Spatial pattern of invasive and native graminoids in the Brazilian *cerrado*

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Abstract

Invasive grasses are an important threat in tropical savannas and grasslands and may be affected by natural and anthropogenic features of the environment. They may affect native species at a variety of scales, but a spatially-explicit assessment of their effects is lacking. We studied the spatial pattern of native and invasive graminoids in Brazilian *cerrado* in southeastern Brazil and assessed the effects of vegetation type, elevation and edges. We sampled native grasses, native sedges, and two invasive grass species (*Urochloa decumbens* and *Melinis minutiflora*) along three 301 to 1334 m-long transects encompassing grassland, forest, and savanna. We used wavelet transforms, generalized additive models, and null model simulations for analysis. Invasive grasses were mostly found in open vegetation. Neither native nor invasive species were consistently affected by elevation or edges. Much of the spatial variation could be explained by small-scale autocorrelation, but *M. minutiflora* had a more heterogeneous pattern than *U. decumbens*. Invasive grasses were negatively related to native ones at a variety of scales, from 1 to 66 m, and we observed both positive and negative relations between the two invasive species, with positive ones a finer scales. We hypothesize that spatial pattern characteristics of different invasive species may be related to their invasion potential.

Keywords: Bivariate wavelets, edge influence, *Melinis minutiflora*, *Urochloa decumbens*, wavelet transform.

Introduction

Plant communities have intrinsic spatial heterogeneity, described by their spatial pattern (Dale

1999), with alternating high-cover areas (patches) and low-cover areas (gaps); the distance between the centers of adjacent patches and gaps is the scale of spatial pattern (Dale 1999). Spatial pattern may be related to competition (Wiegand et al. 2005; Strand et al. 2007), soil properties (Ruggiero et al. 2002; Chudomelová et al. 2017), disturbances (Strand et al. 2007), edges (Harper et al. 2018), and vegetation type, and affects species coexistence and hence biodiversity (Durrett and Levin 1998; Stoll and Prati 2001; Tilman 1994). Intraspecific aggregation (resulting in a more patchy structure) may promote species coexistence, especially where environmental conditions are temporally stable and spatially heterogeneous (Chesson 2000; Snyder and Chesson 2003).

Spatial pattern is an important aspect of biological invasions (Travis and Park 2004; Petrovskaya et al. 2017). Invasive plants often show scales of spatial pattern of a few meters to tens of meters (Chapman et al. 2015, Shields et al. 2015), possibly affecting the spatial pattern of plant communities as a whole. This may be related to many factors, including topography (Jeltsch et al. 1998; Augustine 2003; Ashton et al. 2016) and disturbances (D'Antonio and Vitousek 1992; Dodonov et al. 2013). Topography may affect invasive plants through local variation in water availability in the upper soil layer, a key factor for invasive plants such as grasses (Gibson and Hulbert 1987; Scholes and Archer 1997). Linear disturbances, including roads and trails, may serve as dispersion corridors (LaPaix et al. 2012; Bacaro et al. 2015) and environmental conditions at their edges may facilitate the establishment of invasive plants (Morgan 1998; Cilliers et al. 2008; Dodonov et al. 2013).

Invasive grasses impact biodiversity in different ecosystems worldwide (D'Antonio and Vitousek 1992; Pivello et al. 1999a; Rossiter-Rachor et al. 2009) and may dominate tropical grasslands and savannas, seriously impacting native species (Pivello et al. 1999a, b; Hoffman and Haridasan 2008; Almeida-Neto et al. 2010; MacDonald 2004). Invasive grasses often show intraspecific aggregation and form dense mats, hampering other species (D'Antonio et al. 2011), and characterizing their spatial pattern in patchy environments may aid in understanding grass invasions. Savannas are naturally patchy, with alternating areas of high and low woody cover and corresponding low and high herbaceous cover (Jeltsch et al. 1998), and are thus an interesting model to study the spatial pattern of invasive grasses in a patchy environment. We studied how invasive and native grasses are related to vegetation type, natural topographic variation, and anthropogenic linear disturbances by quantifying their spatial pattern in a highly heterogeneous environment, the Brazilian *cerrado*. Invasive grasses can impact *cerrado* plant communities by suppressing native graminoids (Damasceno et al. 2018; Pivello et al. 1999a, b), hampering the regeneration of woody species (Almeida-Neto et al, 2010; Hoffmann et al, 2008), and changing local disturbance regimes (Gorgone-Barborsa et al, 2005; Hoffmann et al. 2012). Our specific objectives were 1) to compare the cover and spatial pattern of native and invasive graminoids among vegetation types (grassland, savanna, and forest with different disturbance histories), 2) to assess the effects of topography and anthropogenic linear disturbances on these graminoids (by relating their pattern to the topographic gradient and to the proximity of linear disturbance edges), and 3) to assess the relationships of invasive grasses with each other and with native graminoids at different scales. We hypothesized that 1) invasive grasses would be more abundant and be spatially structured at larger scales in the more open and disturbed vegetation types, with the opposite trends for native species; 2) the cover of invasive grasses would decrease up to a certain distance from edge whereas that of native graminoids would increase (Dodonov et al. 2013, Mendonça et al. 2015); and 3) there would be negative relationships in the cover of invasive and native graminoids and of different invasive grasses (Damasceno et al. 2018; Pivello et al. 1999a,b) at a variety of spatial scales.

Methods

Study sites

We sampled two areas in São Paulo state, southeastern Brazil: Itirapina Ecological Station (22°14'46"S, 47°52'39"W) and Federal University of São Carlos (21°58'34"S, 47°52'31"W) (Figure 1a-d). These sites were selected because they were easily accessible and spatially heterogeneous on a small scale. The vegetation types in these sites include riparian forests, savanna known as typical *cerrado*, open savannas known as *campo* sujo, and grasslands (classification according to Coutinho 1978; Ribeiro and Walter 2008). Graminoids account for 30 to 90% of the biomass in these grasslands and savannas (Kauffman et al. 1994).

