Received: 11 September 2019 | Revised: 5 November 2019 | Accepted: 8 November 2019

DOI: 10.1111/jvs.12842

SPECIAL FEATURE ARTICLE

Journal of Vegetation Science IAVS

Where does the forest come back from? Soil and litter seed banks and the juvenile bank as sources of vegetation resilience in a semiarid Neotropical forest

María Lucrecia Lipoma[1,2] | Valentina Fortunato[2] | Lucas Enrico[1,2] | Sandra Díaz[1,2]

[1]Instituto Multidisciplinario de Biología Vegetal (IMBIV), CONICET, Córdoba, Argentina

[2]FCEFyN, Universidad Nacional de Córdoba, Córdoba, Argentina

Correspondence
María Lucrecia Lipoma, Instituto Multidisciplinario de Biología Vegetal (IMBIV), CONICET and FCEFyN, Universidad Nacional de Córdoba, Casilla de Correo 495, 5000 Córdoba, Argentina.
Email: lucrecialipoma@gmail.com

Funding information
This study was supported by FONCyT, CONICET (PIP 11220130100103), SECyT-Universidad Nacional de Córdoba (33620180100767CB and PRIMAR Res 248/18), the Inter-American Institute for Global Change Research (IAI) SGP-HW 090, and the Newton Fund, UK.

Co-ordinating Editor: James Bullock

Abstract

Questions: The existence of reservoirs from which dominant plants recruit after disturbances is a key factor in ecosystem resilience. With this in mind, we ask the following question: where do woody species regenerate from in the semiarid Neotropical Chaco forest? Is land use affecting the floristic composition of biodiversity reservoirs? Are the soil and litter seed banks and the juvenile bank potential sources of resilience of these forests in the face of different land-use regimes?

Location: Chancaní, Northwestern Córdoba, Argentina.

Methods: We selected four ecosystem types subjected to increasing long-term land-use intensity: primary forest (no land use in the last 50 years), secondary forest (low land-use intensity), closed species-rich shrubland (moderate land-use intensity), and open shrubland (high land-use intensity). We monitored four sites per ecosystem type where we recorded adults, saplings and seedlings of all woody species. We collected litter and soil samples that were processed in the laboratory for taxonomic identification and germination of seeds. We compared the floristic composition of the soil and litter banks, as well as of the juvenile bank ("biodiversity reservoirs") with that of established vegetation of the primary forest, considered as the reference ecosystem. We also compared the established vegetation from sites under land use with that of the primary forest.

Results: Woody species were scarcely represented in the soil, but very well represented in the litter and the juvenile banks from different ecosystem types. These two reservoirs showed high similarity with the established vegetation of the primary forest. However, as land-use intensity increased, similarity between the reservoirs and the established vegetation of the primary forest decreased.

Conclusion: Litter and juvenile banks, but not the soil bank, are the main reservoirs for the recruitment of new individuals of woody species in the Chaco forest. However, the ability of these reservoirs to act as sources of resilience decreases as land use intensifies.

KEYWORDS

juvenile plant bank, land use, litter seed bank, semiarid Chaco, soil seed bank, sources of resilience

1 | INTRODUCTION

The concept of ecological resilience, defined here as the capacity of a system to return to its initial or reference state after a perturbation (Holling, 1973; Leps, Osbornova-Kosinova, & Rejmanek, 1982), has received considerable attention (Bellwood, Wainwright, Fulton, & Hoey, 2006; MacGillivray & Grime, 1995; Sankaran & McNaughton, 1999), but studies clarifying which elements of the ecosystem promote resilience are still uncommon (Oliver et al., 2015; Willis, Jeffers, & Tovar, 2018). Resilience can be influenced by different ecosystem components or *sources of resilience* (Lipoma, Funes, & Díaz, 2018; Oliver et al., 2015). One of the most important of these is biodiversity reservoirs from which dominant species could recruit after disturbance. If these reservoirs have "memory", i.e., if their floristic composition resembles that of the initial or reference state, they can operate as a pool for regenerating it (Bekker et al., 1997; Fenner, 2000; Hopfensperger, 2007; Thompson & Grime, 1979).

The soil seed bank — the assemblage of seeds that remain dormant in the soil (Simpson, Leck, & Parker, 1989) — is by far the most studied biodiversity reservoir for community regeneration in sub-humid Holarctic ecosystems. However, information is still scarce for semiarid Neotropical ones (Henderson, Petersen, & Redak, 1988; Khurana & Singh, 2001). Equally understudied are the *litter seed bank* and the *juvenile bank* (Chambers, 2000; Fenner, 2000; Khurana & Singh, 2001; Ribbens, Silander, & Pacala, 1994).

When seeds reach the ground, after primary dispersal, they can either enter the *soil seed bank*, or keep moving by different dispersal agents to a more distant location (Chambers & MacMahon, 1994; Chambers, MacMahon, & Haefner, 1991). Seeds that neither penetrate the soil, nor keep moving to a remote location can be trapped by vegetation debris on the soil surface; this prevents their loss and eventually promotes in-situ regeneration of the plant community (Chambers, 2000; Chambers & MacMahon, 1994; Chambers et al., 1991; Lipoma, Díaz, Cuchietti, & Gorne, 2019; Márquez, Funes, Cabido, & Pucheta, 2002). Litter and soil seed banks are two very different reservoirs, affecting seed survival and thus community regeneration in different ways (Facelli & Facelli, 1993; Facelli & Pickett, 1991; Rotundo & Aguiar, 2005). For instance, depending on the functional composition of the vegetation, these reservoirs acquire different relative importance. The soil bank is known to be important for small, quasi-spherical seeds, which can be buried more easily (Thompson, Band, & Hodgson, 1993). In contrast, large, unevenly-shaped seeds are more likely to get trapped in the litter layer. In addition to seed banks, regeneration — particularly of woody species — sometimes depends on the presence of seedlings and saplings that remain in a suppressed state until they have the opportunity to grow to adult size, forming a *juvenile bank* (Canham, McAninch, & Wood, 1994; Fenner, 2000; Grubb, 1977). Understanding the relative importance of these different reservoirs in the regeneration of a community after disturbances requires knowing the 'memory' of each of these reservoirs, i.e., how similar they are to the reference vegetation.

