

The role of roadsides in conserving Cerrado plant diversity

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Abstract The structure of Cerrado vegetation (*sensu stricto*) along roadsides was compared with that of protected areas (reserves). The superior stratum of reserves had 2.7 times more individuals and 1.4 times more species than on roadsides, while in the intermediate stratum there were 1.7 times more individuals and 25 % more species in reserves. Additionally, roadsides had a lower prevalence of tree species with thin bark and from forest physiognomies. In the intermediate stratum of roadsides there was a lower proportion of forest species, and also fewer species dispersed by animals. These differences occur, possibly because the vegetation of their edges is cleared during the construction of the roads and part of the soil is taken as landfill. Later, they suffer from a higher fire frequency and high coverage of exotic grasses (80 % average). Moreover, it is likely that the absence of some dispersers on roadsides may affect the recruitment of young plants. Despite these differences, the roadsides are able to maintain at least 70 % of tree species and 72 % of shrub species found in reserves. These results show that roadside vegetation can contribute

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to the conservation of the flora of Cerrado. This is particularly important considering that over 60 % of the original area of this ecosystem has been destroyed and that less than 4 % is protected. With 32,012 km of roads in the Cerrado alone, the roadside vegetation may represent a cumulative area of 96,000 of hectares, an area larger than many of the Cerrado's national parks.

Keywords Conservation · Exotic species · Fire · Highway · Resilience · Road verge

Introduction

Roads are very important to local and national economic development. However, they can also be major causes of biodiversity loss (Fearnside 1990; Forman and Alexander 1998; Trombulak and Frissell 2000) because the access provided by them to previously isolated areas increases rates of deforestation (Trombulak and Frissell 2000; Fearnside et al. 2009). Roads may also affect hydrological processes via erosion and the disruption of water-courses (Campbell and Doeg 1989; Jones et al. 2000), act as barriers to dispersal (Mader 1984; Shepard et al. 2008), and alter animal behavior due to noise pollution (Reijnen et al. 1996). Finally, vehicle traffic can kill wild animals (Clevenger et al. 2003; Coelho et al. 2008; Bager and Rosa 2010) and generate dust and pollutants that have deleterious effects on roadside vegetation (Rogers et al. 1979; Thompson et al. 1984).

One of the principal negative impacts of roads is the introduction and spread of exotic and invasive plant species (Parendes and Jones 2000; Gelbard and Belnap 2003). Road construction exposes soil in which the seeds attached to tires (Veldman and Putz 2010) can germinate, increases light availability, and results in frequent fires that reduce native plant biomass and the availability of some soil nutrients (Dantonio and Vitousek 1992). While the way in which roads lead to the establishment of invasive taxa is increasingly well understood, surprisingly little is known about the structure of native plant communities along roadsides and the extent to which they persist through the associated disturbances (Way 1977; Dunnett et al. 1998; Spooner and Smallbone 2009). If a sufficient proportion of native plant species are able to persist in roadsides verges, these areas could be an important component of conservation and restoration strategies (*sensu* Haan et al. 2012).

Not all native plant species will have the same likelihood of persisting when biotic and abiotic conditions change along roadsides. For example, frequent fires can favor species with thick bark and greater capacity for regrowth, both of which are traits that are positively correlated with resistance to fire (Coutinho 1990; Uhl and Kauffman 1990; Hengst and Dawson 1993). Similarly, the reduced density of animals along roadsides (Clevenger et al. 2003; Coelho et al. 2008; Bager and Rosa 2010) and absence of some birds due to noise pollution (Reijnen et al. 1996) may limit the recruitment of plant species that depend on these animals for dispersal. Nevertheless, few studies have evaluated the characteristics of the species that survive in roadside environments (Parendes and Jones 2000; Zeng et al. 2011).

Most investigations of plant communities along roadsides have been conducted in the temperate zone, especially grasslands in Europe (Way 1977; Ullmann and Heindl 1989; Dunnett et al. 1998; Cousins 2006) and China (Zhao et al. 2008; Leung et al. 2009; Zeng et al. 2011). However, the economic expansion of many developing countries in the tropics has led to a tremendous increase in road construction. For instance, Brazil currently has a network of paved and unpaved roads that extend more than 1.7 million kms (DNIT 2013). Besides, a major Brazilian government plan for economic growth (named “Programa de

Aceleração do Crescimento”) proposes investments of over US\$ 25 billion for the construction of 8,000 km of new roads and the widening of 55,000 km of existing roads by 2014 (Agência Brasil 2013). This proposed expansion is taking place with a paucity of data on the ecological impacts of road construction beyond a few studies focusing on wildlife roadkill (Vieira 1996; Gumier-Costa and Sperber 2009; Bager and Rosa 2010). Similar plans for the expansion of road networks have been put forward in other species-rich tropical locations (e.g., the Trans-African Highway, the Indian North–South–East–West Corridor; Laurance et al. 2006).

