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Influence of grazing intensity on patterns and structuring processes in plant–pollinator networks in a subtropical grassland

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Abstract

Understanding how disturbances influence interaction networks is a central but still poorly explored issue in ecology and management. The goal of this study was to test how the structure of plant–pollinator networks and the structuring processes are influenced by grazing in a subtropical grassland community on the southern hemisphere. Twelve sampling plots were allocated in order to cover a grazing gradient ranging from overgrazed to ungrazed sites. For each plot, we created a quantitative matrix containing all observed pairwise insect–plant interactions and described morphology, phenology and abundances of each species. We fitted a series of models to test the influence of grazing intensity on metrics describing networks structure. We finally used probabilistic matrices, maximum likelihood and model selection to investigate the processes influencing frequencies of interactions across the gradient of disturbance. Grazing intensity influenced connectance, specialization and interaction evenness, while the number of species and links, nestedness and modularity were less variable. Species abundance was the most important determinant of interaction frequencies regardless of grazing intensity. In contrast to northern hemisphere pollination networks studied so far, these subtropical plant–pollinator networks and their structuring processes were remarkably consistent along the grazing gradient. We argue that this results from the dominance of generalist Asteraceae species, which are selectively avoided by cattle and play a core role in attracting a wide range of pollinators and thereby structuring plant–pollinator interactions, providing therefore stability.

Keywords Asteraceae · Grazing management · Interactions network · Moderate disturbance · Land use

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Introduction

Understanding how disturbances influence species interactions is a central goal in ecology and biodiversity management (Tylianakis et al. 2007; Lázaro et al. 2016). Pollination interactions are considered a crucial ecosystem service which contributes to the maintenance of biodiversity, ultimately influencing and being influenced by the spatial distribution, richness (Costanza et al. 1997; Potts et al. 2010; Moeller et al. 2012) and assembly processes of plant communities (Wolowski et al. 2016). One important question is how mutualistic interactions between plants and pollinators that emerge as complex networks at the community level (Memmot 1999, Olesen et al. 2007) change along ecological gradients (Basilio et al. 2006; Bascompte and Jordano 2007; Nielsen and Bascompte 2007, Welti and Joern 2017). Plant–pollinator networks frequently exhibit highly conserved properties such as low connectance, asymmetric distribution of interactions, nestedness and modularity (Vázquez et al. 2009a). These patterns are mostly driven

by species abundances (i.e., neutral-based processes) and exploitation barriers or trait matching among partners (i.e., niche-based processes) (Vázquez et al. 2009a, Vizentin-Bugoni et al. 2018). However, the processes are not mutually exclusive, and mechanisms related to relative abundances, species traits, phenology and phylogenetic relationships may act simultaneously as determinants on the structure of mutualistic networks and also being influenced by different levels of disturbance (Vázquez et al. 2009a; Vizentin-Bugoni et al. 2014; Martín-González et al. 2015; Bastazini et al. 2017). Indeed, their relative importance still is debated and may be variable in distinct pollination systems (Vizentin-Bugoni et al. 2018).

Several structural properties have been suggested to influence the stability of plant–pollinator networks (Tscharntke and Tylianakis 2010; Thébault and Fontaine 2010). Notably, theoretical and empirical studies indicate that generalization increases network robustness by promoting high connectance and redundancy of links (Bascompte et al. 2003), while high nestedness and modularity may indicate higher resistance to species loss (Okuyama and Holland 2008; Heleno et al. 2012). Thus, these structural properties not only describe patterns of interactions but may also inform community response to disturbances such as habitat fragmentation and loss due to land use (Klein et al. 2007; Spieman and Inouye 2013; Nielsen and Totland 2013; Tylianakis et al. 2007; Kaiser-Bunbury and Blüthgen 2015).

Disturbances are important processes in many ecosystems including natural grasslands where fire and grazing have promoted species adaptations to cope with such stressors (Cingolani et al. 2005). Intermediate intensities of fire and grazing have been reported to increase plant species richness and vegetation heterogeneity, produce more complex species composition (Overbeck et al. 2005) and influence plant phenology and abundance (Grant et al. 1996; Pykälä 2004). Indirectly, these disturbances may affect most trophic levels in grassland ecosystems, including soil organisms (Lupatini et al. 2013), predators such as spiders (Podgaiski et al. 2013) and birds (Baker and Guthery 1990; Develey et al. 2008; Dias et al. 2017), and might also influence pivotal ecological processes such as pollination (Vázquez and Simberloff 2004; Mayer et al. 2006; Vanbergen et al. 2013; Lázaro et al. 2016, Welti and Joern 2017). Effects of grazing on plant–pollinator interactions, pollinator diversity and reproductive success of plants have been investigated so far in grazing exclusion experiments (Vázquez and Simberloff 2004; Mayer et al. 2006; Vanbergen et al. 2013); however, the effects of variable grazing intensity on plant–pollinator networks remain poorly understood. A recent study in the Mediterranean phrygana shrublands found high number of links, species diversity, generalization and interaction evenness at moderate grazing intensities (Lázaro et al. 2016). In

shrublands in northern Scotland, the diversity of both floral visitors and plants was higher at moderate and higher grazing intensities (Vulliamy et al. 2006; Vanbergen et al. 2013). Contrastingly, a pollination network in a Mongolian steppe presented lower diversity and generalization at moderate grazing intensities (Yoshihara et al. 2008). Thus, the effects of grazing vary among different ecosystems, and generalizations may be difficult. Notably, the existing studies are focused on network patterns, while the effects of grazing on the relative importance of distinct processes structuring interactions (e.g., species abundances, phenotype and phenology) remain unexplored, limiting the understanding of the mechanisms behinds such complex patterns of response at the community level.

In grasslands in southern South America, overgrazing by cattle often leads to the dominance of prostrate grasses and increased abundances of unpalatable Asteraceae shrubs (e.g., Baccharis, Vernonanthura and Senecio) and rather ruderal small forbs (e.g., Mercadonia, Oxalis and Euphorbia; Boldrini and Eggers 1996). Conversely, low-intensity grazing promotes the dominance of tall grass tussocks and also shrubs, such as Baccharis (Overbeck et al. 2007). Consequently, plant richness and functional diversity peaks at intermediate grazing intensities in these systems (Boldrini and Eggers 1996; Pillar and Focht 2003). Moreover, moderate grazing is also associated with higher cattle performance and economic profitability and, therefore, strategies of management usually focus on the maintenance of moderate grazing (Milchunas et al. 1988; Soares et al. 2005). However, no study until now has investigated the influence of grazing on pollination networks in southern Brazilian grasslands.

