1 Vegetation composition and structure changes following roller-chopping deforestation in 2 **Central Argentina woodlands** 3 Steinaker Diego F. 1,2, Jobbágy Esteban G. 3, Martini Juan P. Arroyo Daniel N. 2 & Pacheco Jorge 4 L². Marchesini Victoria A. ^{3,4} 5 6 ¹ Department of Biology, University of Regina, Regina SK, Canada S4S 0A2. 7 8 ² Instituto Nacional de Tecnología Agropecuaria, Casilla de Correo 17, Villa Mercedes, San Luis, 9 5730, Argentina. ³ Grupo de Estudios Ambientales, IMASL – CONICET- Universidad Nacional de San Luis, 10 Ejército de los Andes 950, San Luis, 5700, Argentina 11 12 ⁴ School of Plant Biology. The University of Western Australia 35 Stirling Highway Crawley, 13 14 WA, 6009, Australia. 15 16 17 Corresponding author: victoriamarchesini@gmail.com 18 19 **ABSTRACT** 20 21 Driven by the pressure of increasing forage production for cattle, dry forests and woodlands of 22 Argentina are suffering one of the highest deforestation rates in the world. In this study we 23 combined field work and a remote sensing approach to assess the successional trajectory in terms 24 of functional group diversity and ecosystem phenology, following roller chopping deforestation 25 in a woodland of central Argentina. The first year after disturbance, shrub cover decreased at the 26 same proportion than grass cover increased while tree cover was drastically reduced. After 3 27 years, shrubs recovered 70% of the original cover and grasses maintained a relatively high 28 proportion, but tree cover remained low. Roller-chopping favoured early over late successional 29 species in the case of woody plants, but had the inverse effect in the case of grasses. At 30 ecosystem scale the length of the growing season was drastically shortened by 100 days 31 following disturbance. Roller chopping improves ecosystem services of provision by enhancing 32 forage's offer but at the same time deteriorated the system by reducing functional plant diversity

33 and by shortening the growing season, with potential cascade-consequences on other ecosystem 34 processes such as the carbon and water dynamics. 35 36 Keywords: Argentina woodlands, ecosystem phenology, functional group diversity, NDVI, 37 roller- chopping. 38 39 1. INTRODUCTION 40 41 In central Argentina, like in many semiarid regions around the world, deforestation is advancing 42 in order to increase forage production and accessibility to cattle (Gasparri et al., 2013; Rueda et 43 al., 2013; Bestelmeyer, 2014). Argentinean dry Chaco is the largest remaining continuous dry 44 forest unit in the continent (Eva et al., 2004) and one of the fastest expanding agriculture 45 frontiers of the world (Zak et al., 2008; FAO, 2010). 46 47 The ecological succession after deforestation has been object of extensive literature (Noble and 48 Slatyer, 1980; Guariguata and Ostertag, 2001; Staus et al., 2002; Lohbeck et al., 2012; Lohbeck 49 et al., 2014a; Lohbeck et al., 2014b). Classical studies have shown that this disturbance usually 50 follows a succession with a first occurrence of shade intolerant and annual species followed by 51 shade tolerant, perennials and endemic species (White, 1979; Connell and Slatyer, 1977; 52 Dorrough and Scroggie, 2008). These changes are generally accompanied by other changes in 53 ecosystem functioning. For example, a reduction in functional group diversity could affect 54 primary production and ecosystem phenology with significant-cascade effects at all trophic levels (Tilman, 1997; Clark and McLachlan, 2003; Leniére and Houle, 2009). Additionally, 55 56 changes in the length of the growing season could eventually affect the carbon cycle and water 57 balance (Körner and Basler, 2010). 58 59 Trees and shrubs represent the biomass-dominant plant life form in dry forests and woodlands. 60 Traditionally, climatic conditions have restricted the use of these semiarid areas of central 61 Argentina to extensive grazing and selective logging. In the last decades, however, increments in 62 regional precipitation along with livestock expansion and new technologies have intensified land 63 use in these areas (Oesterheld, 2005; Viglizzo et al., 2010) promoting the reduction of shrubby