The savanna woodland of central Brazil known as the Cerrado, is a biodiversity hotspot with an estimated 12,000 plant species, of which approximately one third are endemic (Mendonça et al. 2008). Like many savanna ecosystems, the Cerrado is actually a gradient of vegetation types from open grasslands to closed canopy forests, all of which are influenced by frequent fires (Ribeiro et al. 1985; Oliveira-Filho and Ratter 2002). Because of its size (2 millions km²) and the critical role it plays in Brazil’s emergence as a global agricultural power (FAO 2004), the Cerrado’s extensive road network has been planned for expansion, making it an ideal model system to understand how roads alter the structure of native plant assemblages. The vegetation along roadsides were compared with that of nearby reserves to address the following questions:

- (1) Are there differences in the abundance and species richness of native and exotic plants between roadside vegetation and nearby Cerrado reserves? We predict lower abundance and richness on disturbed roadsides than in reserves given the frequent burning and other impacts in roadsides.
- (2) Are there differences in the proportion of individuals and species with thick bark and typical of savanna physiognomies (both proxies for adaptation to fire) between roadsides and reserves? We predict that roadsides will have a greater proportion of individuals with thick bark and from savanna physiognomies because frequent fires on roadsides lead to the loss of fire-sensitive species.
- (3) Are there differences in the proportion of species dispersed by animals between roadsides and reserves? We predict that roadsides will have lower proportions of species and individuals dispersed by animals due to the cumulative effects of reduced animal abundance.

Methods

Study sites

The study was conducted in areas of Cerrado *sensu stricto* in Minas Gerais State, Brazil. This vegetation type represents approximately 70 % of the Cerrado biome and is characterized by scattered trees, shrubs, and an herbaceous layer dominated by grasses (Eiten 1994). Average monthly temperature in the region where we conducted our surveys is 22.8 °C; the average annual rainfall is 1600 mm with more than 70 % occurring between November and March (Rosa et al. 1991; Cardoso et al. 2009). The dominant soils of the region are oxisols, with poor nutrient availability and moderate to strong acidity (Lopes and Cox 1977; Haridasan and Araújo 1987).

The surveys took place from May 2009 to March 2010. We surveyed 19 sites with remnant Cerrado vegetation along roadsides (Appendix A, Supplementary material) and 10 sites in private Cerrado reserves ranging in size from 17 to 441 hectares (Appendix B,

Supplementary material). The roadside vegetation surveys were conducted in the area adjacent to the roads (Appendix C, Supplementary material) where legislation prevents any activity except the expansion of the road itself (DNIT 2013). These areas are subjected to disturbance during building of the road including the removal of vegetation and often topsoil for using in road surfacing. After the construction of the road is concluded, an area of about 20 m wide on each side of the road is abandoned allowing vegetation to regenerate. The 19 roadside sites were chosen based on their proximity to the reserves studied to minimize potential problems of geographic variation in plant species composition between sites. The sites also had similar geographic characteristics such as soil drainage and topography. There were no fires in the private reserves in the 10 years prior to our surveys (Carmo et al. 2011).

Sampling

Three strata were considered for vegetation sampling: an superior stratum predominantly of trees with trunks of circumference at breast height (CBH) ≥ 15 cm; an intermediate stratum comprising shrubs and trees with CBH < 15 cm and ≥ 1 m in height, and a lower stratum composed primarily of herbaceous species with some individuals of woody taxa 20–100 cm tall. In each of the 29 sites we sampled the superior stratum in a 20×250 m² (0.5 ha) plot with the exception of six roadside sites that were < 20 m in width, in which case we established two plots of 10×250 m² (one on each side of the road). For the intermediate stratum, we sampled an area of 10×250 m² in all sites. The line intercept method (Canfield 1941; Munhoz and Araújo 2011) was used to determine the species composition and coverage of each species in the lower stratum. In each site we established two lines of 250 m each, one meter above the ground. In every other meter we recorded the length of the line that was intercepted by each individual bellow the line. To estimate the relative area covered by each species in each site the area intercepted by that species was divided by the total length of line (500 m). The species were grouped into the following categories: exotic grasses, native grasses, herbs, shrubs, trees. We recorded whether the soil was exposed or covered with litter in cases where no plants were found at a sampling point.

Vouchers of all plants we were unable to identify in the field were collected and identified with the assistance of plant taxonomists, keys to local flora, or comparison with material in the Herbarium Uberlandense (HUFU). The plants were classified according to APG III classification system (Chase and Reveal 2009).

Species traits

Three individuals of each species with CBH > 20 cm were selected in the largest of our Cerrado reserves to measure the bark thickness of the species found in the superior stratum. The thickness of pieces of bark collected 30 cm above the soil surface was measured with calipers and classified each species as having thin (≤ 0.9 cm) or thick bark (≥ 1 cm). These categories were based on previous studies with 56 Cerrado tree species demonstrating that those with bark thickness > 0.9 cm had a 50 % chance of surviving a fire (Hoffmann and Solbrig 2003; Hoffmann et al. 2009; Hoffmann et al. 2012).