Here, we investigated the extent to which grazing intensity influences plant–pollination networks in grasslands of southern Brazil. First, we tested the expectation that both ends of the grazing gradient encompass more complex networks, i.e., should be larger, more connected, generalized, and highly nested. This expectation is due to (1) the dominance of ruderal unpalatable Asteraceae species and pollinator-dependent herbs at high grazing intensities and; (2) the dominance of generalist Baccharis species at lower grazing intensities, which would attract higher pollinator diversity and promote high generalization. Secondly, we investigated how grazing influences the relative importance of distinct determinants of interaction frequencies. We hypothesized that, at low or high grazing intensity, species abundances would be more important than constraints imposed by traits due to the dominance of abundant ruderal Asteraceae species with unspecialized flowers. In contrast, at intermediate grazing intensities, phenological overlap and morphological matching between flowers and pollinators mouthparts are expected to play more important roles because of increasing functional diversity promoted by higher plant diversity and lower dominance of Asteraceae (Fontaine et al. 2005).

Materials and methods

Study area

Data were collected at the Agricultural Experimental Station (EEA) of the Universidade Federal do Rio Grande do Sul in the municipality of Eldorado do Sul, Rio Grande do Sul state, Brazil, from September 2014 to February 2015 (spring and summer seasons during the peak flowering period in the southern hemisphere, Pinheiro et al. 2008, Oleques et al. 2016). The climate is subtropical in this region which is characterized by dominance of species rich grasslands (Overbeck et al. 2007; Andrade et al. 2019). Livestock ranching is one of the main economic activities of the region and plays an important role in the maintenance of grasslands and conservation of their biodiversity (Nabinger et al. 2000). Our study took advantage of in a progress long-term experiment (> 25 years experiment) in which paddocks are maintained at different herbage allowance (i.e., availability of dry forage per kg animals), resulting in distinct grazing intensities (Boldrini and Eggers 1996; Nabinger et al. 2000). The treatments are daily forage allowances of 4, 8, 12, and 16 kg of dry matter mass (DM) per 100 kg of live weight (LW), where 4% indicates the highest grazing intensity and 16% the lowest grazing intensity (Junges et al. 2016). Additionally, we included an adjacent ungrazed sampling plot which had not been grazed by large mammals for at least ten years, representing a scenario of extremely low grazing.

Within these areas, we selected twenty 100 m² sampling plots that visually represented a grazing intensity gradient. In each plot, we measured vegetation height at five 1m2 subplots (measurements were taken on each corner and the center of each subplot) which was used as a proxy for grazing intensity. The twenty plots were then classified according to the mean vegetation height, and we selected twelve plots scattered along the grazing intensity gradient, in order to encompass plots ranging from ungrazed to overgrazed sites (Fig. 1). Plots were distant at least 100 m from each other, which made the sampling logistically possible and allowed sampling of multiple sites within the same day which reduces biases derived from temporal variation in weather conditions. We acknowledge that an individual flying insect may potentially visit multiple plots during the study; however, their responses to resources availability are known to take place at multiple scales, including at local scales (Essemberg 2013). This suggests that, despite the capacity to explore resources in multiple sites, even fairly close sites may differ in the patterns of plant–pollinator interactions depending on the resource availability (i.e., flower) at the local scale. Thus, how visitors respond to local variation in resources availability and how it influences local network structure is of direct interest of our study.
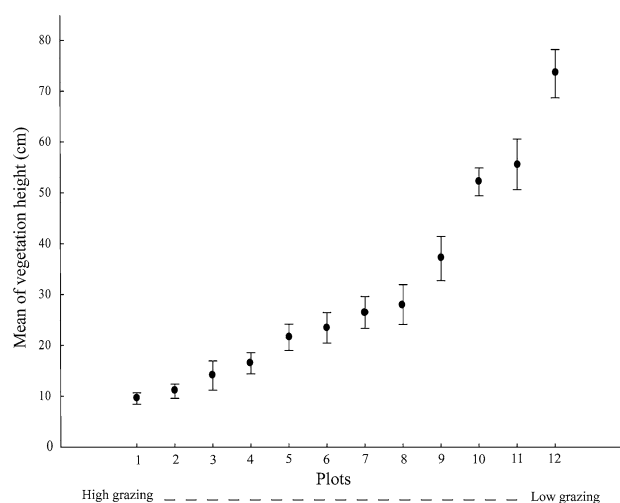

Fig. 1 Vegetation height (mean ± standard error) in the twelve plots sampled. Low vegetation height values correspond to high grazing intensities (left) and high values indicate low grazing intensities (right)

Sampling of interactions

In each plot, all flowering plant species, except Poaceae, Cyperaceae and Juncaceae (whose flowers are not attractive to insect, in general), were observed monthly during 6 months. All flowering species were observed for 15 min during three periods of the day (9–12 h, 12–14 h and 15–17 h). For each plant species, all potential pollinators (visitors touching reproductive structures of the flowers) were collected and identified.

Phenology, abundance and morphology of plants and pollinators

In each plot, we recorded presence of flowers for each plant species as a measure of temporal distribution of floral resources (hereafter 'phenology'). As a measure of plant abundance, we also quantified the number of open flowers (or inflorescences, for Asteraceae) per flowering individual. We considered that flower abundance better represents resource availability from a pollinator perspective than abundance of individual plants (Vázquez et al. 2009a; Vizentin-Bugoni et al. 2014; Olito and Fox 2015). For pollinators, phenology was described by presence of each species (or morphotype for specimens not identified at the species level) during each month in each plot. Pollinator abundance was measured as the total frequency of occurrence in each plot along the period of study (sensu Vizentin-Bugoni et al. 2014). We also quantified species morphology for each species by measuring corolla tube length and pollinator tongue length for at least five individuals per species.