Above-ground disturbances related to land use, such as fire, grazing or cropping, can affect established vegetation by decreasing plant biomass, survival and seed production (Fenner, 2000; Garnier et al., 2007; Laliberté et al., 2010; Thompson & Grime, 1979). In the long term, this affects the density and floristic composition of reservoirs: species whose seeds are not replenished into the soil bank and do not have other regeneration mechanisms become increasingly likely to disappear from the community. It follows that changes in land-use intensity, by modifying the established vegetation, can compromise biodiversity reservoirs, affecting the "memory" of the system and, as a consequence, its ecological resilience (Bakker, Poschlod, Strykstra, Bekker, & Thompson, 1996; Bossuyt & Honnay, 2008; Hopfensperger, 2007).

The Chaco forest — the most extensive seasonally dry forest in South America — has experienced important land-use changes in the last few decades (Cabido, Acosta, Carranza, & Díaz, 1992; Cabido, Manzur, Carranza, & González Albarracin, 1994; Hoyos et al., 2013). There is ample evidence for the effects of these changes on established plant communities (Cabido et al., 1992, 2018) and ecosystem structure and processes (Conti et al., 2016; Díaz, Acosta, & Cabido, 1992; Jobbágy, Nosetto, Santoni, & Baldi, 2008; Magliano et al., 2016; Marchesini, Fernández, Reynolds, Sobrino, & Di Bella, 2015). However, the effects of land-use change on processes related to ecosystem recovery and resilience are still poorly known.

In this study, we aimed to characterize the biodiversity reservoirs for recruitment of new individuals of woody species in different ecosystem types resulting from different past and present land-use regimes in the semiarid Neotropical Chaco forest.

Specifically we asked:

1. Where do woody species regenerate from in the Chaco forest?
2. Is land use affecting the floristic composition of biodiversity reservoirs in this ecosystem?
3. Are the soil or the litter seed banks, or the juvenile bank potential *sources of resilience* of these forests in the face of different land-use regimes?

Based on Thompson et al. (1993), who propose that burial mechanisms will operate more effectively on small seeds, we hypothesize that the main source of regeneration would not be the soil bank, because the seeds of the woody species in the Chaco tend to be large (Funes, Díaz, & Venier, 2009), making their burial difficult. Additionally, since the Chaco forest has been subjected to land use at least for several decades, we expected that, as the established vegetation changes with increasing land-use intensity, floristic composition of the different biodiversity reservoirs would change accordingly. Consequently, similarity between the established vegetation of the reference system and the biodiversity reservoirs from disturbed sites should decrease as land-use intensity increases.

2 | METHODOLOGY

2.1 | Study area and experimental design

The study was carried out in the southernmost and driest extreme of the Gran Chaco, in central Argentina (c. 31°15′–31°44′

S and 65°16′–65°40′ W). The climate is subtropical with a mean annual precipitation of c. 600 mm distributed in spring–summer (October–March) and a mean annual temperature of 18°C. Soils are mainly sandy-loam aridisols (typical Camborthids) of alluvial origin (Gorgas & Tassile, 2003). The dominant vegetation is an open xerophytic forest with *Aspidosperma quebracho-blanco* and *Prosopis flexuosa* as canopy and sub-canopy dominants, respectively. The shrub layer is often dense and dominated by *Mimozyganthus carinatus*, *Senegalia gilliesii*, *Celtis ehrenbergiana* and *Larrea divaricata* (Cabido et al., 1992, 2018).

The study area was established in 2007 to analyze the effects of land-use change, a process that has been modifying the landscape in the last decades (Cabido et al., 1992; Zak, Cabido, Cáceres, & Díaz, 2008), on ecosystem functioning and resilience. Within the study area, we selected different ecosystem types initially corresponding to the same vegetation, developed under the same climate and on very similar parental material but having experienced contrasting combinations of historic and present livestock grazing and logging (Cabido et al., 1994; Conti & Díaz, 2013). The ecosystem types identified were: (a) primary forest, a three-strata forest (trees, shrubs and herbs) dominated by *Aspidosperma quebracho-blanco*, with no significant logging or livestock grazing during the past six decades; (b) secondary forest, a three-strata forest (trees, shrubs and herbs) dominated by *Aspidosperma quebracho-blanco* and *Prosopis flexuosa*, recently managed with light selective logging and low cattle and goat stocking rates; (c) closed species-rich shrubland, with two strata (shrubs and herbs) dominated by *Larrea divaricata*, *Mimozyganthus carinatus* and *Senegalia gilliesii*, with some isolated trees of *Aspidosperma quebracho-blanco* and *Prosopis flexuosa*, where logging as well as cattle and goat stocking rates are moderate at the present, but have been historically (>two decades ago) heavy; and (d) open shrubland, also with two strata (shrubs and herbs) strongly dominated by *Larrea divaricata* with a high percentage of bare ground, and historically characterized by heavy logging and high cattle and goat stocking rates. There were no records or physical signs of fire, plowing or application of soil fertilizer in any of the sites during the past few decades, and based on historical sources, they were unlikely to have been tilled during at least the past 150 years (detailed information about the different ecosystem types can be found in Conti & Díaz, 2013).

