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Understorey vegetation gradient in a *Eucalyptus grandis* plantation between a savanna and a semideciduous forest

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Abstract

Background: Plant community assemblage is influenced by many factors, including soil characteristics and the arrival of diaspores from surrounding areas. These factors may be especially important in transition areas, leading to spatial gradients in the plant community.

Methods: This study was performed in the understorey of an abandoned *Eucalyptus grandis* W. Hill ex Maiden plantation between a savanna and a forest, 490 m apart, in south-eastern Brazil. This study assessed whether the spatial variation in several variables related to the understorey's structure and composition is best described by linear or non-linear (quadratic) models. The linear model would indicate a gradient between the two vegetation types, whereas the quadratic model would indicate a stronger effect of the plantation's edges.

Results: There was a gradient in species composition between the two edges of the plantation. Mean vegetation height was greatest at the savanna edge and lowest in the centre of the plantation. The total number of individuals per plot and the phylogenetic diversity decreased with distance from the savanna edge. Different patterns were observed for different dispersal syndromes, with animal dispersal being more common at the savanna edge, wind dispersal in the centre of the plantation and self dispersal at the forest edge.

Conclusions: The greater number of individuals at the savanna edge may indicate that dispersal and arrival of diaspores are the most important factors influencing community structure and composition of the understorey of this abandoned *E. grandis* plantation, with most propagules coming from the savanna area. The smaller vegetation height in the centre of the fragment may also indicate older colonisation at the edges. Therefore, in addition to highlighting the recovery potential of undergrowth beneath abandoned *Eucalyptus* spp. plantations, these results show that this recovery is spatially heterogeneous and that dispersal plays a large role in it. This should be taken into account in restoration projects. The authors recommend careful consideration before removing regenerating *Eucalyptus* spp. trees as part of the site restoration. Instead the focus should be on the recovery potential of the undergrowth, with gradual removal of *Eucalyptus* trees, if necessary.

Keywords: Cerrado; Community composition; Dispersal; Diversity; Ecotone; Restoration; Structure

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Background

Reconstructing a natural community is one of the greatest challenges for restoration ecology, partly because community assemblage is determined by several distinct factors such as environmental filters, diaspore availability, competition between and within species, and species potential for colonisation (Webb et al. 2002; Chase 2003). Natural recolonisation may aid in community reconstruction by allowing communities to regenerate with species from neighbouring vegetation patches. However, a successful application of this process requires a better understanding of how species colonise or recolonise disturbed areas (Török et al. 2011). Colonisation is limited mostly by three factors: 1) diaspore availability in the neighbouring species pool and the dispersal capacity of different species (Török et al. 2011); 2) ecological traits that determine the survival and establishment of different species under different environmental conditions (Lebrija-Trejos et al. 2010); and 3) biotic interactions, such as facilitation and competition, that determine the patterns of species co-occurrence (Cianciaruso et al. 2009). This is also true for natural recolonisation of disturbed environments, in which resprouting from pre-existent underground structures may also play an important role (Durigan et al. 1998). Therefore, knowledge of how these factors affect transition area is essential for successful restoration planning.

Transition areas between different vegetation types, for example between savanna and forest, are usually characterised by a gradual shift in environmental conditions and species composition (Furley et al. 1992). In some areas, however, abrupt changes in soil and other environmental characteristics may result in a sharp edge between the different vegetation types (Ruggiero et al. 2002, Durigan and Ratter 2006). In either case, both savanna and forest patches influence the transition area, and the influence is stronger closer to each patch (Cadenasso et al. 2003). This is likely to result in a spatial gradient in species composition during the recolonisation of a transition area, as the occurrence and density of different species will vary with the distance from the source of diaspores (Wolters et al. 2005). The environmental conditions found in the transition area also affect the resulting species composition, as species originating from different environments are adapted to different environmental constraints. For example, savanna species are adapted to decreased soil fertility and water availability (Ruggiero et al. 2002) and to regular fires (Moreira 2000; Miranda et al. 2002), factors that may lead to the local extinction of forest species.

Ecotones between forest and savanna are common in the São Paulo state, south-eastern Brazil, where cerrado *sensu stricto*, a savanna formation that is part of the larger floristic domain known as the Cerrado, occurs alongside semideciduous forests (Ruggiero et al. 2002; Durigan and Ratter 2006). Transition areas in this region are often replaced by agricultural and silvicultural land uses. Silviculture, a large part of which uses exotic *Eucalyptus* spp. trees, is the fifth most frequent land use adjacent to cerrado fragments in the São Paulo state (Durigan et al. 2007). One characteristic of these *Eucalyptus* spp. plantations is that they often contain an understorey composed of native species (Saporetti Jr et al. 2003; Neri et al. 2005). This understorey may be used as a resource and refuge by animal species and also function as stepping stones or corridors linking natural areas that would not be connected otherwise (Machado and Lamas 1996; Lyra-Jorge et al. 2008). In addition, the understorey can increase local biodiversity by offering regeneration sites for plant species from different vegetation types (Saporetti-Jr et al. 2003).

This understorey may also be used as a starting point to restore native vegetation when the plantation is no longer used, which makes assessments of its composition important for restoration ecology. Other studies (e.g. Durigan et al. 1998, Jepson 2005, Neri et al. 2005) have already shown the potential of natural regrowth in abandoned *Eucalyptus* spp. plantations; however, these studies have not discussed large-scale spatial variation in the regrowth's structure and composition. The objective of this study was to test for linearity or non-linearity of the gradient in vegetation structure, composition and diversity of the understorey of an abandoned *Eucalyptus grandis* W. Hill ex Maiden plantation located between a cerrado *stricto sensu* and a semideciduous forest to provide insights for restoration. The following questions were addressed in this study: (1) Are there gradual changes in species composition, richness, diversity and phylogenetic diversity between the two areas? These gradual changes are expected because both proximity to natural areas and edges affects vegetation structure and species occurrence and distribution (Harper et al. 2005, Wolters et al. 2005). (2) Are these patterns linear or non-linear pattern, with a trough or peak in the middle? As colonisation starts from the edges, greater density of individuals and mean vegetation height should be found closer to the edges. (3) Are there more pronounced gradients on wind- and self-dispersed species than on animal-dispersed species? If this area is used homogeneously by the local frugivorous fauna, animals could disperse seed evenly through the area. (4) Do abundant species show a gradient in their distribution between the two areas? Differences in ecological processes and species composition between the savanna and forest areas are likely to affect the distribution of the dominant species in the study area. This article reports the actual compositional and structural variability of the woody species in the study area, discusses its probable causes and whether the results matched expected composition. Conclusions have been drawn and recommendations made for the restoration of natural vegetation in similar areas.
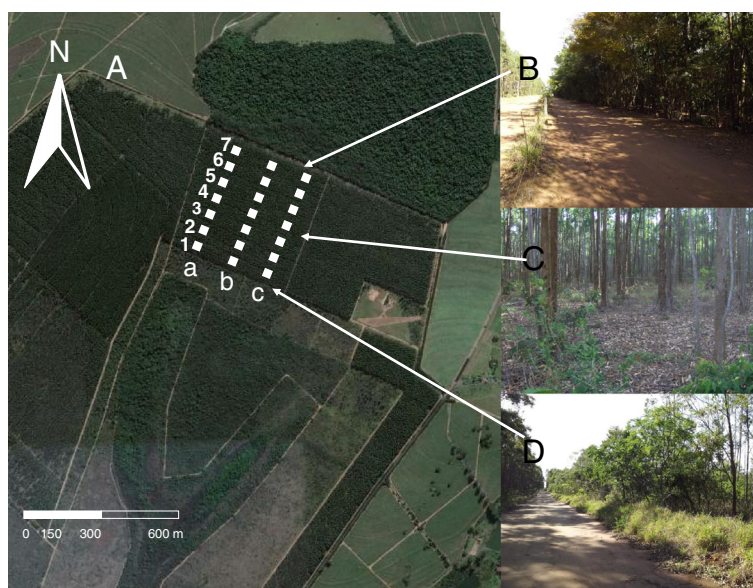
Figure 1 Study areas. A: Satellite image of the study site, located in the north-eastern portion of the Federal University of São Carlos (21°57′50″ S, 47°51′55 W) between a semideciduous forest to the north and a savanna to the south (white lines represent the transects); **B**: the forest edge; **C**: the interior of the site; **D**: the cerrado edge.

