

Do alien species dominate plant communities undergoing restoration? A case study in the Brazilian savanna

Espécies exóticas dominam comunidades vegetais em restauração?
Um estudo de caso no Cerrado

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Resumo

Entre os princípios estabelecidos pela Sociedade Internacional para Restauração Ecológica - Society for Ecological Restoration International – SER, consta que o uso de espécies exóticas para fins de restauração deve ser evitado, e isso é delineado nos dois primeiros atributos esperados de um ecossistema restaurado pelo SER Primer. Essa recomendação é provavelmente baseada na hipótese de que as espécies exóticas dominarão comunidades em restauração e prejudicarão a biodiversidade local. Nós avaliamos a comunidade atual de plantas em uma área de Cerrado em restauração, onde 42 espécies – 6 nativas e 36 não nativas – foram plantadas, e comparamos com comunidade nativa adjacente. Nós visamos verificar se a comunidade nativa adjacente foi invadida pelas exóticas, e se essas espécies tendem a dominar a comunidade em restauração, que seria então distinta da flora nativa. Oito anos após o plantio, não detectamos a presença das espécies exóticas no ecossistema natural adjacente. Na comunidade em restauração, mesmo sendo exóticas 94% das árvores plantadas (86% das espécies), apenas 3% das plantas regenerantes (14% das espécies) pertencem a espécies não nativas, indicando que a similaridade florística tende a aumentar ao longo do tempo. Consideramos que as espécies não nativas utilizadas neste projeto não estão oferecendo perigo aos ecossistemas naturais situados nas proximidades e que, em longo prazo, espécies nativas dominarão o ecossistema em restauração. No entanto, recomendamos que políticas públicas priorizem e viabilizem o uso de espécies nativas do Cerrado, melhor adaptadas para a restauração deste ecossistema.

Palavras-chave: invasão biológica, Cerrado, restauração ecológica, espécies invasoras, efeito de prioridade.

Abstract

Among the principles established by the Society for Ecological Restoration International – SER is that the use of exotic species for restoration purposes should be avoided, and this is outlined on the two first attributes expected of a restored ecosystem by the SER Primer. This recommendation is possibly based on the hypothesis that exotics will dominate the restored communities and jeopardize the local biodiversity. We assessed the current plant community in an area of the Brazilian Cerrado undergoing restoration, where 42 species – 6 natives and 36 non-natives – were planted, and compared it with the contiguous native community. We aimed at verifying if the surrounding native community has been invaded by alien species, and if the community being restored has been dominated by the latter, not resembling the native flora. Eight years after planting, the alien species were not recorded in the surrounding native ecosystem. In the community undergoing restoration, despite 94% of the planted trees being exotics (86% of the species) they corresponded to only 3% of plants regenerating (14% of the species), indicating that floristic similarity with the native vegetation is increasing over time. We consider that the non-native species planted do not offer threat to the native ecosystems in the vicinity, and tend to be defeated by the natives in the long term. Even though, public policies should prioritize and make feasible the use of native species, better adapted to the harsh environmental conditions of the Cerrado.

Keywords: biological invasion, Cerrado, ecological restoration, invasive species, priority effect.

INTRODUCTION

The importance of invasive plant species has been highlighted because of their economic costs as weeds and because they may cause na-

tive biodiversity losses (WILCOVE et al., 1998; MACK et al., 2000; LEVINE et al., 2003) and alter ecosystem functions (VITOUSEK 1996; RAIZADA et al. 2008; EHRENFELD 2010). Ecological restoration aims at promoting natural

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succession, enabling high biodiversity and establishing a vegetation community similar to the pristine ecosystems. Among the principles established by the Society for Ecological Restoration International – SER is that ‘a restored ecosystem consists of indigenous species to the greatest practicable extent’, and ‘contains a characteristic assemblage of the species that occur in the reference ecosystem’ (SER 2004). Under these principles, we conclude that the use of exotic species for restoration purposes should be avoided. This recommendation is certainly based on the hypothesis that exotics can behave like Greek soldiers that were hidden on the huge wooden horse and brought as a gift into the city walls of Troy, defeating the native soldiers and conquering the new territory. Bringing this metaphor to the context of ecological restoration and biological invasions, we named this as “the Trojan horses’ hypothesis”, which we tested in the Brazilian savanna. This hypothesis is related to the priority effects, which occur when the arrival or earlier growth of one or more species leads to a different community structure than it would be if all species began growth simultaneously (SHULMAN et al. 1983). It has been tested in the context of native x alien species, and the advantage of exotics has been confirmed for herbs, grasses and shrubs (MCEWAN et al., 2009; DICKSON et al., 2012; WAINWRIGHT et al., 2012), but was never tested for tropical trees.