Descriptors of network structure

For each plot, we created a quantitative matrix of interactions (S) with pollinator species in rows (i), plants species in columns (j) and the number of visits of animal i on plant j in each cell (sij) (Edwards and Auger-Méthé 2018). For each matrix, we calculated metrics encompassing distinct aspects of the network structure, namely number of species, number of links, connectance, specialization, interaction evenness, nestedness and modularity. Network structure analyses were performed in the R package bipartite (Dormann et al. 2008). Connectance (C) is the proportion of realized links in the network. Interaction evenness (IE) measures how the number of visits is distributed among the distinct pairwise species (i.e., links) within the community. Complementary specialization was calculated by the index H'_2 which measures network-level specialization for quantitative matrices (Blüthgen et al. 2008). Nestedness was calculated by the wNODF metric which is based on Non-Overlap and Decreasing Fill of the matrix (Almeida-Neto and Ulrich 2011), ranging from 0 (no nestedness) to 1 (perfect nestedness). A nested structure occurs when specialists species interact with subsets of partners of those more generalist species. Modularity (M) describes the existence of subgroups of species interacting more among themselves than with other members of the networks; it was calculated using the QuanBiMo algorithm which uses simulated annealing to search for the optimal modularity (set to steps = 1e7, Dorman and Strauss 2014).

Differences in network size and asymmetry hamper direct comparisons of metrics among networks. To account for these potential sources of biases, we used a correction based on null models (Δ-transformation) which calculates the extent in which a metric differs from a null expectation (see Dalsgaard et al. 2017). For each network, we performed Δ-transformation for metrics affected by network dimensions (i.e., IE, H'_2, wNODF and M) by subtracting the observed value of a metric by the mean expected value obtained by 1000 randomizations of the null model (Vázquez et al. 2007). This null model keeps the same dimension and connectance as the observed matrix (Dalsgaard et al. 2017) and is implemented as the function vaznull in the R-package bipartite (Dormann et al. 2008).

In order to test whether grazing intensity affects network structure, we subsequently related Δ-transformed metrics to vegetation height (a proxy for grazing intensity) using generalized linear models. For each metric (response variable), we fitted null linear, exponential and quadratic models to the grazing gradient (explanatory variable) with functions *lm()* and *nls()*. We performed model selection based on Akaike Information Criterion corrected for small sample sizes (AICc), selecting models with the highest AICc weight. When two models had ΔAICs > 2, the simplest model was considered the best (Burnham and Anderson 2002). These

analyses were implemented using an iterative maximum likelihood algorithm function lme() from the R package *bbmle* (Bolker and R Development Core Team, 2014). At the species level, we calculated species strength (s strength) to identify the keystone species within each network. This allowed us to quantify a species' relevance across all its partners based on the sum of dependencies of each species (Bascompte et al. 2006).

Processes structuring networks

In order to evaluate whether abundances, phenological overlap or morphological matching predicted the observed frequencies of interactions along the grazing gradient, we used the framework proposed by Vázquez et al. (2009b) and adapted by Vizentin-Bugoni et al. (2014), based on probabilistic matrices, maximum likelihood and model selection. First, we created probabilistic matrices based on abundances (A), phenological overlap (P) and morphological matching (M). A assumes that interaction is driven by the chance of encounter so that the probability of an interaction is the product of the abundances of a given plant and a given pollinator species; P assumes that the probability of interactions is proportional to the amount of temporal overlap (i.e., number of months) in occurrence of a plant and a pollinator; and M assumes that probabilities of interaction depend on the morphological matching between flower shape and pollinator mouthpart. To this end, we first classified flower tubes and animal mouthparts into three categories of corolla/mouthpart length: < 1 mm, 1 − 5 mm and > 5 mm. We then assumed that the probabilities of interaction were: '1' when the pollinator's mouthpart was shorter than a tubular corolla; '2' when plants and animals belonged to distinct categories, except the previous situation, and '3' when both plants and pollinators belonged to corresponding classes. In this sense, interaction at the category '1' had half the chances of those in category '2' and one-third of the chance of those in category '3'.

In order to convert matrices into probabilities, cells values were divided by the matrix sum prior; therefore, sij in each matrix represents a probability of interactions ranging between 0 and 1, and each matrix sums up 1. To evaluate the combined effect of the variables in the determination of interactions, we created additional matrices based on all possible combinations of **A**, **M** and **P** among them (**AM**, **AP**, **PM** and **APM**). Each combined matrix was also normalized by dividing each cell's value by the matrix sum. As a standard for comparison with the other matrices, we created a Null model assuming that all interactions have exactly the same probability. Each of the probabilistic matrices represents a distinct model (i.e., **A**, **M**, **P**, **AM**, **AP**, **PM**, **APM** and **Null**) and was related to the observed matrix of interactions of each plot using a maximum likelihood estimation

and assuming a multinomial distribution. The resulting AIC of each model was then used to evaluate the ability to predict frequencies of interactions. Finally, we performed a model selection based on the ΔAICc (i.e., the difference between AICc of a model and the lowest AICc among the candidate models) and AICc weight to find the best predictor of interaction frequencies in each plot along the gradient. Model complexity was defined as number of matrices used to assemble each model. It varies from 0 for Null model, as its assumption is that all species have the same probability to interact, to 3 for AMP (Vázquez et al. 2009a).

Results

Plants and pollinator diversity, abundance and phenology

We recorded 163 morphospecies of pollinators visiting 65 flowering plant species. The most common pollinator groups were flies, beetles, butterflies, bees, wasps and ants (Fig. 2, Online Resource 1). Plant families with highest numbers of species were Asteraceae, Fabaceae, Rubiaceae and Verbenaceae (Online Resource 2). Plant species with higher number of pollinators were Asteraceae species such as *Vernonanthura nudiflora* (38 species), *Aspilia montevidensis* (35), *Senecio leptolobus* (34), *Baccharis crispa* (33) and *B. articulata* (30). *Aspilia montev*idensis presented the highest species strength (s strength), for seven of the twelve plots (Online resource 3, Fig. 3), while *B. crispa*, *B. articulata* and *V. nudiflora* were the species with higher species strength values in the other five plots. Flowering period was relatively similar for most plants (approximately two months), with only six species (9.0%) flowering longer than three months and ten species (15.6%) flowering only one month. Flower abundance was variable: 23 species (35.9%) produced more than 100 flowers, and only three species (4.7%) produced more than 1000 flowers, including *B. crispa* (1824 flowers), *V. nudiflora* (1117) and *B. articulata* (1100) (Online Resource 3).

For pollinators, only 25 morphospecies (14.8%) had more than ten records and 12 had more than 50 records. The most frequent insects were *Apis mellifera* (224 records) and *Camponotus blandus* (172 records). Most pollinators were rare (occurring only in one month) and only 30 morphospecies (17.9%) occurred during more than two months (Online Resource 4). The most abundant plant species was variable along the grazing gradient, and higher total abundance of Asteraceae species was observed in low-intensity grazed plots (Online Resource 3). Regarding flower morphology, 24 plant species (36.0%) did not present corolla tubes, and few plant species had mean corolla length greater than 10.0 mm.