Itirapina Ecological Station is mostly occupied by *campo sujo*, often associated with a shallow water table in this area (Leite et al. 2018), gallery forests, savanna-forest ecotones, and degraded *campo sujo* areas occupied mostly by African grasses (Figure 2a, c, f). The creation of Itirapina Ecological Station began in 1957 and was completed in 1984 (Zanchetta et al. 2006). The area has a long history of human impacts prior to becoming a protected area (pers. comm. from the station’s employees) and the station’s most recent management plan states that nearly all grassland and savanna areas therein contain African grasses (Zanchetta et al. 2006). The area in São Carlos was previously occupied mostly by eucalypt plantations and pastures, which were removed between 1972 and 1988 (Fushita et al 2017). Currently, this area contains degraded *campo sujo* dominated by African grasses, typical *cerrado* in intermediate and advanced states of regeneration, riparian forests and savanna-forest ecotones (Figure 2b, d, e, g, h). Invasion by African grasses in this area possibly began in the 1960s (Marcelo Nivert, pers. comm.). The predominant soils are oxisols and entisols in Itirapina (Reis and Zanchetta 2006) and dystrophic oxisols in São Carlos (Dantas and Batalha 2011). The climate is humid subtropical in both areas, with an annual precipitation of around 1400 mm and an average annual temperature of around 22^{o}C (Oliveira and Batalha 2005; Reis and Zanchetta 2006). A large part of the study site in São Carlos was hit by a dry-season fire in August 2006; we are unaware of more recent fires affecting our sampling locations, and the sampling locations in Itirapina have been protected from fire for at least 15-20 years..

Sampling

We located one transect in Itirapina (transect I1, 733 m long) and two in São Carlos (transects S1 and S2, 1334 and 301 m) (Figure 1). Transects I1, S1 and S2 were sampled, respectively, between September 2012 - February 2013, August 2011 – August 2012, and March - August 2014. To avoid confouding seasonal variation with spatial pattern along the longest transect, we sampled it non-sequentially, e.g. started sampling at its middle rather than at one extremity. The transects traversed different vegetation types (Table 1, Figure 2), and anthropogenic linear disturbances, mostly narrow firebreaks (that also act as forest roads), and were placed subjectively to maximize the variation in vegetation types and the number of firebreaks. Total variation in altitude was 15, 26.5, and 8 m along I1, S1, and S2, respectively (Figure 1e-g). Transect I1 traversed degraded *campo* sujo, *campo sujo*, an ecotone, and riparian gallery forest. Transect S1 traversed typical *cerrado* (intermediate and advanced regeneration) and degraded *campo sujo*. Transect S2 included typical *cerrado*, riparian gallery forest, and ecotone. Each transect crossed 4-5 narrow linear disturbances (5-20 m-wide), resulting in a total of 24 edges along three transects (Table 1).

We sampled graminoids along each transect using 1 x 1 m contiguous quadrats . Contiguous quadrats permit the detection of spatial patterns at different scales, enabling a thorough assessment of spatial variation in the response variables (Xiaobing and van der Maarel 1997; Dale 1999). Within each quadrat, we visually estimated the cover of four graminoid types: two species of invasive grasses (*Urochloa decumbens* **(**Stapf) R.D.Webster and *Melinis minutiflora* P. Beauv - Poaceae), native grasses (Poaceae), and native sedges (Cyperaceae). *U. decumbens* and *M. minutiflora* are C4 African grasses (Klink and Joly 1989) and are considered serious threats to *cerrado* vegetation (Hoffmann and Haridasan 2008; Xavier et al. 2017). *U. decumbens* usually forms a continuous cover, whereas *M. minutiflora* tends to have a patchy distribution (Pivello et al. 1999b). We did not differentiate native grasses from other exotic but non-invasive grasses (e.g. *Melinis repens* (Willd.) Zizka) because these exotic species occur with low frequency and are not considered a conservation threat in the *cerrado* (Xavier et al. 2017, Xavier et al. 2019). We had six cover classes: 0%, 0 - 12.5%, 12.5 - 25%, 25 - 50%, 50 - 75%, and 75 - 100%, and used their mid-points in the analyses.

Data analysis

We analyzed each graminoid group along each transect separately for all analyses. The scales of spatial pattern (see below) were always determined for the full transects and for each vegetation type individually. For the first objective (comparing graminoids among vegetation types), we assessed the frequency, average cover, and scales of spatial pattern in each vegetation type. We calculated the frequency (proportion of quadrats containing each graminoid type) and average cover (excluding zero-cover quadrats, as they were already considered in the frequency calculation) and compared these values to a null model representing homogeneous vegetation along the transects. For this, we calculated two-tailed 95% confidence intervals for a first-order Markov chain (MC1) model including spatial autocorrelation but assuming there are no differences among the vegetation types; we used MC1 because complete spatial randomness is usually an ecologically unrealistic null model (Fortin and Jacquez 2000, James et al. 2010). In our MC1 model, the cover of a graminoid in a quadrat is a stochastic function of its cover in the adjacent quadrat, as calculated from the data (Dodonov 2015; Online Resource 1), representing small-scale dispersal especially by vegetative spread. We simulated the data by 1) selecting a random position along the transect, 2) assigning the cover of the graminoid in question in a random quadrat to the selected position, 3) randomly determining the cover in the next quadrat based on the current quadrat's cover, and 4) repeating step 3 until reaching the end of the transect (Dodonov 2015). This procedure was applied in both directions, i.e. towards the end and the beginning of the transect, 4999 times, resulting in 5000 datasets for each response variable along each transect (the observed data and 4999 simulations, Manly 2007).

We used wavelets (Percival and Walden 2000; Dong et al. 2008; Rouyer et al. 2008) to assess the scales of spatial pattern (which can be understood as the average distance between patch and gap centers - Dale 1999), up to a maximum scale of 75 m. We used the continuous wavelet transform (CWT), a highly redundant transformation of the data that shows its adjustment to a wavelet template at contiguous scales of 1, 2... *j* meters, where *j* is the maximum scale examined. This is done by multiplying the graminoid cover data by the wavelet template centered at the first position, then at the second position, and so on until the last position along the transect. The wavelet template is then expanded and this analysis is repeated for a larger scale. The result shows how similar the signal is to the shape of the wavelet template at each position along the transect at different scales, and thus depends on the wavelet template used (Percival and Walden 2000; Dong et al. 2008; Rouyer et al. 2008). The amount of variation at each scale, or scale variance, is calculated by squaring the CWT coefficients and averaging the squared values across all positions for a given scale (Dale and Mah 1998; Rosenberg and Anderson 2011).

We calculated scale variance based on the Mexican Hat wavelet, a second derivative of a Gaussian function (Dale and Mah 1998; Percival and Walden 2000), for scales up to 75 m, except when limited by the number of quadrats or by their proximity to the transects' limits. For this wavelet template, maximum variance values are observed at scales at which the template overlaps high-cover areas (patches) surrounded by low-cover areas (gapes) or vice-versa. We assessed significance by comparing the variance at each scale with one-tailed 95% confidence intervals for the MC1 models. As the differences among vegetation types in graminoid frequency and cover were assessed in the previous analysis, we simulated MC1 models separately for each vegetation type. Thus, the null hypothesis was that the spatial pattern within each vegetation type is determined by small-scale autocorrelation, but there may be other differences among vegetation types (Dodonov 2015). As above, we used 4999 simulated datasets plus the original data.

