cerrado. Conserv. Biol. 19, 707–713.
Lugo, A.E., Helmer, E., 2004. Emerging forests on abandoned land: Puerto Rico's new forests. For. Ecol. Manag. 190, 145–161. https://doi.org/10.1016/j.foreco.2003.09.012.
Marsden, S.J., Whiffin, M., Galetti, M., 2001. Bird diversity and abundance in forest fragments and Eucalyptus plantations around an Atlantic forest reserve, Brazil. Biodivers. Conserv. 10, 737–751.
Martins, C.R., Hay, J.D.V., Carmona, R., 2009. Potential invasor de duas cultivares de Melinis minutiflora no Cerrado brasileiro – características de sementes e estabelecimento de plântulas. Rev. Árvore 33, 713–722.
Martins, C.R., Hay, J.D.V., Walter, B.M.T., Proença, C.E.B., Vivaldi, L.J., 2011. Impacto da invasão e do manejo do capim-gordura (Melinis minutiflora) sobre a riqueza e biomassa da flora nativa do Cerrado sentido restrito. Braz. J. Bot. 34, 73–90.
Modna D, Durigan G, Vital MVC 2010 *Pinus elliottii* Engelm como facilitadora da regeneração natural da mata ciliar em região de Cerrado, Assis, SP, Brasil. Sci. Forestalis 38: 73-83.
Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.
Neri AV, Campos EP, Duarte TG, Neto JAAM, Silva AF, Valente GE 2005 Regeneração de espécies nativas lenhosas sob plantio de Eucalyptus em área de Cerrado na Floresta Nacional de Paraopeba, MG, Brasil. Acta Bot. Bras. 19: 369-376.
Oksanen, J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, H.H., Szoecs, E., Wagner, H., 2017. Vegan: community ecology package. R package version 2.4-4. https://CRAN.R-project.org/package=vegan.
Oliveira, A.D., Leite, A.P., Botelho, S.A., 1998. Avaliação econômica da vegetação de Cerrado submetida a diferentes regimes de manejo e de povoamentos de eucalipto plantado em monocultivo. Cerne 4, 34–56.
Ostertag, R., Giardina, C.P., Cordell, S., 2008. Understory colonization of Eucalyptus plantations in Hawaii in relation to light and nutrient levels. Restor. Ecol. 16, 475–485.
Parsons, J.J., 1972. Spread of African pasture grasses to the American tropics. J. Range Manag. 25, 12–17.
Pivello, V.R., Shida, C.N., Meirelles, S.T., 1999. Alien grasses in Brazilian savannas: a threat to the biodiversity. Biodivers. Conserv. 8, 1281–1294.
R Core Team, 2018. In: R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL. https://www.R-project.org/.
Richardson, D.M., 1998. Forestry trees as invasive Aliens. Conserv. Biol. 12, 18–26.
Ridenour, W.M., Callaway, R.M., 2001. The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. Oecologia 126, 444–450.
Robinson, J.B., 1991. The growth of Chloris gayana within and adjacent to a plantation of Eucalyptus grandis. Trop. Grassl. 25, 287–290.
Santos, J.E., Paese, A., Pires, J.S.R., 1999. Unidades da paisagem (biótopos) do Campus da UFSCar. EdUFSCar. São Carlos. Available at: http://www.lapa.ufscar.br/livros/unidades-da-paisagem-biotopos-do-campus-da-ufscar.
Saporetti Jr., A.W., Neto, J.A.A.M., Almado, R., 2003. Fitossociologia de sub-bosque de Cerrado em talhão de *Eucalyptus grandis* W. Hill ex Maiden no município de Bom Despacho- MG. Rev. Árvore 27, 905–910.
Sartori, M.S., Poggiani, F., Engel, V.L., 2002. Regeneração da vegetação arbórea nativa no sub-bosque de um povoamento de *Eucalyptus saligna* Smith. localizado no Estado de São Paulo. Sci. Forestalis 62, 86–103.
Silva, M.C., Scarano, F.R., Cardel, F. de S., 1995. Regeneration of an Atlantic forest formation in the understorey of a *Eucalyptus grandis* plantation in South-eastern Brazil. J. Trop. Ecol. 11, 147–152.
Stape, JL, Binkley, D, Ryan, MG, Fonseca, S, Loos, RA, Takahashi, EN, Silva, CR, Silva, SR, Hakamada, RE, Ferreira, JMA, Lima, AMN, Gava, JL, Leite, FP, Andrade, HB, Alves, JM, Silva, GGC, Azevedo, MR, 2010. The Brazil Eucalyptus potential productivity project: influence of water, nutrients and stand uniformity on wood production. For. Ecol. Manag. 259, 1684–1694.
Stur, W.W., Humphreys, L.R., 1988. Defoliation and burning effects on the tillering of Brachiaria decumbens. J. Appl. Ecol. 25, 273–277.
Viani, R.A.G., Durigan, G., Melo, A.C.G., 2010. A regeneração natural sob plantações florestais: desertos verdes ou redutos de biodiversidade? Ciência Florest. 20, 533–552.
Williams, D.G., Baruch, Z., 2000. African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology. Biol. Invasions 2, 123–140.
Wilson, J.R., Hill, K., Cameron, D.M., Shelton, H.M., 1990. The growth of *Paspalum notatum* under the shade of a Eucalyptus grandis plantation canopy or in full sun. Trop. Grassl. 24, 24–28.
Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. Roy. Stat. Soc. 73, 3–36.
Xavier, R.O., D'antonio, C.M., 2017. Multiple ecological strategies explain the distribution of exotic and native C4 grasses in heterogeneous early successional sites in Hawai'i. J. Plant Ecol. 10, 426–439.
Xavier, R.O., Leite, M.B., Silva-Matos, D.M., 2017. Stress responses of native and exotic grasses in a Neotropical savanna predict impacts of global change on invasion spread. Austral Ecol. 42, 562–576.
Zenni, R.D., Sampaio, A.B., Lima, Y.P., Pessoa-Filho, M., Lins, T.C.L., Pivello, V.R., Daehler, C., 2018. Invasive Melinis minutiflora outperforms native species, but the magnitude of the effect is context-dependent. Biol. Invasions 21, 657–667.
Zenni, R.D., Sampaio, A.B., Lima, Y.P., Pessoa-Filho, M., Lins, T.C.L., Pivello, V.R., Daehler, C., 2019. Invasive Melinis minutiflora outperforms native species, but the magnitude of the effect is context-dependent. Biol. Invasions 21, 657–667.
Zhang, C., Fu, S., 2009. Allelopathic effects of eucalyptus and the establishment of mixed stands of eucalyptus and native species. For. Ecol. Manag. 258, 1391–1396.
Zhang, C., Li, X., Chen, Y., Zhao, J., Wan, S., Lin, Y., Fu, S., 2016. Effects of Eucalyptus litter and roots on the establishment of native tree species in Eucalyptus plantations in South China. For. Ecol. Manag. 375, 76–83.
Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York.