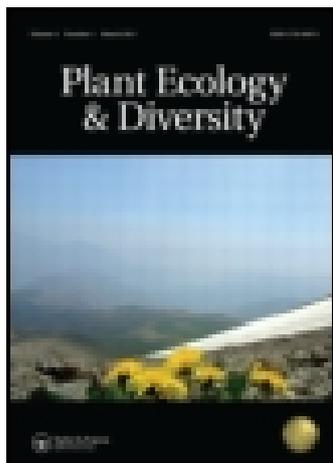


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## Factors affecting the genesis of vegetation patches in anthropogenic pastures in the Atlantic forest domain in Brazil

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**Background:** Forest succession in tropical pastures usually starts from woody vegetation patches. Patches may arise within the grass matrix at microsites with favourable soil conditions or through facilitation by established nurse plants.

**Aims:** We report the formation of woody vegetation patches in tropical pastures after investigating whether patch formation was associated with micro-scale terrain features and whether facilitation was important for patch initiation.

**Methods:** The study was conducted in three pasture sites in the Atlantic forest domain of Brazil. We compared soil, terrain and species abundance patterns among pairs of woody patch and open pasture plots.

**Results:** The effect of variation in soil physical and chemical attributes was limited. Some species were able to establish in the grass matrix and survive disturbance from grazing and fire, while other species only established in patches, under other already established trees or shrubs. Some of these species were exotics, which are commonly eliminated in restoration efforts.

**Conclusions:** Allowing the establishment of species capable of withstanding pasture environments, including exotics, can accelerate succession. Furthermore, the abilities to endure competition from grasses and survive fire are key features of species suitable for the initial stages of forest restoration in tropical pastures.

**Keywords:** facilitation; *Paspalum notatum*; slope; soil fertility; *Urochloa decumbens*

### Introduction

Re-establishment of native forest vegetation in pasture sites can be gradual, and it depends on several factors including microclimate, availability of propagules, range-land management regimes and competitive ability of dominant grasses (Marcano-Vega et al. 2002; Zanini et al. 2006; Griscom et al. 2009; Nadkarni and Haber 2009; Leitão et al. 2010). Management can result in highly compacted soil with low fertility (Carvalho et al. 2010; Merino-Martín et al. 2012), while high cattle density and high fire frequency can heavily damage woody species (Davis et al. 1999; Holl 2002; Martinez-Garza and Howe 2003; Santiago-García et al. 2008; Griscom et al. 2009; Brooks et al. 2010; Gunaratne et al. 2010). However, establishment of woody species in the grass matrix can create favourable microclimates under their canopies and promote seedling establishment by attracting seed dispersers, thereby improving soil conditions and ultimately facilitating the development of a woody vegetation patch (Davis et al. 2005). This process has been widely described, and tree and shrub species capable of having a facilitation effect have been called 'nurse plants' or 'focal plants' (Benjamin and Sanderson 2000; Saïd 2001; Callaway et al. 2002; Marcano-Vega et al. 2002; Lanta and Lepš 2008; Baniya et al. 2009; Modna et al. 2010).

The establishment of nurse plants may itself be influenced by both microsite characteristics, such as microtopography, and by traits such as drought tolerance and

nutrient requirements, of the potential nurse species (Scholz et al. 2010; Merino-Martín et al. 2012). Ecological restoration activities have been devoted to deal with either site limitation or the selection of the best facilitating species, and even a combination of the two strategies, presenting inconsistent results (Lopez-Pintor et al. 2003; Hooper et al. 2005; Zanini et al. 2006; Lanta and Lepš 2008; Massad et al. 2011).

Another source of variation in the preliminary results of both active and passive forest restoration efforts in pastures is the identity of the dominant grass (Brooks et al. 2010). Some tropical grasses, such as *Urochloa* spp., have been reported to act as barriers in tropical forest regeneration (Barbosa et al. 2008; Leitão et al. 2010), while others appear to be less restrictive to the establishment of woody species (Fehmi et al. 2004; Cheung et al. 2009; Brooks et al. 2010; Flory and Clay 2010). For example, *Paspalum notatum*, a South American grass, is known among restoration practitioners to be less restrictive of forest regeneration than African grasses introduced in Brazil. Thus, along with site characteristics, the availability of seed sources and facilitation effects, interactions with extant grass species may influence the genesis of woody vegetation patches in pastures (Brooks et al. 2010).