For the second objective (assessing effects of edges and topography), we adjusted, for each transect, binomial generalized additive models with logit link functions (GAMs – Zuur et al. 2009) relating the cover of each graminoid type to either either distance to the nearest firebreak or elevation and including vegetation type in all models, resulting in a total of 24 GAMs. We included vegetation type to avoid confounding differences among vegetation types with effects of other explanatory variables, as, for example, forest vegetation was farther from edges and on lower ground than other vegetation. Quadrats on linear disturbances were excluded because we were interested in determining how edge distance affects the remaining vegetation. The optimal degree of smoothing was determined by cross-validation, but we set a maximum limit of 5 effective degrees of freedom to avoid overfitting (Zuur et al. 2009).

We calculated the significance of each GAM by comparing them to MC1 models considering spatial autocorrelation and differences among the vegetation types, as above. We adjusted the two GAMs for each simulated dataset, extracted the proportion of deviance explained by the model (analogous to an R^2), and calculated one-tailed significance as the proportion of simulated datasets in which the proportion of explained deviance was at least as great as that obtained for the original data.

For the third objective (assessing the relationships between native and invasive graminoids), we used wavelet scale covariance, also known as bivariate wavelet analysis, to assess the relationship between invasive and native graminoids and between the two invasive species (Hudgins and Huang 1996; Rosenber and Anderson 2011). Wavelet scale covariance is calculated by multiplying the CWT coefficients of two response variables and calculating the average of this product across all positions for each scale (Rosenberg and Anderson 2011); the result shows at which scales the two response variables are positively or negatively correlated. We used the Mexican hat wavelet and a maximum scale of 75 m, as above. We calculated 95% confidence intervals based on MC1 models as in the previous analysis, using one-tailed confidence intervals for the relationships between invasive and native graminoids to focus on negative relations only and two-tailed intervals for the relations between the two invasive species.

All analyses were performed in R 3.2.3 (R Core Team 2015), with the packages *wmtsa* (Constantine and Percival 2012) for wavelet analyses and *mgcv* (Wood 2011) for GAMs. Pseudocode for the MC1 models is available as Online Resource 1. The datasets and the full R code used, including functions for the MC1 simulations and for wavelet variance and covariance, are available as Online Resource 2 and 3, respectively.

Results

The frequency and cover of the different graminoid types varied among transects and vegetation types (Figure 3, Tables 2 and 3). The cover of *U. decumbens* was lower than predicted by the MC1 models (i.e. lower than would be expected if spatial autocorrelation alone determined its cover) in some *campo sujo* and typical *cerrado* areas, but it was more frequent and had higher cover than predicted in degraded *campo sujo*. Cover and frequency of *M. minutiflora* generally did not deviate from the MC1 models. Native grasses were less frequent than predicted by the MC1 models in degraded *campo sujo* (Tables 2 and 3). *U. decumbens* and *M. minutiflora* were completely or nearly absent from ecotones in Itirapina and from forest areas. Native sedges were absent from the degraded *campo sujo* areas in São Carlos. Otherwise, all graminoids were found in all vegetation types along all transects.

There were few significant scales of spatial pattern (*i.e.* deviations from the MC1 model predictions); larger scales, over 30-40 m, were predominant and no scales were significant for transect S2 (Table 4). *U. decumbens* had significant scales of approx. 10-13 and 40-55 m in degraded *campo sujo*. Scales of pattern were significant for *M. minutiflora* only for transect S1, with scales of 40-75 m in all vegetation types and an additional scale of 16-17 m in degraded *campo sujo*. Native grasses showed significant scales of 22 to 75 m depending on the vegetation type. Smaller scales, of 17-51 m, were observed for native sedges.

Effects of edges and topography were minimal, with only five significant or marginally significant relations ($p < 0.08$). *U. decumbens* and native grasses had maximum cover at intermediate elevation at some transects ($p<0.07$; Figure 4 a-c). Sedge cover increased slightly with distance from the edge whereas native grass cover was greatest at intermediate distances along one transect each (Figure 4 d-e).

Negative relationships between invasive and native graminoids were observed along all transects and in most vegetation types, with finer scales being dominant for *M. minutiflora* (Table 5). Negative relationships between *U. decumbens* and native grasses were observed at scales of 1, 5-13, and 19-66 m. Those between *U. decumbens* and native sedges were less common, but were also observed at scales of 1, 11-22 and 69-75 m. *M. minutiflora* was negatively related to native grasses at scales of 1-18 and 36-66 m, and to native sedges at scales of 1-4 and 23-46 m. The two invasive grasses were largely uncorrelated with each other (Table 6), but positive relationships were observed at scales of 2-10, 41-51 and 66-75 m, and negative ones at scales of 1-2 and 12-18 m.

Discussion

Vegetation type affected both native and invasive graminoids. Both study sites had a substantial cover of invasive grasses, but these species were rare or absent in forests. This is consistent with the environmental constraints associated with these vegetation types, as *U. decumbens* and *M. minutiflora* may be more limited by shade than native graminoids (Xavier et al. 2017). Likewise, both invasive grasses were absent from ecotones in the Itirapina transect, which are transitions between wet grasslands and riparian forests dominated by floodplains species (pers. obs.). The hydrological regime may explain the absence of invasive grasses in these sites (Xavier et al. 2017), even though *M. minutiflora*, unlike *U. decumbens* (Dias-Filho and Carvalho 2000), is moderately resistant to waterlogging periods (Xavier et al. 2017). The extensive variation within the expected range for the MC1 models shows the high importance of small-scale autocorrelation in this system.

Spatial patterns also differed between the invasive grasses: *M. minutiflora* tended to occur in clumps, unlike the more continuous cover of *U. decumbens*, as has also been observed previously (Pivello et al. 1999b). *M. minutiflora* produces many wind-borne seeds (Martins et al. 2009) and is stress-tolerant (Baruch and Jackson 2005; Xavier et al. 2017; Xavier and D'Antonio 2017). Dispersal ability is closely related to spatial dynamics and persistence of species in patchy environments (Hassell et al. 1994), such as Neotropical savannas (Jeltsch et al. 1998; Gonçalves and Batalha 2011; Dodonov et al. 2014b). We hypothesize that a synergism between effective seed dispersal and phenotypic plasticity enables *M. minutiflora* to arrive and establish under less suitable conditions than *U. decumbens*, with the subsequent formation of dense monospecific patches and the patchy spatial structure observed here. As our MC1 models were designed to incorporate small-scale dispersal, the few significant scales observed for *U. decumbens* may indicate that it relies more on local dispersal to surrounding favorable sites, resulting in a more homogeneous spatial pattern with larger and more spread-out patches, possibly due to its producing comparatively fewer and heavier seeds (Gardener et al. 1993) and being less stress-tolerant (Xavier et al. 2017). The larger scales of spatial pattern up to 30 to 75 m for native graminoids may be related to factors such as woody vegetation and fire severity, which may be spatially structured on scales up to 60 m or more in the *cerrado* (Gonçalves and Batalha 2011; Dodonov et al. 2014b).

