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Soil Seed Banks of Dry Tropical Forests under Different Land Management

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Abstract: The objectives of this study were to evaluate woody-species composition and seed density in the soil seed bank (SSB) in a dry subtropical forest with different disturbance regimes and assess the role of leaf litter as a seed reservoir in disturbed forests. Study area: the western Argentine Chaco region. Climate is seasonal and semiarid, and the fire season coincides with the dry and cool periods. In the first step, we evaluated the composition of species and seed density in the soils of forests with four different combinations of disturbances (wildfires, livestock, roller-chopping, and logging) using a systematic sampling design. In the second step, we assessed the seed density in the soil and litter fractions under focal individuals of six native woody species in two forest types (undisturbed/disturbed by roller-chopper and wildfires). Soil samples were extracted by core following standard methods for SSB studies. Eleven woody species were found in the SSB. The seed density varied between 17.78 seeds/samples in the reference condition forest and 5.46 seeds/samples in the more intensively disturbed forest (wildfires and livestock). The tree seed abundance was reduced in the disturbed forest SSB and the shrubby species increased. There were no significant differences in the seed density among the soil and litter fractions of each type of forest, but disturbances reduced the seed density in the litter fraction. The leaf litter is a seed reservoir in the soils of the Chaco forests, but this localization could promote loss by fires and desiccation. Our results could improve the forestry management plans in areas exposed to climate and land-use change.

Keywords: soil seed banks; woody species; wildfires; logging; roller-chopping



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1. Introduction

Seed banks represent a source of viable propagules to establish new individuals in natural environments and influence the dynamics of plant communities. Seeds can be stored in soils or on aerial-organ-conforming soil seed banks or aerial seed banks, respectively [1,2]. The seed viability maintenance in seed banks is a relevant aspect for the persistence of plant communities, especially in arid and semiarid regions, where vegetation can be exposed over several months to water availability restrictions [3] and disturbances such as fires, unplanned forest exploitation, and grazing, among others [4].

The species composition, seed density, and persistence of soil seed banks (SSBs) allow for comprising a pattern of plant regeneration and responses to perturbations [5,6]. The species composition of SSBs can widely vary from the standing vegetation; moreover, the seed density of a particular species in a SSB could be nonlinearly related to the standing individual density [7,8]. These biological concerns are key to plant community resilience, since the absence of a species in the SSB could hamper or limit the recruitment or become dependent on seed rains [9,10]. As well, seed traits such as seed quality, health state, dormancy, and viability, among others, influence the SSB persistence and the aptitude of species to propagate sexually in disturbed areas. Therefore, the changes in the SSB in response to disturbances and climate change are the main topics currently studied in threatened environments.

In the world, tropical and subtropical forests are the most threatened ecosystems due to climate and land-use changes [11,12]. Knowledge about regeneration strategies and the effectiveness of sexual reproduction in disturbed environments is a valuable baseline for environmental managers and stakeholders of decisions about natural resources. The background information usually required comprises biological aspects such as seed viability, seed dormancy and heat shock, and desiccation tolerance [9,13], as well as the environmental requirements of species to germinate and seedling growth (water, space, and light availability) [14,15]. In semiarid environments, the leaf litter plays a relevant role in the recruitment of new individuals, since it represents a natural barrier against soil water loss by evapotranspiration and mitigates the seasonal and daily thermal amplitude [14,16]. Leaf litter could also represent a reservoir of seeds in environments where the decomposition rates are slow due to restrictions in water availability [17]. Nevertheless, the retention of seeds in leaf litter exposes them to greater risks of desiccation, pathogen attacks, and fires [5], thus influencing SSB persistence [18].

Chaco-region forests are one of the most altered vegetation units in South America by deforestation, wildfires, unplanned forest exploitation, and extensive livestock [19,20]. The postdisturbance regeneration of the native woody species from the Chaco Forest has been mainly related to the resprouting strategy [21,22]. On the one hand, [23,24], and [8] reported that the woody species of Chaco-region forests are scarcely represented in the SSBs, and the resilience of these systems does not seem dependent on recruitment from the SSB. However, on the other hand, [10] identified litter and seedlings banks as reservoirs of woody species regeneration and established that anthropic disturbances reduce their similarity with standing vegetation. Ref. [16] have studied the role of vegetation complexity and wind in the recovery on a short time-lapse, indicating that the manipulation of soil cover should influence resilience. Therefore, more studies about forest SSBs, their persistence, and the controlling factors are desirable to improve the comprehension of risks under climate and land-use changes [6].