In this context, the objective of our study was to investigate the main factors affecting the formation of woody patches in tropical pastures of the Atlantic forest domain through the systematic sampling of spontaneous

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woody patches and open pastures in three sites dominated by the tropical grasses *Urochloa decumbens* Stapf. (R. D. Webster) and *P. notatum* Flüggé. We sought to determine (1) whether patch formation was associated with terrain characteristics such as soil depth, slope or fertility; and (2) whether facilitation was important for patch formation.

## Materials and methods

### Study sites

Study sites were located in the northern Paraná state of Brazil, where the natural vegetation was seasonal Atlantic forest at three pasture sites: Refugio farm (23° 21' 92" S, 51° 06' 89" W), Barra Grande farm (23° 29' 59" S, 51° 08' 68" W) and Mafre farm (23° 29' 29" S, 51° 10' 01"), hereafter referred to as sites 1, 2 and 3, respectively. The three sites have similar terrain morphology (gentle slopes with small mounds and shallow gullies), soil type (a mosaic of eutroferric red nitosols and lithosols, with occasional rock outcrops) and surrounding landscape (a mosaic of pastures and soybean plantations interspersed with small forest fragments). The remnant forest cover (excluding early secondary forests) around the three sites ranges from 5% to 8%, and the distance from the nearest remnant forest fragment ranges from 1100 m (site 1) to 2500 m (site 3). All these sites are used to raise cattle at low densities (<1.0 cattle per hectare) and are occasionally burned in the late dry season. None of the sites has been burned in the five years prior to sampling. Site 1 is dominated by *U. decumbens* (Stapf) R. D. Webster (formerly *Brachiaria decumbens*), an exotic grass species, and sites 2 and 3 by the native *P. notatum* Flüggé. No remnant trees from the original forest exist in any of the three sites. Thus, all trees present established in the pasture after deforestation.

The regional climate is Köppen Cfa, subtropical with hot summers and infrequent winter frosts. The average annual air temperature is 21 °C and the average annual rainfall is 1600 mm, with more rain during summer and a weak winter dry season (Iapar 2000).

### Sampling design

Sampling was made in pairs of circular plots (radius 5.65 m, area ca. 100 m<sup>2</sup>). One plot was placed in a woody vegetation patch of up to 500 m<sup>2</sup> in area, and the other was placed in nearby open pasture. Woody patches were randomly selected and the centre of the plot corresponded to the centre of the patch, which was defined as the intersection of the two longest patch axes. An open pasture plot was placed 20 m north of the border of each woody patch. The minimum distance between plots of different pairs was 20 m. Grass cover in all pasture plots reached 100%. The number of pairs in each site was limited by the pasture area and the number of vegetation patches; 30, 12 and 15 pairs of plots were selected within sites 1, 2 and 3, respectively. Grass cover, vegetation

features, and soil and terrain characteristics were evaluated at each plot.

### Soil and terrain data

Soil depth was measured with a steel rod at four equally spaced points per plot. The presence of rocks at the surface and in the soil profile was also recorded. The presence of surface water inside the plots was recorded by observation on dry days during the rainy season. Slope was estimated from the average of two measurements per plot. Measurements were made by using a 2-m-long ruler, a measuring tape and a spirit level.

One soil sample per plot was prepared from four equally spaced 0–20 cm drill holes per plot and were analysed for pH, cation exchange capacity, base saturation and the concentrations of C, P, Ca, Mg and Na. Only the data for pH, P concentration and base saturation are presented here due to the high correlation among soil chemical variables.

### Vegetation sampling

Grass cover was estimated visually in 20% increments with the aid of a measuring tape. The cover of the two predominant grasses, *U. decumbens* and *P. notatum*, was recorded separately, but the cover of all other grasses, which was lower than 5%, was later pooled with the dominant grass.

All woody plants with a height of ≥10 cm were sampled. Height was recorded for all sampled plants and for those with a diameter at soil height (DSH) ≥ 5 cm (large plants), the DSH was also recorded. Plants with a DSH < 5 cm were considered 'small plants'. Botanical identification was made in the field whenever possible, and voucher samples were collected for later herbarium confirmation. Woody species were classified according to origin (native or exotic), dispersal syndrome (biotic or abiotic), habit (trees, shrubs or lianas) and successional status (pioneer or late successional species).