Fig. 2 Plant–pollinator interactions recorded in grasslands from southern Brazil: **A** *Xylocopa* sp. visiting *Senecio heterotrichius*, **B** Curculionidae beetles visiting *Eryngium horridum*, **C** *Apis mellifera* on *Richardia grandiflora* flower and **D** *Campsomeris* sp. on *S. heterotrichius*
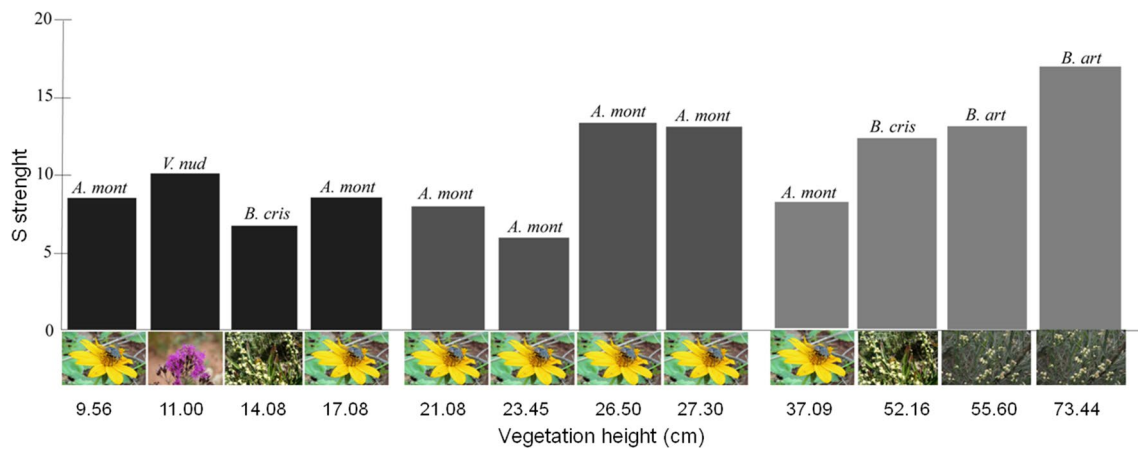
Fig. 3 Species with the highest S strength values for each plot along the grazing gradient

Similarly, only nine pollinator species had mouthpart length greater than 10.0 mm (Online Resources 1 and 2).

Grazing gradient and networks structure

The largest numbers of visits were recorded at a plot with intermediate grazing intensity and an ungrazed plot, with 565 and 404 links, respectively (Table 1, Fig. 4). In general, networks showed low connectance ($C = 0.10 \pm 0.01$; Mean $\pm$ SE) and moderate specialization ($H2' = 0.62 \pm 0.03$) and interaction evenness ($IE = 0.52 \pm 0.05$). Most networks attributes, such as number of links and species, modularity and weighted nestedness did not change predictably across the grazing gradient, i.e., the intercept-only model was the best model

(Table 2). However, connectance was lower at intermediate grazing intensities ($R^2 = 0.528$, Fig. 5A) with quadratic regression as the best model fitted, while interaction evenness decreased linearly with grazing intensity ($R^2 = 0.396$; Fig. 5B). Furthermore, specialization increased linearly toward lower grazing or ungrazed sites; however, the relation was notably weak ($R^2 = 0.058$, Fig. 5C; Table 2).

Determinants of network properties

Regardless of grazing intensity, species abundance was a far better predictor of the frequency of interaction among plants and pollinators than morphological matching and phenological overlap (Table 3, Fig. 6).

Table 1 Normal and Δ- transformed metrics calculated from each network interaction along the grazing gradient

Plot/vegetation height (cm)		NS	NL	C	IE	ΔIE	H'_2	$\Delta H'_2$	M	ΔM	W.NODF	ΔW.NODF
Plot 1	9.560	51	175	0.115	0.590	0.000	0.640	0.121	0.590	0.103	14.710	−2.280
Plot 2	11.000	55	241	0.107	0.547	−0.002	0.590	0.266	0.478	−0.017	6.180	−9.070
Plot 3	14.080	55	304	0.106	0.530	−0.006	0.674	0.286	0.263	−0.016	11.636	−0.946
Plot 4	17.087	54	130	0.106	0.581	0.033	0.571	0.102	0.670	0.014	8.360	−3.551
Plot 5	21.600	68	363	0.100	0.583	−0.031	0.606	0.269	0.525	−0.006	13.140	−14.838
Plot 6	23.458	57	253	0.080	0.520	0.001	0.652	0.284	0.531	−0.009	8.060	−11.887
Plot 7	26.500	60	318	0.076	0.430	−0.025	0.623	0.398	0.383	0.001	8.520	−15.487
Plot 8	27.304	88	565	0.068	0.500	−0.016	0.601	0.329	0.143	0.008	12.580	−6.872
Plot 9	37.091	56	170	0.095	0.580	−0.01	0.065	−0.311	0.620	0.002	12.970	−4.775
Plot 10	52.160	38	262	0.118	0.410	−0.017	0.647	0.362	0.293	0.028	12.690	−9.389
Plot 11	55.609	46	258	0.116	0.500	−0.024	0.641	0.353	0.465	−0.019	17.410	−15.736
Plot 12	73.440	55	404	0.125	0.510	−0.045	0.647	0.405	0.209	−0.014	16.733	−12.135