Methods
Study area and sampling methods
This study was conducted in the understorey of a site 490 m wide and 490 m long in the north-eastern portion of the Federal University of São Carlos (21°57′50″ S, 47°51′55″ W, 815–890 m a.s.l.; Santos et al. 1999), in São Paulo state, Brazil. This site had been used previously as a *Eucalyptus grandis* plantation and was last harvested approximately 15 years prior to the study. It had not been managed since then and *E. grandis* trees had re-grown from stumps left after the last harvest. These trees were approximately 15 m tall at the time of the study, with a highly homogeneous tree cover throughout the study site. This site is located between two natural areas: a semi-deciduous forest to the north and a regenerating cerrado *sensu stricto* savanna to the south (Figure 1). The predominant vegetation of the cerrado was fully grown native trees but there were also a few, widely spaced *Eucalyptus* spp. trees that had regenerated for more than 20 years from an previous *Eucalyptus* spp. plantation. The regional climate is seasonal, with dry winters and wet summers. Soils are acidic and nutrient-poor Oxisols with high aluminium content (Santos et al. 1999).

Three transects were placed between the cerrado and forest edges, with 150 m between adjacent transects (Figure 1). Seven 25 x 25 m plots were delimited in each transect, leaving 50 m between consecutive plots. The first and last plot of each transect were placed approximately 10 m from the cerrado and forest edges, respectively. The three transects were labelled as "a", "b" and

"c", and the plots in each transect were numbered from 1, corresponding to the plot closest to the cerrado edge, to 7, corresponding to the plot closest to the forest edge. Therefore, plot a1 is the plot of transect "a" that is closest to the cerrado and plot c7 is the plot of transect "c" that is closest to the forest. The three transects were treated as replicates and used the distance between the centre of each plot and the cerrado edge (i.e. 22.5 m for plot 1 and 472.5 m for plot 7) as the explanatory variable. Within each plot, all woody non-vine plants with height greater than 50 cm were sampled, considering stems that were clearly separated at soil level as different individuals, and classified them into four height classes: < 1.4 m, 1.4 − 1.6 m, 1.61 − 3 m, and > 3 m. All individuals to were then identified species level by consulting specialised literature and a taxonomist (see Acknowledgments) and classified all species into dispersal syndromes (wind-, self- and animal-dispersed) based on literature reviews or on the information available for other species of the same genus. As the *E. grandis* trees had been planting without prior removal of the underground plant structures (pers. comm., Maria Inês S. Lima), native species in this area may have originated either by resprouting or from recruitment. However, it was not possible to differentiate between these two types in the field.

Data analysis
Ordination analysis of vegetation composition
General differences in species composition among the sampling plots were assessed by means of a non-metric

multidimensional scaling (NMDS) analysis, performed on untransformed data with the algorithm developed by Taguchi & Oono (2005), using Past 2.10 sofware (Hammer et al. 2001). Two similarity indices were used to assess the presence-absence and abundance patterns: the Jaccard index, which takes into account only the presence of a given species, and the Horn index, which considers the relative abundance of all the species (Jost et al. 2011).

Vegetation variables

The data were described with 23 response variables related to species diversity, phylogenetic diversity, vegetation structure, dispersal syndrome, and distribution of abundant species. For species diversity, two measures of species richness were used, namely the number of species and the Fisher's alpha diversity index, as well as Shannon's diversity index and the corresponding Pielou's evenness index (Magurran 1988), calculated in Past 2.10. The Fisher's alpha diversity index was used because species richness per se usually increases with increasing number of individuals, whereas the Fisher's alpha diversity index is a robust species richness estimate that is not influenced by biases in the number of individuals (Maurer and McGill 2011). To use Fisher's alpha diversity index, the species abundance distribution should not be different from the log-series (Maurer and McGill 2011), which was the case for our data ($p = 1$, as calculated using the Past 2.10 software).

Phylogenetic diversity was assessed by means of two indices, phylogenetic diversity (PD) and phylogenetic diversity-rate (PD-rate). The Phylomatic module of the Phylocom software was used to construct a phylogenetic tree of all the species sampled (Webb and Donoghue 2005; Webb et al. 2008). The lengths of the branches were estimated based on the current Phylomatic tree (tree R20091110; Webb et al. 2008) with APG III (Angiosperm Phylogeny Group 2009) and Wikström ages (Wikström et al. 2001). The root node and all the dated nodes were fixed, and the undated nodes were placed evenly between the dated nodes or between the dated nodes and the terminal nodes by means of the "bladj" algorithm in the Phylocom software (Webb et al. 2008). The calculation of PD was done by summing the lengths of the branches of the phylogenetic tree obtained for each plot (Faith 1992). The units used for PD were millions of years (My). PD-rate was calculated by dividing PD by the number of species in each plot. Whereas PD is a measure of the phylogenetic distance between species in a community, PD-rate permits to verify whether the variation in PD is due to the number of species present or to the phylogenetic differences between the species. A low PD-rate indicates that the PD value at a site is due mostly to the number of species present, whereas a high PD-rate indicates that the PD is a result of the phylogenetic distances between the species.