### Statistical analyses

All continuous variables were checked for normality using the Kolmogorov–Smirnov test and for homogeneity of variance using the Levene test. Comparisons between woody patches and open pasture among sites were made by using analysis of variance (ANOVA) and Tukey's tests for soil chemical properties, slope, species richness and abundance. Species richness and abundance were square-root transformed. Proportions of dispersal syndromes and successional groups, as well as the frequency of the presence of rocks, were compared by  $\chi^2$  tests in contingency tables. The relationship between vegetation data and terrain characteristics was analysed by means of Spearman's rank correlation. Results were considered significant when  $P < 0.05$ . Similarity in species composition was assessed via Jaccard and Bray–Curtis indices. The relationship

between total species abundance in patches and open pasture was estimated through Spearman's rank correlation.

A  $\chi^2$  goodness-of-fit test for the proportion of individuals in each size class (small or large plants) occurring in woody and pasture plots was carried out for the 39 species with >20 individuals. The null hypothesis was that both proportions (woody and pasture) were the same. Statistica 8.0 software (StatSoft Inc., Tulsa, OK, USA) was used to carry out the statistical analyses.

## Results

### Soil and terrain features

Soil depth and the presence of rocks in the soil profile or at the surface did not differ among sites or between woody plots and open pasture plots (Table 1). These features also had no relationship with vegetation features, such as species richness and abundance. Neither gullies nor surface water were observed in any of the plots. Field observations revealed that some gullies had sparse vegetation, but no trees or shrubs, while microsites with surface water only had herbaceous vegetation, mostly from the Cyperaceae family.

Woody plots had a steeper slope than open pasture plots at site 1 (ANOVA,  $P < 0.005$ ), but not at sites 2 and 3. Slope also did not differ among sites (Table 1). Slope was correlated with some of the vegetation features, albeit inconsistently. At site 1, the richness of woody plots decreased with slope (Spearman  $r = -0.52$ ,  $P < 0.01$ ) and there was no correlation in open pasture plots. At site 2, no relationship was observed in woody plots, but in open pasture plots both species richness (Spearman  $r = 0.80$ ,  $P < 0.01$ ) and abundance (Spearman  $r = 0.65$ ,  $P < 0.01$ ) increased with slope. In contrast, no relationship was observed in woody plots or in open pasture plots at site 3. Taking sites 2 and 3 together, however, slope correlated with both species richness (Spearman  $r = 0.59$ ,  $P < 0.01$ ) and abundance (Spearman  $r = 0.51$ ,  $P < 0.01$ ).

The soil pH differed between sites 1 and 3 (Tukey,  $P < 0.001$ ), but did not differ between the woody and open pasture plots within any of the sites. The P concentration

was lower at site 1 than at sites 2 and 3 (Tukey,  $P = 0.005$  and  $0.026$ , respectively); however, at site 3, P concentration was higher in the woody plots than in the open pasture plots (Tukey,  $P = 0.043$ ). Base saturation differed only between sites 1 and 2 (Tukey,  $P = 0.005$ ), and did not differ between the woody plots and open pasture plots at any of the sites (Table 1).

### Vegetation features

Grass cover in the woody plots was higher at site 1 (mean 90% cover) than at sites 2 (33%) and 3 (47%) (Tukey, both  $P < 0.001$ ). Given that site 1 is dominated by *U. decumbens* while sites 2 and 3 are both *P. notatum*-dominated pastures, this suggests that *U. decumbens* has a higher shade tolerance than *P. notatum*. Overall, both the richness and abundance of woody species were higher in all woody patch plots than open pasture plots. Likewise, richness and abundance were higher in sites 2 and 3, which are dominated by *P. notatum* grass, than in site 1 (Tukey,  $P < 0.001$  and  $P = 0.034$ , respectively, Table 2 and Supplemental data).

Native species predominated in all sites and plot sets (open pasture and woody patches), but some exotic species had a high abundance. No differences in successional groups of species were observed among sites or between plot sets. Woody patches had a higher richness of zoochoric species in all sites ( $\chi^2$ ,  $P < 0.001$ ), with no differences among sites. Shrub density and species richness did not differ between patches and open pasture plots, but among the 10 most abundant species in open pastures, six (at site 1) and three species (at sites 2 and 3) were shrubs.