We found few relationships with edges or topography, and these were not consistent among sites. The effects of elevation may be related to soil water availability, as water table depth and soil water availability vary with topography in Itirapina (Leite et al, 2018; Xavier et al, 2017). Elevation effects on spatial patterns and invasion success are often complex and depend on interactions with other environmental factors (Davis et al. 2015; Chudomelová et al. 2017). The lack of edge influence was surprising, as previous studies detected effects of linear disturbances on adjacent savanna vegetation (Smit and Asner 2012; Dodonov et al. 2013, 2017; Krix et al. 2017). Roads and other linear corridors may facilitate the dispersal of invasive (Gelbard and Belnap 2003; Penone et al. 2012) and native (Suárez-Esteban et al. 2013; Dodonov et al. 2014a) species. However, firebreaks in our study area had little vehicle movement, reducing the dispersal of invasive plants. Edge influence in some studies could have resulted in part from small-scale dispersal, which was incorporated into our MC1 modelos.

Negative effects of *M. minutiflora* on native species, such as we observed for graminoids at scales of 10-30 m, are well-known (Almeida-Neto et al. 2010; Hoffmann and Haridasan 2008). Similar negative correlations have been observed for *U. decumbens* in our study and as a decreased abundance of native graminoids at edges dominated by *U. decumbens* by Dodonov et al. (2013). Still, these negative effects were not observed at all the scales evaluated, indicating that the effects of invasive species are generally scale-dependent (Powell et al, 2011; Pauchard and Shea, 2006).

Positive relationships between the two invasive species were more common than negative ones, which may reflect similar environmental requirements (e.g. low canopy cover). By hampering the establishment and growth of woody species (Hoffman and Haridasan 2008), these may species favor each other by decreasing overall shading. Positive interactions between co-occurring invasive species may enable their long-term persistence to the detriment of native species (Simberloff and Von Holle 1999; Vitousek and Walker 1989). However, typical competitive interactions may also be observed (Belote and Weltzin 2006; Xavier and D'Antonio

2017). Our results show that, regardless of the mechanism, negative interaction between invasive grasses may take place at smaller scales than positive ones.

Overall, we found that vegetation type was the best predictor of the cover of invasive and native graminoids, whereas elevation and edges had only minor roles. In addition, much of the variation could be explained by fine-scale autocorrelation, as incorporated into our MC1 models. *Cerrado* graminoid communities appeared to be structured at scales of approx. 20-70 m, with interactions between invasive and native graminoids occurring on similar scales. However, *U. decumbens* had negative effects at larger scales than the more patchily distributed *M. minutiflora* and thus the interaction between different invasive grasses may be scale-dependent. As both invasive species were not limited to edges, control and monitoring actions must consider the entire area where these grasses may occur: even if control of invasive grasses in a patch is successful, the existence of other nearby patches is likely to enable reinvasion. Because complete eradication of an invasive species is rarely feasible once this species is well-established and considering that the effects of invasive grasses on native ones occur at different scales, management actions may be directed towards scales at which these effects are strongest. This management has to be species-specific. Because *M. minutiflora* had effects at smaller scales than *U. decumbens*, we recommend controlling, even small patches of *M. minutiflora* when possible, but focusing on larger patches for managing *U. decumbens*. Spatial scales must be considered in studies on the impacts of an control invasive grasses.

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Supplementary material

Online Resource 1: Pseudocode for the MC1 null models.

Online Resource 2: Datasets used for the analyses.

Online Resource 3: R code used for the analyses.

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Tables

Table 1. Land uses and vegetation types along the two study transects in São Carlos and Itirapina. The length and elevation is indicated for each section of different land use or plant community.

Section number	Land use or vegetation type	Length (m)	Mean elevation (m a.s.l.) (range in parentheses)
Itirapina (I1)			
1	Railroad	12	704 (704-704)
2	Degraded *campo sujo*	107	702 (700-705)
3	Firebreak	13	700 (700-700)
4	*Campo sujo*	287	697 (693-700)
5	Firebreak	12	693 (693-693)
6	Ecotone	31	692 (692-693)
7	Forest	135	691 (690-692)
8	Ecotone	31	693 (691-694)
9	*Campo sujo*	40	695 (694-696)
10	Firebreak	14	696 (696-696)
11	*Campo sujo*	52	696 (696-697)
São Carlos 1 (S1)			
1	Degraded *campo sujo*	32	853 (852-854)
2	Firebreak	3	854 (854-854)
3	Degraded *campo sujo*	69	857 (854-860)

4	Firebreak	4	860 (860-861)
5	Typical *cerrado*	223	865 (861-870)
6	Firebreak	5	870 (870-870)
7	Typical *cerrado* (intermediate regeneration)	209	874 (869-877)
8	Firebreak	4	876 (876-876)
9	Typical *cerrado* (intermediate regeneration)	779	873 (862-879)
10	Firebreak	6	862 (862-862)
São Carlos 2 (S2)			
1	Firebreak	8	864 (864-864)
2	Typical *cerrado* (intermediate regeneration)	47	863 (863-864)
3	Firebreak	6	863 (863-863)
4	Typical *cerrado*	9	863 (863-863)
5	Firebreak	5	863 (863-863)
6	Ecotone	39	863 (862-863)
7	Forest	124	859 (857-862)
8	Typical *cerrado*	57	862 (859-864)
9	Firebreak	6	865 (864-865)

* Railroad: a railroad on the border of the Itirapina study site; firebreak: a dirt road with almost no vegetation

Table 2. Frequency (% quadrats) of the different graminoids in each vegetation type along the three transects. The first value is the observed frequency and the numbers in parentheses are 95% confidence intervals for the null hypothesis of no difference among the vegetation types. Values outside the confidence interval were considered significantly different from the null model and are underlined.