The total number of individuals, the average vegetation height, the standard deviation of height and the coefficient of variation (calculated by dividing the standard
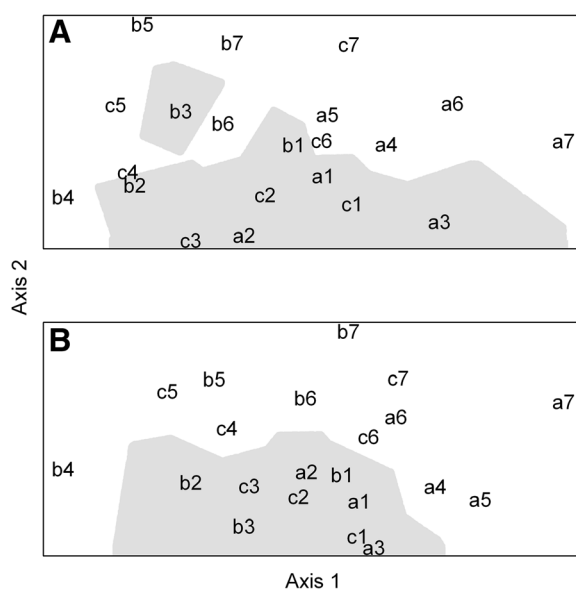

Figure 2 Gradient in the floristic composition in the understorey of the study site. Non-metrical multi-dimensional scaling using: **A**: Jaccard distance; and **B**: Horn distance. Letters *a*, *b* and *c* represent the three transects, and numbers 1 to 7 represent plots at the following distances from the cerrado edge: (1) 10–35 m; (2) 85–110 m; (3)160-185 m; (4) 235–260 m; (5) 310–335 m; (6) 385–410 m; and (7) 460–485 m. Grey areas represent areas of the ordination plot that are closer to plot 1, 2 and 3 than to the other plots, showing a pattern in the analysis performed with Horn distance. Stress: **A** = 0.3223, **B** = 0.2489.

Table 1 Floristic composition of the study area

Species	N	Rank	Distances	Dispersal
Anacardiaceae				
Astronium graveolens Jacq.	21	24	1-7	Wind[23]
Tapirira guianensis Aubl.	6	36	1-3,5	Animal[15]
Annonaceae				
Annona coriacea Mart.	18	26	2-5,7	Animal[15]
Annona crassiflora Mart.	2	40	1,4	Animal[15]
Duguetia furfuracea (A.St.-Hil.) Saff.	19	25	1-5	Animal[15]
Guatteria nigrescens Mart.	1	41	7	Animal[17]
Xylopia aromatica (Lam) Mart.	13	30	1-5,7	Animal[1]
Xylopia frutescens Aubl.	11	32	5,7	Animal[34]
Aquifoliaceae				
Ilex cerasifolia Reissek	3	39	5-7	Animal[31]
Araliaceae				
Schefflera vinosa (Cham. & Schltdl.) Frodin & Fiaschi	204	1	1-7	Animal[14]
Asteraceae				
Baccharis dracunculifolia DC.	33	18	1-6	Wind[9]
Chromolaena cf. *laevigata* (Lam.) R.M. King & H. Rob.	2	40	6	Wind[32]
Eupatorium cf. *megaphyllum* Baker	1	41	7	Wind
Gochnatia pulchra Cabrera	16	28	1,3,4	Wind[28]
Piptocarpha axillaris (Less.) Baker	4	38	3,6,7	Wind[16]
Piptocarpha macropoda (DC.) Baker	11	32	1,5-7	Wind[31]
Piptocarpha rotundifolia (Less.) Baker	24	21	1-7	Wind[15]
Piptocarpha sp. Hook. & Arn.	6	36	3-5	Wind[35]
Vernonanthura cf *puberula* (Less.) H. Rob.	1	41	2	Wind[33]
Vernonanthura phosphorica (Vell.) H. Rob.	5	37	1-3	Wind[14]
Vernonia rubriramea Mart. ex DC.	12	31	1-4,6,7	Wind[28]
Bignoniaceae				
Handroanthus chrysotrichus (Mart. ex DC.) Mattos.	2	40	1,3	Wind[31]
Handroanthus ochraceus (Cham.) Mattos	4	38	2,3,5	Wind[15]
Jacaranda caroba (Vell.) DC.	24	21	3-7	Wind[28]
Tecoma stans (L.) Juss. ex Kunth	23	22	1-7	Wind[18]
Zeyheria montana Mart.	3	39	3	Wind[28]
Zeyheria tuberculosa (Vell.) Bureau ex Verl.	1	41	6	Wind[31]
Burseraceae				
Protium heptaphyllum (Aubl.) Marchand	2	40	5	Animal[26]
Caryocaraceae				
Caryocar brasiliense A.St.-Hil.	10	33	2-5	Animal[15]
Celastraceae				
Tontelea micrantha (Mart. ex Schult.) A.C. Sm.	1	41	3	Animal[24]
Connaraceae				
Connarus suberosus Planch.	9	34	2,3	Animal[15]
Rourea induta Planch.	5	37	3,5	Animal[15]
Ebenacae				
Diospyros hispida A.DC.	26	20	1-7	Animal[15]

Table 1 Floristic composition of the study area (Continued)

Erythroxylaceae				
Erythroxylum cf. *deciduum* A.St.-Hil.	5	37	2,4	Animal[24]
Erythroxylum cuneifolium (Mart.) O.E. Schulz	9	34	2,3,5-7	Animal[28]
Erythroxylum suberosum A.St.-Hil.	4	38	1,2,4	Animal[15]
Euphorbiaceae				
Alchornea triplinervia (Spreng.) Müll. Arg.	36	16	1.4-7	Animal[11]
Sapium glandulosum (L.) Morong	9	34	1,3,4,7	Animal[31]
Fabaceae				
Acacia recurva Benth.	2	40	2	Self[31]
Acosmium dasycarpum (Vogel) Yakovlev	1	41	2	Wind[26]
Acosmium subelegans (Mohlenbr.) Yakovlev	10	33	2,5,6	Wind[15]
Anadenanthera peregrina (L.) Speg.	1	41	2	Self[29]
Andira inermis (Wright) DC.	3	39	5	Animal[25]
Bauhinia rufa (Bong.) Steud.	51	13	1-7	Self[15]
Bowdichia virgilioides Kunth	1	41	4	Wind[15]
Chamaecrista flexuosa (L.) Greene	2	40	3	Self[24]
Copaifera langsdorffii Desf.	74	8	1-7	Animal[1]
Dalbergia miscolobium Benth.	5	37	2-4	Wind[15]
Dimorphandra mollis Benth.	2	40	2	Animal[15]
Machaerium acutifolium Vogel	7	35	1,4,7	Wind[1]
Machaerium nyctitans (Vell.) Benth.	2	40	4,7	Wind[4]
Machaerium stipitatum (DC.) Vogel	1	41	7	Wind[31]
Pterogyne nitens Tul.	1	41	3	Wind[27]
Senna rugosa (G. Don) H.S. Irwin & Barneby	2	40	4	Self[28]
Senna splendida (Vogel) H.S. Irwin & Barneby	2	40	2,7	Self[34]
Stryphnodendron adstringens (Mart.) Coville	2	40	4,5	Animal[28]
Stryphnodendron obovatum Benth.	16	28	1-5,7	Self[15]
Lamiaceae				
Aegiphila lhotzkiana Cham.	22	23	1-7	Animal[29]
Lauraceae				
Endlicheria paniculata (Spreng.) J.F. Macbr.	1	41	1	Animal[33]
Ocotea pulchella (Nees & Mart.) Mez	171	2	1-7	Animal[8]
Malpighiaceae				
Byrsonima intermedia A. Juss.	35	17	1-7	Animal[15]
Malvaceae				
Eriotheca gracilipes (K. Schum.) A. Robyns	17	27	2-4,6	Wind[29]
Melastomataceae				
Leandra lacunosa Cogn.	6	36	1,3,5	Animal[14]
Miconia albicans (Sw.) Steud.	68	9	1-7	Animal[15]
Miconia cf. *ligustroides*(DC.) Naudin	1	41	7	Animal[15]
Miconia fallax DC.	17	27	1-4	Animal[15]
Miconia ligustroides (DC.) Naudin	4	38	2,3	Animal[15]
Miconia rubiginosa (Bonpl.) DC.	29	19	1-7	Animal[12]
Miconia stenostachya DC.	4	38	1,2	Animal[29]