We established four 50 m × 50 m plots (replicates) in each of the four different ecosystem types, with a minimum distance of 1 km between plots (Figure 1). Each plot was as homogeneous as possible in terms of vegetation, soil and topography (see Conti & Díaz, 2013 for details on site selection).

2.2 | Data collection

At each site, we analyzed floristic composition, i.e., presence and relative abundance of each species, of the different biodiversity compartments (established vegetation, soil seed bank, litter seed bank and juvenile bank). The measurements were carried out in different years, because they are part of a long-term monitoring project. However, the history of land management in each ecosystem type has been maintained for more than two decades. Additionally, because woody species are dominants in this ecosystem (Cabido et al., 1992, 1994), we evaluated this group as a good indicator of the potential recovery of the system.

2.2.1 | Established vegetation sampling

We quantified the abundance of each woody species as visually estimated ground cover inside a 16-m^2 area within each plot, every summer between 2014 and 2019, and the average of the cover of each species was used in the analysis. This allowed us to include the whole period in which different reservoirs were measured. Cover was estimated at 5% intervals, following Cabido, González, Acosta, and Díaz (1993) and Díaz, Cabido, and Casanoves (1998). Cover values were preferred over abundances of adult individuals because they better represent how dominance is distributed between individuals in these communities, where different species have a particular architecture and biomass that does not correspond with their abundance.

2.2.2 | Soil seed bank and litter seed bank sampling

In each plot, we defined a 50m transect that crossed the center of the plot from north to south. Along the transect and every 5m, we collected three soil samples with a 12 cm diameter and 5 cm-depth bore (30 samples per plot), removing the litter layer present in the soil surface. Sampling was carried out during May 2019 immediately after seed set in order to include both the transient and persistent seed banks (sensu Thompson & Grime, 1979).

The litter seed bank (seeds that are retained in the dead plant material lying on the soil surface, such as branches, leaves, inflorescences, bark) was sampled in the same 50-m transect during June 2015, right after the end of the seed dispersal period for woody vegetation (Martin, Nicosia, & Lagomarsino, 1997) and before the beginning of the rainy season (October). Along the transect, we obtained a compound litter seed bank sample by setting a 50 × 50 cm quadrat (10 quadrats per plot) every 5 m, where we gathered all the litter with a soft brush, which enabled collection without disrupting the first centimeters of the soil. If no litter was found at the point allocated to a quadrat, the quadrat was moved to one of the sides within a maximum distance of 1 m. Samples were processed in the laboratory in search for seeds. Soil and litter samples were sieved with a 2-mm mesh (selected according to previous knowledge of prevalent seed sizes in the area) and seeds belonging to woody species were identified using the CORDOBASE seed collection. Complementarily, a tetrazolium test was developed in order to assess seed viability (ISTA, 2014; Ruiz, 2009). Seed abundance was quantified as the number of viable seeds per species for each ecosystem type.

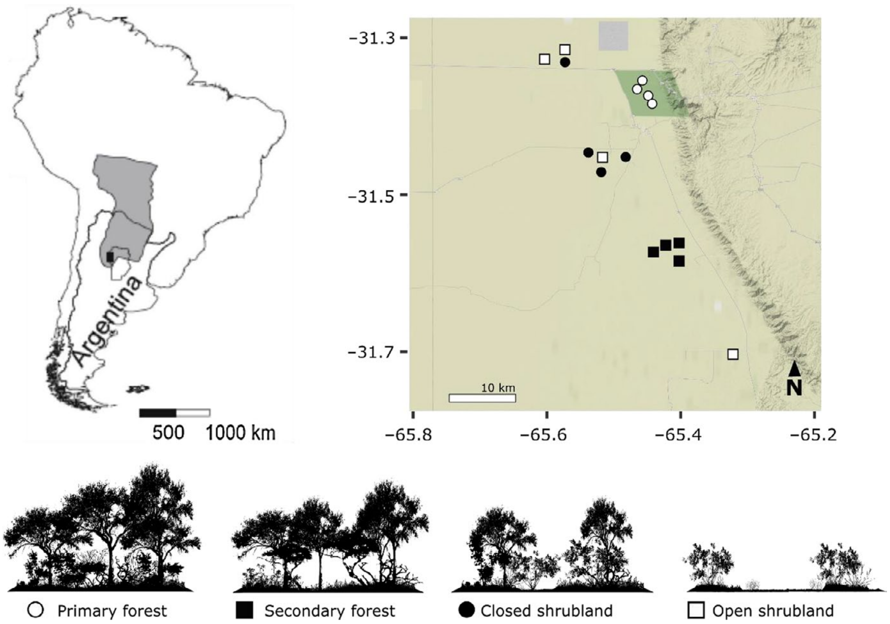

FIGURE 1 Study area location in central Argentina. The map shows the area represented by the Gran Chaco forest in Southern South America (in gray), the framed area corresponds to Córdoba province in central Argentina and the black area situates the study area in the southern portion of the Gran Chaco region. Sampling plots are located in the area and are represented with different symbols for each ecosystem type. Ecosystem types are also presented with an illustration

2.2.3 | Juvenile bank sampling

During February 2016, we quantified the abundance of individuals in the juvenile banks by counting all juvenile individuals of woody species inside the 16-m^2 area established in each plot. Juveniles were defined as individuals that had not reached sexual maturity, including both seedlings (with cotyledons) and saplings (in general including individuals with a diameter <0.5 cm and <1 m in height, with no signs of flowers or fruits during the seasons of observation). For this study, we recorded only the individuals without obvious signs of originating from resprouting.