The species compositions of small plants (mostly juveniles) and larger plants and of woody patches and pastures were dissimilar, both qualitatively (Jaccard index) and quantitatively (Bray–Curtis index) (Table 3). At site 1, out of the 30 species with higher abundance in the DSH < 5 cm class (small plants or juveniles), only 14 were not observed in pastures. However, of the total of 61 species in the DSH < 5 cm class, only 19 (31%) were also observed in pastures. Taking sites 2 and 3 together, the same pattern holds, with 9 of 11 species that have a higher abundance

Table 1. Terrain and soil features in three pasture sites near Londrina, Paraná, Brazil.

Sites →	Site 1 (n = 60)			Site 2 (n = 24)			Site 3 (n = 30)		
	Patch	Open	All	Patch	Open	All	Patch	Open	All
Slope (%)	26*	20*	23	32	28	30	24	20	22
Soil depth (cm)	49	48	48.5	48.1	48.3	48.2	43	42.5	42.7
Rocks in surface (%)	13.3	0	13.3	16	12.5	14.3	13.3	0	13.3
Rocks in profile (%)	28.3	25	26.6	29	29	29	43	37	40
pH	5.5	5.5	5.5a	5.4	5.3	5.4ab	5.3	5.2	5.3b
P (mg dm <sup>-3</sup> )	12.7	9.9	11.3a	33.1	14.1	23.6b	28.5*	10.0*	19.3b
V (%)	79	78.1	78.5a	84.3	80.1	82b	81.1	77.7	79.4b

Notes: Data were derived from circular 100 m<sup>2</sup> plots placed in open pastures and woody vegetation patches. Site 1 is dominated by *U. decumbens* and sites 2 and 3 are dominated by *P. notatum*. Patch, woody vegetation patches amidst pastures; Open, open, grass-dominated pasture sites; \*significant difference between patch and open site (ANOVA, Tukey's test,  $P \leq 0.05$ ); lower-case alphabets after values indicate differences among sites.

Table 2. Proportion of species richness and abundance of the woody species in three pasture sites near Londrina, Paraná, Brazil.

S/N	Total	Origin		Dispersal		Habit			Succession	
		Native	Exotic	Abiotic	Biotic	Shrub	Liana	Tree	Pioneer	Late
<i>S</i> (%)										
Site 1	64	78	22	47	53	27	3	70	97	3
Site 2	64	87.5	12.5	45	55	31	2	67	89	11
Site 3	57	88	12	44	56	23	–	77	88	12
<i>N</i> (%)										
Site 1	1.01	80	20	26	74	18.9	0.03	81.1	98	2
Site 2	1.57	94	6	58	42	25.3	0.02	74.7	89	11
Site 3	1.35	80	20	49	51	28	–	72	96	4

Notes: Data were collected in circular 100 m<sup>2</sup> plots placed in open pastures and woody vegetation patches. Site 1 is dominated by *U. decumbens* ( $n = 60$ ) and sites 2 ( $n = 24$ ) and 3 ( $n = 30$ ) are dominated by *P. notatum*. *S*, species richness; *N*, individuals per square metre; Origin, dispersal syndromes, habit and succession category are expressed in percentage.

Table 3. Species richness, shared species and similarity indexes for woody species in three pasture sites near Londrina, Paraná, Brazil.

	Samples		Richness			Similarity index	
	First	Second	First	Second	Shared	Jaccard	Bray–Curtis
Site 1	VPL	VPS	28	60	25	0.397	0.282
	VPL	OP	28	19	12	0.343	0.385
	VPS	OP	60	19	19	0.317	0.248
Sites 2 and 3	VPL	VPS	26	79	25	0.313	0.055
	VPL	OP	26	29	10	0.222	0.11
	VPS	OP	79	29	29	0.367	0.262

Notes: Data are from circular 100 m<sup>2</sup> plots placed in open pastures and woody vegetation patches. Site 1 is dominated by *U. decumbens* ( $n = 60$ ) and sites 2 ( $n = 24$ ) and 3 ( $n = 30$ ) are dominated by *P. notatum*. VPL, vegetation patch plots, large plants (i.e. diameter at soil height, DSH > 5 cm); VPS, vegetation patch plots, small plants (DSH < 5 cm); OP, open pasture plots; Jaccard, qualitative index; Bray–Curtis, quantitative index.

of the small size class in patches also occurring in pastures, but with the majority of species (49 from 78 species, or 63%) occurring only in woody patches. Thus, there was a trend for the most abundant species in the patches as juveniles also tend to be common in pastures (Spearman  $r = 0.36$ ,  $P < 0.05$ ). However, most of the species found as juveniles in woody patches did not occur in pastures (65 out of 97 species).