Table 1 Floristic composition of the study area (Continued)

Meliaceae				
Cabralea canjerana (Vell.) Mart.	3	39	5,7	Animal[30]
Cedrela fissilis Vell.	2	40	2,7	Wind[9]
Moraceae				
Brosimum gaudichaudii Trécul	9	34	1,5-7	Animal?[1]
Ficus cf *citrifolia* Mill.	2	40	2,4	Animal[31]
Myristicaceae				
Virola sebifera Aubl.	14	29	2,4,5	Animal[29]
Myrtaceae				
Calyptranthes concinna DC.	5	37	5,6	Animal[13]
Calyptranthes lucida Mart. ex DC.	2	40	5,6	Animal[13]
Campomanesia adamantium (Cambess.) O. Berg	57	11	1-7	Animal[15]
Campomanesia pubescens (Mart. ex DC.) O. Berg	2	40	3	Animal[15]
Campomanesia sp. Ruiz & Pav.	2	40	5	Animal[13]
Eugenia cf *klotzschiana* O. Berg	1	41	3	Animal[13]
Eugenia dysenterica DC.	4	38	3,4	Animal[1]
Eugenia obversa O. Berg	17	27	4-7	Animal[13]
Eugenia punicifolia (Kunth) DC.	1	41	2	Animal[15]
Eugenia pyriformis Cambess.	3	39	4,5	Animal[13]
Myrcia bella Cambess.	57	11	1-7	Animal[15]
Myrcia cf. *tomentosa* (Aubl.) DC.	6	36	1,2,5,6	Animal[13]
Myrcia fallax DC.	37	15	1-7	Animal[15]
Myrcia lingua (O. Berg) Mattos & D. Legrand	100	4	1-7	Animal[13]
Myrcia tomentosa (Aubl.) DC.	2	40	1,3	Animal[13]
Psidium grandifolium Mart. ex DC.	26	20	1-6	Animal[24]
Psidium guajava L.	2	40	1,2	Animal[13]
Psidium laruotteanum Cambess.	12	31	2-5,7	Animal[24]
Nyctagenaceae				
Guapira noxia (Netto) Lundell	14	29	1-6	Animal[15]
Guapira opposita (Vell.) Reitz	4	38	1,4	Animal[10]
Ochnaceae				
Ouratea spectabilis (Mart. ex Engl.) Engl.	12	31	1-7	Animal[15]
Peraceae				
Pera glabrata (Schott) Poepp. ex Baill.	56	12	1-6	Animal[15]
Phyllantaceae				
Phyllanthus acuminatus Vahl	123	3	1-7	Self[22]
Seguieria cf. *americana* L.	7	35	1,4-6	Wind[6]
Primulaceae				
Myrsine coriacea (Sw.) R.Br. ex Roem. & Schult.	90	7	1-7	Animal[20]
Myrsine umbellata Mart.	93	6	1-7	Animal[31]
Proteaceae				
Roupala montana Aubl.	7	35	2,5,7	Self[15]
Rubiaceae				
Chomelia cf. *obtusa* Cham. & Schltdl.	1	41	1	Animal[11]
Cordiera concolor (Cham.) Kuntze	1	41	4	Animal[31]

Table 1 Floristic composition of the study area (Continued)

Cordiera sessilis (Vell.) Kuntze	1	41	2	Animal[28]
Palicourea rigida Kunth	3	39	2,5	Animal[15]
Psychotria nuda (Cham. & Schltdl.) Wawra	5	37	1,2,6,7	Animal[3]
Rudgea viburnoides (Cham.) Benth.	11	32	1,3,5-7	Animal[29]
Tocoyena formosa (Cham. & Schltdl.) K. Schum.	2	40	1	Animal[15]
Rutaceae				
Zanthoxylum cf. *fagara* (L.) Sarg.	2	40	2	Animal[5]
Zanthoxylum rhoifolium Lam.	10	33	1-3,6	Animal[10]
Salicaceae				
Casearia silvestris Sw.	12	31	2-6	Animal[15]
Siparunaceae				
Siparuna guianensis Aubl.	29	19	1-4,6,7	Animal[4]
Solanaceae				
Solanum lycocarpum A. St.-Hil.	48	14	1,2,4,7	Animal[2]
Solanum mauritianum Scop.	58	10	1-7	Animal[7]
Solanum paniculatum L.	95	5	1,2,4-7	Animal[14]
Solanum pseudoquina A. St.-Hil.	1	41	5	Animal[30]
Solanum reflexum Schrank	1	41	2	Animal[35]
Solanum viarum Dunal	14	29	2,4,6,7	Animal[19]
Styracaceae				
Styrax ferrugineus Nees & Mart.	10	33	1,2,4,5	Animal[15]
Thymelaeaceae				
Daphnopsis fasciculata (Meisn.) Nevling	6	36	1,3,4,6,7	Animal[21]
Urticaceae				
Cecropia pachystachya Trécul	1	41	5	Animal[23]
Vochysiaceae				
Qualea cf. *multiflora* Mart.	1	41	3	Wind[15]
Vochysia tucanorum Mart.	5	37	1,2	Wind[31]

Species are shown with the corresponding total number of sampled individuals (N), abundance rank (from the most to the least abundant), the plots at which the species was found (from 1 – closest to the cerrado edge to 7 – closest to the forest edge), dispersal syndrome (wind-, self- or animal-dispersed), and reference for the dispersal syndrome as superscripts. Families, authors, synonyms and accepted names were checked on The Plant List (2010) or Tropicos (Missouri Botanical Garden 2012) databases with the Plantminer software (Carvalho et al. 2010).