The Cerrado – the Brazilian savanna, with its squat trees of thick bark, twisted trunks and thick twigs, spread over a grass layer, is the second largest biome in Brazil the most extensive savanna in South America, and the richest savanna in the world. It covered more than 2 million km², but has lost about half of this area in the last four decades and is possibly the most threatened tropical savanna in the world (SILVA; BATES, 2002; KLINK; MACHADO, 2005), rapidly replaced by agriculture. As for other degraded biomes in the world, ecological restoration has becoming a priority action for biodiversity conservation of the Cerrado. Restoring the Cerrado vegetation, however, has been by far more difficult than restoring forest biomes in Brazil (DURIGAN; MELO, 2011; PILON; DURIGAN, 2013). The low availability of water and nutrients in the soil, and the unlikely propagation of its native plant species by seeds (LABORIAU et al., 1963; HOFFMANN, 1998; HOFFMANN et al., 2004; MELO et al., 2005) are the natural factors which, besides the invasion by African

grasses, are constraining restoration success in the Cerrado (HOFFMANN; HARIDASAN, 2008; DURIGAN; MELO, 2011). Pilon and Durigan (2013), when indicating framework species to recover the Cerrado vegetation, adopted as criteria the ability of the species to overcome the obstacle posed by the invasive grasses.

Ecological restoration or rehabilitation of the Cerrado vegetation is legally required in some situations (DURIGAN; MELO, 2011), but under the inexistence of seedlings available of native species, which are mostly endemic from this biome, there is not much option left but using species from other biomes or other countries. Many of the exotic species which have been planted in Cerrado restoration are already included in lists of invasive species in Brazil or elsewhere (Instituto Horus, Global Invasive Species Database, ZENNI; ZILLER, 2011). The impact of these non-native species on the Cerrado community, however, has not yet been assessed.

The presence of exotic species in plant communities undergoing restoration must not be considered a problem *per se* (ZAVALETA et al., 2001; D’ANTONIO; MEYERSON, 2002; EWEL; PUTZ, 2004; MARTÍNEZ, 2010; BRUDVIG, 2011). In fact, there are reports on exotics facilitating natural regeneration of native species and helping ecosystem reestablishment (LANTA; LEPS, 2008; SANTIAGO-GARCIA et al., 2008, MARTÍNEZ, 2010; MODNA et al., 2010) or improving ecosystem functioning (PARROTA; KNOWLES, 1999; VANDERHOEVEN, et al., 2005). The performance of exotic and natives often depends on growing conditions and no species can equally invade all ecosystems (DAEHLE, 2003; COLAUTTI; MCISAAC, 2004). Biological invasion proceeds when invasivity of the species matches with invasibility of the ecosystem (REJMÁNEK, 1999; ALPERT, et al., 2000; PYSEK; RICHARDSON, 2007; RICHARDSON; REJMÁNEK, 2011), and a species can be an effective invader only inside a particular ecological region (COLAUTTI; MCISAAC, 2004).

We assessed the current plant community in a stand of Cerrado vegetation undergoing restoration where a number of non-native species were inadvertently planted, and compared it with the contiguous native community. First, we investigated if the non-native species planted were colonizing the native vegetation around, already performing as invasive. In the community undergoing restoration, we verified if there is a tendency of the non native species planted to dominate the

community over time, on the basis of their proportion among the trees planted and individuals spontaneously regenerating in the understory.

METHODS

Study site

The Assis State Forest (Assis, state of Sao Paulo, Brazil, coordinates 22° 37' 41" S, 50° 21' 27" W) is a protected area in the southern borders of the Cerrado biome, in altitudes ranging from 500 to 588 m.a.s.l. The regional climate is between Cwa and Cfa subtropical climates (Köppen's classification), with a rainy summer and a dry winter. Mean annual precipitation is around 1.400 mm, and mean temperature is 21.8°C (PINHEIRO; DURIGAN, 2009). The soil at the study site is classified as Red Dystrophic Oxysol, which is deep, sandy, acid and poor as are most of Cerrado soils (REATTO et al., 2008). The local native vegetation is classified as Cerrado *sensu lato*, being the cerradão (woodland savanna) the dominant physiognomy. The woodland savanna has a forest physiognomy with a continuous arboreal stratum, shading about 90% of the ground (PINHEIRO; DURIGAN, 2009). This study encompasses an area of 20 ha undergoing restoration and a remnant of woodland savanna of 8 ha in the vicinity, both situated more than 200 m far from the riparian zone.

Restoration background

In order to duplicate the width of an existing road near the Assis State Forest, a number of isolated trees and small fragments of native vegetation were removed. The Brazilian legislation requires compensation of the environmental impacts caused by an enterprise and that includes ecological restoration in the same region, and recovering the same vegetation type which was destroyed (see ARONSON et al., 2011; DURIGAN; MELO, 2011). For the Cerrado, in the state of São Paulo, an area four times greater than the impacted area must be restored (SÃO PAULO, 2009). To comply with the law by compensating the removal of native vegetation along the road, a restoration planting was carried out at Assis State Forest, aiming to recover an area previously occupied by pasture, and thus increasing the areas of habitat for the native species of the Cerrado biome.