The Chaco region has had a long history of natural resource management since the late XVII century [20]. Aborigines and pre-Columbian settlers scorched grasslands and savannas for long periods to increase grass availability for animals, and the land management practice persists today. Fire frequency has increased over the last century [25]. Additionally, Chaco-region forests were intensively exploited for 1800 years for low-value uses such as tannins extraction, charcoal, and sleepers for train reels. The livestock has increased since the early 1900s at a regional scale, and in recent decades, the silvopastoral systems have introduced new disturbance combinations to enhance livestock productivity [20,26].

The objectives of this work were (a) to evaluate seed density in the soil of Chaco-region native forests managed with different disturbance regimes and (b) to assess the role of leaf litter as a seed reservoir in these forests. These hypotheses were tested: (a) The forestry management practices such as prescribed fires, grazing, and logging represent anthropogenic disturbances reducing the seed density and species richness in soil seed banks, and (b) leaf litter is a significant reservoir of seeds in Chaco forests, and disturbances reduce its biomass, affecting the SSBs.

2. Materials and Methods

2.1. Study Area

The study area is located in the western Argentine Chaco region. This region is included in the named semiarid diagonal from South America, with the Cerrado and Caatinga from Brazil (Figure 1). The Argentine Chaco region shows a decreasing precipitation gradient from east to west and the western Chaco region is characterized by a seasonal semiarid climate [27]. Mosaics of grasslands, savannas, and forests with different structures and species compositions [20] represent the native vegetation. The study was carried out in the Experimental Ranch Francisco Cantos (28°01'57" S, 64°15'41" W), belonging to the Instituto Nacional de Tecnología Agropecuaria (INTA), in the province of Santiago del

Estero, Argentina (Figure 1). This experimental ranch has 8000 ha with logged forests, silvopastoral systems, a forest reserve area, and grazed grasslands and savannas.



Figure 1. Localization of study area in the western Argentine Chaco region with the satellite image of the Experimental Ranch Francisco Cantos, Instituto Nacional de Tecnología Agropecuaria, Santiago del Estero (INTA).

Our study was carried out in typical native forests from the Chaco region called the “two quebrachos”. In the forest canopy (c. 15–22 m tall) *Schinopsis lorentzii* (quebracho colorado santiagueño), Anacardiaceae, and *Aspidosperma quebracho-blanco* (quebracho blanco) dominate, while Apocynaceae, *Neltuma nigra* (algarrobo negro), *Sarcomphalus mistol* Griseb. (mistol), *Parkinsonia praecox* (brea), and *Geoffroea decorticans* (chañar) are common species in the intermediate forest stratum. Several species, such as *Atamisquea emarginata* (atamisqui), *Senegalia praecox*, *Senegalia gilliesii*, *Vachellia aroma*, *Jodina rhombifolia* (sombra de toro), *Ximena americana* (pata), *Condalia microphylla* (piquillín), *Celtis erhenbergiana*, and *Schinus* spp characterize the shrubby lower stratum [28]. Typical grasslands of Chaco region are dominated by *Trichloris crinita*, *Trichloris pluriflora*, *Gouinia paraguariensis*, *Gouinia latifolia*, *Setaria argentina*, *Setaria gracilis*, *Digitaria sanguinalis*, *Papophorum pappiferum*, and *Papophorum mucronulatum*. In the savannas, the dominant grass species is *Elionorus muticus* Spreng. (“aibe”, “espartillo”, “paja amarga”), a caespitosus plant commonly between 30 and 40 cm tall. Tree species such as *A. quebracho-blanco*, *N. nigra*, and *V. aroma*, and shrubs such as *Schinus* sp. and *C. erhenbergiana*, are scattered across the savannas in small patches of woody vegetation [25,29].

2.2. Sampling Sites Selection

Sampling sites were located in native forests from the Chaco region with five different land-management types: (a) a forest without productive activities for at least the last 34 years was considered as the reference condition (RC), (b) a forest with grazing cattle and implanted tropical pasture (L + Ps), (c) a forest with roller-chopping and logging (Rch + log), (d) a forest with cattle grazing and fires (L + Wf), and (e) an overgrazed and burnt forest that was abandoned for the last 9 years (L + F + A). These types of land management represent different disturbance combinations applied eight years before the study.