[1] Almeida et al. 1998; [2] Batalha and Mantovani 2000; [3] Borgo 2010; [4] Campos et al. 2009; [5] Candiani 2006; [6] Catharino et al. 2006; [7] Coelho et al. 2010; [8] Francisco and Galetti 2002; [9] Frenedoso 2004; [10] Galetti et al. 2011; [11] Giehl et al. 2007; [12] Goldenberg and Shepherd 1998; [13] Gressler et al. 2006; [14] Ishara and Maimoni-Rodella 2011; [15] Jardim and Batalha 2009; [16] Liebsch et al. 2009; [17] Lobão and Mello-Silva 2007; [18] Grau et al. 1997;; [19] Paise and Vieira 2005; [20] Pascotto 2007; [21] Polisel and Franco 2010; [22] Ressel et al. 2004; [23] Reys et al. 2005; [24] Silva et al. 2009; [25] Spina et al. 2001; [26] Stefanello et al. 2009; [27] Takahasi and Fina 2004; [28] Tannus et al. 2006; [29] Weiser and Godoy 2001; [30] Wiesbauer et al. 2008; [31] Yamamoto et al. 2007; [31] Yamamoto et al. 2007 (for *Myrsine umbellata*); [32] Ye et al. 2004 (for *Cedrela odorata*); [33] Zipparro et al. 2005; [34] Moura et al. 2011; [35] based on species from the same genus.

deviation by the mean height) were used to characterise the vegetation structure. To calculate average vegetation height, we considered that the height of each individual corresponds to the mid-value of its height class (4.5 m for the last class, as most tall trees were still under 6 m in height) and calculated the mean of these mid-values. We used the same mid-values to estimate standard deviation, which was used as a measure of structural variability within the plot. The number and proportion of wind-, self-, and animal-dispersed individuals and species within each plot were used to analyse the dispersal syndromes. We also analysed the distribution of the seven species with at least 90 individuals because patterns of abundant species may indicate important ecological processes.

Regressions

Both quadratic and linear regressions were examined to assess the existence and shape of the gradient with respect to the 23 response variables, in the software R 2.13 (R Core Development Team, 2012). Distance from the cerrado edge was specified as the explanatory variable. We chose quadratic regressions because they fit with the expected pattern of more extreme values at both edges,

with either a trough or a peak at intermediate distances. In contrast, a linear regression would show a linear increase in the response variable along each transect. We considered a quadratic regression significant only when its quadratic term (x^2) was also significant; otherwise we considered the linear regression to be a better model. We considered a significance level of 0.05 for all tests.

Results

Vegetation composition
Non-metrical multidimensional scaling ordination was conducted using both the Jaccard and Horn distance indices, Figure 2A & B, respectively. No clear separation among sites was generated with the Jaccard distance index but was more obvious when the Horn distance index was used. Specifically, the three plots of each transect that were closer to the cerrado edge were placed more closely together on the ordination plot with the Horn distance index. This resulted in a trend in species composition that may be represented by two zones, up to 185 m (plot 3) from the cerrado edge and further (Figure 2B). These results indicate that, even though there is a change in species abundances along the gradient, complete species replacement does not occur. Furthermore, in the ordination diagrams, plots located along the same transect appear to be more similar to one another than plots of different transects, although this separation is not as clear as for edge distances (Figure 2).

Vegetation variables
There were 2235 individuals, which corresponded to 1702 individuals per hectare. These individuals belonged to 123 species from 81 genera and 39 families (Table 1).

Number of species and Fisher's alpha diversity index varied from 24 to 44 among the plots. Shannon's diversity index varied between 2.8 and 3.4 natural logarithm digits (nats) per individual. Pielou's evenness index varied between 0.46 and 0.88. The PD varied between 1958 and 2995, PD-rate varied between 68 and 82, and the number of individuals per plot varied from 40 to 199. Most of the plants encountered were small (75.7% of individuals in the first height class, 9.6% in the second, 11.9% in the third and 2.8% in the fourth). The most abundant dispersal syndrome was animal dispersal, with 1776 individuals and 83 species, followed by wind dispersal, with 253 individuals and 31 species, and self dispersal, with 206 individuals and 9 species (Table 1).

The most abundant species were *Schefflera vinosa* (Cham. & Schltdl.) Frodin & Fiaschi (Araliaceae, N = 204), *Ocotea pulchella* (Nees & Mart.) Mez (Lauraceae, N = 171), *Phyllanthus acuminatus* Vahl (Phyllanthaceae, N = 123), *Myrcia lingua* (O. Berg.) Mattos & D. Legrand (Myrtaceae, N = 100), *Solanum paniculatum* L. (Solanaceae, N = 95), *Myrsine umbellata* Mart and *Myrsine*

coriacea (Sw.) R.Br. ex Roem. & Schult. (Primulaceae, N = 93 and 90 respectively). The most abundant families were Myrtaceae, Solanaceae, Araliaceae, Fabaceae, and Primulaceae, with 336, 217, 204, 185 and 183 individuals respectively, and the most species-rich families were Fabaceae, Myrtaceae, Asteraceae, Melastomataceae, and Rubiaceae, with 19, 18, 11, 7 and 7 species respectively (Table 1).

Analysis of vegetation variables using quadratic and linear regressions
A single outlier, located at 322.5 m from the cerrado edge was removed from the analysis of variables related to vegetation height because this plot was partially occupied by the invasive fern *Pteridium esculentum arachnoideum*. The presence of this fern may have affected the size structure of the plot by reducing the number of plants in the smaller size classes. Ten out of the 23

Table 2 Coefficient of determination (R^2) of linear and quadratic regressions between the response variables and distance from cerrado edge along the transects

Response variable	Linear R^2	Quadratic R^2
Number of species	0.36**	0.38
Fisher's alpha diversity index	< 0.01	0.28*
Shannon H index	0.01	0.35**
Pielou Evenness index	0.20*	0.41*
PD	0.23*	0.25
PD rate	0.41**	0.43
Number of individuals	0.37**	0.55*
Mean height	0.03	0.41**
SD of height	0.18	0.42*
CV of height	0.23*	0.35
Wind-dispersed individuals	0.01	0.28*
Self-dispersed individuals	0.21*	0.22
Animal-dispersed individuals	0.21*	0.35
Wind-dispersed species	<0.01	<0.01
Self-dispersed species	<0.01	0.02
Animal-dispersed species	<0.01	0.01
Abundance of *Schefflera vinosa*	0.68***	0.78*
Abundance of *Ocotea pulchella*	0.19*	0.27
Abundance of *Phyllanthus acuminatus*	0.04	0.33*
Abundance of *Myrcia lingua*	0.17	0.17
Abundance of *Solanum paniculatum*	0.09	0.09
Abundance of *Myrsine coriacea*	0.19*	0.43*
Abundance of *Myrsine umbellata*	0.33**	0.48*