2.3 | Data analysis

Because abundance estimation in the different compartments was naturally different, we standardized it prior to comparisons. We did this by transforming, in each case, the absolute abundance of each species into relative abundance (values between 0 and 1). In the case of ground cover of the established vegetation, the abundance of each species was standardized against the summation of all the estimated ground covers in each plot. The abundance of each species in the juvenile bank and in the soil and litter seed banks was standardized against the total number of juvenile individuals, or the total number of viable seeds counted in each plot. Then, comparisons between compartments were evaluated in terms of species composition (presence and absence of species) and relative abundance of each species.

To assess similarities in floristic composition between different compartments, we performed a nonmetric multidimensional scaling (NMDS) analysis, using the species × relative abundance matrix as input for each site. Ordination was carried out using the ‘metaMDS’ function from the vegan package (v 2.4-1) in R (R Core Team, Foundation for Statistical Computing, Vienna, Austria). MetaMDS automatically applies a square-root transformation and calculates the Bray–Curtis distances for the community-by-site matrix.

We calculated Sorensen (accounting only for species presence/absence) and Bray–Curtis similarity indices (including both species presence and the relative abundance), between different compartments and the established vegetation of primary forest. We used GLMMs (generalized linear mixed models) to account for differences in both similarity indexes between ecosystem types. To model the lack of independence we included two random effects: plot (indicating the identity of one of the 16 replicates where each reservoir was being analyzed that was being compared with the established vegetation of the primary forest) and forest (indicating the identity of one of the four replicates of the primary forest that was being used as a reference). We used the Akaike information criterion to evaluate the effect of the ecosystem type by comparing each model with a null model without the factor of interest. Then, we used the R a-posteriori test to analyze differences between ecosystem types. Data were analyzed to meet the assumptions of normal distribution and homogeneous variance. Analyses were carried out in R (version 3.3.1; R Core Team, 2015). GLMMs were developed using the “lme” function from the “nlme” package and the “lmer” function from the “lme4” package (Bates, Machler, Bolker, & Walker, 2014; Pinheiro, Bates, DebRoy, & Sarkar, 2016).

3 | RESULTS

A total of 15 species, belonging to 10 families, were detected in different compartments (Table 1). The soil seed bank was the compartment with the lowest richness (five species), followed by the litter seed bank (11 species), the juvenile bank (12 species), and the established vegetation (15 species). There was only one species (*Ximenia americana*) that was present in the established vegetation but not in any other compartment.

Floristic composition changed among ecosystem types and among compartments (Figure 2). The established vegetation and the litter seed bank differed between ecosystem types, especially between sites with no land use and those with intermediate or high land-use intensity. Under no land use (primary forest), *Aspidosperma quebracho-blanco*, *Celtis ehrenbergiana* and *Capparis atamisquea* dominated the established vegetation and the litter seed bank; sites with high land-use intensity (open shrubland) were dominated mainly by *Larrea divaricata*. On the other hand, the soil seed bank and the juvenile plant bank did not show a clear differentiation among ecosystem types. *Parkinsonia praecox*, found only in low proportions in the established vegetation, was dominant in the soil seed bank in all ecosystem types; in addition, the juvenile bank of all ecosystem types showed a high proportion of species typical of the primary forest.

The floristic composition of seed banks of all the ecosystem types showed very low similarity with the floristic composition of the established vegetation of the primary forest (Figure 3a, b). The floristic composition of the litter seed banks and the juvenile banks showed higher similarity with the established vegetation of the primary forest (Figure 3c–f) in all cases, but this similarity decreased with increasing land-use intensity. In the case of the litter seed bank, similarity decreased with intermediate and high land-use intensities, especially when the index included the relative abundance of species (Bray–Curtis index; Figure 3c, d). Similarity between the juvenile bank and the established vegetation of the primary forest showed higher values in the ecosystem types with low and intermediate land-use intensities and decreased with high intensities (Figure 3e, f). Finally, similarity between the established vegetation from different ecosystem types and the primary forest also decreased with increasing land-use intensity, but species composition was less affected than relative abundance (Figure 3g, h).

4 | DISCUSSION

We focused on how land use, through its effects on different biodiversity reservoirs, can compromise the "memory" of the Chaco forest and thus its resilience. Most studies have focused on the soil seed bank as the main biodiversity reservoir and, although some of them have included the litter seed bank in the surveys, they have not analyzed it separately (Henderson et al., 1988; Hopfensperger, 2007; Khurana & Singh, 2001). We found, however, that the litter seed bank and the juvenile plant bank, but not the soil seed bank, are acting as effective reservoirs for the woody community in this ecosystem.