	Urochloa decumbens	*Melinis minutiflora*	Native grasses	Native sedges
Itirapina I1				
Degraded *campo sujo*	<u>97.2</u> (0.9 - 55.1)	4.7 (0 - 10.3)	<u>25.2</u> (36.4 - 83.2)	9.3 (8.4 - 28)
Campo sujo	8.4 (7.4 - 37.7)	4.5 (0.8 - 6.6)	<u>85.5</u> (47.5 – 72.6)	16.1 (12.7 - 23)
Ecotone	0 (0 - 62.9)	0 (0 - 12.9)	87.1 (29 - 88.7)	<u>35.5</u> (6.5 – 32.3)
Forest	<u>0.7</u> (1.5 - 51.9)	0 (0 - 9.6)	<u>7.4</u> (39.3 - 80)	16.3 (9.6 - 26.7)
São Carlos S1				
Degraded *campo sujo*	<u>77.2</u> (5.9 - 39.6)	59.4 (26.7 - 65.3)	<u>54.5</u> (57.4 - 86.1)	<u>0</u> (5.9 - 28.7)
Typical *cerrado* (intermediate regeneration)	<u>13.3</u> (14.3 - 25.7)	42.3 (39.4 - 51.4)	<u>77.9</u> (68.1 - 77.2)	<u>21.1</u> (12.8 - 20)
Typical *cerrado* (intermediate regeneration)	22.9 (9.4 - 32.3)	57 (32.7 - 58.3)	64.1 (62.8 - 82.1)	<u>4</u> (9.4 - 24.2)
São Carlos S2				
Typical *cerrado* (intermediate regeneration)	17 (0 - 23.4)	36.2 (4.3 - 55.3)	59.6 (17 - 70.2)	2.1 (0 - 34)
Typical *cerrado*	10.6 (0 - 19.7)	<u>57.6</u> (7.6 - 50)	48.5 (21.2 - 65.2)	18.2 (0 - 28.8)
Ecotone	7.7 (0 - 23.1)	46.2 (2.6 - 59)	15.4 (15.4 - 74.4)	15.4 (0 - 35.9)
Forest	<u>0</u> (1.6 - 16.1)	<u>0</u> (12.1 - 43.5)	45.2 (25 - 59.7)	6.5 (0.8 - 23.4)

Table 3. Average cover (%) of the different graminoids in each vegetation type along the three transects. The first value is the observed cover and the numbers in parentheses are 95% confidence intervals for the null hypothesis of no difference among the vegetation types. Values outside the confidence interval were considered significantly different from the null model and are underlined.

	Urochloa decumbens	*Melinis minutiflora*	Native grasses	Native sedges
Itirapina I1				
Degraded *campo sujo*	61.4 (6.3 - 66.4)	6.3 (0 - 37.5)	9 (24.3 - 52.1)	23.1 (9.1 - 29.3)
Campo sujo	28.1 (31.1 - 59.9)	18.4 (6.3 - 24.6)	41.4 (31.9 - 46.4)	16.5 (12.6 - 23.4)
Ecotone	0 (0 - 69.1)	0 (0 - 37.5)	51.3 (19.8 - 55.3)	32.7 (7 - 34.4)
Forest	6.3 (6.3 - 65.4)	0 (0 - 31.3)	8.8 (26.4 - 50.8)	8.8 (9.9 - 28.6)
São Carlos S1				
Degraded *campo sujo*	52 (6.3 - 51.1)	41.4 (16.6 - 43.5)	42.2 (15.9 - 30.9)	0 (6.3 - 19.2)
Typical *cerrado* (intermediate regeneration)	23.3 (24 - 38.4)	27.7 (25.4 - 33.9)	23.2 (20.9 - 25.7)	11.3 (9 - 13.5)
Typical *cerrado*	24 (15.1 - 45.1)	31.1 (20.6 - 38.6)	16.7 (18.4 - 28.5)	9.7 (7 - 16.4)
São Carlos S2				
Typical *cerrado* (intermediate regeneration)	16.4 (0 - 62.5)	19.9 (6.3 - 33.7)	22.5 (6.3 - 32.2)	37.5 (0 - 57.2)
Typical *cerrado*	10.7 (0 - 49)	15.1 (6.3 - 31.8)	17.4 (8.5 - 30.4)	45.8 (0 - 57.5)
Ecotone	10.4 (0 - 62.5)	10.1 (6.3 - 35)	6.3 (6.3 - 33.3)	15.6 (0 - 57)
Forest	0 (6.3 - 37.5)	0 (7.3 - 26.9)	19.5 (10.5 - 27)	7.8 (6.3 - 53.4)

Table 4. Significant scales (m) of spatial pattern for the different graminoid types for the vegetation types along each transect up to a maximum scale of 75 m*. Significance was asssessed via Markov Chain models controlling for differences among the vegetation types. Results for transect S2 are not shown because there were no significant scales of spatial pattern.

	Urochloa decumbens	*Melinis minutiflora*	Native grasses	Native sedges
Itirapina I1				
Overall (entire transect)	ns	ns	43-75	ns
Degraded *campo sujo*	44-58	ns	ns	17-31
Campo sujo	ns	ns	ns	34-39
Ecotone	N/A**	N/A	60	ns
Forest	ns	N/A	22-75	ns
São Carlos S1				
Overall (entire transect)	ns	43-75	28-75	33-48
Degraded *campo sujo*	10-13, 41-51	16-17, 44-51	ns	N/A
Typical *cerrado* (intermediate regeneration)	ns	51-75	23-75	30-51
Typical *cerrado*	ns	18, 39-63	ns	ns

* The maximum scales assessed were smaller for some sections either because they were on the limit of transect or because they were too short to make the assessment of larger scales meaningful: transect I1, ecotone (62 m) and invaded grassland (58 m); transect S1, invaded grassland (51 m); transect S2, regenerating *cerrado* (26 m), *cerrado* (34 m) and ecotone (39 m).

** N/A: this species was absent from this vegetation type.

Table 5. Spatial scales at which there were negative relationships between invasive grasses (U. decumbens and M. minutiflora) and native grasses and sedges, up to a maximum scale of 75 m*. Significance was assessed via a first-order Markov chain model controlling for differences between vegetation types. The ecotone and forest in I1 and forest in S2 were not included because the invasive species were absent or nearly absent in these environments.