The primary habitat preference (i.e., exclusive of savannas vs. from savannas and/or forests) of all species in both the superior and intermediate strata was identified using published studies (Mendonça et al. 2008; Rossatto et al. 2008) and our prior experience. We also used previously published literature to determine dispersal mechanisms (i.e.,

zoochoric vs. anemochoric/autochoric; Silva Júnior 2005; Saravy et al. 2003; Gottsberger and Silberbauer-Gottsberger 2006; Figueiredo 2008).

Data analyses

The density of individuals, species richness, and Fisher α diversity index (Fisher et al. 1943) were calculated for both the superior and intermediate strata. Fisher α was chosen because it is less influenced than other commonly used diversity indices by differences in sample size or the abundance of the most common species (Taylor et al. 1976). We used t tests to test if these parameters differed between roadsides and reserves. The density of individuals was $\log(x + 1)$ transformed to meet the assumptions of the test. The species composition of roadsides and reserves were compared using a non-metric multidimensional scaling. The NMDS ordination technique is considered one of the most effective ordination methods for ecological communities because it does not require a linear relationship between variables (McCune and Grace 2002); the ordinations were based on the relative abundance of species in each study site using the Bray–Curtis index as the similarity measure. T tests were also used to measure differences between roadsides and reserves in proportion of individuals and species with different characteristics (dispersal system, predominant physiognomy of occurrence, and bark thickness). Finally, t-tests were used with Bonferroni correction to measure for differences between roadsides and reserves in the coverage and number of species of exotic grasses, native grasses, herbs, shrubs, tree seedlings, litter, bare soil. All statistical analyzes were performed using the program Systat 10.2 (SPSS 2000).

Results

Structure and species composition of the superior stratum

A total of 6,649 plants were recorded in the 10 Cerrado reserves and 5,152 in the 19 roadside sites. There were a total of 108 species from 40 families in the reserves, including four families sampled only in these sites (Combretaceae, Lauraceae, Myristicaceae, Symplocaceae). Roadside sites had a total of 99 species from 39 families, including the only representatives of the Meliaceae, Solanaceae, and Urticaceae (Appendix D, Supplementary material). The five most common species in reserves were *Qualea grandiflora*, *Miconia albicans*, *Caryocar brasiliense*, *Qualea parviflora*, and *Ouratea hexasperma* (Fig. 1a), which occurred in 90 % of the reserves sampled and together accounted for 28 % of individuals found. In contrast, these species occurred in only 34 % of the roadsides, representing only 6 % of the total individuals sampled there. The most common species on roadsides were *Dalbergia miscolobium*, *Aspidosperma tomentosum*, *Pouteria ramiflora*, *Qualea grandiflora*, *Pouteria torta* (73 % of the roadside sites, 25 % of all individuals), while these species occurred in 86 % of the reserves and represented 15 % of the individuals sampled.

The 2.4 fold difference in plant density between reserve and roadside plots ($1,329.8 \pm 333.4$ SD individuals ha^{-1} vs. 542.3 individuals $\text{ha}^{-1} \pm 154.4$ SD, respectively) was significantly different ($t = 8.17$, $P < 0.001$, Fig. 2). Species richness per site was also significantly higher in reserves than along roadsides (53.2 ± 8.5 SD and 38.7 ± 5.4 SD, respectively; $t = 5.57$, $P < 0.001$). Fisher α , however, did not differ between the two habitats ($t = 1.26$, $P = 0.219$). In addition to the differences in plant