For the variables related to vegetation height, we removed a single outlier, located at 322.5 m from the cerrado edge. We chose to remove this outlier because this plot was partially occupied by the invasive fern *Pteridium esculentum arachnoideum*, which may have affected the size structure of the plot by reducing the number of plants in the smaller size classes. *p < 0.05; **p < 0.01; ***p < 0.001.
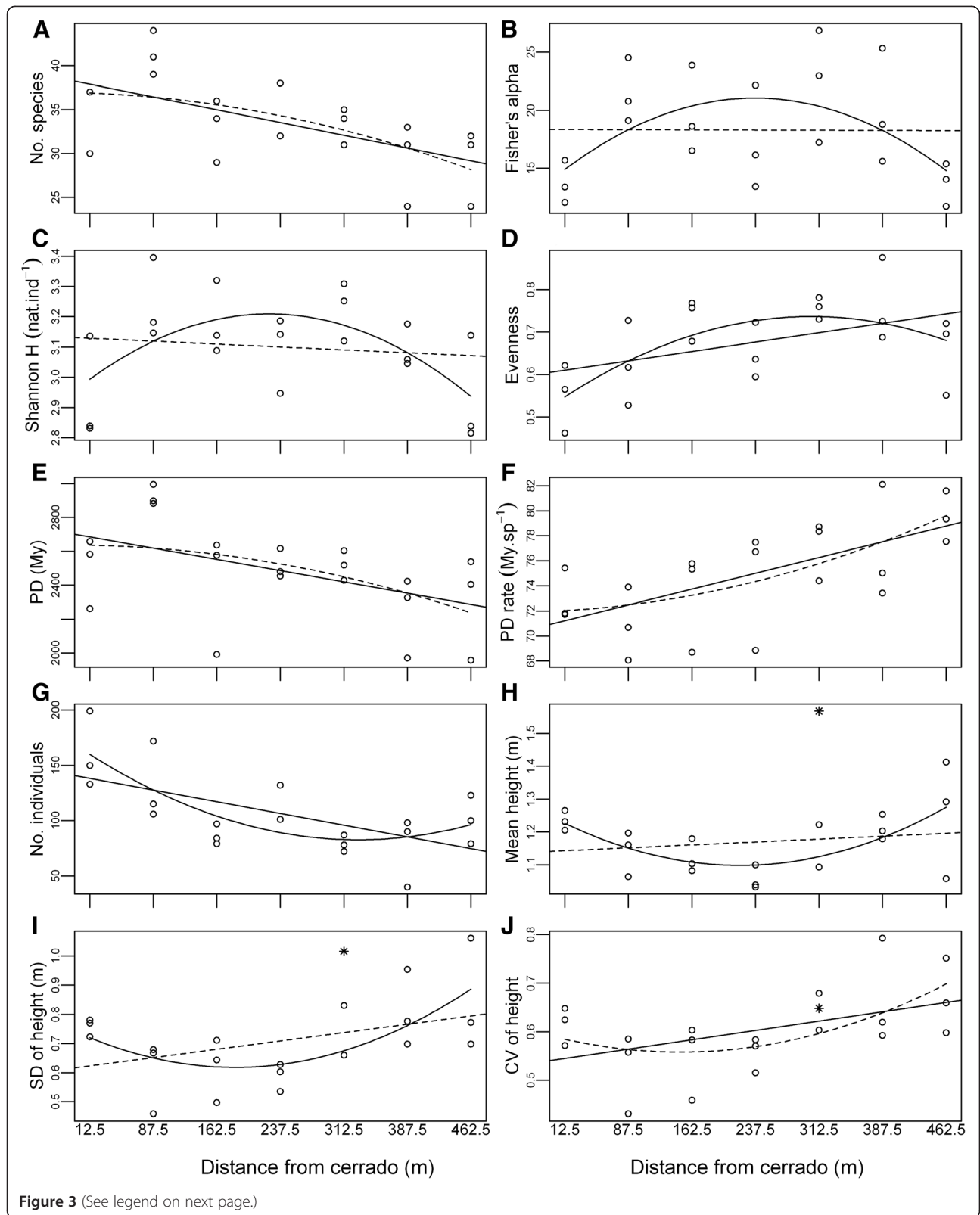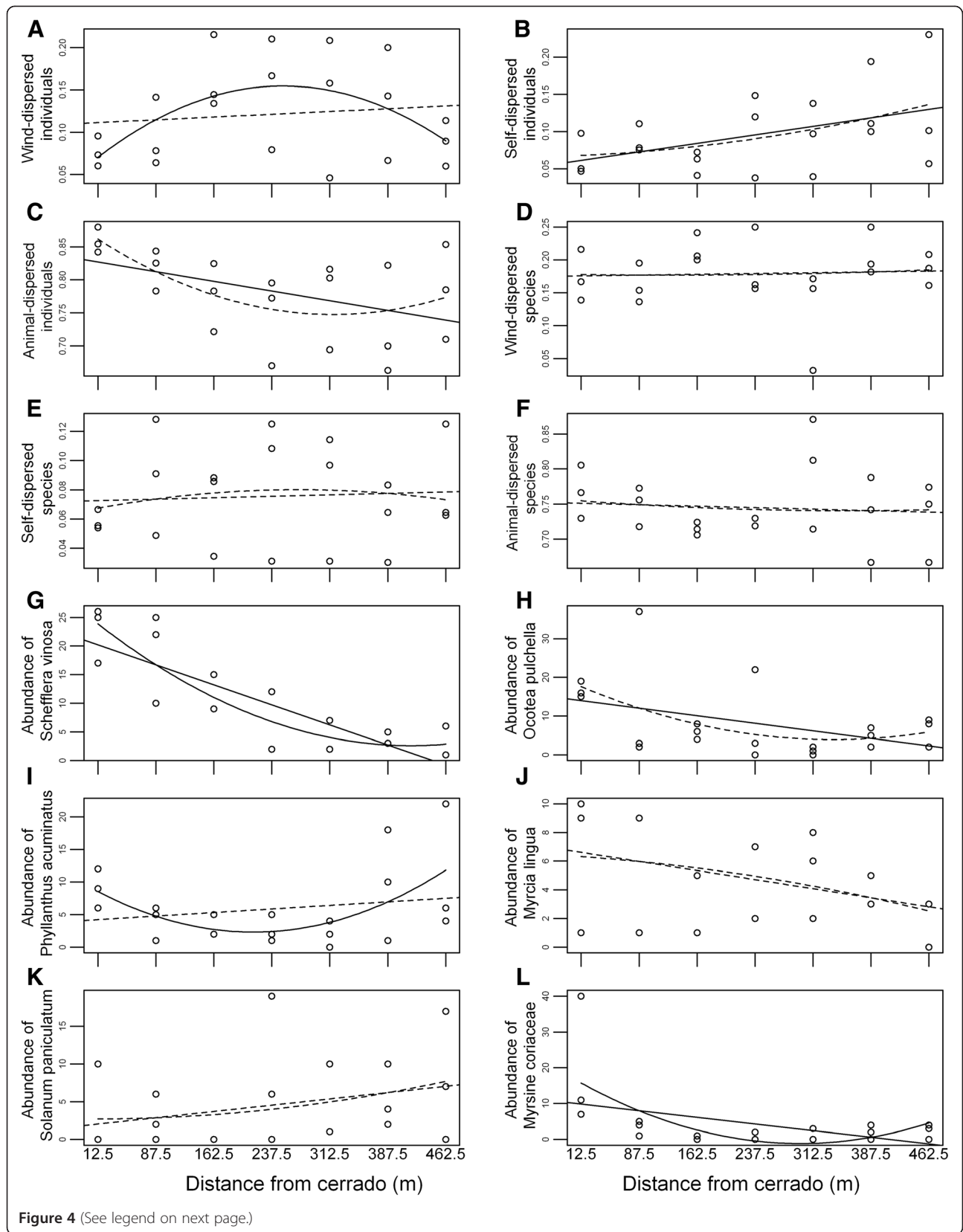
Figure 3 (See legend on next page.)