	U. decumbens vs. Native grasses	*U. decumbens* vs. Native sedges	*M. minutiflora* vs. Native grasses	*M. minutiflora* vs. Native sedges
Itirapina I1				
Overall (entire transect)	1	1	5-18	26-44
Degraded *campo sujo*	1, 55-58	1, 14-22	ns	ns
Campo sujo	ns	2	5-18	25-46
São Carlos S1				
Overall (entire transect)	1, 7-11, 28-66	ns	1-12	23-33
Degraded *campo sujo*	5-13, 31-51	ns	34-51	N/A**
Typical *cerrado* (intermediate regeneration)	36-55	ns	1-16	23-34
Typical *cerrado*	ns	69-75	1-3, 36-66	ns
São Carlos S2				
Overall (entire transect)	19-29	ns	ns	2-4
Typical *cerrado* (intermediate regeneration)	ns	ns	ns	ns
Typical *cerrado*	ns	ns	6-9	1-4
Ecotone	21-25	11-12	4-10	ns

* The maximum scales assessed were smaller for some sections either because they were on the limit of transect or because they were too short to make the assessment of larger scales meaningful: transect I1, ecotone (62 m) and invaded grassland (58 m); transect S1, invaded grassland (51 m); transect S2, regenerating *cerrado* (26 m), *cerrado* (34 m) and ecotone (39 m).

** Native sedges were absent from this vegetation type along this transect.

Table 6. Scales at which there were significantly positive or negative relationships between the two invasive grasses (U. decumbens and M. minutiflora).

	Negative relationship	Positive relationship
Itirapina I1		
Overall (entire transect)	ns	75
Degraded *campo sujo*	ns	ns
Campo sujo	ns	66-75
São Carlos S1		
Overall (entire transect)	1-2, 12-18	ns
Degraded *campo sujo*	1-2, 12-18	41-51
Typical *cerrado* (intermediate regeneration)	1	ns
Typical *cerrado*	ns	ns
São Carlos S2		
Overall (entire transect)	ns	ns
Typical *cerrado* (intermediate regeneration)	ns	ns
Typical *cerrado*	ns	ns
Ecotone	ns	2-10

Figure captions

Fig. 1 Location of the study sites (a) and of the transects sampled therein (b), altimetric profiles (in meters above sea level - m a. s. l) of the three transects (c), and a schematic representation of the transect I1, showing the different vegetation types and the linear disturbances (darker lines) (d). In C, the black line represents elevation and the background colors show the land use or vegetation type: white for linear disturbances (firebreaks and railroad) and shades of gray representing, from lighter to darker, *campo sujo*, typical *cerrado*, ecotone, and forest (Table 1). Satellite images were obtained with the OpenLayers plugin in Quantum GIS software and the schematic representation used drawings from Open Clip Art. Figure widths in C) are proportional to the transect lengths.

Fig. 2 Examples of the vegetation types examined in this study: a) degraded *campo sujo* at transect I1, b) degraded *campo sujo* at transect S1, c) *campo sujo* at transect I1, d) typical *cerrado* (intermediate regeneration) at transect S1, e) typical *cerrado* at transect S1, f) ecotone at transect I1, g) ecotone at transect S2, h) riparian forest at transect S2. The areas in a) and b) are mostly occupied by invasive grasses, whereas native grasses predominate in the *campo sujo* in c).

Fig. 3 Cover of *Urochloa decumbens*, *Melinis minutiflora*, native grasses and native sedges along the three study transects.The background colors show the land use or vegetation type: white for linear disturbances (firebreaks and railroad) and shades of gray representing, from lighter to darker, *campo sujo*, typical *cerrado*, ecotone, and forest (Table 1). Figure widths are proportional to transect lengths.

Fig. 4 Effects of elevation on the cover of native grasses at transect I1 (a; p=0.012), *Urochloa decumbens* at transect S1 (b; p=0.011), and native grasses at transect S2 (c; p=0.060), and effects of distance to edge on native sedges at transect S1 (d; p=0.0010) and native grasses at transect S2 (e; p=0.078). The lines correspond to generalized additive models for different vegetation types, which were controlled for in the analysis.