Restoration planting took place in January 2003, after more than three decades of use as pasture of *Urochloa decumbens* (Poaceae), an

invasive African grass that has been one of the most severe threats to the Cerrado biome (PIVELLO et al., 1999; KLINK; MACHADO, 2005; DURIGAN et al., 2007). Cattle had been excluded for some years and a natural regeneration process was taking place (data published by DURIGAN et al., 1998). Two years before the restoration planting, the entire area was accidentally burned and the high biomass of invasive grasses resulted in total destruction of the native biomass. From the set of tree species planted, only a small portion were native from the local Cerrado, and the majority came from other biomes in Brazil or from other countries. Some of the species planted are included amongst the most aggressive invasive species in the world according to the Global Invasive Species Database (2005), such as *Leucaena leucocephala* (Fabaceae Mimosoideae), *Schinus terebinthifolius* (Anacardiaceae) and *Spathodea campanulata* (Bignoniaceae). Others are amongst the species considered invasive in Brazil (ZENNI; ZILLER, 2011), including *Clitoria fairchildiana* (Fabaceae Faboideae), *Hovenia dulcis* (Rhamnaceae) and *Tecoma stans* (Bignoniaceae). The explanation from the company in charge of restoration for including this high number of non-native species was, as usual, the lack of seeds and seedlings from Cerrado species promptly available. Seedlings were planted in an average density of 1000 ind.ha⁻¹, about 3 x 3 m spacing. The area being restored is bordered in its full extent by a fragment of native vegetation – the woodland savanna. We used this fragment as a reference ecosystem for the native flora and it was also surveyed in search of invasive individuals from the non-native species introduced in the planted stand.

Data collection and analyses

We sampled 40 plots of 200 m² each (40 m x 5 m) randomly distributed in the area undergoing restoration, at eight years after planting, and 10 plots (the same size) in the reference ecosystem. In each plot, all woody plants from 50 cm in height were identified and recorded. In addition to the origin of the species (native or non-native), we categorized each individual sampled as planted (in regularly spaced lines) or not planted (naturally established). We also described the species by dispersal syndrome and shade tolerance, on the basis of previous studies (DURIGAN et al., 2004; PILON; DURIGAN, 2013), and literature on exotic species (LORENZI et al., 2003). We separated the individuals in

three size classes: a) stem diameter taken at 30 cm above ground – $D_{30} < 1$ cm; b) $1 \text{ cm} \leq D_{30} < 5$ cm; and c) $D_{30} \geq 5$ cm. Reproductive individuals were recorded, in order to indicate if the species could, potentially, leave descendants.

The stem diameter was measured for all individuals with $D_{30} \geq 5$ cm, in order to estimate the basal area of the community. In addition, canopies and grass cover were estimated by the line interception method (CANFIELD, 1941), over a line 40 m long in the middle of each plot.

Absolute and relative densities of the species in the community being restored and in the native vegetation were calculated separately by size class, species origin (native or non-native) and for planted or naturally established individuals. Relative density was calculated as the proportion of individuals of a particular group among all individuals in the community. We applied Chi-square test to verify if the proportions differ between groups.

The Jaccard's similarity index - ISj (MÜLLER-DOMBOIS; ELLENBERG, 1974) between the floristic composition of the reference ecosystem and that being restored was calculated for each size class. We considered the smaller plants as the last to arrive at the community (the youngest). The Jaccard's similarity index between two communities corresponds to the proportion of the total number of species sampled which is common to both communities. Two communities are considered floristically similar if at least 25% of the species ($ISj = 0.25$) are in common (MÜLLER-DOMBOIS; ELLENBERG, 1974).

For each non-native species planted, we compared the relative density among the planted individuals and among those naturally regenerating. We considered as potentially invasive a species if its frequency (relative density) was higher among plants in natural regeneration than among the planted individuals.

RESULTS & DISCUSSION

Community structure: The reference ecosystem presented a basal area of $19.76 \text{ m}^2 \cdot \text{ha}^{-1}$, canopy cover of 90% and grasses were absent. The density was 1225 individuals ha^{-1} in the arboreal layer and 6040 individuals ha^{-1} in the understory (stem diameter below 5 cm), from 53 species. In the community undergoing restoration, basal area was $5.12 \text{ m}^2 \cdot \text{ha}^{-1}$, canopy cover was 66% and invasive grasses occupied 67% of the area; density was 489 individuals ha^{-1} of planted trees

and 2418 individuals ha^{-1} of plants in natural regeneration, summing up 78 species (Table 1).

Origin of the species: In the Cerrado fragment (reference ecosystem), all individuals surveyed in the arboreal layer as well as in the understory were from native species (53 species recorded). In the community being restored, among the 42 species planted, 14% were native (6 species) and 86% were non-natives (36 species). From the regenerating community, 86% of the species (38 species) were native and 14% were non-natives (6 species) (Table 1).

The evidence from this study indicates that the woodland savanna has been resistant to invasion by the exotic species, since not even a single individual from the alien species already reproducing was recorded in the native ecosystem. However, considering that a lag phase is common between establishment and spread, when the invasive species adapt to the new community (SAKAI et al., 2001; BARNEY, 2006), the time period since the introduction of the non-natives was too short for a conclusion, requiring monitoring of the native ecosystem in the long term. Studies have shown that the community assembly in the woodland savanna is mediated by competition for light and soil water (ABREU et al., 2011; ASSIS et al., 2011), and these are, probably, the ecological filters locally constraining the establishment of the alien species in the native ecosystem.

The alien species planted are not colonizing the area being restored either. It was hypothesized that alien species are not adapted to the harsh environmental conditions of the Cerrado and, therefore, do not reproduce or regenerate in the study site. Soil water deficiency in addition to acid and poor soils, can have either delayed or inhibited those species to reach their reproductive stage or to establish. In fact, Figure 1 reveals that, among the species planted, the natives have been relatively better succeeded than exotics in reproduction.