64 vegetation and the consequent increment on grass production (Rueda et al., 2013). Like in other 65 dry woodlands around the world, shrub cover is reduced by using "roller choppers", heavy 66 cylinders equipped with transversal blades and moved by bulldozers that chop and crush smalland medium-size woody vegetation. This practice promotes grass production and facilitates 67 68 cattle foraging (Kunst et al., 2012). However, some woody species in our study area have re-69 sprout capabilities and they readily initiate new growth from their base (Villagra et al., 2004; 70 Fernández and Maseda, 2006). Although thousands of hectares of dry forests are cleared every 71 year in the Chaco's region (Boletta et al., 2006; Hoyos et al., 2013), few studies have analysed 72 the impact of this disturbance on vegetation composition, phenology and primary productivity. 73 74 In this study we assess the successional trajectory, in terms of species and functional group 75 composition, and its associated phenological shifts, in response to roller-chopping deforestation 76 in a woodland area of central Argentina. We selected contiguous deforested sites, which vary on 77 the elapsed time from disturbed (1, 2 and 3 years after rolled-chopping), and adjacent 78 undisturbed sites, to assess impacts on vegetation composition, productivity and phenology; 79 combining in situ and remote sensing observations. 80 81 2. METHODS 82 83 2.1 Study area 84 85 Field work was performed in San Luis province, on the west-central region of Argentina (33.5° S 66.49° W, 420 m.a.s.l.). Vegetation is a xerophytic woodland of shrubs and emergent trees 86 87 (Prosopis flexuosa), with a discontinuous gramineous understory layer. Dominant woody species 88 includes the genera Larrea, Prosopis, Condalia, Lycium and Senna. Common grass genera are 89 Pappophorum, Trichloris, Setaria, Aristida, Chloris, and Neobouteloua and represent the main 90 forage resource in the area (Morello, 1955; Morello, 1958). Growing season generally extends 91 from September to April for woody species and from November to March for grasses. Growing 92 season matches the seasonal precipitation distribution. Precipitation is 400 mm per year and 93 usually occurs in events exceeding 20 mm (Salinas del Bebedero, Weather Station). Mean annual temperature is 24° C. Soil has been classified as regosol with a low content of organic matter and sandy-loam texture (Kirby et al., 2001).

2.2 Experimental design

The study was based on the existence of areas that were subject to roller chopping (disturbed areas) and adjacent "untreated" woodlands (undisturbed areas). Roller chopping deforestation was performed by using a cylindrical 18 T roller or drum, 4 m in length and 1.8 m in diameter, pulled by a bulldozer. The roller was equipped with 20 cm high blades running parallel to the axis and spaced 50 cm apart around the cylinder surface. *In situ*, field measurements were performed in March 2007 on contiguous large forest extensions that were roller-chopped in August-December 2004 (29 ha), 2005 (132 ha), and 2006 (91 ha), and on their adjacent undisturbed-control sites (<100 m from them, and >100 ha of extension). On each one of these large rolled-chopped and undisturbed sites we set 3 permanent experimental transects to measure changes in plant life forms and ecological strategies. Thus, there were 3 replicates per each roller-chopped treatment and 3 control-undisturbed sites transects. Until deforestation began, the area was covered by natural woodlands and experienced the same land use history with no intense grazing, logging or fire activity over the last decades. No differences were found between soil texture (n=3 boreholes per site, F=2.79, site x depth P=0.12) and bulk density (n=2 boreholes per site, F=1.15, site x depth P=0.37) between treatment and control sites.

2.3 Plant life forms and ecological strategies

We measured plant species cover (%) by using the line intercept method (Canfield, 1941), on three-100-m linear transects randomly located in each disturbed and control site. Percentage of bare soil and litter was also estimated from each interception line. Each species was later categorized by life forms (trees, shrubs, grasses and forbs) and plant ecological strategies (early and late successional). Plant ecological strategies were defined considering shade tolerance, growth rate, number and size of seeds and seed dispersion strategies (Steinaker *pers. communication*).