Nonetheless, it is difficult to explore positive species-specific relationships for the 32 species recorded in open pasture plots, which could potentially serve as facilitators. The presence of adult individuals of any of the 10 species most abundant in open plots did not influence either the species richness or abundance of the species in the small size class. Furthermore, several patches included two or more of these species, which prevents disentangling their specific effects even through multivariate analysis (see Supplemental data).

The most abundant species differed among sites. One native species, *Lonchocarpus muehlbergianus* Hassl., and two exotics, *Psidium guajava* L. and *Tecoma stans* (L.) Juss. ex Kunth, were the most abundant at site 1. At sites 2 and 3, the native species *Croton urucurana* Baill. and *Eupatorium maximilianii* Schrad and the exotic species *P. guajava* and *Citrus limonia* (L.) Osbeck were the most abundant. When considering only woody plants with a DSH > 5 cm, the most abundant species were

*L. muehlbergianus*, *T. stans*, *Bauhinia forficata* Link and *P. guajava* at site 1; and *Tabernaemontana catharinensis* A. DC., *Parapiptadenia rigida* (Benth.) Brenan, *B. forficata* and *P. guajava* at sites 2 and 3.

Three different patterns of species abundance were observed when taking the three sites together. Some species were only recorded in woody patch plots (shown in sector A of Figure 1). Other species were observed in higher abundance in woody patch plots, but were also recorded in pasture plots (sector B of Figure 1;  $\chi^2$ ,  $P < 0.05$ ). While capable of establishing in an open pasture, these species benefited from the woody vegetation patches, reaching higher densities there. Finally, some species were equally or more abundant in pasture plots than in woody patch plots (sector C of Figure 1). Of the 39 most abundant species listed in Figure 1, only one (*C. limonia*) had individuals recorded in the ‘large’ size class in pasture plots.

## Discussion

### Soil and terrain features

Our results suggest that soil depth and the presence of rocks in the soil profile or at the surface did not affect the formation of woody vegetation patches in pastures. The inconsistent effects of slope suggest complex interactions of vegetation with topography. Positive correlations of