The RC forest is a three-strata forest (shrubby, tree intermediate, canopy) which we considered as a control site, since it remains without disturbance from 34 years ago [24,30]. The L + Ps forest is a grazed forest where exotic grasses were sown to increase forage production. It is a common practice in silvopastoral systems that use Buffel grass (*Cenchrus ciliaris* L.) and Gatton panic (*Megathyrsus maximum* (Jacq.) B.K. Simon and S.W.L. Jacobs) due to their relative tolerance to dryness and shadow, respectively [26].

The roller-chopper is a management practice applied to improve the forage capacity of degraded shrublands, control the shrubby stratum in silvopastoral systems, or facilitate forestry operations in central-western Argentina. The treatment consists of a passage of heavy cylinders tracked by a small tractor on woody vegetation to open the shrubby strata [26,31]. The Rch + log forest has been roll-chopped with a low severity (a simple passage of cylinder) and then logged (30% of initial basal area) for obtaining firewood. This forestry management is considered conservative relative to other, more intensive, forestry management plans. Under unusual environmental conditions, such as dryness or great fuel accumulation, savanna fires are incoming to forests [25]. The L + Wf and L + F + A forests were grazed and burnt by wildfires, but the last more intensively than the first, causing a significant environmental degradation that has facilitated its abandonment over the last decade. These forests represent management types widely spread in the Chaco region [32].

We located two 50 m × 50 m plots in each sampling site and extracted eight soil samples per plot with a systematic sampling design. This design established four subplots determined by the interceptions of two 50 m perpendicular transects crossing the center of each plot (Figure 2A). A 13.5 cm diameter core borer extracted the samples of the soil seed bank at a 5 cm depth. Were extracted eight soil samples from each plot, and samples with an average weight of 800 g were stored in plastic bags and then were sieved at the laboratory (n = 80) using a 2 mm × 2 mm metal mesh. The selection of the size of the mesh aperture considered the dimensions of dispersal units of woody species and was small enough to avoid seed loss. The identifications of the seeds found in the soil samples were made by descriptions and previous studies available for the study area [32,33]. The species composition of the SSB of each type of forest included all species identified in the samples. An important number of samples without seeds suggested a high variability in the spatial distribution of the seeds in the study area. Therefore, after this first study, we carried out a sampling of the SSBs under the focal individual of a set of species [7]. We expected that this sampling of the SSB could reduce the number of without-seed samples and identify the role of leaf litter as a seed reservoir.

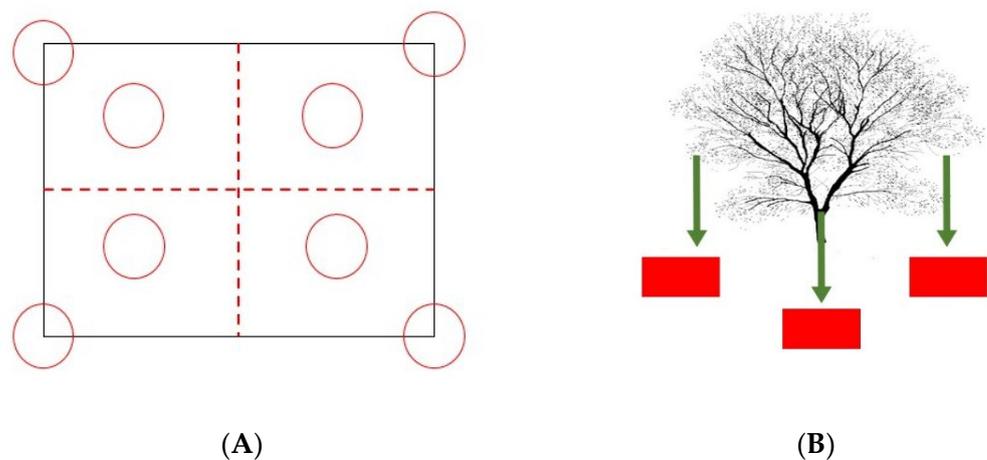


Figure 2. Sampling design of soil seed banks in Chaco-region forests, Argentina (A). Diagram of the soil samples extraction following the systematic sampling design (B). Localization of soil samples extracted under focal individuals.