Figure 1

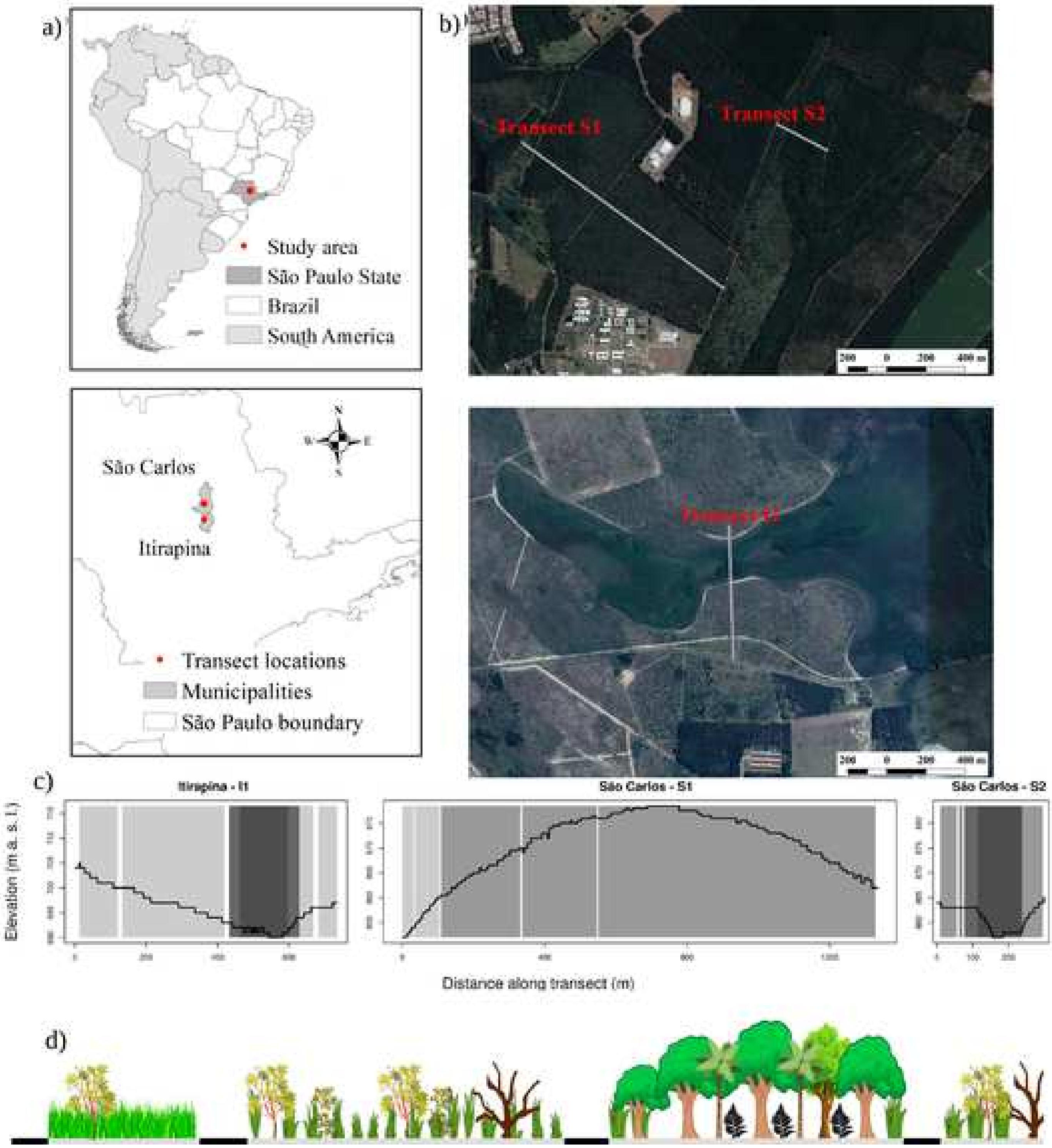

a)
Study area
São Paulo State
Brazil
South America
São Carlos
Itirapina
Transect locations
Municipalities
São Paulo boundary
b)
Transect S1
Transect S2
c)
Itirapina - I1
São Carlos - S1
São Carlos - S2
Elevation (m a. s. l.)
Distance along transect (m)
d)