Reproductive stage: 42 of all 78 species sampled in the community undergoing restoration (planted or regenerating) were already in reproductive age in the restored area or in the native vegetation around. From these species, 26 species are native from Cerrado, while the others (16) do not occur in the study region. Considering only the planted trees, 20 species have reached reproductive stage, being four natives and 16 non-natives. The proportion of species reproducing among those planted ($\chi^2 = 10.021$; $p < 0.05$; $d.f = 1$) is higher among natives than non-natives (Figure 1).

Table 1. Arboreal species sampled in the Cerrado area undergoing restoration, their functional attributes (shade tolerance and dispersal syndrome), if planted or not, reproducing or not, native or non native, status as invasive in Brazil, and relative density among planted trees, among individuals in natural regeneration and in the reference ecosystem (Assis State Forest, Assis, SP, Brazil).

Tabela 1. Espécies arbóreas amostradas na área de restauração de Cerrado, atributos funcionais (tolerância à sombra e síndrome de dispersão), se plantadas ou não, reprodutivas ou não, nativas ou não, status como invasoras no Brasil, e densidade relativa entre árvores plantadas, entre indivíduos em regeneração natural e no ecossistema de referência (Floresta Estadual de Assis, Assis, SP, Brasil).

Species	Shade tolerance	Dispersal syndrome	Planted species	Reproducing	Geographical origin	Status as invasive	Relative density (%)		
							Among planted trees	Among regenerating individuals in the restored area	In the Reference ecosystem
<i>Acacia mangium</i>	Intolerant	Barochory	Planted	Yes	non native	Invasive	0.26	0.00	0.00
<i>Acacia paniculata</i>	Intolerant	Barochory	Planted		native		0.51	0.10	0.00
<i>Actinostemon conceptionis</i>	Tolerant	Barochory		Yes	native		0.00	0.00	0,08
<i>Aegiphila lhotskiana</i>	Intolerant	Zoochory		Yes	native		0.00	0.78	0,04
<i>Albizia lebbbeck</i>	Intolerant	Barochory	Planted		non native		1.28	0.00	0.00
<i>Amaioua intermedia</i>	Tolerant	Zoochory		Yes	native		0.00	0.00	0,04
<i>Anadenanthera falcata</i>	Intolerant	Barochory	Planted	Yes	native		1.54	0.00	0.00
<i>Anadenanthera macrocarpa</i>	Intolerant	Barochory	Planted	Yes	non native		11.03	0.16	0.00
<i>Annona dioica</i>	Intolerant	Zoochory		Yes	native		0.00	0.62	0.00
<i>Annona muricata</i>	Intolerant	Zoochory	Planted		non native		0.51	0.00	0.00
<i>Astronium graveolens</i>	Tolerant	Anemochory			native		0.00	0.00	0,04
<i>Baccharis dracunculifolia</i>	Intolerant	Anemochory		Yes	native		0.00	21.93	0.00
<i>Bauhinia longifolia</i>	Tolerant	Barochory	Planted	Yes	non native		1.79	0.26	0.00
<i>Bauhinia variegata</i>	Intolerant	Barochory	Planted	Yes	non native		3.85	0.00	0.00
<i>Bixa orellana</i>	Intolerant	Zoochory	Planted	Yes	non native		1.03	0.00	0.00
<i>Bredemeyera floribunda</i>	Intolerant	Anemochory		Yes	native		0.00	1.98	0,12
<i>Byrsonima intermedia</i>	Intolerant	Zoochory			native		0.00	0.78	0,29
<i>Byrsonima laxiflora</i>	Tolerant	Zoochory			native		0.00	0.10	0,08
<i>Caesalpinia ferrea</i>	Tolerant	Barochory	Planted		non native		0.10	0.05	0.00
<i>Caesalpinia peltophoroides</i>	Intolerant	Barochory	Planted		non native		2.05	0.00	0.00
<i>Callicarpa reevesii</i>	Intolerant	Zoochory	Planted		non native		0.26	0.00	0.00
<i>Caryocar brasiliense</i>	Intolerant	Zoochory		Yes	native		0.00	0.00	0,62
<i>Casearia silvestris</i>	Tolerant	Zoochory		Yes	native		0.00	0.10	0.00
<i>Cecropia pachystachya</i>	Intolerant	Zoochory	Planted	Yes	native		2.05	0.00	0.00
<i>Cedrela fissilis</i>	Tolerant	Anemochory	Planted		non native		1.28	0.00	0.00
<i>Ceiba speciosa</i>	Intolerant	Anemochory	Planted		non native		0.26	0.00	0.00
<i>Clitoria fairchildiana</i>	Intolerant	Barochory	Planted	Yes	non native	Invasive	4.62	0.00	0.00
<i>Cojoba sophorocarpa</i>	Intolerant	Barochory	Planted		non native		0.77	0.00	0.00
<i>Copaifera langsdorffii</i>	Tolerant	Zoochory			native		0.00	0.05	4,44
<i>Cordia sellowiana</i>	Tolerant	Zoochory		Yes	native		0.00	0.00	0,29
<i>Couepia grandiflora</i>	Intolerant	Zoochory		Yes	native		0.00	0.00	0,21
<i>Croton floribundus</i>	Intolerant	Barochory	Planted	Yes	non native		0.26	0.31	0,25
<i>Croton urucurana</i>	Intolerant	Barochory	Planted	Yes	non native		1.79	0.00	0.00
<i>Cupania tenuivalvis</i>	Tolerant	Zoochory		Yes	native		0.00	0.00	0,99
<i>Dimorphandra mollis</i>	Intolerant	Barochory		Yes	native		0.00	0.16	0.00
<i>Diospyros hispida</i>	Intolerant	Zoochory			native		0.00	0.05	0.00
<i>Diospyros inconstans</i>	Tolerant	Zoochory			native		0.00	0.16	0.00
<i>Duguetia furfuracea</i>	Intolerant	Zoochory		Yes	native		0.00	0.26	0,08
<i>Enterolobium contortisiliquum</i>	Intolerant	Barochory	Planted		non native		0.26	0.00	0.00
<i>Erythroxylum pelleterianum</i>	Tolerant	Zoochory		Yes	native		0.00	0.00	0,21
<i>Eugenia lambertiana</i>	Tolerant	Zoochory		Yes	native		0.00	0.00	0,25
<i>Eugenia punicifolia</i>	Intolerant	Zoochory			native		0.00	0.21	0,41
<i>Genipa americana</i>	Intolerant	Zoochory	Planted		non native		0.77	0.00	0.00
<i>Gochnatia barrosii</i>	Intolerant	Anemochory			native		0.00	5.82	0,33
<i>Gochnatia polymorpha</i>	Intolerant	Anemochory		Yes	native		0.00	0.16	0,21
<i>Helicteres lhotzkyana</i>	Intolerant	Anemochory	Planted	Yes	native		0.26	0.00	0.00
<i>Hovenia dulcis</i>	Tolerant	Zoochory	Planted		non native	Invasive	3.85	0.00	0.00