In the second step, we studied the SSBs of six native woody species from Chaco-region forests in two different forest types: the reference condition forest (RC) and the rolled-chopping and burnt forest (Rch + F). The selection of these sampling sites was based on the inclusion of a new combination of disturbances, commonly used in silvopastoral systems of the Chaco region. Prescribed fires are often applied one year after roller-chopping to reduce plants of diameter below 5 cm and to facilitate the grass sown for livestock in silvopastoral systems [26,31]. The woody species selected for this study considered their representativeness in the different forest strata as follows: (a) canopy: *A. quebracho-blanco* (quebracho blanco) and *S. lorentzii* (quebracho colorado); (b) medium stratum: *S. mistol* (mistol) and *N. nigra* (algarrobo negro); (c) shrubby understory: *S. gilliesii* (garabato, teatín) and *V. aroma* (tusca). Two mature and healthy individuals of each species were selected as focal individuals in the RC and Rch + F forests. Three 13 cm × 17 cm × 5 cm soil samples were extracted below the canopy of each individual, with an angular distance of 120° among them (Figure 2B). The samples, including the leaf litter, were stored in plastic bags, and then analyzed at the laboratory, separating the soil and leaf-litter fractions. The weight from each soil fraction was recorded on the same date of the collection using a precision scale with 0.001 mg.

2.3. Statistical Analysis

The variable number of seeds per sample is referred to in this work as the seed density, considering a relatively constant soil volume of the extracted samples. It showed a negative binomial data distribution. We performed tests using the generalized linear model (GLM), using the number of seeds per sample as a response variable and the function of forests with different managements as explanatory variables. A combined zero-inflated model was utilized, as it is considered convenient for modeling count variables when excessive zeros usually overdispersed the data. The GLM was fitted using the `glm.nb` function from the MASS package in R Core Team statistical software version 4.1.1 [34].

3. Results

Eleven species corresponding to eleven genera and seven botany families were identified in the soil samples (Table 1). The most represented botany families were Fabaceae, Anacardiaceae, and Rhamnaceae. Shrubby species predominated in the SSBs ($n = 7$). The highest S in the SSBs was observed in the Rch + log forest, where 63.6% of species present in the SSB were identified. Twenty percent of soil samples did not have seeds. A higher number of samples without seeds was observed in the L + Wf forest (7.5%), followed by the L + Wf + A forest (5.6%; Table 2).

The relative abundance of woody species seeds in the SSBs varied among the different forest types. The tree species had a higher abundance in the soil samples from the RC forest. *S. lorentzii* was the only tree species present in the soil samples from all types of forests, whereas *A. quebracho-blanco* was absent in the Rch + log and L + F + A forests (Table 1). *S. mistol* and *N. nigra* were absent or drastically reduced their abundance in the SSBs from the L + Ps, L + F, and L + F + A forests. Among the shrubby species, *S. gilliesii* was found exclusively in the RC forest, whereas *S. fasciculatus*, *V. aroma*, *X. americana*, *C. microphylla*, and *C. ehrenbergiana* were exclusively in the disturbed forests.

Table 2 shows the median and average values of the seed number per sample, species richness, and diversity indexes in the SSB from native forests with different land-management types. The average seed density per sample varied from 17.78 seeds/sample in the RC forest to 5.46 seeds/sample in the L + F + A forest. The RC, L + Ps, and Rch + Log forests showed greater soil seed density than in other forest types, without significant differences among them (Figure 2, Tables 2 and 3). The species richness (S) and the Shannon and Simpson Indexes were greater in the Rch + log forest, and the lowest observed was in the L + Ps forest and the L + Wf forest.

Only 11.38% of the SSB samples extracted under focal individuals (the second sampling method) did not have seeds. In the RC forest, only 11.11% of soil samples extracted under

focal individuals did not have leaf litter, and this percentage increased to 22% in the samples extracted from the Rch + F forest. Independently of species, there were no significant differences between the weights of leaf litter or soil fractions from the RC and Rch + Wf forests ($p = 0.214$, Table 4).

Table 1. Species composition, growth habit, and relative abundance of woody species in soil seed banks from the western-Chaco-region forests, Argentina, with different land-management types. T = tree; S = shrub; RC = reference condition; L+Ps: grazed forest with tropical pasture sowing; Rch+log = rolled-chopping and logged forest; L + WF = grazed and burnt forest; L + F + A = overgrazed, burnt, and abandoned forest.