NS number of species, *NL* number of links, *C* connectance, *IE* interaction evennes, *H'₂* specialization, *M* modularity, *W.NODF* weighted nestedness
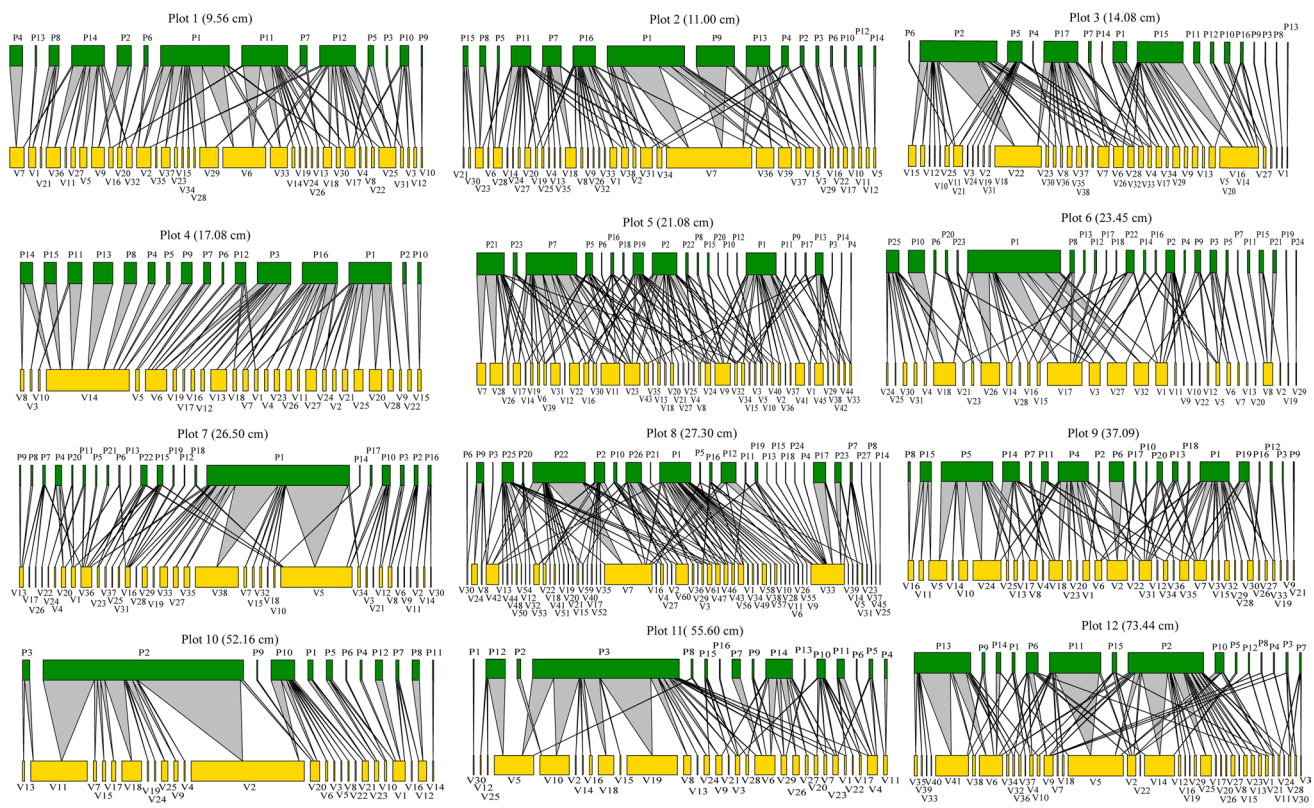
Fig. 4 Plant-pollinator networks along the grazing gradient. Above (green): plant species and below (yellow): pollinators. Grey links indicated the frequency of interactions

Discussion

Despite the influence of grazing on plant species diversity and composition has been widely recognized (Boldrini and Eggers 1996; Olff and Ritchie 1998; Adler and Lauenroth 1998), our results suggest that the structure and main processes structuring plant–pollination interaction networks remained consistent regardless of grazing intensity. Contrary to our predictions, grazing intensity influenced few network structures (i.e., connectance, interaction evenness and specialization) while other properties such as number of links and species, nestedness and modularity did not change predictably along the grazing gradient. This indicates that most network properties are not strongly affected grazing intensity in the system despite the variation in the identity of most generalist species along the gradient. To the best of our comprehension, this is the first study to investigate how distinct structuring processes respond to grazing intensity in the southern hemisphere. We found that species abundances is the most influential driver of interaction frequencies regardless of grazing intensity, rejecting our prediction of higher relative importance of niche-based processes (i.e., morphological matching or phenological overlap) at moderately grazed sites. As we argue below, the dominance of

Asteraceae species is likely of crucial importance in the maintenance of the structural properties of plant–pollinator networks in this community.

Plant and pollinator diversity

Asteraceae was the richest plant family in the studied grasslands which is not surprising due to the high diversity of this family in southern Brazilian grasslands (Boldrini and Eggers 1996; Beretta et al. 2008). Asteraceae species were frequently visited by a wide range of insects demonstrating the importance of this group for pollinators. These results agree with previous studies in South America also report the high importance of Asteraceae species as resources for pollinators (Torres and Galleto 2002; Antonini and Martins 2003; Pinheiro et al. 2008; Oleques et al. 2017).

Regarding pollinators, the alien honeybee *Apis mellifera* and the ant *Camponotus blandus* were the most frequent species recorded on flowers. Honeybees are highly abundance in many ecosystems which is possible because they form long lived societies that are active even in the colder seasons (Westerkamp 1991) as well as for their generalist foraging behavior and potential for competitive displacement of native bee populations (Aizen and Feisinger

Table 2 - Regression models of each network metric and mean vegetation height

Network metric	Intercept (α)	Coefficient (β_1, β_2)	AICc	ΔAICc	AICc weight
Number of species					
Linear (Y′=a+bX)	62.150	−0.170	101.000	2.700	0.176
Exponential Y′=a+b*logX	66.970	−3.107	101.700	3.300	0.127
Quadratic (Y′=a+(b1)X+(b2)X^2)	55.100	0.320–0.000	105.300	6.900	0.021
Null (Y′~1)	**56.920**	**1.000**	**98.300**	**0.000**	**0.675**
Number of links					
Linear (Y′=a+bX)	240.882	1.498	155.700	2.900	0.155
Exponential Y′=a+b*logX	110.300	54.580	155.400	2.500	0.182
Quadratic (Y′=a+(b1)X+(b2)X^2)	286.920	2.685–0.015	160.400	7.600	0.015
Null (Y′~1)	**224.070**	**1.000**	**152.900**	**0.000**	**0.649**
Connectance*					
Linear (Y′=a+bX)	0.090	0.000	−56.000	2.500	0.134
Exponential Y′=a+b*logX	0.086	0.004	−54.400	4.000	0.062
Quadratic (Y′=a+(b1)X+(b2)X^2)	**0.013**	**−2.16E03 to 3.17E05**	**−58.400**	**0.000**	**0.467**
Null (Y′~1)	0.100	1.000	−57.800	0.700	0.337
Interaction evenness**					
Linear (Y′=a+bX)	**0.013**	**0.000**	**−55.800**	**0.000**	**0.538**
Exponential Y′=a+b*logX	0.052	−0.018	−54.100	1.700	0.225
Quadratic (Y′=a+(b1)X+(b2)X^2)	3.89E−04	2.37E−04–1.16E−05	−51.800	4.000	0.074
Null (Y′~1)	−0.007	1.000	−53.400	2.400	0.162
Specialization (H$_2$′)***					
Linear (Y'=a+bX)	**0.165**	**0.002**	**2.400**	**0.000**	**0.355**
Exponential Y′=a+b*logX	0.040	0.058	2.700	0.300	0.310
Quadratic (Y′=a+(b1)X+(b2)X^2)	0.306	−0.007 to 0.001	6.400	4.000	0.047
Null (Y′~1)	0.238	1.000	138.3	135.900	<0.001
Modularity					
Linear (Y′=a+bX)	0.024	0.000	−40.500	2.600	0.159
Exponential Y′=a+b*logX	0.068	−0.019	−41.200	1.900	0.232
Quadratic (Y′=a+(b1)X+(b2)X^2)	0.004	0.002–2.39E−05	−36.200	6.900	0.018
Null (Y′~1)	**0.062**	**1.000**	**−43.100**	**0.000**	**0.590**
Weighted NODF					
Linear (Y′=a+bX)	−6.863	−0.089	76.600	1.700	0.207
Exponential Y′=a+b*logX	0.655	−3.173	76.000	1.000	0.291
Quadratic (Y′=a+(b1)X+(b2)X^2)	−4.489	0.257–0.002	81.000	6.000	0.024
Null (Y′~1)	**−9.62**	**1.000**	**75.000**	**0.000**	**0.478**