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Figure 3 Quadratic and linear regressions between the diversity or structural response variables and distance from cerrado edge, represented as the mid-point of each plot, along three transects in the understorey of the study site. Each plot presents two lines, one for quadratic regression, and other for linear regression. Significant regressions are presented with a continuous line, non-significant ones with an interrupted line. Please note that some of variables presented significance for both quadratic and linear regression. **A**: number of species (i.e. species richness), **B**: Fisher's alpha diversity index, **C**: Shannon's H index, **D**: Pielou's evenness index, **E**: Phylogenetic diversity (PD), **F**: Phylogenetic diversity rate, **G**: total number of individuals, **H**: mean vegetation height, **I**: vegetation height standard deviation, **J**: vegetation height coefficient of variation. For the variables related to vegetation height, we removed a single outlier, located at 322.5 m from the cerrado edge and indicated by a *.

response variables tested exhibited significant quadratic relationships with edge distance, with R^2 ranging from 0.29 to 0.55 (Table 2), except for the distribution of *Schefflera vinosa*, which had an R^2 of 0.78. Shannon's H index, Fisher's alpha diversity index, and the proportion of wind-dispersed individuals had peak values in the middle of the study site, whereas total number of individuals, mean height, height SD, and the distributions of *S. vinosa*, *Myrsine umbellata* and *Myrsine coriacea* all had a trough in the middle plots (Figures 3 and 4). Shannon's evenness, PD-rate, height CV, and proportion of self-dispersed individuals increased from the cerrado to the forest edge, and species richness, PD, number of individuals, number of animal-dispersed individuals, and the distributions of *S. vinosa*, *M. umbellata* and *M. coriacea*, *Phyllantus acuminatus* and *Ocotea pulchella* all decreased from the cerrado to the forest edge (Figures 3 and 4). The R^2 of the linear regressions ranged from 0.19 to 0.36. Only five variables, namely the proportion of wind-dispersed, self-dispersed and animal-dispersed species and the abundances of *Myrcia lingua* and *Solanum paniculatum*, did not present any significant distance-driven relationships (Figure 4).

Discussion

The primary result of this study was the large number of species (126) found in the understorey of the study site. Other surveys of understorey in cerrado areas containing *Eucalyptus* spp. trees have found much lower numbers (between 39 and 47 species) (Saporetti Jr et al. 2003, Neri et al. 2005). This variation may be at least partially due to differences in methodology as these earlier studies only included individuals with at least 3 cm diameter at soil level. The density of individuals of native species (1700 ind.ha^{-1}) in the current study was between two and five times smaller than observed in two nearby cerrado areas, where density ranged between 4000 and 8250 ind.ha^{-1} (Dantas and Batalha 2011, Gonçalves and Batalha 2011). This difference in density is even more pronounced given that the sampling criterion used in the current study included individuals with less than 3 cm diameter. Even so, the density observed in our study is within the recommended density of pre-existent or planted trees for the restoration of cerrado areas, which ranges from 1000 up to 2000 ind.ha^{-1} (Durigan et al.

2003), showing that land used previously as *Eucalyptus* plantations may have a large potential for natural regeneration and restoration. The potential for regeneration of cerrado vegetation has already been documented for areas previously used as pasture or as *Eucalyptus* plantation (Durigan et al. 1998, Jepson 2005, Neri et al. 2005). For example, in one study in eastern Mato Grosso state, central Brazil, over 50% of once-cleared cerrado areas experienced regeneration during the 13-year study period, mostly without human intervention (passive restoration) (Jepson 2005). In addition to the results of these studies, our study showed that the regenerating vegetation is a phylogenetically diverse community, showing that not only many species occurred but that these species belonged to phylogenetically distant groups.

The undergrowth vegetation was spatially heterogeneous, with a conspicuous gradient in the undergrowth between the cerrado and the semideciduous forest. Of the above-mentioned studies, only one (Neri et al. 2005) explored the spatial variation in the regenerating vegetation, but on a much smaller scale than our study. As expected, the proximity to native vegetation of either cerrado or semideciduous forest influenced species composition in the transition area. It appears that the species composition of plots between 0 and 185 m from the cerrado edge was more similar to that of the cerrado than plots further away (Figure 2). Changes in relative abundances were more evident than changes in species composition, as indicated by the lack of an obvious pattern in the NMDS ordination plot based on the Jaccard Index, which is a presence-absence similarity index. The most abundant species, i.e. those that were better able to recolonise this altered area, were from distinct families at the cerrado and forest edges. Species in the family Meliaceae were more abundant at the forest edge and members of the Araliaceae more abundant at the cerrado edge. The distribution of some of the most abundant species, *S. vinosa* and *O. pulchella*, decreased from the cerrado to the forest edge. In fact, of the most abundant species, only *M. lingua* and *S. paniculatum* did not present a distance-related trend. The importance of the semideciduous forest in determining the composition of this area is emphasised by the presence of typical forest species (e.g. *Cedrela fissilis* and *Cabralea canjerana*) closer to the forest edge. Thus, even though most

Figure 4 (See legend on next page.)