The soil seed bank showed very low species richness and was dominated (in all ecosystem types) by *Parkinsonia praecox*, a species that is not well represented in the established vegetation of the primary forest, but is very common at disturbed sites (Cabido et al., 1992; Cabido, Giorgis, & Tourn, 2010; Paez & Marco, 2000). The low number of species in the soil is possibly related to the fact that seeds of many woody species, because of their shape and size, often do not penetrate the soil surface and are lost or trapped in the surface (Bekker et al., 1997; Esmailzadeh, Hosseini, & Tabari, 2011; Thompson et al., 1993). Nevertheless, we found a small number of seeds in the soil that were not viable (data not shown), indicating that a small proportion of seeds are able to penetrate the soil, but are not effectively available for germination, as reported previously in the literature (Ray & Brown, 1995). The soil seed bank is one of the most studied biodiversity reservoirs for community regeneration, mainly because the species present in this compartment have the potential to colonize after disturbances. However, in forest ecosystems the seed bank does not always ensure the recovery of the reference vegetation (Bakker et al., 1996; Hopfensperger, 2007), because it tends to be dominated by a few, often weedy species, highlighting the conservation and restoration value of other biodiversity reservoirs (Bakker, de Graaf, Ernst, & van Bodegom, 2005; Bossuyt & Hermy, 2003; Esmailzadeh et al., 2011; Hopfensperger, 2007).

Our results show, for the first time for the Chaco forest, that the litter seed bank and the juvenile bank — both with high similarity to the floristic composition of the established vegetation — could be acting as much more effective reservoirs for the regeneration of the woody Chaco forest if major disturbances are halted. Other studies have highlighted the role of the litter as an effective trap for seeds and as a factor modifying abiotic conditions, facilitating germination in situ (Chambers, 2000; Facelli & Pickett, 1991; Gross & Vary, 2014; Paez & Marco, 2000; Rotundo & Aguiar, 2005; Seidl, Vigl, Rossler, Neumann, & Rammer, 2016). An experimental study in the same area (Lipoma, Cuchietti, Gorne, & Díaz, 2019) indicates that sites with higher litter cover and vegetation complexity retain a higher number of seeds on the ground. Additionally, Paez and Marco (2000) showed that litter cover and depth were two factors affecting the floristic composition of seedlings of woody species in the Chaco forest. Barberis, Boccanelli, and Alzugaray (2011) also showed for Chaco forest that understorey plants, particularly bromeliads, are favorable microsites for the accumulation of seeds of woody species. Together, these studies empirically demonstrate the importance of the litter layer for both seed retention and the establishment of woody species in the Chaco forest. Furthermore, our study indicates that this pattern could be driven by land-use intensity. In addition, the juvenile bank of this ecosystem is an important reservoir due to the fact that some of the species found in this reservoir have the capacity to persist in a juvenile stage for a long time until the right conditions appear for maturation. This is particularly clear for *Aspidosperma quebracho-blanco*, the emblematic canopy dominant of this ecosystem (Barchuk & Del Pilar Díaz, 1999). Additionally, during this extended seedling stage, some species have the ability to resprout, promoting their persistence in the community in spite of disturbances (Barchuk, Campos, Oviedo, & Díaz, 2006; Barchuk & Díaz, 1999; Vieira, Scariot, Sampaio, & Holl, 2006).

Predictably, land use altered the floristic composition of the established vegetation, whose similarity with the primary forest decreased as land-use intensity increased, although these effects were much

TABLE 1 Relative abundance of woody species in the established vegetation and the three biodiversity reservoirs in different ecosystem types (PF, primary forest, SF, secondary forest, CS, closed species-rich shrubland and OS, open shrubland)

	Established vegetation				Juvenile bank				Litter seed bank				Soil seed bank			
Species	PF	SF	CF	OP	PF	SF	CF	OP	PF	SF	CF	OP	PF	SF	CF	OP
Aspidosperma quebracho-blanco Schltdl.	36.17	41.54	22.55	0.95	69.46	57.84	27.96	33.33	37.50	0.47	–	–	–	–	–	–
Capparis atamisquea Kuntze	17.41	6.95	–	–	0.99	4.90	–	–	9.72	7.58	–	–	–	7.69	–	–
Celtis ehrenbergiana (Klotzsch) Liebm.	18.84	5.46	2.85	1.08	6.40	1.96	1.61	5.56	13.89	25.12	2.86	3.17	33.33	–	–	–
Condalia microphylla Cav.	2.32	0.64	0.04	–	3.94	4.90	0.54	–	1.39	–	2.86	–	–	–	–	–
Geoffroea decorticans (Gillies ex Hook. & Arn.) Burkart	1.91	3.17	–	0.03	1.48	5.88	0.54	–	–	–	–	–	–	–	–	–
Larrea divaricata Cav.	4.17	6.19	10.75	86.30	3.45	3.92	6.99	5.56	5.56	0.95	57.14	76.19	–	–	–	33.33
Monteverdia spinosa (Griseb.) Biral	6.14	3.81	–	–	0.99	–	–	–	–	–	–	–	–	–	–	–
Mimozyganthus carinatus (Griseb.) Burkart	3.01	5.11	34.75	4.70	1.48	–	48.92	22.22	–	–	–	–	–	–	–	–
Parkinsonia praecox (Ruiz & Pav. ex Hook.) Harms	0.14	6.31	0.05	1.16	0.49	4.90	–	–	18.06	54.50	–	3.17	66.67	69.23	100.00	66.67
Prosopis flexuosa DC.	0.29	13.38	20.11	0.12	0.99	5.88	1.61	16.67	–	1.90	11.43	15.87	–	23.08	–	–
Prosopis torquata (Cav. ex Lag.) DC.	0.12	–	–	–	–	–	–	–	4.17	6.16	–	–	–	–	–	–
Sarcomphalus mistol (Griseb.) Hauenschild	0.04	–	–	–	–	–	–	–	1.39	–	2.86	1.59	–	–	–	–
Schinus fasciculatus (Griseb.) I.M.Johnst.	1.54	0.06	0.01	–	4.93	–	1.08	–	2.78	–	–	–	–	–	–	–
Senegalia gilliesii (Steud.) Seigler & Ebinger	7.19	3.90	4.67	0.75	3.94	8.82	7.53	11.11	5.56	3.32	22.86	–	–	–	–	–
Ximenia americana L.	–	0.009	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Note: Species were identified following Zuloaga (1994) and Zuloaga and Morrone (1996a, 1996b).