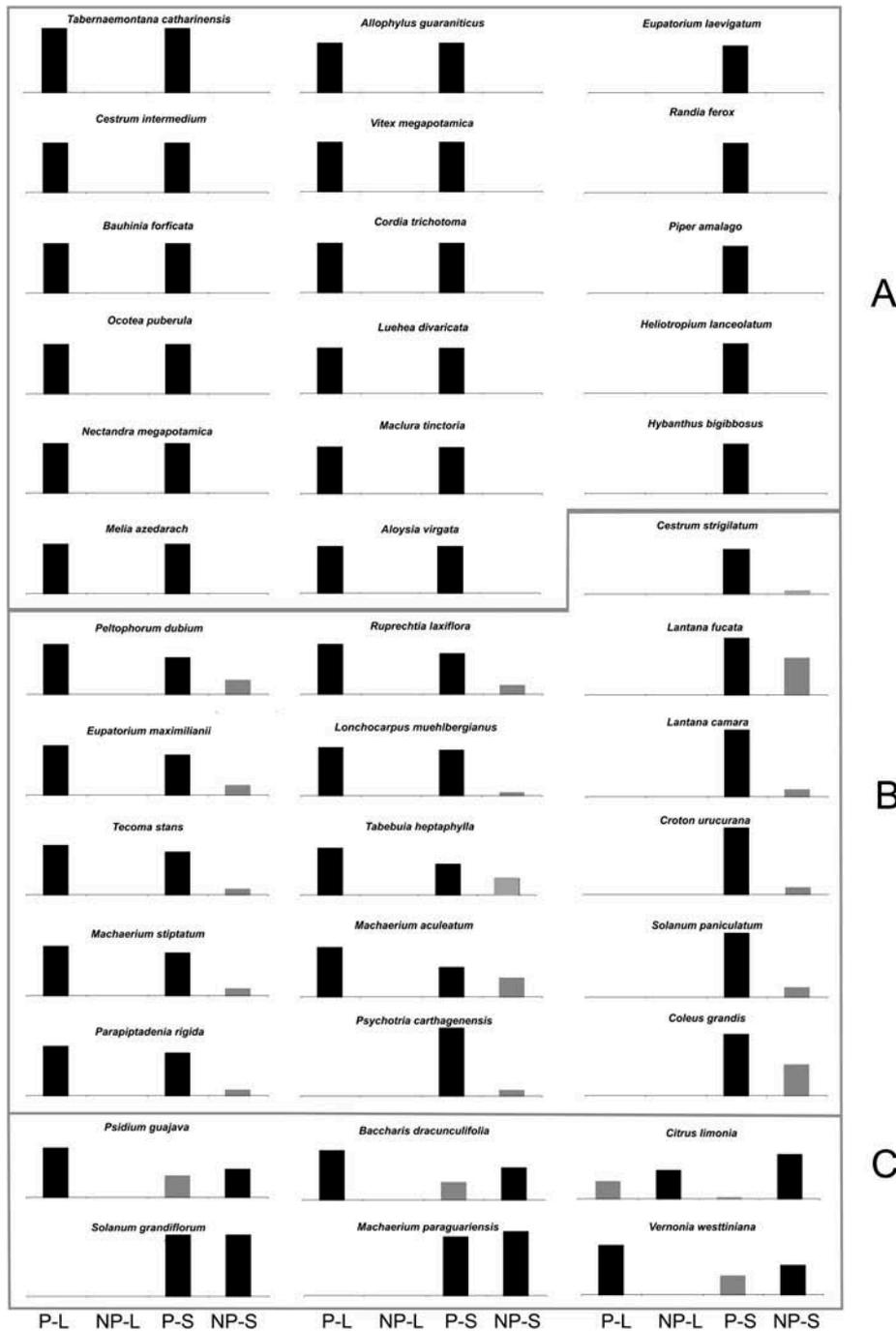


Figure 1. Relative abundance of 39 species with 20 or more individuals found in low cattle density pastures in north Paraná state, Brazil (see Table S2 for the complete set of species). The capital letters P indicate plots in  $<500\text{ m}^2$  vegetation patches and NP plots in nearby open pastures. Relative abundance were calculated for two size classes: S, woody plants higher than 10 cm and up to 5 cm in diameter at soil height (DSH); L, woody plants with  $\text{DSH} > 5$  cm. Bars of the same colour for the same size class have no statistical difference ( $\chi^2$ ,  $P < 0.05$ ). Capital letters at the right side of the figure indicate groups of species: A, patch-only, facilitated species; B, species able to establish in pastures, but benefited by patch formation; C, species able to establish in pastures with higher abundance or abundance similar to that in patches.

vegetation features with slope may be related to lower trampling and foraging rates by cattle at steep sites, which could facilitate plant establishment within the grass cover (Saïd 2001; Milchunas and Noy-Meir 2002; Gunaratne et al. 2010). Steep slopes can influence woody patch initiation, but can also limit the further

development of patch species richness after grass displacement (Saïd 2001).

Soil in all sites was highly fertile with high levels of base saturation and a high concentration of nutrients, including P. However, site 1 (dominated by *U. decumbens*) was less fertile than the sites dominated by *P. notatum*, but

the lack of replication of sites dominated by *U. decumbens* prevents conclusions regarding the effect of grass species on soil fertility. Nonetheless, there were no consistent differences in soil fertility between woody patches and open pasture plots across sites, suggesting that microsite differences in soil chemical composition are not associated with patch development.

#### Vegetation features

*P. notatum*-dominated sites had both higher species richness and higher abundance than the *U. decumbens*-dominated site. Differences in competitive ability with native flora are expected for different grass species, especially for exotics (Fehmi et al. 2004; Davis et al. 2005; Brooks et al. 2010). In particular, *U. decumbens* is reported by Cheung et al. (2009) to be a strong inhibitor of native Atlantic forest regeneration. However, as with soil fertility, the lack of site replicates with *U. decumbens* prevents definitive conclusions.

As expected, woody plots had higher species richness and abundance, and higher zoochoric species richness, than did the open pasture plots, suggesting both positive microclimatic effects and the attraction of dispersal agents to shrubs and trees that had established in formerly open pasture sites (Zanini et al. 2006; Gunaratne et al. 2010). Valiente-Banuet and Verdú (2008) pointed out that when positive interactions are important it is common to find vegetation in a clumped spatial pattern.

Shrubs are among the most abundant species in open pasture plots, which suggests an important role of shrubs in facilitating pasture colonisation by other native species (Benjamin and Sanderson 2000; Saïd 2001). However, this suggestion can only be tested by means of temporal series data sets. Most shrub species are shade intolerant and tend to disappear with increasing vegetation height and density in patches; therefore, they are not detectable in the late stages of patch formation (see the discussion of species groups below). Indeed, a positive interaction between plants can shift to a negative one when facilitated plants reach the adult phase (Valiente-Banuet and Verdú 2008).