Table 1 - Continuation. Arboreal species sampled in the Cerrado area undergoing restoration, their functional attributes (shade tolerance and dispersal syndrome), if planted or not, reproducing or not, native or non native, status as invasive in Brazil, and relative density among planted trees, among individuals in natural regeneration and in the reference ecosystem (Assis State Forest, Assis, SP, Brazil).

Tabela 1 - Continuação. Espécies arbóreas amostradas na área de restauração de Cerrado, atributos funcionais (tolerância à sombra e síndrome de dispersão), se plantadas ou não, reprodutivas ou não, nativas ou não, status como invasoras no Brasil, e densidade relativa entre árvores plantadas, entre indivíduos em regeneração natural e no ecossistema de referência (Floresta Estadual de Assis, Assis, SP, Brasil).

Species	Shade tolerance	Dispersal syndrome	Planted species	Reproducing	Geographical origin	Status as invasive	Relative density (%)		
							Among planted trees	Among regenerating individuals in the restored area	In the Reference ecosystem
<i>Hymenaea courbaril</i>	Tolerant	Zoochory	Planted		non native		1,03	0.00	0.00
<i>Hymenaea stigonocarpa</i>	Tolerant	Zoochory		Yes	native		0.00	0.00	0,04
<i>Inga laurina</i>	Intolerant	Zoochory	Planted		non native		1.28	0.00	0.00
<i>Jacaranda caroba</i>	Intolerant	Anemochory		Yes	native		0.00	0.52	0,99
<i>Jacaranda cuspidifolia</i>	Intolerant	Anemochory	Planted		non native		4.10	0.00	0.00
<i>Lacistema hasslerianum</i>	Tolerant	Zoochory		Yes	native		0.00	0.00	0,04
<i>Lafoensia pacari</i>	Tolerant	Anemochory	Planted	Yes	native		0.26	0.05	0.00
<i>Luehea candicans</i>	Tolerant	Anemochory			native		0.26	0.05	0.00
<i>Mabea fistulifera</i>	Tolerant	Barochory		Yes	native		0.00	4.99	5,80
<i>Machaerium aculeatum</i>	Intolerant	Anemochory		Yes	native		0.00	0.00	0,21
<i>Machaerium acutifolium</i>	Intolerant	Anemochory		Yes	native		0.00	0.00	0,99
<i>Machaerium brasiliense</i>	Intolerant	Anemochory		Yes	native		0.00	0.68	0.00
<i>Maprounea guianensis</i>	Tolerant	Zoochory		Yes	native		0.00	0.00	4,03
<i>Melia azedarach</i>	Intolerant	Zoochory	Planted		non native	Invasive	0.77	0.00	0.00
<i>Memora axillaris</i>	Intolerant	Anemochory		Yes	native		0.00	0.10	0.00
<i>Miconia albicans</i>	Tolerant	Zoochory			native		0.00	0.16	4,57
<i>Miconia ligustroides</i>	Tolerant	Zoochory		Yes	native		0.00	0.00	0,08
<i>Miconia stenostachya</i>	Tolerant	Zoochory		Yes	native		0.00	0.00	0,95
<i>Mimosa caesalpinifolia</i>	Intolerant	Barochory	Planted	Yes	non native	Invasive	11.54	0.00	0.00
<i>Mimosa setosa</i>	Intolerant	Barochory	Planted	Yes	non native		3.08	2.23	0.00
<i>Myrcia fallax</i>	Tolerant	Zoochory			native		0.00	0.10	3,13
<i>Myrcia guianensis</i>	Tolerant	Zoochory		Yes	native		0.00	0.57	12,59
<i>Myrcia lingua</i>	Intolerant	Zoochory		Yes	native		0.00	0.00	0,04
<i>Myrcia multiflora</i>	Tolerant	Zoochory		Yes	native		0.00	0.00	2,18
<i>Myrciaria floribunda</i>	Tolerant	Zoochory		Yes	native		0.00	0.00	0,62
<i>Nectandra cuspidata</i>	Tolerant	Zoochory		Yes	native		0.00	0.00	1,73
<i>Nerium oleander</i>	Intolerant	Anemochory	Planted		non native		0.26	0.00	0.00
<i>Ocotea corymbosa</i>	Tolerant	Zoochory			native		0.00	0.99	7,32
<i>Peltophorum dubium</i>	Intolerant	Anemochory	Planted	Yes	non native		13.59	0.10	0.00
<i>Pera obovata</i>	Tolerant	Barochory		Yes	native		0.00	0.10	0.00