125 2.4 Dynamics of NDVI and ecosystem phenology 126 127 We evaluated ecosystem seasonality and changes in phenology by analysing the dynamics of the 128 Normalized Difference Vegetation Index (NDVI) in undisturbed and disturbed areas, throughout 129 eight growing seasons (2001-2009). We used MODIS-TERRA images with 6.2 ha and 16 days 130 of spatial and temporal resolution respectively. The sites for assessing NDVI dynamics were 131 selected considering two criteria: a) They had to be located in the same areas that the 132 experimental transects and b) they had to cover a minimum of four pure MODIS pixels. Both 133 criteria were met since all roller-chopped sites were larger than the required extension. 134 Ecosystem seasonality was characterized by the start, end and length of growing season, and the 135 moment of maximum NDVI "greenness". We also measured the inter-annual stability of NDVI 136 by using the temporal coefficient of variation (CVt = (standard deviation/mean)*100). All the 137 analyses were performed by using TIMESAT software (Jönsson and Eklundh, 2004) which 138 process time series data by considering 23 images per year. Maximum, minimum and peak 139 values of NDVI and the start, end and the length of the growing season before and after 140 disturbance were calculated using a filtering function (Savitzky-Golay) that suppress extreme 141 values produced by extraordinary events. Starting from the NDVI integral curve as 100%, the 142 beginning or the end of the growing season is then calculated as the time for which the left/right 143 edge of the curve has increased to a user defined level. NDVI thresholds for the beginning and 144 the end of the growing season were defined following Jobbágy et al. (2002). 145 146 2.5 Statistical Analysis 147 148 As measurements were conducted on the same experimental unit over time, we used the PROC-149 MIXED repeated measurement analysis to compare NDVI dynamics of each treatment over 150 time. For texture and bulk density we performed a repeated measurement analysis considering 151 depth as a repeated measure and using the same procedure. Comparisons of plant cover (%)

among different sites (disturbed and undisturbed sites) were performed using a one-way

ANOVA. All analyses were completed using SAS version 6.12 (SAS Institute, Cary, North

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Carolina, USA).

3. RESULTS

Plant life-form considerably changed after roller-chopping, mainly from woody to herbaceous vegetation. The first year after disturbance, shrub cover decreased almost at the same proportion (3:1) than grass cover increased (shrubs from 80 to 26% and grasses from 24 to 87%, Fig. 1). However, after 3 years, shrubs recovered 70% of their initial cover while grasses maintained a relatively high cover (74%, Fig. 1). Trees were the most affected group with their cover being reduced from the 20% to 2% in the first year and no recovery found afterwards. Forbs showed a variable pattern, without significant differences between undisturbed and disturbed areas (Fig. 1). Litter cover raised from 60 to 75% and the bare soil area was reduced from 34 to 16%.

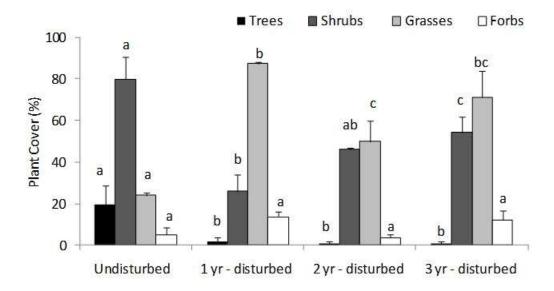


Figure 1. Tree, shrub, grass and forbs cover (%) in undisturbed and disturbed woodland areas of 1, 2 and 3 years old. Bars show mean values and standard errors. Letters compare undisturbed and disturbed areas within each plant life-form (Dunkan's post-hoc test, P<0.05).

3.1 Plant ecological strategies

Roller-chopping changed plant ecological strategies within plant life-forms, from late to early successional species in woody species, but conversely in grasses (Table 1). Although all woody

species (shrubs and trees) were affected, early successional shrubs such as *Larrea divaricata*, *Lycium chilense* and *Senna aphylla* recovered from the disturbance, but late successional *Condalia microphilla* and *Prosopis flexuosa* do not (Table 1). On the other hand, early successional grasses *Aristida mendocina*, *Sporobolus pyramidatus* and *Gounia paraguayensis* tended to diminish after roller chopping, but late successional *Setaria leucopila*, *Digitaria californica* and *Trichloris crinita* significantly increased their cover (Table 1).

Table 1: Mean plant cover (%) of dominant grass and woody species in undisturbed forest and 1, 2 and 3 year disturbed areas. LS: late successional species, ES: early successional species. Letters compare undisturbed and deforested areas within each species (Dunkan 's post-hoc test, P<0.05).