Species	Botany Family	Growth Habit	Relative Abundance of Seeds from Different Species in Soil Samples of Different Forest Types				
			RC	L + Ps	Rch + log	L + Wf	L + F + A
<i>Schinopsis lorentzii</i>	Anacardiaceae	T	27.7	25.9	16.7	16.1	13.6
<i>Aspidosperma quebracho-blanco</i>	Apocynaceae	T	63.6	18.2	0.0	18.2	0.0
<i>Sarcomphalus mistol</i>	Rhamnaceae	T	41.2	0.0	35.3	11.8	11.8
<i>Neltuma nigra</i>	Fabaceae	T	49.0	28.5	22.5	0.0	0.0
<i>Atamisquea emarginata</i>	Capparaceae	S	45.5	0.0	45.5	9.1	0.0
<i>Senegalia gilliesii</i>	Fabaceae	S	100.0	0.0	0.0	0.0	0.0
<i>Vachellia aroma</i>	Fabaceae	S	0.0	0.0	21.6	64.9	13.4
<i>Celtis ehrenbergiana</i>	Cannabaceae	S	0.0	0.0	0.0	0.0	100
<i>Condalia microphylla</i>	Rhamnaceae	S	0.0	0.0	0.0	0.0	100
<i>Schinus fasciculatus</i>	Anacardiaceae	S	0.0	60.0	22.2	0.0	17.8
<i>Ximena americana</i>	Olacaceae	S	0.0	0.0	100.0	0.0	0.0

Table 2. Average, median, and standard deviations of seed density per sample, and species diversity in soil seed banks from Chaco-region forests with different land-management types. RC = reference condition forest; L + Ps: grazed forest with tropical pasture sowing; Rch + log = rolled-chopping and logged forest; L + Wf = grazed and burnt forest; L + Wf + A = overgrazed, burnt, and abandoned forest.

Types of Forests	Seed Density per Sample in Forest Soils					
	Median	Average	Standard Deviation	Richness (S)	Shannon Index	Simpson Index
Reference condition (RC)	6.00	17.78 ^a	21.63	6	0.876	2.144
Livestock + exotic pasture (L + Ps)	6.00	12.66 ^a	15.52	4	0.869	2.079
Roller-chopping + logging (Rch + Log)	7.5	9.87 ^a	8.29	7	1.211	2.653
Livestock + wildfires (L + Wf)	2.00	7.71 ^b	13.93	5	0.760	1.930
Overgrazed + fire + abandonment (L + WF + A)	3.00	5.46 ^b	8.17	6	0.883	1.722

Different letters in the same column indicate significant differences with $\alpha < 0.05$.

Table 3. Results of generalized linear model (number of seeds per sample-types of forests, data = seeds, link = log, init. Theta = 0.5899), AIC = 1054.2. Fixed effects: forests with different land-management types. Overgrazed + fire + abandonment forest (L + WF + A) does not appear because it is included in the intercept.

Fixed Effects	Estimate	EE	z-Score	Significance Level
Reference condition (RC)	10.598	0.3371	3.144	0.00167 **
Livestock + exotic pasture (L + Ps)	0.8391	0.3378	2.484	0.01300 *
Roller-chopping + logging (Rch + Log)	0.5910	0.3389	1.744	0.08118
Livestock + wildfires (L + Wf)	0.3446	0.3402	1.013	0.31105

Significance Codes: ** 0.01 * 0.05.

All studied species were found in both leaf litter and soil fractions in both the RC and Rch+Wf forests. The seed density did not vary significantly between both fractions within each forest type, except for *A. quebracho-blanco*, which diminished significantly the number of seeds in the leaf litter of the disturbed forest (Table 5). *S. lorentzii* and *S. gilliesii* showed a lower number of seeds in the soil fractions of the disturbed forest (Rch + Wf) than in the RC forest (Table 5; $p < 0.05$). On the other hand, *A. quebracho-blanco*, *S. lorentzii*, and *S. gilliesii* showed a lower number of seeds in the leaf litter fraction of the disturbed forest than in the RC forest (Table 5; $p < 0.05$).

Table 4. Statistical data of weight (grams) of leaf litter and soil fractions in samples of soil seed banks from Chaco forests with different land-management types. RC = reference condition forest, Rch + Wf = rolled-chopper and burnt forest.