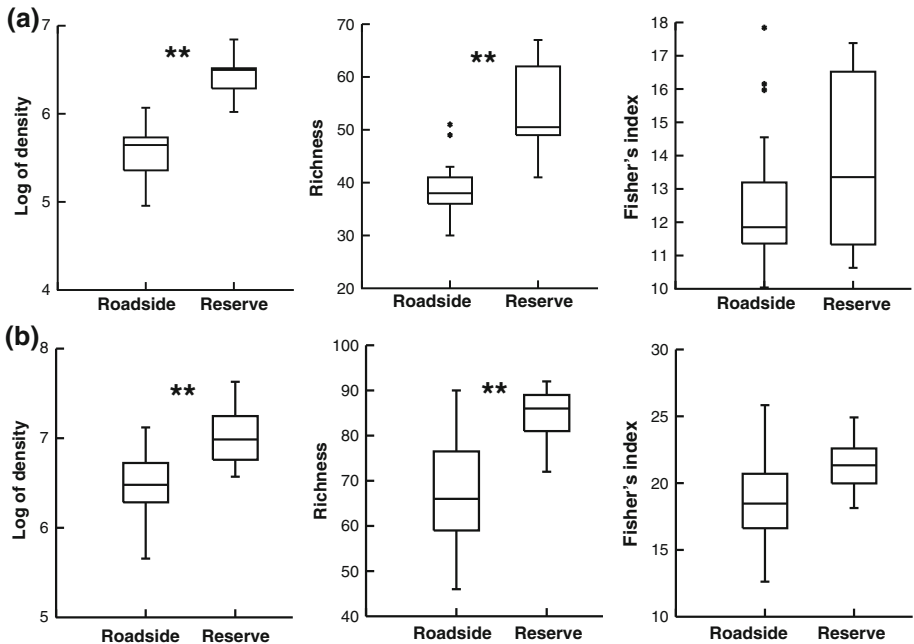


Fig. 1 Mean abundance of species in the **a** superior and **b** intermediate strata in reserves ($n = 10$) and roadsides ($n = 19$). The species were ranked according to their mean abundance in reserves and presence in more than half of the 29 sampled sites. Of the 64 species in the superior stratum, 44 had a higher mean abundance in the reserves while 20 were more abundant in the roadsides. Of the 104 species of the intermediate stratum, 70 had a higher mean abundance in reserves while 34 were more abundant in roadsides. We highlight the five most abundant species in reserves (*bold*) and roadsides

abundance and species richness, there were also clear differences in community composition based on the NMDS (stress = 0.196; proportion of variance explained = 0.783; Fig. 3).

Roadsides had a significantly lower percentage of ‘forest’ species (25.2 ± 5.9 SD vs. 19.6 ± 4.0 SD, $t = 3.00$, $P = 0.006$; Fig. 4a) and individuals (33.1 ± 14.8 SD vs. 18.5 ± 7.5 SD; $t = 3.54$, $P = 0.001$; Fig. 4b). There was no significant difference in the proportions of animal-dispersed species ($t = 0.05$, $P = 0.957$) and individuals ($t = 1.80$, $P = 0.082$) between roadsides and reserves. Finally, 37.4 % \pm 7.7 SD of the individuals in the reserves belong to thin-bark species group, while in the roadsides the figure was only 24.1 % \pm 6.5 SD ($t = 4.66$, $P < 0.0001$). There were also proportionately more species with thin bark in reserves than roadsides 36.1 % \pm 3.8 SD vs. 31 % \pm 4.5 SD; $t = 3.0922$, $P = 0.0044$).

Structure and species composition of the intermediate stratum

A total of 11,596 individual plants occurred in reserves and 12,855 along roadsides. There were 180 species from 50 families in reserves and including the only representatives of the Amaranthaceae, Myristicaceae, Oxalidaceae, Peraceae, Siparunaceae, Symplocaceae. Roadsides plots had a total of 239 species from 50 families with the Convolvulaceae, Emmotaceae, Menispermaceae, Phyllanthaceae, Polygalaceae, and Smilacaceae unique to

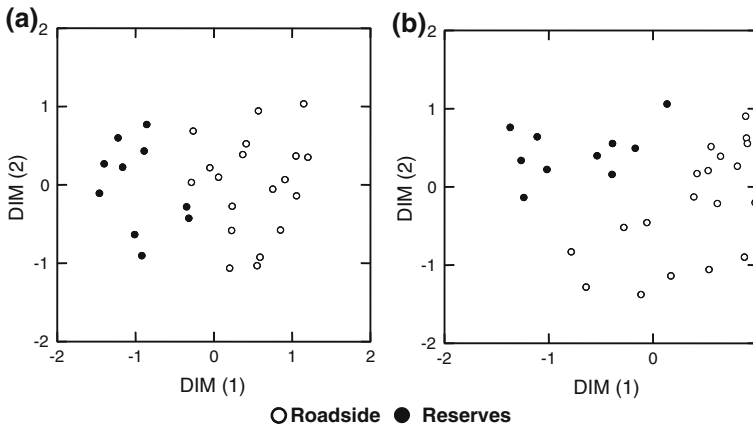


Fig. 2 Mean (\pm SD) number of individuals ($\log + 1$), richness, and Alfa Fisher index of the **a**) superior and **b**) intermediate strata of roadsides ($n = 19$) and reserves ($n = 10$) in cerrado *sensu stricto* (* $P < 0.05$; ** $P < 0.001$)

roadsides (Appendix E, Supplementary material). The five most common species in the reserves were *M. albicans*, *Matayba guianensis*, *Q. grandiflora*, *Eugenia calycina*, *Davilla elliptica* (Fig. 1b). Together these species accounted for 32 % of individuals sampled and occurred in 94 % of the reserves. On roadsides, 34.5 % of individuals were from one of five species—*Matayba guianensis*, *Banisteriopsis malifolia*, *Brosimum gaudichaudii*, *Bauhinia holophylla*, *Byrsonima intermedia*—and these species occurred in 79 % of all roadsides sites.