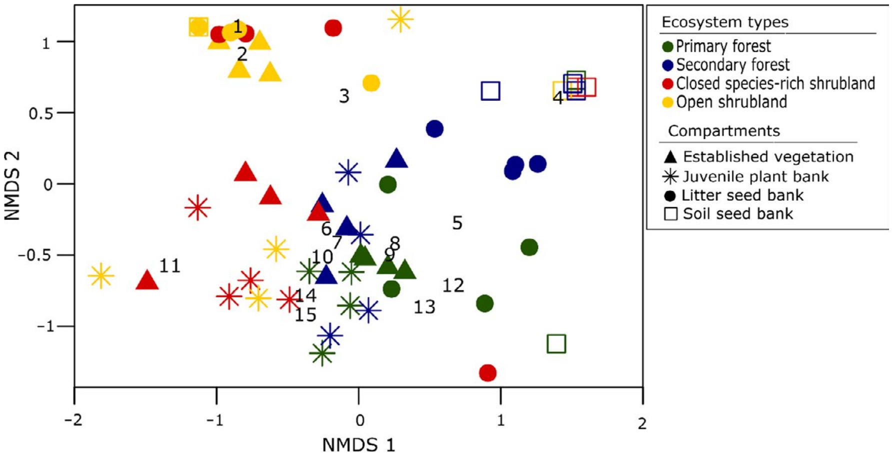

FIGURE 2 NMDS ordination of the proportions of abundance of woody species × ecosystem types matrix. Species are indicated with numbers: (1) *Sarcomphalus mistol*, (2) *Larrea divaricata*, (3) *Prosopis flexuosa*, (4) *Parkinsonia praecox*, (5) *Prosopis torquata*, (6) *Geoffroea decorticans*, (7) *Condalia microphyla*, (8) *Senegalia gilliesii*, (9) *Capparis atamisquea*, (10) *Monteverdia spinosa*, (11) *Mimozyganthus carinatus*, (12) *Celtis ehrenbergiana*, (13) *Schinus fasciculatus*, (14) *Aspidosperma quebracho-blanco*, (15) *Ximenia americana.* Colours represent different ecosystem types. The positions of some replicates of the soil seed bank overlap, so not all of them are represented in the graph

more marked in the relative abundance of species than in the list of species present. Our results show that high land-use intensities also affect the floristic composition of the litter seed bank and the juvenile plant bank. Nevertheless, under low land-use intensities, both the litter seed bank and the juvenile bank were similar to, and therefore showed some degree of "memory" for, the floristic composition of the primary forest. It has been suggested that in highly disturbed areas, where above-ground vegetation has been strongly modified, seed availability is very low (Corrià-Ainslie, Julio Camarero, & Toledo, 2015; Nathan & Muller-landau, 2000; Wijdeven & Kuzee, 2000) and abiotic conditions for the germination and establishment of new individuals are adverse (Corrià-Ainslie et al., 2015; Khurana & Singh, 2001; Paez & Marco, 2000; Rotundo & Aguiar, 2005), preventing the replenishment of these biodiversity reservoirs. However, because the presence of species was less affected than their relative abundance, our results suggest that the presence of few individuals of some species in the established vegetation — and also in neighboring patches acting as sources of propagules — can guarantee the preservation of species composition of these reservoirs (Chazdon, 2003; Derroire, Coe, & Healey, 2016; Török, Helm, Kiehl, Buisson, & Valkó, 2018).

The juvenile bank showed higher similarity, both in terms of species presence and relative abundance, with the primary forest and a lower decrease with land-use intensity than did the litter seed bank. This indicates that there are some species present in the established vegetation and in the juvenile bank that are underrepresented or absent from the litter seed bank, suggesting that, although the litter has an important effect on seed retention for dominant species of the Chaco forest ecosystem, it seems not to be the only source for regeneration. Other regeneration strategies could be involved like seeds that do not form seed banks and germinate immediately after they reach the ground (Drake, 1998; Esmailzadeh et al., 2011; Hille Ris Lambers, Clark James, & Lavine, 2005), and also vegetative regeneration (Klimešová & Klimeš, 2007). Although these strategies are not well documented for this ecosystem, studies in neighboring biogeographical regions and involving several genera and some species in common with ours (Gurvich, Enrico, & Cingolani, 2005; Jaureguiberry & Díaz, 2014; Lipoma, Gurvich, Urcelay, & Díaz, 2016) suggest that resprouting in particular can be both common and important.