Δ-transformed metrics for specialization, modularity and nestedness

Bold represent the best fit model

*R^2=0.528

**R^2=0.396

***R^2=0.058

1994). While the role of ants as effective pollinators is still debated (Gómez 2000; Ashman and King 2005; Blancafort and Gómez 2005; Dutton and Frederickson 2012), these insects were an important group of floral visitors. A high number of plant species is known to have flowers visited by ants (García et al. 1996), including in other grassland communities (Herrera et al. 1984), suggesting their widespread influence on plant–pollinator interactions in open vegetation communities. Nonetheless, we highlight the need of further studies to clarify whether they are effective pollinators or antagonist toward on plant reproduction at the community level.
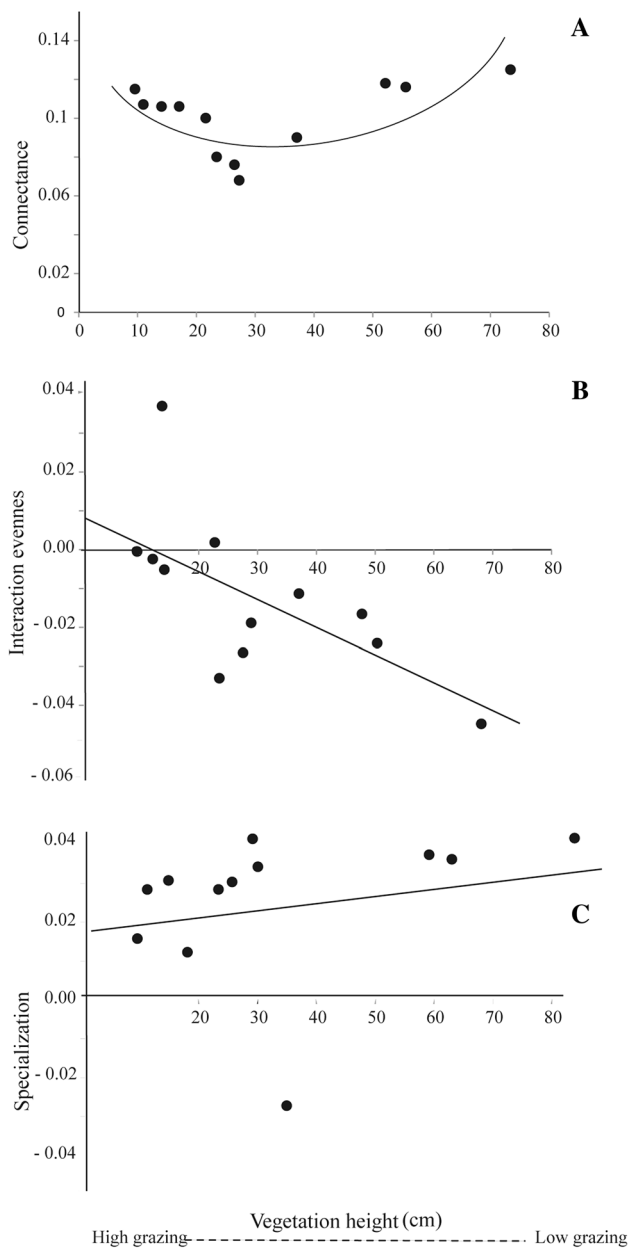
Fig. 5 Response of **A** connectance ($R^2 = 0.528$), **B** interaction evenness ($R^2 = 0.396$) and **C** specialization ($R^2 = 0.058$) to grazing intensities, described as mean vegetation height

Grazing gradient and network structure

Our results reveal that intermediate intensity grazing by cattle does not increase the generalization and complexity of plant–pollinator networks, contrasting with previous findings in grazed Mediterranean shrubland communities (Lázaro et al. 2016). Instead, we found lower connectance at intermediate grazing and decreasing interaction evenness, and weakly increasing specialization with increasing grazing intensity. These two latter associations indicate that

most plants receive similar numbers of visits by their shared pollinators, but also suggest that there is a certain level of specificity in the identity of the visitors on each plant species. This could be because under lower grazing intensities, unpalatable shrubs such as Baccharis species reach high abundance and stature, producing abundant floral resources and thereby concentrate interactions with visitors that do not interact with many other plants. Similarly, a previous study found that higher pollinator richness and network generalization are related to encroachment by shrubs in European grasslands (Lara-Romero et al. 2015). Altogether, this suggest that the dominance of unpalatable and generalist Asteraceae shrubs critically drives network properties in these regions.

Beyond the well-documented increase in plant diversity under moderate disturbance in South Brazilian grasslands (Boldrini and Eggers 1996; Isselstein et al. 2005; Nabinger et al. 2000), our findings suggest that this does not translate into greater complexity of pollination networks. This likely is because grazing acts primarily on the proportions of rhizomatous and tussock grasses, with the latter increasing in cover at lower grazing intensities (Boldrini and Eggers 1996). However, as we show here, changes in the vegetation structure do not substantially influence the structure of plant–pollinator networks, as plant species critically affected by grazing such as grasses are wind-pollinated and not directly important for pollinators.