Figure 2

Click here to access/download;Figure;EIgrasses_fig2_vegetation.jpg

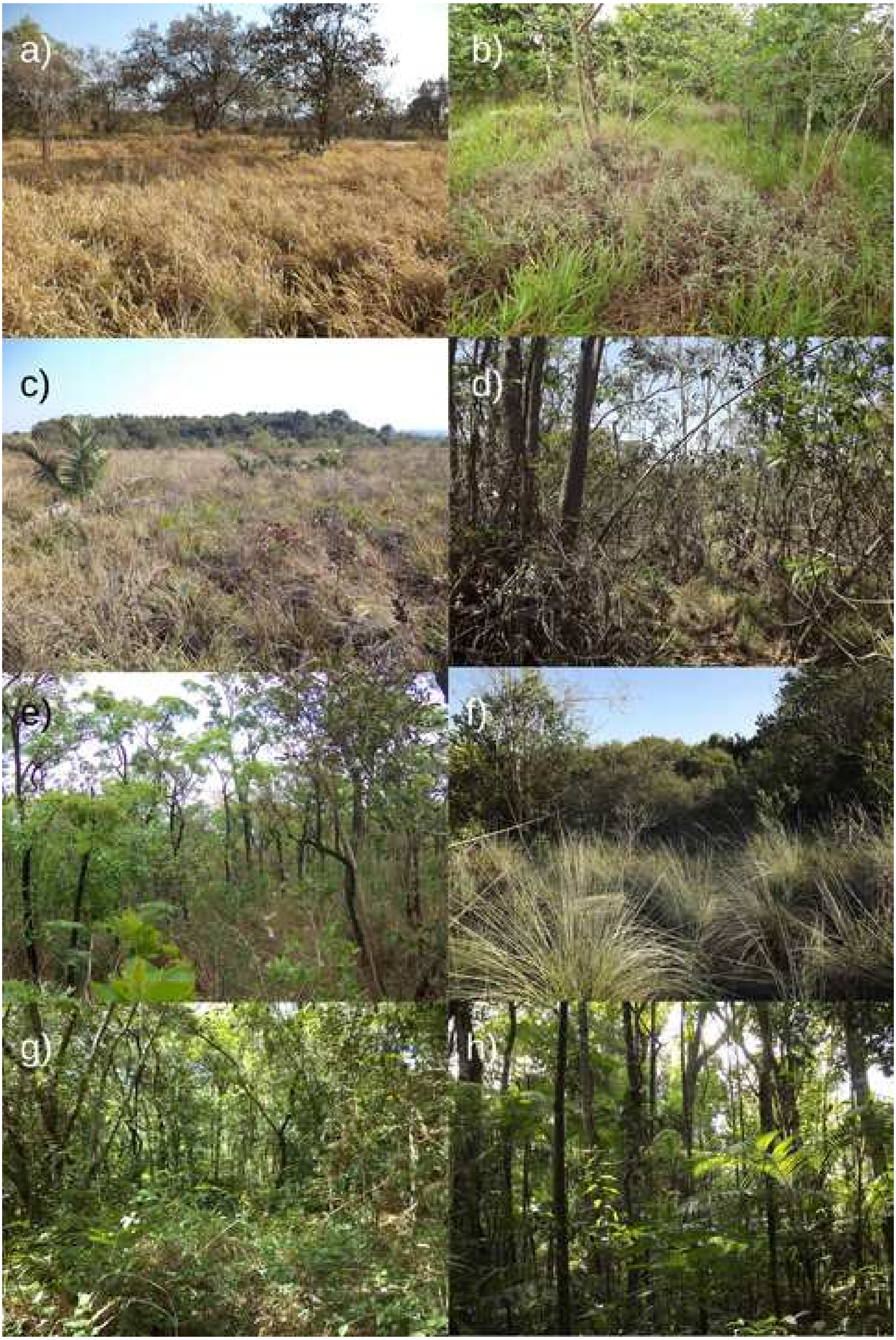


Figure 3

Click here to access/download;Figure;Elgrasses_fig3_distribution_subm3.png

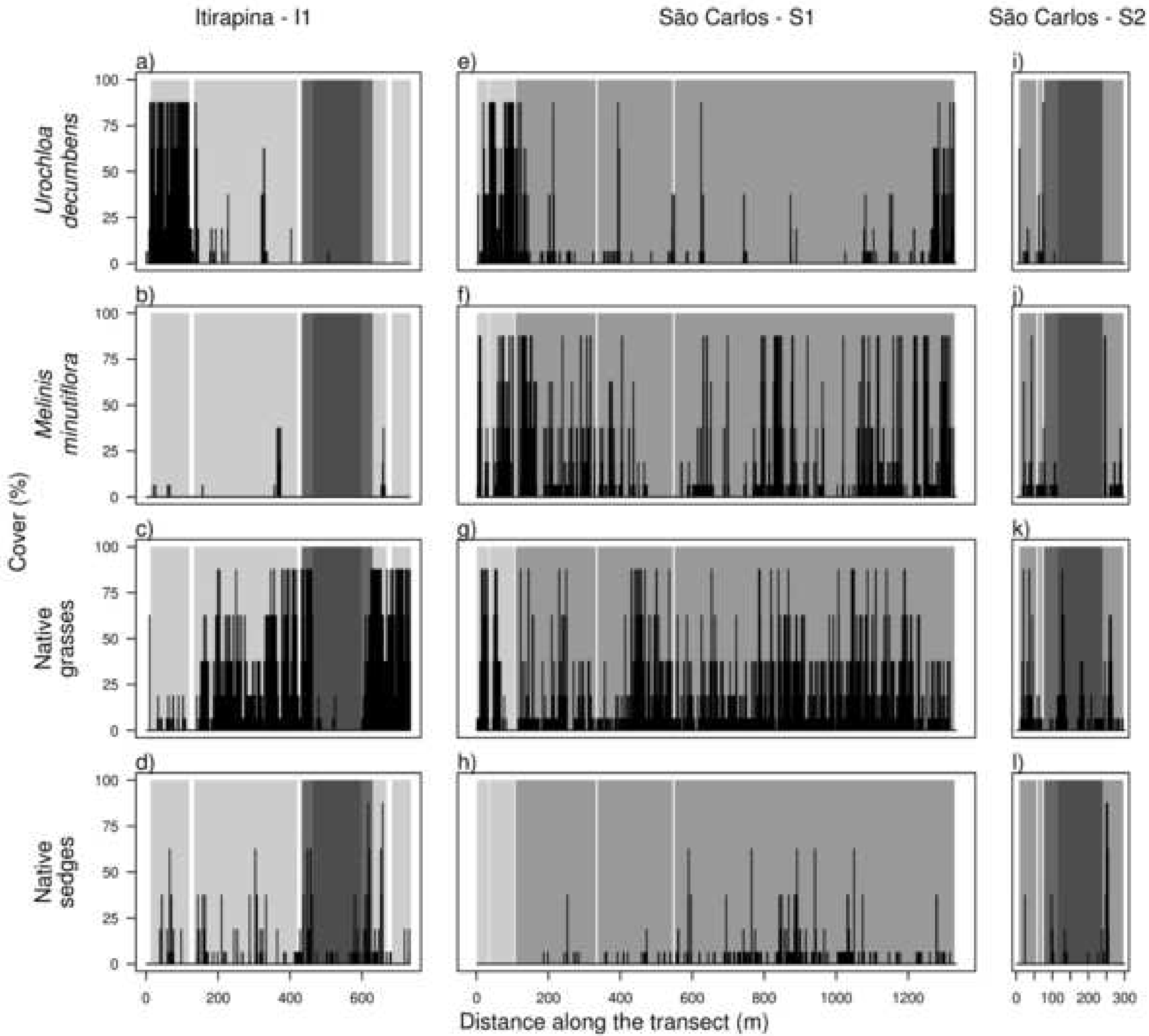
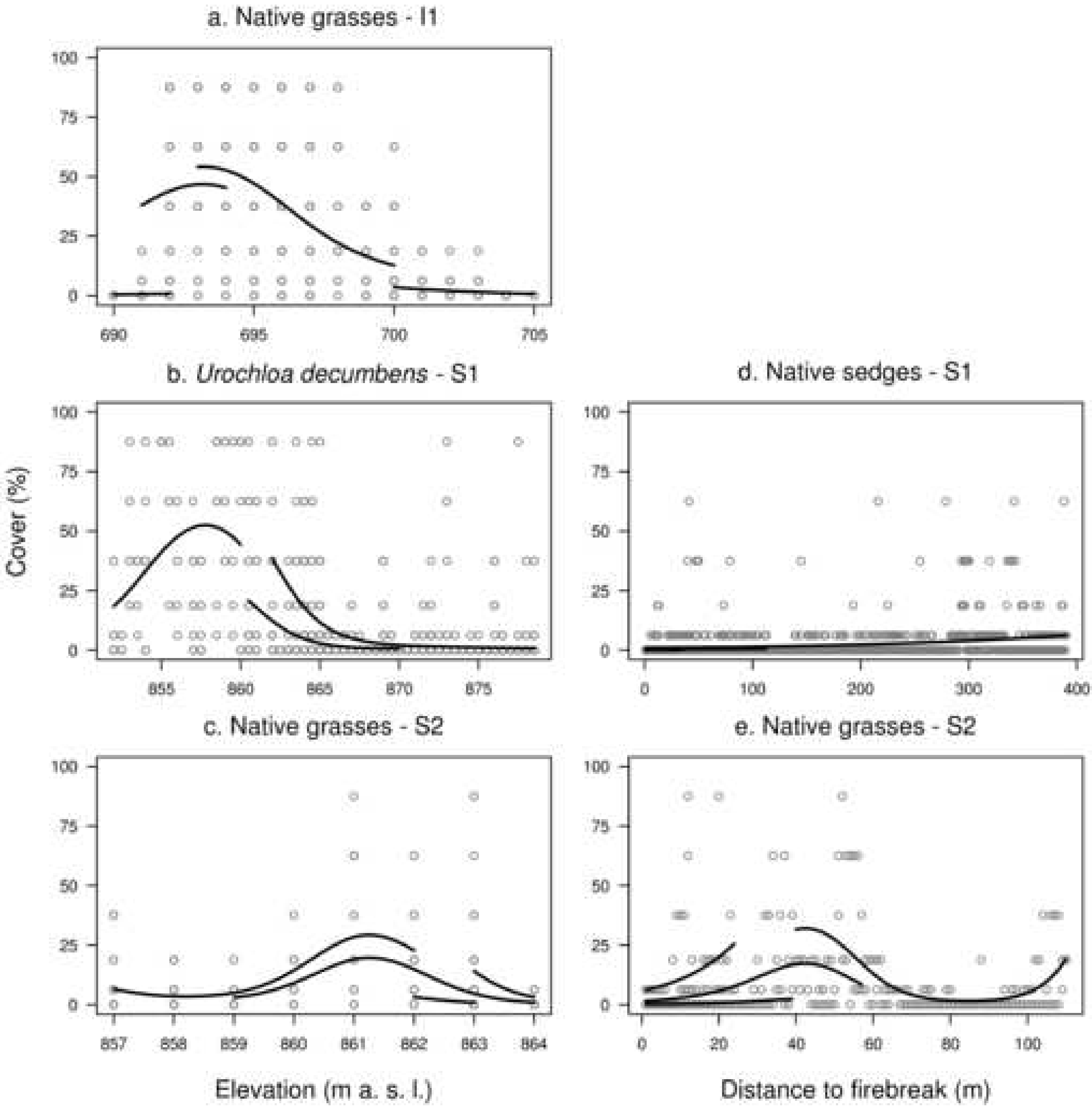


Figure 4



a. Native grasses - I1
b. Urochloa decumbens - S1
c. Native grasses - S2
d. Native sedges - S1
e. Native grasses - S2
Cover (%)
Elevation (m a. s. l.)
Distance to firebreak (m)