	Median Value (g)	Average (g)	Standard Deviations (g)
Leaf litter of reference condition forest (RC)	46.3	60.1 ^a	41.12
Leaf litter of roller-chopping + burnt forest (Rch + Wf)	40	49.1 ^a	41.21
Soil fraction of reference condition forest (RC)	662.6	691.0 ^b	188.47
Soil fraction of roller-chopping + burnt forest (Rch + Wf)	766.1	730.8 ^b	134.51

Different letters in the same column indicate significant differences with $\alpha < 0.05$.

Table 5. Average seed density in soil and leaf litter fractions of six native woody species from Chaco-region forests with different land-management types. RC = reference condition forest, Rch + Wf = rolled-chopping and burnt forest.

Species	Average Seed Density per Soil Sample			
	Reference Condition Forest (RC)		Rolled-Chopping + Wildfire Forest (Rch + Wf)	
	Soil Fraction	Leaf Litter	Soil Fraction	Leaf Litter
<i>Schinopsis lorentzii</i>	48.5 ^a (31.13)	30.66 ^a (30.98)	1.66 ^b (1.86)	2.6 ^b (3.32)
<i>Aspidosperma quebracho-blanco</i>	10.00 ^a (9.27)	16.00 ^a (10.43)	11.50 ^a (21.53)	3.8 ^b (5.7)
<i>Sarcomphalus mistol</i>	12.33 ^a (12.14)	24.33 ^a (24.32)	7.83 ^a (3.92)	10.5 ^a (7.5)
<i>Neltuma nigra</i>	12.00 ^a (7.46)	6.83 ^a (11.26)	5.00 ^a (5.36)	5.5 ^a (8.7)
<i>Vachellia aroma</i>	4.17 ^a (4.79)	4.16 ^a (6.58)	0.83 ^a (1.16)	0.1 ^a (0.4)
<i>Senegalia gilliesii</i>	32.66 ^a (43.33)	14.66 ^a (12.90)	0.83 ^b (2.04)	0.83 ^b (1.60)

Different letters in the same row indicate significant intraspecific differences ($p < 0.05$) among sites and soil fractions. Standard deviations among brackets.

4. Discussion

This work describes variations in seed density in soils from Chaco-region forests exposed to different land-management practices. The management practices of dry forests include the use of fires, roller-chopping, logging, and extensive livestock, as in other world regions [26]. The S observed in the SSBs of both RC forests and disturbed forests is lower than the species richness of standing native vegetation. Ref. [28] recently found 22 woody species in forests from the same study area, most of them belonging to the shrubby stratum. Ref. [24] reported that only 43% of woody species from Chaco-region forests are present in the soil seed banks. Refs. [8,23] agree with these findings. In this work, it has been identified that less of the 50% of woody species from the standing vegetation are present in the SSBs [28]. The most represented botany families are typical of arid and semiarid environments, suggesting an adaptation of the dispersal units to the environmental conditions and the ability to incorporate into the soil. However, the lower

S in the SSB than in the aboveground vegetation suggests the difficulty of a significant number of woody species for recruiting from the SSBs.

The heterogeneity in the composition and abundance of species in the SSBs from forests with different land-management practices could indicate changes generated by different disturbance regimes [6,28,30,32]. As well, the percentage of soil samples without seeds in the first-step analysis could be attributed to the patchiness of the vegetation by disturbances such as roller-chopping, wildfires, and livestock. *S. lorentzii* was the most frequent species in all sampling sites. This result is especially significant, since this species has a great conservation interest and was intensively exploited in the past century [19]. However, both canopy species (*S. lorentzii* and *A. quebracho-blanco*) diminished their seed density in the SSBs of the disturbed forests. The absence of *A. quebracho-blanco* seeds in the SSBs from the Rch + Log and L + Wf + A forests could be related to the extraction of mature individuals for fuel charcoal, thereby reducing the sources of seeds. The diminishing of *S. mistol* and *P. nigra* abundance in the SSBs from the disturbed forests could be attributed to the biomass removal by herbivores, fires, and seed predation by rodents and mammals [11,33,35]. *S. gilliesii* was found exclusively in the SSB from the RC forest, which is possibly related to the high seed predation in disturbed environments [9,35], since mature individuals of this species have been observed in other sampling sites. On the other hand, the shrubby species seeds of *X. americana*, *C. erhenbergiana*, and *C. microphylla* were found exclusively in the SSBs from disturbed forests, where environmental conditions and dispersal agents (mainly small birds and mammals) favor early successional species maturing in shorter times than later successional species [30,33,35].