There are several reports regarding the role of woody species in facilitating succession in pastures, mostly focusing on microclimatic effects, the attraction of seed dispersers, and the reduction in seed predation and grass competition (Esquivel et al. 2008; Miranda et al. 2009; Leitão et al. 2010; Baylão et al. 2011). Nonetheless, a key aspect is the origin of the 'nurse plant' (Esquivel et al. 2008). Original forest fragments remaining after habitat conversion may consist of several species with varying capacities to establish in the open, and the species composition of these fragments can strongly influence succession in pasture sites (Harvey and Haber 1999; Carrierre et al. 2002). At our study sites, deforestation was completed decades prior to our study, and subsequent fires killed any remnant native woody plants; therefore, no remnant trees were observed. Thus, all isolated trees

and shrubs existing in the pasture must have been the result of successful dispersal and establishment under open pasture conditions, except those established under other trees or shrubs. Some of the larger plants from woody patch plots were present as juveniles in open pasture plots, suggesting that some species have the ability to establish themselves in the open and initialise vegetation patches with limited influence of microsite soil and terrain conditions. Indeed, although we found some species exclusively in patches (i.e. dependent on facilitation), there are two other groups of species that are potential facilitators (sectors B and C of Figure 1). These two groups differ in their ability to last in the shade of patches and in their level of abundance in open pastures. However, the patches may be initialised by species from either group B or C, which can establish within grass cover. Consistently, the sampled woody patches contained a mixture of facilitated species (group A), facilitative shade-tolerant species with high abundance (group B) and declining shade-intolerant facilitative species, mostly shrubs (group C). However, this coexistence of facilitative and facilitated species in the same size class and the relatively high species richness recorded in patches in this study prevent the investigation of possible species-specific positive relationships (Valiente-Banuet and Verdú 2008; but see Duarte et al. 2006).

In our study, some of the most abundant species capable of establishing in pastures are reported by south Brazilian cattle ranchers as 'pests', as they endure fire, pruning and cattle herbivory. Not surprisingly, three of these species are exotics, and one is a disturbance-adapted shrub. The fate of the exotic species has been controversial, but some authors claim that there is a place for them in ecological restoration efforts (Modna et al. 2010). In the context of our study, the exotics play a role in vegetation patch development as 'rustic' species able to colonise pastures under dry, hot microclimate conditions and despite competition from grasses (Baylão et al. 2011).

Species vary in their facilitation potential and mechanism (Whittaker and Jones 1994; Callaway et al. 2002). Such variation can be related to differences in the dependence of plants on seed-dispersing fauna and differences in development potential under canopy cover (Carrierre et al. 2002; Zanini et al. 2006; Nadkarni and Haber 2009; Cole et al. 2010). However, in the context of tropical pastures, where the fire regime and the existence of grasses with high competitive abilities overlap with harsh soil and microclimate conditions, nurse plants must have additional characteristics, such as the abilities to survive fire and outcompete grasses (Brooks et al. 2010; Lawes and Clarke 2011). Such a restrictive set of conditions prevents most native species, even forest gap specialists, from acting as nurse plants in a tropical pasture, creating a role for exotic species. Indeed, there are many reports of facilitation by exotics under specific contexts (Zanini et al. 2006; Lanta and Lepš 2008; Modna et al. 2010).

## Conclusions

Micro-scale terrain features play a minor role in the formation of woody vegetation patches in pastures. Small variations in slope under certain conditions will influence patch formation probably by reducing the impact of cattle trampling and herbivory. Soil chemical differences between woody patches and open pasture were almost absent and thus are not important factors in patch development. However, this may not be true in landscapes with lower overall soil fertility.

The establishment of highly competitive woody species in pastures with low cattle density is the proximate cause of vegetation patch formation. These species are able to germinate and grow in a dense grass matrix (ca. 100% soil cover) and to survive certain levels of disturbance from grazing and fire. Some of these species are exotics, which are often eliminated in restoration plans. However, allowing the establishment of these species in sites that are already 'contaminated' can actually speed succession in pastures. Furthermore, the ability to outcompete grasses and to regrow after fire should be considered as crucial features of the species used in the reforestation of fire-prone tropical pastures.

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## Notes on contributors

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