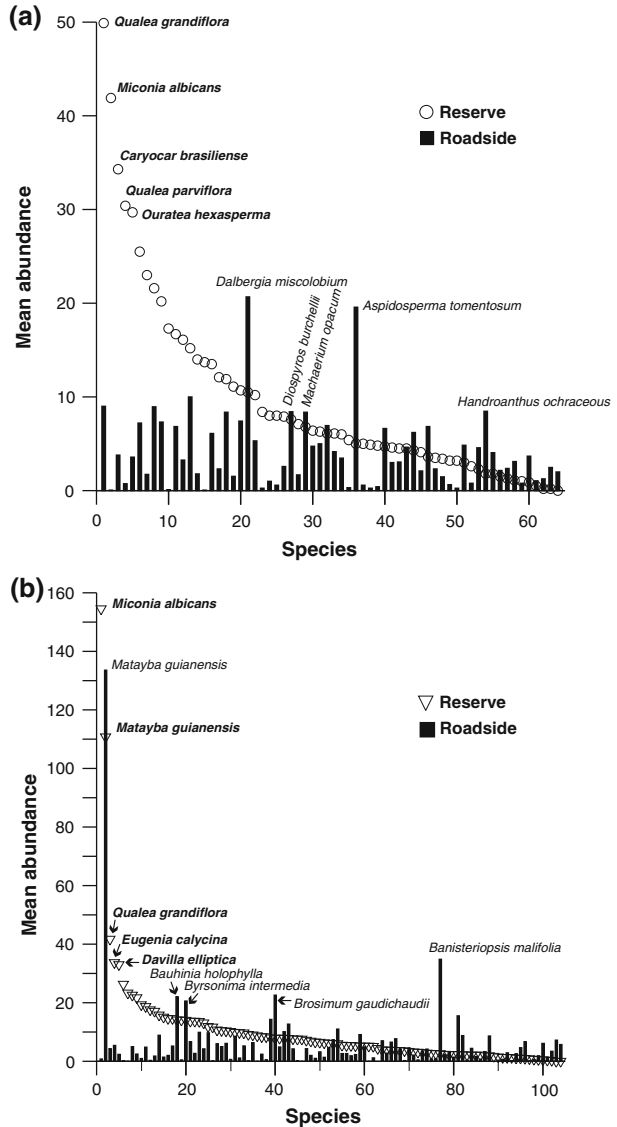
On average there were 1.7 times more individuals ($t = 3.82$, $P < 0.001$) and 25 % more species ($t = 3.77$, $P < 0.001$) in reserves than on roadsides (density: 2319.3 ± 780.69 SD individuals ha^{-1} vs. 1353.1 ± 495.86 SD individuals ha^{-1} ; Fig. 2b). Although, there was only a marginal significance of higher α diversity in reserves than on roadsides ($t = 1.96$, $P = 0.06$), the NMDS indicated that the two communities clearly differed in their species composition (Stress = 0.207; Proportion of variance explained = 0.760; Fig. 3b).

The proportion of “forest” species was 28 % higher in the reserves (0.222 ± 0.046 SD vs. 0.173 ± 0.032 SD, respectively; $t = 3.33$, $P = 0.002$; Fig. 4a), whereas the proportion of “forest” individuals did not differ significantly between habitat types (0.3984 ± 0.161 vs. 0.305 ± 0.147 SD, respectively; $t = 1.56$, $P = 0.128$; Fig. 4b). There were 15 % fewer individuals (0.717 ± 0.083 SD vs. 0.611 ± 0.112 SD, respectively; $t = 2.61$, $P = 0.015$) and 11 % fewer species (0.656 ± 0.0359 SD vs. 0.585 ± 0.052 SD, respectively; $t = 3.79$, $P = 0.001$) that depend on specialized dispersal agents in roadsides than in reserves.

Structure and species composition of the lower stratum

A total of 221 species were recorded in the lower stratum of the reserves: 37 native grasses, three exotic grasses, 44 herbaceous species, and 137 woody species. In roadsides there were 240 species, including 25 native grasses, six exotic grasses, 73 herbaceous species, and 136 woody species. Plots in reserves contained three times more species of native grasses (12.8 ± 2.52 SD vs. 3.9 ± 2.73 SD, respectively; $t = 8.48$, $P < 0.001$, Fig. 5) covering $35 \% \pm 16.1$ SD of the soil surface while in roadsides they covered only