4.1 | Biodiversity reservoirs and resilience

Our results support the idea that litter seed banks and juvenile plant banks have the potential to regenerate the Chaco forest. The presence of biodiversity reservoirs that can promote the recovery of the reference vegetation can be considered as "sources of resilience" in the sense that they are critical components underpinning ecosystem resilience (Lipoma, 2018). Although our study is a snapshot of the dynamic of ecosystems subjected to land-use change, it yielded useful insights. According to our results, ecosystems that have been subjected to low and intermediate land-use intensity will have more chances to recover the floristic composition of primary forest, because they preserve the "memory" of the past vegetation in the litter seed bank and in the juvenile bank. However, the same fact, i.e., the regeneration process being more dependent on litter seed banks and juvenile banks and not so much on soil seed banks, suggests that the process of regeneration could be highly vulnerable to disturbances acting at the ground level, such as fire, and seed predation (Velez, Chacoff, & Campos, 2018; Villagra, 2000) or herbivory on seedlings, which often do not affect seeds buried in the soil.

5 | CONCLUSION

The present study showed that in the Chaco forest, the litter and juvenile banks, but not the soil seed bank, are acting as the main biodiversity reservoirs for woody species. These reservoirs showed some

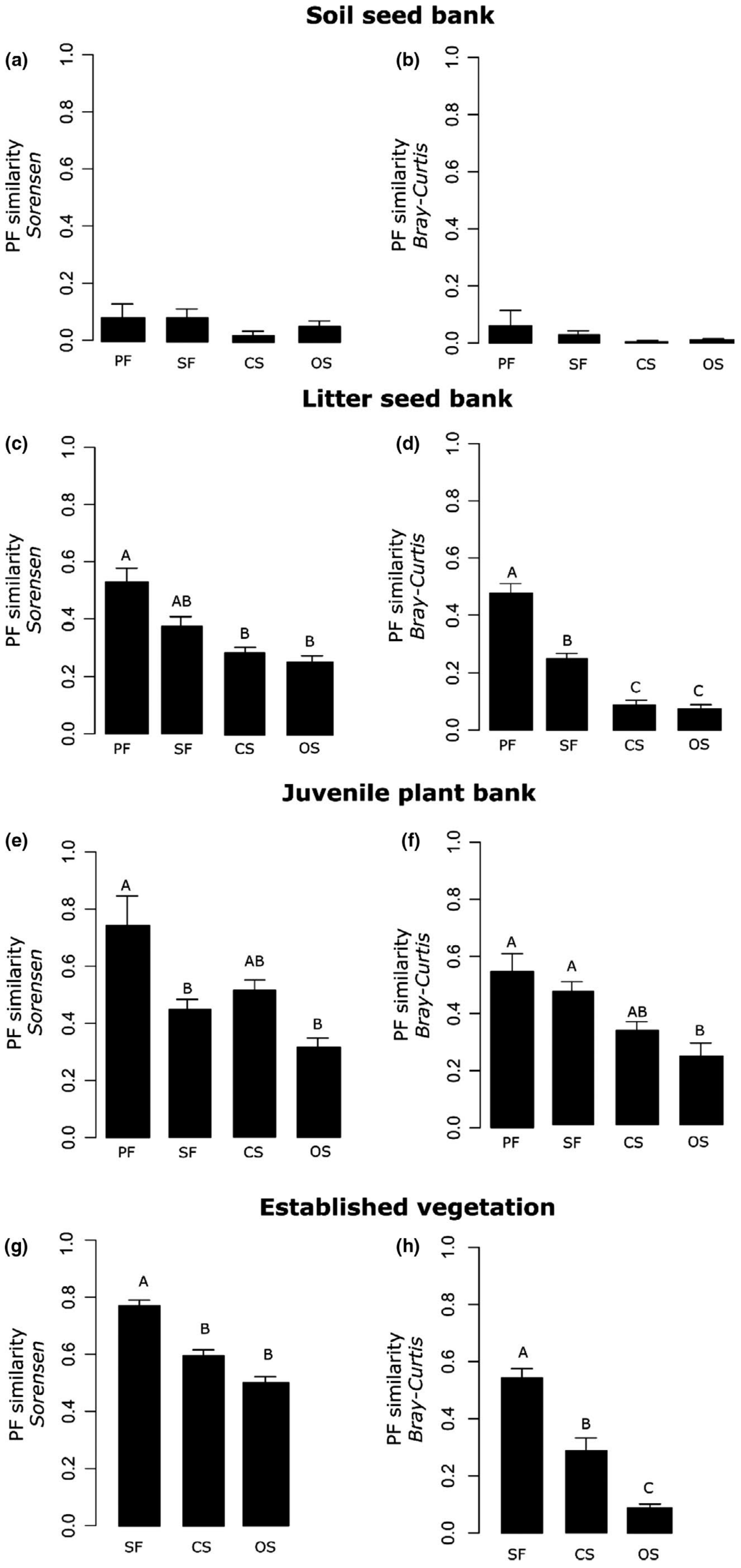

FIGURE 3 Sorensen and Bray–Curtis similarities between the floristic composition of different compartments (soil seed bank, litter seed bank, juvenile plant bank and established vegetation) in each ecosystem type and that of the established vegetation of the primary forest (PF similarity). PF, primary forest; SF, secondary forest; CS, closed species-rich shrubland; OS, open shrubland. When present, different letters indicate significant differences ($p < 0.05$). Bars indicate standard error

degree of "memory" with low land-use intensities, but such "memory" decreases as land use intensifies, compromising their ability to act as sources of ecosystem resilience. If land use ends, those plant communities that have been subjected to low or intermediate land-use intensities will have more chances to recover the floristic composition of the reference vegetation. However, some questions remain, for example, which other regeneration strategies are acting (e.g. vegetative resprouting) and what is their relative contribution to the resilience of this ecosystem.