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Figure 4 Quadratic and linear regressions between the dispersal mode and species abundance response variables and distance from the cerrado edge, represented as the mid-point of each plot, along three transects in the understorey of the study site. Each graph presents two lines, one for quadratic regression, and other for linear regression. Significant regressions are presented with a continuous line, non-significant ones with an interrupted line. Please note that some of variables presented significance for both quadratic and linear regression. **A**: proportion of wind-dispersed individuals, **B**: proportion of self-dispersed individuals, **C**: proportion of animal-dispersed individuals, **D**: proportion of wind-dispersed species, **E**: proportion of self-dispersed species, **F**: proportion of animal-dispersed species, **G**: distribution of *Schefflera vinosa*, **H**: distribution of *Ocotea pulchella*, **I**: distribution of *Phyllanthus acuminatus*, **J**: distribution of *Myrcia lingua*, **K**: distribution of *Solanum paniculatum*, **L**: distribution of *Myrsine coriacea*. The pattern observed for *Myrsine umbellata* was similar to that of *Myrsine coriacea* and is not shown.

species occur throughout the entire area, the composition of the whole community follows the cerrado-forest gradient, probably as a result of a variety of dispersal and establishment characteristics (Wulf and Heiken 2008, Pouliot et al. 2012) of cerrado and forest species. In disturbed areas, plasticity and order of establishment usually have more pronounced effects on species' abundances than biotic interactions (Pouliot et al. 2012). Competition among native species is expected to be low at the current study site due to the low density of native trees. Therefore, the spatial structure encountered suggests that dispersal and recruitment are the main determinants of the species composition in this and other altered areas.

Measures of species diversity, phylogenetic diversity, vegetation structure, dispersal syndromes and distribution of abundant species also formed spatial gradients. Notwithstanding the small sample size and large variability between plots, many quadratic regressions were significant, suggesting that the forest and cerrado areas do in fact influence the gradients in composition, structure and distributions of this understorey community. The observed gradients are not likely to be explained by resprouting, which is common for, e.g., *S. vinosa* and species of the genus *Miconia* (pers. obs.), among many others (Hoffmann and Solbrig 2003), because resprouting would be expected to be more homogeneous throughout the study site. As large changes in soil properties are not expected at this spatial scale (Dantas and Batalha 2011), the observed gradient in species diversity and other characteristics probably resulted from the distance to the source of diaspores, similarly to what we observed for species composition.

Phylogenetic diversity decreased from cerrado to the forest edge, mainly due to decreasing richness towards the forest edge. As speciation is not important at the time scale addressed here, the colonisation process alone turns out as the major factor in determining patterns of phylogenetic diversity. It is likely that more individuals successfully reached and established closer to the cerrado edge because of higher propagule pressure. Edge-interior gradients in species richness, density, and dispersal have also been found previously in the first 25 m from a cerrado edge with a *Eucalyptus* spp. plantation

understorey elsewhere (Neri et al. 2005). The current study indicates that such gradients may also occur over larger distances (up to 185 m) and also occur for phylogenetic diversity and distributions of abundant species. Furthermore, the PD-rate increased modestly from the cerrado to the forest edge, while both PD and species number decreased. This indicates that: 1) at cerrado edge, there were more species which were phylogenetically similar, so that each of them added little phylogenetic diversity to these sites; 2) conversely, there were fewer species at the forest edge, but the phylogenetic distances among these species were greater. For example, *Cabralea canjerana* and *Cedrela fissilis* (Meliaceae), species that are more common in forest than in cerrado, appeared only close to the forest edge and are from a different family than the most abundant species (*Schefflera vinosa*, *O. pulchella*, *P. acuminatus*, *Myrcia lingua*, *Solanum paniculatum*, *Myrsine umbellata* and *M. coriaceae*). Myrtaceae and Fabaceae were among the most abundant and species-rich families and were distributed more or less evenly along the transects.

Plants inside the study site were smaller than those at either edge. These differences were more pronounced than could be explained solely by increased light near the edges of the study site (Bowering et al. 2006; Delgado et al. 2007; Pohlman et al. 2007). Time since establishment is a plausible alternative explanation. This explanation is also consistent with the results for height standard deviation and coefficient of variation, indicating that plant height in the interior of the site is more homogeneous and consequently that understorey plants had a shorter time to develop in the interior of the site than at the edges. In addition, allelopathic effects of *Eucalyptus* spp. could hinder development of trees, causing the trough pattern observed for height, as these effects would be stronger in the centre of the fragment (del Moral and Muller 1970; May and Ash 1990; Khan et al. 2008). Overall density of all understorey species decreased linearly from the cerrado to the forest edge. This may be because cerrado species are more adapted than forest species to the nutrient-poor soils present at this study site (Haridasan 2000; Ruggiero et al. 2002) and so are more likely to colonise the study site than forest species. This also indicates that allelopathic effects of

Eucalyptus grandis do not affect the establishment of new individuals in a spatially explicit manner. Thus, even though forest species are capable of being dispersed into the site, the establishment and survival of species dispersed from the cerrado would be greater, explaining the observed gradient. Other factors, such as differences in soil or shading, may also have played a role. However, their importance was probably smaller, as these characteristics appeared to be reasonably homogeneous in the area and the light levels were sufficient for the establishment and growth of the cerrado species.

With regard to dispersal, the proportion of animal- and self-dispersed individuals, but not species, varied along the gradient. Animal dispersal was the predominant syndrome, as expected for cerrado vegetation (Batalha and Mantovani 2000; Jardim and Batalha 2009), and the proportion of animal-dispersed plants decreased from the cerrado to the forest edge. A decrease in the number of animal-dispersed plants from edge to interior of a *Eucalyptus* sp. plantation has also been observed in a smaller-scale study (Neri et al. 2005), whereas a study in native cerrado vegetation showed an opposite pattern, with the number of animal-dispersed individuals being smallest at the edge (Jardim and Batalha 2009). From these results, it seems that the fauna in the cerrado that is capable of dispersing seeds avoids both agricultural land (Jardim and Batalha 2009) and the interior of ex-plantation areas (Neri et al. 2005 and present study). It is known that *Eucalyptus* plantations may be used as corridor and habitat by top predators such as *Puma concolor* and *Chrysocyon brachiurus* (Lyra-Jorge et al. 2010). However, the use of such areas by seed-dispersing fauna in general seems to be reduced, indicating that this is a poor habitat for a large proportion of the fauna, especially birds. This is similar to what has been observed in a study of avifauna in fragments of Atlantic Forest and *Eucalyptus* sp. plantation, where the number of birds recorded in the plantation was less than half of that recorded in the forest fragments in spite of a well-developed undergrowth (Dário et al. 2002). Thus, the use of study area as a dispersal corridor by animals is probably below the desired levels.

Conclusions

The area studied here was located between two different vegetation types and gradients were observed in both species composition and vegetation structure. The results from this study indicate that the presence of *Eucalyptus grandis* trees from an abandoned plantation does not preclude colonisation of native species from neighbouring cerrado and forest patches. The understorey composition resulting from the succession process was spatially heterogeneous, with a clear pattern in vegetation structure and composition. Thus, the main driving factor of heterogeneity is the distance to areas of native vegetation. Natural regeneration under *Eucalyptus* plantations may be a viable form of restoration given adequate management, and any removal of residual *Eucalyptus* trees should be done gradually to prevent damage to the existing understorey.

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