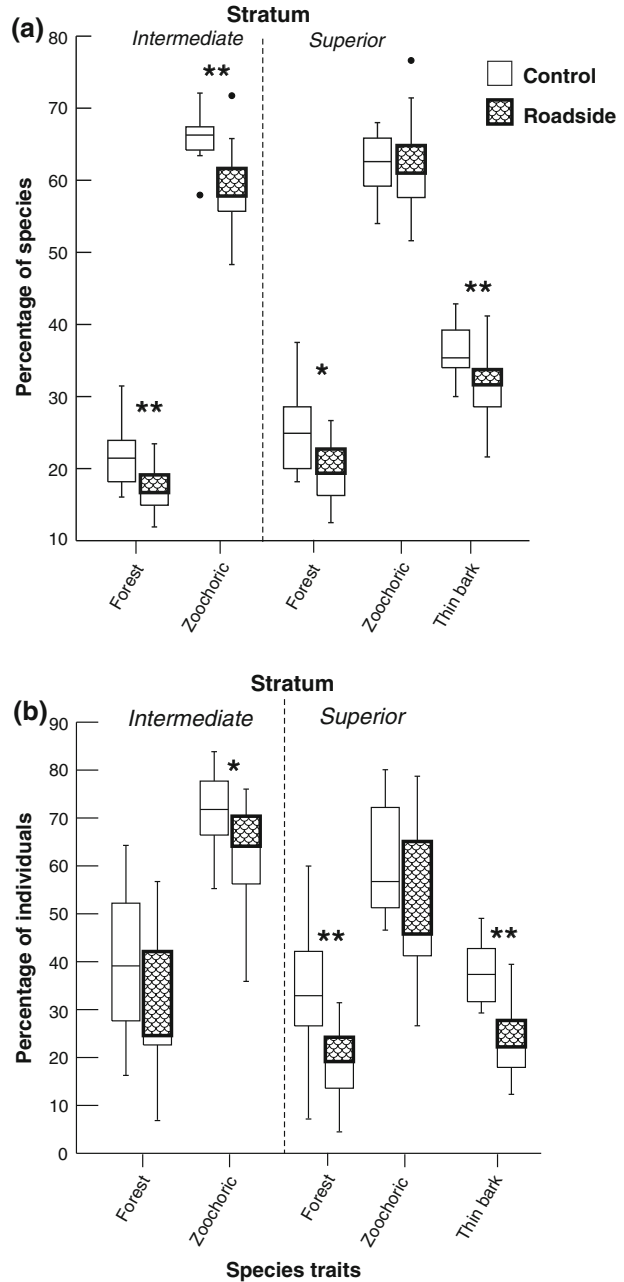
Fig. 3 Community composition of Cerrado *sensu stricto* reserves and roadsides in the superior (a) and b intermediate strata based on non-metric multidimensional scaling. The ordinations were made based on relative abundance of the species in each study site using the Bray-Curtis similarity index



4 % \pm 5 SD ($t = 7.59$, $P < 0.001$). Differences between roadsides and reserves in the species richness of exotic grasses were not significant (1.5 ± 0.7 SD vs. 2.21 ± 1.13 SD; $t = 1.79$, $P = 0.084$). However, on roadsides exotic grasses covered 81.5 ± 6.9 SD of the surface, with most of this coverage of species of the genera *Brachiaria* (79.8 ± 8 SD of total coverage). This is in sharp contrast to the reserves, in which exotic grasses covered only 3 ± 5.4 SD of the soil surface ($t = 31.12$, $P < 0.001$). *Echinolaena inflexa*, *Tri-stachya leiostachya*, and *Loudetiopsis chrysothrix* were the most common of native grasses in the reserves.

There was no significant difference between roadsides and reserves in either the number of herbaceous species per plot (9.9 ± 3.7 SD vs. 9.6 ± 4.4 SD; $t = 0.13$, $P = 0.896$), nor

Fig. 4 Mean (\pm SD) proportion of **a** species and **b** individuals in cerrado *sensu stricto* reserves and roadsides that are forest species, zoochoric species (superior and intermediate strata) or have thin bark (superior stratum only; * $P < 0.05$; ** $P < 0.001$)



in their total coverage per plot (3.2 ± 1.9 SD vs. 2.47 ± 1.6 SD; $t = 1.07$, $P = 0.290$). However, the dominant species in each habitat were different. *Ananas ananassoides* and *Andira humilis* were $42 \% \pm 27.8$ SD of the herbaceous ground cover in reserves, whereas on roadsides the dominant herbaceous species were *Stylosanthes* sp. 3 and *Stylosanthes guianensis* ($21 \% \pm 28.3$ SD of herbaceous cover).