<i>Persea wildenovi</i>	Tolerant	Zoochory		Yes	native		0.00	0.00	0,25
<i>Pouteria ramiflora</i>	Tolerant	Zoochory			native		0.00	0.05	2,71
<i>Protium heptaphyllum</i>	Tolerant	Zoochory		Yes	native		0.00	0.00	0,04
<i>Pseudolmedia laevigata</i>	Tolerant	Zoochory		Yes	native		0.00	0.00	0,25
<i>Psidium guajava</i>	Intolerant	Zoochory	Planted	Yes	non native	Invasive	0.26	0.00	0.00
<i>Qualea cordata</i>	Intolerant	Anemochory		Yes	native		0.00	0.00	0,21
<i>Qualea grandiflora</i>	Intolerant	Anemochory		Yes	native		0.00	0.00	0,25
<i>Roupala montana</i>	Tolerant	Anemochory		Yes	native		0.00	0.57	0,45
<i>Schefflera vinosa</i>	Intolerant	Zoochory		Yes	native		0.00	0.00	1,60
<i>Schinus molle</i>	Intolerant	Zoochory	Planted		non native		1.03	0.00	0.00
<i>Schinus terebinthifolius</i>	Intolerant	Zoochory	Planted	Yes	non native		10.51	0.16	0.00
<i>Senna alata</i>	Intolerant	Barochory	Planted	Yes	non native		0.26	0.00	0.00
<i>Senna rugosa</i>	Intolerant	Zoochory		Yes	native		0.00	0.78	0,04
<i>Senna siamea</i>	Intolerant	Barochory	Planted		non native		0.26	0.00	0.00
<i>Siparuna guianensis</i>	Tolerant	Zoochory		Yes	native		0.00	0.00	15,14
<i>Solanum paniculatum</i>	Intolerant	Zoochory		Yes	native		0.00	37.32	0.00
<i>Spathodea nilotica</i>	Intolerant	Anemochory	Planted		non native		0.77	0.00	0.00

Table 1 - Continuation. Arboreal species sampled in the Cerrado area undergoing restoration, their functional attributes (shade tolerance and dispersal syndrome), if planted or not, reproducing or not, native or non native, status as invasive in Brazil, and relative density among planted trees, among individuals in natural regeneration and in the reference ecosystem (Assis State Forest, Assis, SP, Brazil).

Tabela 1 - Continuação. Espécies arbóreas amostradas na área de restauração de Cerrado, atributos funcionais (tolerância à sombra e síndrome de dispersão), se plantadas ou não, reprodutivas ou não, nativas ou não, status como invasoras no Brasil, e densidade relativa entre árvores plantadas, entre indivíduos em regeneração natural e no ecossistema de referência (Floresta Estadual de Assis, Assis, SP, Brasil).

Species	Shade tolerance	Dispersal syndrome	Planted species	Reproducing	Geographical origin	Status as invasive	Relative density (%)		
							Among planted trees	Among regenerating individuals in the restored area	In the Reference ecosystem
<i>Strychnos brasiliensis</i>	Intolerant	Zoochory			native		0.00	0.26	1,85
<i>Stryphnodendron obovatum</i>	Intolerant	Barochory		Yes	native		0.00	14.40	0,99
<i>Tabebuia impetiginosa</i>	Intolerant	Anemochory	Planted		non native		4.87	0.00	0.00
<i>Tabebuia ochracea</i>	Intolerant	Anemochory		Yes	native		0.00	0.00	0,21
<i>Tabernaemontana catharinensis</i>	Tolerant	Zoochory		Yes	native		0.00	0.83	0.00
<i>Tapirira guianensis</i>	Tolerant	Zoochory			native		0.00	0.05	0,78
<i>Tecoma stans</i>	Intolerant	Anemochory	Planted	Yes	non native	Invasive	2.82	0.00	0.00
<i>Terminalia glabrescens</i>	Intolerant	Anemochory	Planted		native		1.03	0.00	1,07
<i>Tibouchina granulosa</i>	Intolerant	Anemochory	Planted	Yes	non native		1.79	0.00	0.00
<i>Vernonia polyanthes</i>	Intolerant	Anemochory		Yes	native		0.00	0.42	0.00
<i>Vochysia tucanorum</i>	Intolerant	Anemochory		Yes	native		0.00	0.10	4,48
<i>Xylopia aromatica</i>	Intolerant	Zoochory		Yes	native		0.00	0.42	15,43