Differences in species composition and the type of grazer are potential reasons why our findings differ from previous studies that found higher network complexity at intermediate grazing (Lázaro et al. 2016). First, robust flowering shrubs make up a diverse group in Mediteranean phrygana vegetation (Hadar et al. 2009) where they play a core role in the pollination networks (Lara-Romero et al. 2015). In contrast, in South American subtropical grasslands, shrub species belong predominantly to the Asteraceae family, which usually present floral resources that are easily accessible to pollinators due to the lack of morphological barriers. Moreover, Asteraceae species have often low abundances at intermediate grazing intensities (Boldrini and Eggers 1996; Pillar and Focht 2003, Baldissera et al. 2010) and do not promote high network complexity.

In addition, grazer feeding preferences may influence species composition and indirectly determine network structure. In the Mediteranean phrygana (Lázaro et al. 2016) and Mongolian steppe (Yoshihara et al. 2008), goats and sheep were the main herbivores. These species present forb-biased foraging and therefore reduce diversity of insect-pollinated species at high and intermediated grazing intensities (Lázaro et al. 2016). Conversely, our study system is grazed by cattle which present grass-biased foraging (Rutter 2006; Vavra et al. 2007; Welti and Joern 2017) and avoid unpalatable Asteraceae, which are key insect-pollinated plants and
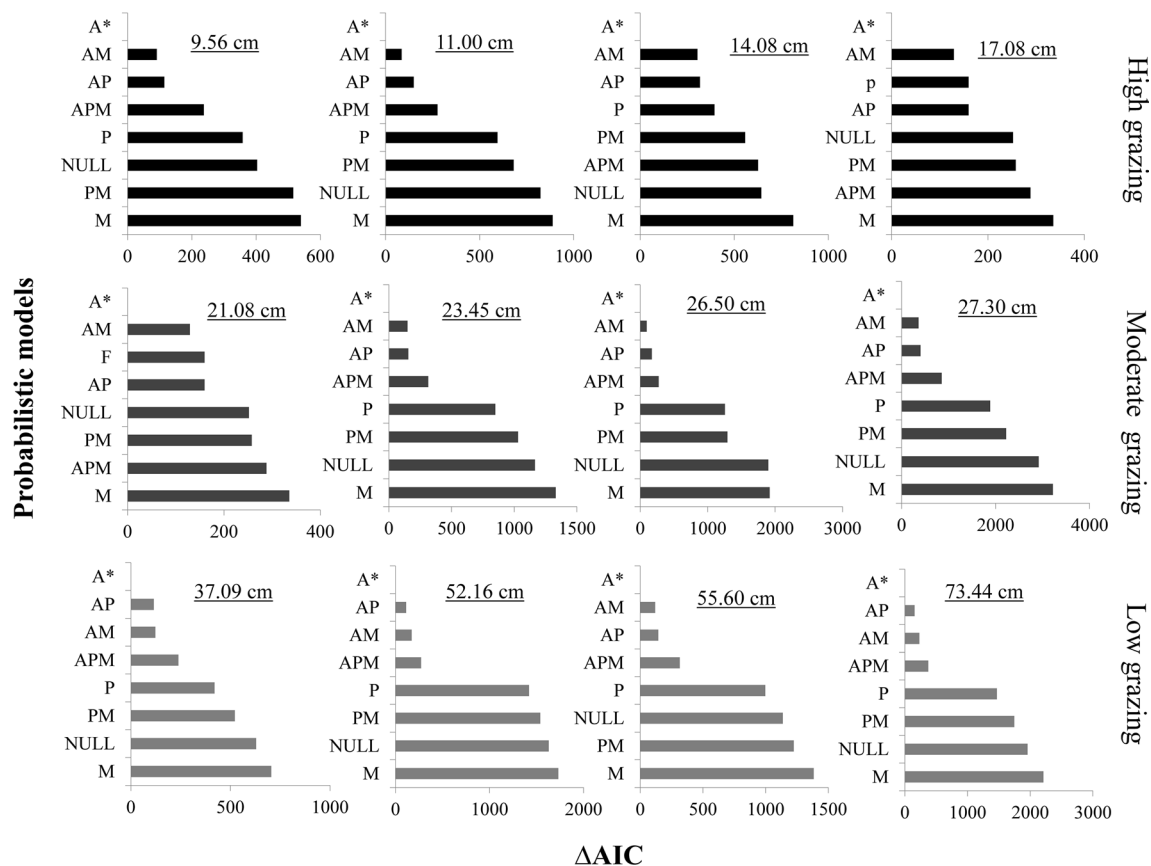
Fig. 6 ΔAIC values of the probabilistic matrices generated from species abundance (A), phenology (P) and morphology (M) and all possible combinations. NULL is the model in which all pairwise interactions have the same probability. Shorter bars indicate better fit of a given model in relation to the observed interaction network. *Best fit model along the grazing gradient; Mean vegetation height is predicted within each graph

notably important for the pollinator community (Mabry et al. 1977; Cruz et al. 2010). Furthermore, studies comparing grazed and ungrazed habitats suggest that grazing disturbance increases plant and pollinator diversity, while certain network properties (i.e., nestedness) decrease in grazed areas (Vanbergen et al. 2013; Welti and Joern 2017). Taken together, these findings suggest that the network response to grazing may vary among communities depending on the herbivores' identity and its effects on plant composition, limiting generalizations across communities.