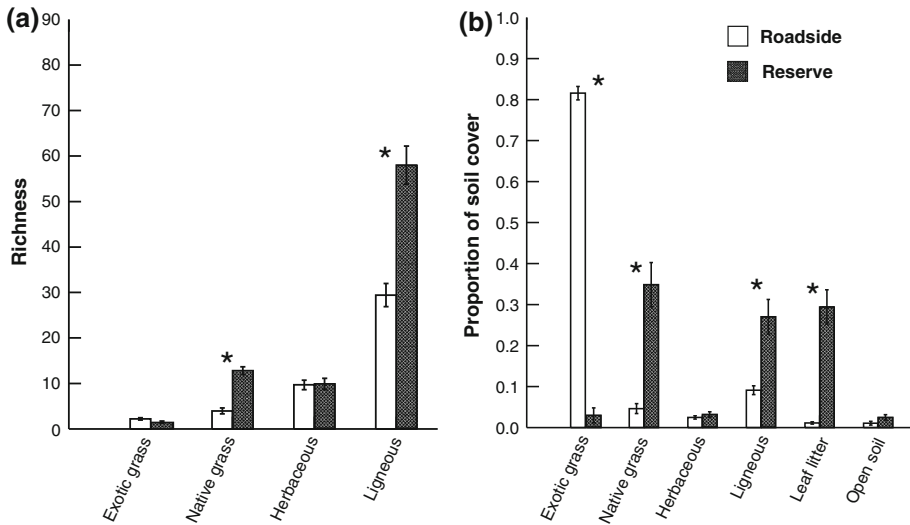


Fig. 5 Mean (\pm SD) **a** number of exotic grasses, native grasses, herbaceous species, and woody species in the understory cerrado *sensu stricto* reserves and roadsides and **b** percent of ground covered by these groups in the same locations (* $P < 0.001$)

Species richness of trees and shrubs (<20 cm in height) in plots located in reserves was double that of roadside plots (58 ± 12.48 SD vs. 29.42 ± 10.78 SD, $t = 6.42$, $P < 0.001$). They also covered an area in plots three times greater than in reserves than roadsides ($27 \% \pm 12.6$ SD vs. 9.1 ± 4.5 SD; $t = 5.60$, $P < 0.001$). The dominant species also tended to differ between habitats: *M. albicans*, *M. guianensis*, *Syagrus comosa*, *Cordia myrciifolia*, *Cordia obtusa* represented 31 % of the woody individuals sampled in the reserves, whereas 38 % of the individuals sampled in roadsides were *M. guianensis*, *B. intermedia*, *B. malifolia*, *Campomanesia adamantium*, *Dalbergia miscolobium*. Roadsides and reserves differed in litter cover ($29 \% \pm 12.4$ SD in reserves and $1 \% \pm 1.2$ SD on roadsides; $t = 9.96$, $P < 0.001$), while there was only a marginal significance of more exposed soil in reserves ($t = 1.86$, $P = 0.074$).

Discussion

The study of roads and their ecological impacts has emerged as an important area of research in conservation biology (Hughes et al. 1997; Forman and Alexander 1998). To date, however, most studies assessing changes in plant communities along roadsides have been conducted in the temperate zone (Dunnett et al. 1998; Way 1977; Zeng et al. 2011 but see Hogbin et al. 1998; Spooner and Smallbone 2009). To our knowledge, the present study is the first of its type conducted in Neotropical savannas—a highly threatened and species rich biodiversity hotspot. Based on our sample of over 36 000 plants, we found that the number of both individuals and species along roadsides is lower than in nearby natural areas, as might be expected given the disturbances that accompany roads. However, we also found that ca. 70 % of the 180 species found in the Cerrado reserves we sampled were also found in our roadside sites. This suggests roadside verges may play an important role

in conserving Cerrado biodiversity, as a stepping stone for isolated animal populations, and as a reservoir of plant genetic diversity.

In the light of the focus on roads as a conduit for plant invasions, it is perhaps not unexpected that so little is known regarding the traits of species that manage to persist in roadside habitats (Parendes and Jones 2000; Zeng et al. 2011). Thick bark enhances survivorship of plants exposed to fire (Uhl and Kauffman 1990; Hengst and Dawson 1993), which is probably the mechanism underlying why plots on roadsides had fewer plants with thin bark than those in reserves. Frequent fires may also be why species and individuals typical of savanna formations were significantly more prevalent in the reserves than in roadsides. Savanna species tend to have a greater capacity for resprouting after fire due to large investments in underground biomass (Hoffmann and Moreira 2002; Hoffmann and Franco 2003), while forest species are adapted to flower and set seeds in environments with little fire (Coutinho 1977; Landim and Hay 1995). Thus, while forest species are selected against on roadsides, they succeed in protected areas with low fire frequency.

We also observed changes in traits related to plant-animal interactions that may also have helped shape plant communities and abundance on roadsides. Seed dispersal on roadsides may be reduced due to the absence of some mammals, birds, or insects (Fahrig and Rytwinski 2009) in much the way it is in other disturbed habitats (Frankel and Soulé 1981); over time this may lead to reductions in the recruitment of obligatory zoochoric species. Our results are consistent with this hypothesis—although it is unknown if disperser abundance is lower on roadsides than in Cerrado reserves, in roadside sites we found a lower number of species and individuals in the intermediate stratum that depend on animals for dispersal. Although this pattern was not observed in the superior strata, this is likely because insufficient time has passed since road establishment to observe changes in the adult tree community resulting from reduced disperser abundance (Vanthomme et al. 2010).