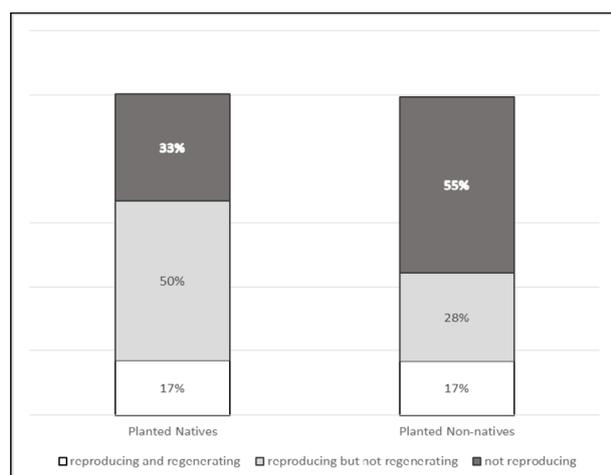


Figure 1. Proportions of the species planted (natives and non-natives) which 1) did not reach the reproductive stage (non-reproductive), 2) are in reproductive stage, but do not leave descendants (reproductive not established) or 3) are naturalized (reproductive and leaving descendants).

Figura 1. Proporção de espécies plantadas (nativas e não nativas) que 1) não atingiram estado reprodutivo (não reprodutivas), 2) estão em estado reprodutivo, mas não deixam descendentes (reprodutivas mas não estabelecidas) e 3) estão naturalizadas (reprodutivas e deixando descendentes).

The relative density (proportion of individuals) by the origin of the species (natives x non-natives) (Figure 2) was distinct between the regenerating stratum and the set of planted trees (Chi-square test: $\chi^2=165$; $p<0.001$, d.f=1, Figure 2). The restoration planting was composed mainly by exotic species, which summed up to

86% of all species. This unbalance, however, has not been sufficient to favor the alien species in colonizing the area being restored, since the regenerating stratum is strongly dominated by the natives (Figure 2 a). The remarkably higher relative abundance of exotics among the planted trees (Figure 2 b) could potentially increase the propagule pressure, which is one of the predictors of invasion success cited in many studies (WILLIAMSON, 1996). The priority effects being stronger for alien than native species (MCEWAN et al. 2009; DICKSON et al. 2012; WAINWRIGHT et al. 2012) were not observed in this study.

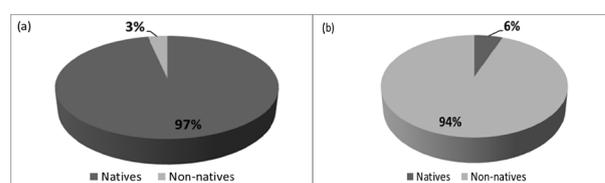


Figure 2. Proportion of individuals from native and non-native species in an area of Cerrado undergoing restoration, southeastern Brazil. (a) among the naturally regenerated individuals; (b) among the planted individuals.

Figura 2. Proporção de indivíduos de espécies nativas e não nativas em área de Cerrado que se encontra em processo de restauração, sudeste do Brasil. (a) entre indivíduos naturalmente regenerantes, (b) entre indivíduos plantados.

When every single species is analyzed, the relative abundance in the community regenerating was never higher for the alien species than the proportion of the species among the

individuals planted (Table 1). *Mimosa setosa* (Fabaceae Mimosoideae) presented the highest relative density among individuals naturally regenerating (2.23%), but it is still lower than among planted trees of this species (3.08%). This is a short lived treelet native from the dry regions of northeastern Brazil, which has adapted to the severity of the local environmental conditions, and requires attention. Since this species is not shade tolerant, however, its persistence in the area undergoing restoration will probably not be possible in the future, when the forest structure of the native vegetation is reached. Four native species not planted – *Solanum paniculatum* (zoochorous and shade intolerant), *Stryphnodendron obovatum* (barochorous and shade intolerant), *Gochnatia barrosii* (anemochorous and shade intolerant) and *Mabea fistulifera* (barochorous and shade tolerant), have higher relative densities than *M. setosa*. These species sum up 62.51% of individuals in the understory (Table 1), clearly dominating the community, and not showing a functional pattern among colonizers. All other non-native introduced species may reproduce occasionally in the community undergoing restoration but have not been able to replace adult trees and rely on repeated introductions to sustain their populations. Although further studies are required to draw definite conclusion, we observe that these species have, actually, performed as nurse trees (CALLAWAY, 1995) for the natives and are expected to go extinct when the adult trees die out. Consequently, they would not result in invasion if used for restoration purposes in the Cerrado region, even if they are invasive elsewhere. The same function, however, should certainly be performed by some native species, like those indicated as framework species for Cerrado restoration by Pilon and Durigan (2013), if there were seedlings available. As observed by Daehler (2003) and Colautti and McIsaac (2004), the performance of exotic and natives within a particular ecological region often depends on growing conditions and no species can equally invade all ecosystems. Richardson et al. (2000) states that “only a small fraction of all introduced taxa reproduce and spread over large areas; most taxa fail at some stage before reaching such levels of success”.