Process affecting network properties

Differences in species abundances lead to higher chances of encounters among abundant species than rarer species. Thus, abundant species are expected to interact more (and more intensely) with their partners than rarer species (i.e., neutral hypothesis, Krishna et al. 2008). Indeed, species abundances have often been reported as crucial drivers of pollination networks structure (e.g., Vázquez et al. 2009a; Olito and Fox 2015); however, no previous study

has evaluated how their importance is influenced on grazing intensity. In contrast, exploitation barriers and trait matching promoted by morphological mismatching and phenological have also been demonstrated to be important determinants of pollination interactions (e.g., Santamaría and Rodríguez-Gironés (2007), especially in specialized plant–pollination networks such as those among tropical plants and hummingbirds or hawkmoths (e.g., Vizentin-Bugoni et al. 2014, 2018). Recently, a 'neutral-niche continuum model' proposed that the variation in the relative importance of neutral and niche-based processes depends on the amount of functional diversity in the system (Vizentin-Bugoni et al. 2018). Communities studied here present notably low variation in flowering span, and morphological constraints do not limit corolla and mouthpart lengths and thus most interactions. Therefore, under a low frequency of exploitation barriers, most species are expected to interact with partners as a function of the resource availability (species abundance), making abundances an essential factor underlying the interactions frequencies as predicted by Vizentin-Bugoni et al. (2018) and reported

Table 3 Likelihood analyses results for each model tested as predictor of frequencies of plant–pollinator interactions along a grazing gradient in Southern Brazil

Vegetation Height (cm)	Null			A*			P			M		
	AIC	ΔAIC	Weight (w)	AIC	ΔAIC	Weight (w)	AIC	ΔAIC	Weight (w)	AIC	ΔAIC	Weight (w)
9.56	1041.7	403.18	<0.001	**638.49**	**0**	**0.999**	996.65	358.16	<0.001	1177.95	539.46	<0.001
11.00	1578.8	823.55	<0.001	**755.29**	**0**	**0.999**	1350.20	594.91	<0.001	1643.68	888.39	<0.001
14.08	2018.2	643.86	<0.001	**1374.30**	**0**	**0.999**	1768.95	394.65	<0.001	2187.56	813.26	<0.001
17.08	782.94	251.89	<0.001	**531.04**	**0**	**0.999**	690.79	159.74	<0.001	866.43	335.38	<0.001
21.60	2374.9	1162.4	<0.001	**1212.5**	**0**	**0.999**	2052.00	839.45	<0.001	2476.55	1264.01	<0.001
23.45	1806.9	1164.9	<0.001	**641.99**	**0**	**0.999**	1491.25	849.25	<0.001	1972.51	1330.52	<0.001
26.50	2614.8	1899.2	<0.001	**715.61**	**0**	**0.999**	1971.53	1255.91	<0.001	2634.87	1919.26	<0.001
27.30	4475.40	2917.6	<0.001	**1557.8**	**0**	**0.999**	3442.30	1884.48	<0.001	4775.87	3218.05	<0.001
37.09	1146	628.97	<0.001	**517.00**	**0**	**0.999**	936.51	419.50	< 0.001	1222.04	705.03	<0.001
52.16	1828.5	1629.7	<0.001	**198.82**	**0**	**0.999**	1618.30	1419.48	<0.001	1929.85	1731.03	<0.001
55.60	1715.8	1137.1	<0.001	**578.66**	**0**	**0.999**	1575.83	997.16	<0.001	1962.18	1383.51	<0.001
73.44	2729.1	1957.4	<0.001	**771.60**	**0**	**0.999**	2240.72	1469.11	<0.001	2982.27	2210.66	<0.001

Vegetation Height (cm)	AP			AM			PM			APM		
	AIC	ΔAIC	Weight (w)	AIC	ΔAIC	Weight (w)	AIC	ΔAIC	Weight (w)	AIC	ΔAIC	Weight (w)
9.56	753.02	114.52	<0.001	729.39	90.90	<0.001	1154.19	515.70	<0.001	875.80	237.31	<0.001
11.00	905.48	150.19	<0.001	840.68	85.39	<0.001	1436.77	681.47	<0.001	1031.96	276.66	<0.001
14.08	1692.05	317.75	<0.001	1678.67	304.37	<0.001	1932.32	558.02	<0.001	2001.34	627.04	<0.001
17.08	690.82	159.77	<0.001	660.36	129.31	<0.001	788.54	257.49	<0.001	819.10	288.06	<0.001
21.60	1374.09	161.55	<0.001	1453.00	240.45	<0.001	2190.61	978.06	<0.001	1610.35	397.80	<0.001
23.45	796.84	154.85	<0.001	790.78	148.78	<0.001	1672.12	1030.13	<0.001	955.91	313.92	<0.001
26.50	887.17	171.56	<0.001	812.25	96.64	<0.001	2008.62	1293.00	<0.001	988.54	272.93	<0.001
27.30	1959.85	402.03	<0.001	1917.33	359.51	<0.001	3782.08	2224.26	<0.001	2409.73	851.90	<0.001
37.09	631.86	114.85	<0.001	639.92	122.91	<0.001	1039.12	522.11	<0.001	755.44	238.43	<0.001
52.16	312.08	113.26	<0.001	370.05	171.23	<0.001	1738.49	1539.67	<0.001	470.31	271.49	<0.001
55.60	722.06	143.39	<0.001	698.10	119.43	<0.001	1803.44	1224.77	<0.001	893.58	314.91	<0.001
73.44	926.65	155.04	<0.001	1003.33	231.72	<0.001	2518.04	1746.43	<0.001	1144.61	373.00	<0.001

Bold values represent the best fit model

A abundance, *P* phenology, *M* morphology

*Represent the best fit model

here. Grazing activity is known to affect plant abundances and indirectly influences pollinators and the role of species abundances on plant–pollinator interactions (Vázquez and Simberloff 2004). In our study system, Asteraceae species were abundant regardless of grazing intensity because cattle avoid them. As these plants are pollinator-generalists and attract a large number of pollinators, they were dominant in the interactions in the studied grasslands and likely increase pollinators abundances. Therefore, we suggest that the dominance of Asteraceae species, their importance as a food source for many pollinators, and the high accessibility of their floral resources, explains why species abundances was a major determinant of interaction frequencies in comparison to morphology and phenology in this grassland community.

Conclusions

In summary, for the subtropical grasslands studied here the effects of cattle grazing on the structure and diversity of plant communities did not lead to profound changes in the structure and complexity of plant–pollinator networks. We provide evidence that species abundance plays a fundamental structuring role in the networks in our study system independent of grazing intensity. Moderate grazing intensity has been argued to be compatible with conservation of plant diversity in grasslands by promoting species coexistence through maintenance of habitat heterogeneity (Boldrini and Eggers 1996; Pillar and Focht 2003, Overbeck et al. 2005). In contrast, we show here that pollinator

richness and interaction complexity are not enhanced at intermediate grazing intensities, but rather are driven by Asteraceae species which are pollinator-generalists and highly abundant at any grazing intensity. Thus, pollination interactions at the community level seem less affected by grazing than it has been shown for particular taxonomic groups of plants and animals. Taken together, our findings suggest that the plant–pollinator network structure in this southern Brazilian grassland is not dramatically affected by grazing disturbance, but rather determined by species abundances and identity.

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