Species/sites	Undisturbed Forest	Deforested area (1 yr)	Deforested area (2 yr)	Deforested area (3 yr)	Change direction
Trees					
Prosopis flexuosa (LS)	19.8 a	0.0 b	0.3 b	0.3 b	•
Shrubs					
Condalia microphilla (LS)	7.7	2.7	5.3	2.0	$lack \Psi$
Lycium chilense (ES)	11.2	11.0	9.7	18.0	1
Senna aphylla (ES)	2.2	1.5	4.8	1.7	^
Larrea divaricata (ES)	50.0 a	8.5 b	22.6 ab	28.7 ab	^
Grasses					
Setaria leucopila (LS)	16.3 a	27.5 a	29.3 a	54.5 b	1
Digitaria californica (LS)	0.3 b	2.5 ab	3.8 ab	6.2 a	1
Trichloris crinita_(LS)	1.2	3.5	2.7	2.8	^
Gounia paraguayensis (ES)	1.5	2.7	0.3	0.5	V
Aristida mendocina (ES)	2.5	1.5	1.8	0	ullet
Sporobolus pyramidatus (ES)	1.7	0.7	1.2	0	$oldsymbol{\Psi}$

3.2 NDVI dynamics and ecosystem phenology

Roller-chopping reduced the integral of the NDVI by 15% and drastically shortened the length of the growing season (Table 2). The shorter growing season in disturbed sites was due to both, a significant delay in the beginning of the growing season along with an early end (Table 2). These

changes in the phenology of the overall plant community were observed immediately after the disturbance and maintained for at least four years (Fig. 2). In accordance with the NDVI integral reduction, the maximum NDVI reached by a site during the season also decreased with the disturbance (Table 2). However, the moment in which that maximum NDVI occurs (Day of Max) was not affected by deforestation (Table 2). Finally, the inter-annual variation of the integral NDVI increased after deforestation (CV: 10 vs. 17% for undisturbed and disturbed sites respectively, data not shown). Before deforestation, undisturbed sites remained without significant changes in all phenological variables (exception: day of maximum NDVI), even though annual rainfall was variable among years (Table 2).

Table 2: Growing season mean values traits in undisturbed and disturbed (roller-chopping deforestation) sites. Ref: START, END and LENGTH (days) of the growing season (day 1: winter start). DAY of MAX: day of maximum Normalized Vegetation Index (NDVI). NDVI MAX: Maximum NDVI. NDVI integral. Standard deviations are shown in parenthesis.* P < 0.05, ** P < 0.01, *** P < 0.001 ns: no statistically significant difference.

Variable	Time	Before	After	Time
	Site	disturbance	disturbance	Comp
START	Undisturbed	64 (3)	62 (4)	ns
	Deforested	57 (3)	97 (16)	***
	Site Comp	ns	***	
END	Undisturbed	349 (3)	349 (5)	ns
	Deforested	357 (2)	295 (24)	***
	Site Comp	ns	***	
LENGTH	Undisturbed	286 (4)	287 (6)	ns
	Deforested	299 (7)	198 (38)	***
	Site Comp	ns	***	
DAY of MAX	Undisturbed	215 (6)	184 (17)	**
	Deforested	214 (7)	181 (10)	**
	Site Comp	ns	ns	
NDVI MAX	Undisturbed	0,67 (0,01)	0,67 (0,01)	ns
	Deforested	0,67 (0,01)	0,63 (0,02)	**
	Site Comp	ns	***	
NDVI Integral	Undisturbed	0,53 (0,01)	0,53 (0,02)	ns
	Deforested	0,52 (0,01)	0,44 (0,01)	***
	Site Comp	ns	***	

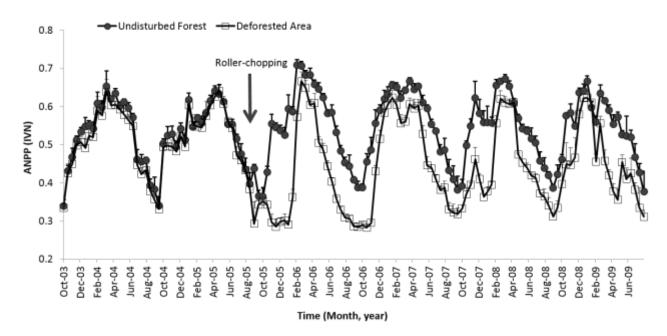


Figure 2: NDVI (mean, SE) of disturbed (white squares) and undisturbed (black circles) areas from October 2003 to July 2009. Black arrow indicates the roller chopping event.

4. DISCUSSION

Rolling-chopping deforestation modified the plant community structure, from a mainly woody to a shrubby-herbaceous system, and modified the plant ecological strategies from early to late successional species for grasses, and conversely for woody species. These changes impacted larger-scale ecosystem processes by drastically reducing the length of the growing season.