Burning also kills woody plant seedlings and adults (Sato and Miranda 1996), which can reduce local density and diversity (Hoffmann 1998) as well as increase the presence of invasive grasses (Milberg and Lamont 1995). These grasses, such as species of *Brachiaria* and *Melinis minutiflora*, produce large amounts of biomass providing fuel for fires (Coutinho 1990). This biomass can also inhibit the establishment of seedlings or reduce their growth and survivorship (Hoffmann et al. 2004; Hoffmann and Haridasan 2008). We found a lower number of regenerating woody species in roadsides, suggesting seedling establishment is indeed reduced in these locations. That an average of 29 woody species are found in the lower stratum, however, suggests the mechanisms underlying recruitment are complex; potential factors permitting these species to become established include larger seeds sizes (Hobbs and Mooney 1998), the absence of predators (Hobbs and Mooney 1998) or presence of secondary dispersers (Bangert et al. 2005), and differences in seed rain and propagule pressure (Gilpin and Soulé 1986). Further observations and careful experiments are needed to distinguish among these possibilities and elucidate why some species appear able to establish despite the detrimental effects of exotic grasses (Hoffmann and Haridasan 2008).

Although roadsides contain a large proportion of the species found in reserves, it is notable that the occurrence of some characteristic Cerrado species is very low in these locations. For instance, *Qualea grandiflora*, *Caryocar brasiliense*, *Miconia albicans* were the three most common species in the superior stratum and were also very common in the intermediate class, but they were rare or missing in roadside plots (Fig. 1a). Despite the similarity of these results, however, the lower occurrence of these species is probably caused by other factors. For *Q. grandiflora* the mechanism appear to be primarily biotic,

namely the poor competitive ability of its seedlings against invasive grasses (Hoffmann and Haridasan 2008). In contrast, *M. albicans* is very sensitive to fire, which can both alter its phenology and topkill large plants (Hoffmann 1998; Hoffmann and Solbrig 2003). These fires may also explain why the five most abundant species on roadsides have thick bark ($1.72 \text{ cm} \pm 0.43 \text{ SD}$), and hence are more characteristic of savanna physiognomies. These results show why one must be cautious when attempting to generalize about the mechanisms responsible for declines of populations on roadsides - failure to identify the correct mechanisms could result in incorrect or inefficient strategies for management and conservation. They also show that while roadsides appear to be reservoirs of a large proportion of Cerrado plant diversity, reserves away from roads are needed to maintain larger populations of some characteristic elements of the Cerrado flora.

Several important caveats to our conclusions should be mentioned. First, we did not make allowance for the age of roads in our analyses. The roads we studied were built 24–48 years ago and while studies of roads of similar ages have revealed patterns comparable to ours (Sýkora et al. 2002; Zeng et al. 2011), older roads have previously been shown to maintain a larger number of individuals (Spooner and Smallbone 2009). With the exception of a major highway (BR-050; Appendix A), however, most of the roads in the Cerrado region are similar in age to those used in our study, suggesting our results will be geographically applicable. Second we have no data on the frequency with which our roadside verges were burned. Some of the negative effects we observed should therefore be interpreted cautiously because fire frequency is an important predictor of vegetation structure (Hoffmann and Moreira 2002). Finally, paved roads may (Barbosa et al. 2010) or may not (Craig et al. 2010) contain more exotic species than those unpaved because of the chemicals used in their construction. Four of our roadside sites were unpaved, but there is no evidence that the vegetation bordering them is different in composition or plant abundance. Nevertheless, we suggest future work should emphasize increased sampling along unpaved roads to study possible effects of paving. Finally, we have no information on plant abundance and community composition in our sites prior to road construction, it is possible—although we believe unlikely—that some of the differences we observed existed prior to road construction.

Conclusion

Even small habitat patches such as the vegetation along roadsides can play an important role in biodiversity conservation (Hogbin et al. 1998; Cousins 2006; Spooner and Smallbone 2009; Zeng et al. 2011). Indeed, in the Netherlands more than half the country's flora can be found on roadsides (Sýkora et al. 2002), while in England plant species diversity in these environments is 43.5 % higher (Way 1977). Roadsides are also important sites for the restoration of native plant communities (Norcini et al. 2008, 2009), and which may reduce the risk of fire (Velloso and Andrade 2008), erosion and pollution (Dolan et al. 2006). In Australia there is a well implemented program that balances road safety and infrastructure with biodiversity conservation of roadsides through management (www.coorong.sa.gov.au/page.aspx?u=439, Stokes et al. 2006). Federal legislation in Brazil (Law N° 6766) requires that a 15 meter buffer strip adjacent to the road remains undisturbed. Based on 32,012 km of roads in the Cerrado alone (DNIT 2013), this represents a total area of over 96,000 hectares—a cumulative area larger than several of the Cerrado region's flagship state and national parks. Our results indicate that while these buffer strips are susceptible to colonization by invasive grasses, they can also harbor a large diversity of native plants. This

could make roadside verges an essential component of conservation strategies for highly fragmented biodiversity hotspots (Cavalcanti and Joly 2002) in which less than 4 % is formally protected in conservation units (Klink and Machado 2005).

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