The relative density of native species regenerating differs among size classes ($\chi^2 = 7.6$; $p < 0.05$; d.f = 2), with natives increasing as the plant size decreases (Figure 3). Considering that

the smaller plants were the last to arrive to the community, the proportion of natives has increased with time after restoration planting.

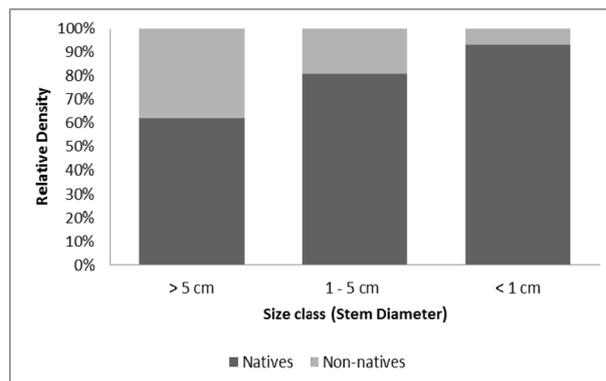


Figure 3. Relative density of native and non-native individuals in the community undergoing restoration, in each size class.

Figura 3. Densidade relativa de indivíduos nativos e não nativos na comunidade em processo de restauração, em cada classe de tamanho.

The floristic similarity with the reference ecosystem (Figure 4) tends to increase with time, considering the youngest plants as the last to arrive to the community. When the younger plants are analyzed (diameter below 1 cm); the community undergoing restoration can already be considered floristically similar to the reference ecosystem ($IS_j > 0.25$).

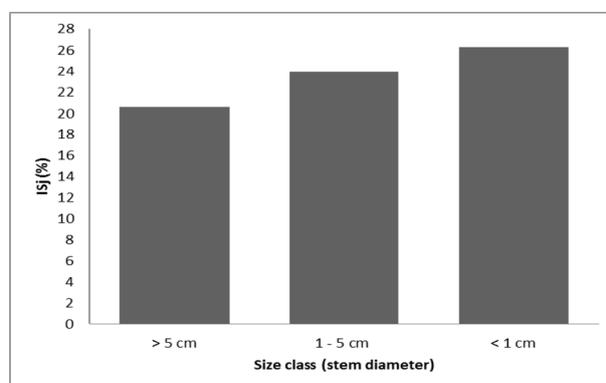


Figure 4. Jaccard's Similarity Index (IS_j) between the floristic composition of the reference ecosystem and the community undergoing restoration, calculated for three size classes according to the stem diameter.

Figura 4. Índice de Similaridade de Jaccard (IS_j) entre a composição florística do ecossistema de referência e a comunidade em restauração, calculado para três classes de tamanho, conforme diâmetro do caule.

Our results revealed that non-native species introduced aiming at restoration made the community floristically distinct from the native vegetation. The young trees regenerating, however, which are mostly native (Figure 3), have already reached floristic similarity with the reference

vegetation (Figure 4), with Jaccard's Similarity Index higher than 25% (MÜLLER-DOMBOIS; ELLENBERG, 1974) if the smaller size class is included in the analysis. That is a consequence of the continuous immigration of native species from the surrounding native vegetation and from native adult trees in the area undergoing restoration (Figure 2). Therefore, the plant community is evolving towards native ecosystem despite of the inadvertently massive introduction of alien species. Apparently, the community assembly has followed the 'self-design' capacity of nature (MITSCH; WILSON, 1996) with the native species assembling by themselves given a long time period (*ca* 15–20 years).

CONCLUSION

Our findings did not support the Trojan's horse hypothesis, since the alien species, even if intentionally introduced, have not proven to be able to spread over the ecosystem undergoing restoration and to dominate the community or invading the native ecosystems around. Alternatively, the natives are winning the battle, and the community is becoming more similar to the native vegetation through time. The presence of exotic species in plant communities being restored has not been considered a problem per se. If native and non-native species are both planted in a restoration project or if there are seed sources in the vicinity, the natives tend to succeed relatively better in regenerating and colonizing areas of woodland savanna (*cerradão*) undergoing restoration. The non-natives tend to be naturally eliminated from the community.

Monitoring the non-native species in the long term is recommended, to identify possible threats of invasion (species to be necessarily banned from restoration) as well as exotic species which can act as nurse trees ("friendly" alien species), fostering the natural regeneration of *Cerrado* species. The use of native species for restoration is always preferable, particularly if seedlings of a set of framework species can be obtained. However, as far as production of seedlings of native *Cerrado* species in large scale persists as a technical obstacle to be surpassed, a pool of friendly non-natives can, potentially, help recovering at least some ecosystem services and catalyzing the latter arrival of the natives in severely degraded areas.

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