The similarity in the SSB size, S, and Shannon Index values among the RC forest and Rch + log forest seems to indicate that the former is a secondary forest in regeneration despite the more than 30 years without disturbances [36]. Nevertheless, all tree species were identified in the SSB of the RC forest, suggesting a better forest structure under the absence of disturbance or low-disturbance frequency [28]. In this work, the seed density diminished significantly only in forests where wildfires and grazing synergistically removed vegetation (L + Wf and L + Wf + A forests), which is in agreement with [11]. Our results confirm the first hypothesis of this work and highlight that sustainable management plans for Chaco forests require consideration of the disturbance frequency and the time needed by plants for reloading the SSBs and/or recovering the growth modules to resprout [4,37]. On the other hand, the better values of the diversity parameters observed in the Rch + log forest seem to reflect the resilience of the Chaco forests when the forest management practices represent low-impact disturbances. Our work suggests that strict management of the intensity and frequency of disturbances is needed to assure the new individual recruitment from the SSBs, chiefly in grazed and burnt forests.

The assessment of the seed density in soil samples under focal species allows a reduction in the number of soil samples without seeds, suggesting the importance of the distance to the mother plant as a variable significant to form SSBs and the efficiency of this sampling method to study the SSBs [7]. All woody species considered in this analysis could include their seeds in the soil, which is very significant for SSB persistence [7,38]. Ref. [38] considered that the buried seeds increase the persistence of the SSB. More studies to assess the seed persistence in the SSBs from Chaco-region forests are desirable to improve forest management plans [13].

The lack of significant differences in the seed density between the soil and leaf litter fractions within each type of forest seems to reaffirm the importance of the litter as a seed reservoir in Chaco-region forests, coinciding with [16,17]. However, the diminishing seed density in the leaf litter of *A. quebracho-blanco*, *S. lorentzii*, and *S. gilliesii* in the disturbed forest (Rch + Wf) suggests that recurrent disturbances could limit or hamper their recruitment [9,10,39]. On the other hand, the seed density diminishing in the leaf litter of these last species, without significant changes in the weight of the soil and leaf litter fractions, suggests some difficulties in the reproductive process in areas with disturbances. These species probably require a higher time-lapse to recover the reproductive growth modules

after disturbances than the other species studied. These results suggest that the recruitment of the canopy species from Chaco-region forests could be affected under recurrent disturbances. The lack of significant changes in the seed density in the leaf litter of *S. mistol*, *P. nigra*, and *V. aroma* in the disturbed forest (Rch + Wf) suggests a better aptitude of these species to recruit in altered environments, coinciding with [15,28,30,32]. The dispersion of indehiscent fruits in these species could promote their permanence in the leaf litter due to the protection of seeds by endocarps [13,33]. Results reaffirm only partially the second hypothesis since the response varied among studied species. More studies about the viability of seeds in soil and leaf litter could improve the interpretation of these results.

5. Conclusions

The results of this study allowed identifying changes in species composition and seed density in the SSBs of Chaco-region forests with different land-management practices. Eleven woody species of Chaco-region forests were found in the SSBs. Shrubby species ($n = 7$) were the most represented species, whereas tree species were absent or reduced their abundance in the SSBs of disturbed forests, especially those with wildfires and livestock. The diversity indexes showed the highest values in the SSBs of the RC, Rch + log, and L + Ps forests, and the lowest in the L + Wf and L + Wf + A forests. The size of the SSB decreased following the same tendency, showing the effects of the disturbances in species composition and diversity of the SSBs. The six native woody species selected for the second objective of this study could incorporate seeds into the soil, indicating the potential to form an SSB. The leaf litter is a large seed reservoir in the semiarid Chaco region. Roll-chopping and wildfires reduced the seed density of *S. lorentzii*, *A. quebracho-blanco*, and *S. gilliessi* in the leaf litter, while they did not significantly change the seed density in the leaf litter of *S. mistol*, *P. nigra*, and *V. aroma*. These results will contribute to improving the knowledge of the effects of disturbances in SSBs and could enhance the sustainability of forestry management plans.

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