The important release of resources (e.g., light, water and nutrients) after removal of aboveground woody biomass by deforestation (Prescott, 2002; Sangha et al., 2006) seems to be capitalized by grasses that tripled their biomass in one season and maintained it during the next three seasons. Shrubs cover retrieved faster than trees after disturbance. Considering that roller-chopping cuts and chops small and medium-size woody stems but does not remove roots and buds on the base of the trunks, it seems that the greater shrub's resilience may be explained by their capacity of regrowth from remaining shoots and roots (Donato et al., 2009).

The considerable increment of forage offer immediately after roller chopping seems to improve some ecosystem conditions for example through a reduction in bare soil cover. A decrease in the proportion of bare soil and runoff after roller chopping has also been recorded by Aguilera et al. (2003) which observed that roller chopping and seeding reduced the proportion of sites susceptible to erosion (such as bare soil or short grass cover types). Despite these effects, longterm results (3-yr old patch) indicate a general impoverishment of the system by encroaching and increases of non-forage species as Larrea spp. and the losses of valuable forage species as *Prosopis flexuosa* which fruits are largely consumed by animals due to its high protein values (Villagra et al., 2004). Roller chopping affected grasses and woody species in opposite ways, favoring early successional shrubs such as Lycium chilense, Senna aphylla and Larrea divaricata, and late successional grasses (i.e., Digitaria californica, Setaria leucopila, Trichloris crinita). This apparent contradiction is actually expected since the roller chopper disturbs shrubs and trees by chopping and crushing woody stems, but it does not disturb herbaceous plants. On the contrary, roller chopping increases availability of resources (i.e., nutrients, water and light) for grasses, and it may accelerate successional processes in grass communities. Resource heterogeneity also favours early successional species (Bazzaz, 1979; Bazzaz and Carlson, 1982). In our study area, as in most arid woodlands around the world, resource distribution is spatially heterogeneous (Rossi and Villagra, 2003; Abril et al., 2009), and it is attributable to shrubs and trees that creates patches of great nutrient uptake and high deposition of organic residues under their canopies (Aguiar and Sala, 1994; Prescott, 2002; Austin et al., 2004). Air and soil temperature, soil moisture and light intensity is also very heterogeneous, allowing early successional species to occupy more stressful sites (Grime, 1977). Roller chopping redistributes and homogenizes distribution of organic residues, increasing water infiltration and water-holding capacity (Aguilera et al., 2003). This more homogeneous and productive sites will allow more competitive late successional species increases their dominance. Although shrub cover recovered with time, NDVI did not show the same trend. If we considered NDVI as a surrogate of above primary productivity (ANPP) the losses in species and functional groups diversity such as nitrogen fixers or species with deep root distribution such as *Prosopis*

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flexuosa could explain NDVI/ANPP lower values since both, species and functional groups richness has been largely shown to increment ecosystem productivity at all levels (Díaz and Cabido, 2001; Flombaum and Sala, 2008). On the other hand, changes in phenology especially during the growing and autumn seasons can have significant influence on carbon dynamics and water balance. Studies on climate change and phenology show different trends according to the nature of the disturbance, for example changes in species composition after shrubs invasion in eastern US forests have been demonstrated to extend leaf autumn phenology due to a delayed in autumn leaf fall compared with natives species (Fridley, 2012) which imply that invasive species continue assimilating carbon during these season. In addition, most of the model simulation predictions on climate change has anticipated early beginning of growing seasons as consequence of global warming and increases in precipitation (Cleland et al., 2007). Studies performed over temperate regions in China showed an advanced in the growing season on average, at a rate of 1.3 days per decade (Cong et al., 2013). Our findings, on the contrary, show a late-beginning of the growing season which could be due to the absence of trees and large shrubs with deep root distribution and rain-independent and which phenology could be more responsive to temperature than to precipitation. In areas near to our field site, studies based on the analysis of isotopic composition of plant water (δ 18O and δ 2H) and fluctuations of water table levels on *Prosopis* spp. site has confirmed this species as ground water dependent showing the same pattern early emergence of leaves during the dry season (Jobbágy et al., 2011). Finally, it is important to clarify that although precipitation slightly increased during the analysed period, our finding seems to be clearly the effects of deforestation than any other variable such as climate change. Additionally, the likely increment in soil moisture as a combined effect of disturbance and precipitation could even accelerate the observed process of encroachment increasing early successional shrubs Senna aphylla and Larrea divarica. By observing both, structural and functional changes after a large disturbance, this study shows the cascade effects of changing the dominance of plant life form and the changes in the abundance of plant life strategies which seems considerably affect phenology at ecosystem level.

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