ACKNOWLEDGEMENTS

We are grateful to land dwellers, owners and managers for allowing us to work on their properties and to the Secretaría de Ambiente de Córdoba and staff of the Reserva Natural Chancaní. We also thank all those who kindly helped during the experiments (in particular G. Funes, G. Conti, G. Bertone, E. Arrieta, D. Cabrol, A. Cuchietti and L. Gorné) and the anonymous reviewer and the Coordinating Editor for their insightful comments on this manuscript.

AUTHORS' CONTRIBUTIONS

MLL and SD designed the research question and methods; MLL, VF and LE collected the field data, MLL and VF analyzed the data; MLL wrote the paper; all authors discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT

Data from this study are available at Zenodo.org, https://doi.org/10.5281/zenodo.3517207

ORCID

María Lucrecia Lipoma https://orcid.org/0000-0001-7409-6015
Lucas Enrico https://orcid.org/0000-0002-8932-0144
Sandra Díaz https://orcid.org/0000-0003-0012-4612

REFERENCES

Bakker, C., de Graaf, H. F., Ernst, W. H. O., & van Bodegom, P. M. (2005). Does the seed bank contribute to the restoration of species-rich vegetation in wet dune slacks? *Applied Vegetation Science*, *8*(1), 39–48. https://doi.org/10.1111/j.1654-109X.2005.tb00627.x

Bakker, J. P., Poschlod, P., Strykstra, R. J., Bekker, R. M., & Thompson, K. (1996). Seed banks and seed dispersal: Important topics in restoration ecology. *Acta Botanica*, *45*, 461–490. https://doi.org/10.1111/j.1438-8677.1996.tb00806.x

Barberis, I. M., Boccanelli, S. I., & Alzugaray, C. (2011). Terrestrial bromeliads as seed accumulation microsites in a xerophytic forest of Southern Chaco, Argentina. *Bosque*, *32*(1), 57–63. https://doi.org/10.4067/S0717-92002011000100007

Barchuk, A. H., Campos, E. B., Oviedo, C., & Díaz, M. D. P. (2006). Supervivencia y crecimiento de plántulas de especies leñosas del Chaco Árido sometidas a remoción de la biomasa aérea. *Ecologia Austral*, *16*(1), 47–61.

Barchuk, A. H., & Del Pilar Díaz, M. (1999). Regeneration and structure of Aspidosperma quebracho-blanco Schl. in the Arid Chaco (Cordoba, Argentina). *Forest Ecology and Management*, *118*(1–3), 31–36. https://doi.org/10.1016/S0378-1127(98)00484-8

Bates, D., Machler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software 67*(1), 1–48.

Bekker, R. M., Verweij, G. L., Smith, R. E. N., Reine, R., Bakker, J. P., & Schneider, S. (1997). Soil seed banks in European grasslands: Does land use affect regeneration perspectives? *Journal of Applied Ecology*, *34*(5), 1293–1310.

Bellwood, D. R., Wainwright, P. C., Fulton, C. J., & Hoey, A. S. (2006). Functional versatility supports coral reef biodiversity. *Proceedings. Biological Sciences/the Royal Society*, *273*(1582), 101–107. https://doi.org/10.1098/rspb.2005.3276

Bossuyt, B., & Hermy, M. (2003). The potential of soil seedbanks in the ecological restoration of grassland and heathland communities. *Belgian Journal of Botany*, *136*(1), 23–34.

Bossuyt, B., & Honnay, O. (2008). Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. *Journal of Vegetation Science*, *19*(6), 875–884. https://doi.org/10.3170/2008-8-18462

Cabido, M., Acosta, A. T., Carranza, M. L., & Díaz, S. (1992). La vegetación del Chaco Árido en el W de la provincia de Córdoba, Argentina. *Documents Phytosociologiques*, *17*, 447–456.

Cabido, M., Giorgis, M. A., & Tourn, M. (2010). Guía para una excursión botánica en las sierras de Córdoba. *Boletin De La Sociedad Argentina De Botanica*, *45*, 209–219.

Cabido, M., González, C., Acosta, A., & Díaz, S. (1993). Vegetation changes along a precipitation gradient in Central Argentina. *Vegetatio*, *109*(1), 5–14. https://doi.org/10.1007/BF00149541

Cabido, M. R., Manzur, A., Carranza, L., & Gonzalez Albarracin, C. (1994). La vegetación y el medio físico del Chaco Arido en la provincia de Córdoba, Argentina Central. *Phytocoenología*, *24*, 423–460. https://doi.org/10.1127/phyto/24/1994/423

Cabido, M., Zeballos, S. R., Zak, M., Carranza, M. L., Giorgis, M. A., Cantero, J. J., & Acosta, A. T. R. (2018). Native woody vegetation in central Argentina: Classification of Chaco and Espinal forests. *Applied Vegetation Science*, *21*(2), 298–311. https://doi.org/10.1111/avsc.12369

Canham, C. D., McAninch, J. B., & Wood, D. M. (1994). Effects of the frequency, timing, and intensity of simulated browsing on growth and mortality of tree seedlings. *Canadian Journal of Forest Research*, *24*(4), 817–825. https://doi.org/10.1139/x94-107

Chambers, J. C. (2000). Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: Implications for restoration. *Ecological Applications*, *10*(5), 1400–1413.

Chambers, J. C., & MacMahon, J. (1994). A day in the life of a seed: Movements and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics*, *25*(1), 263–292. https://doi.org/10.1146/annurev.es.25.110194.001403

Chambers, J. C., MacMahon, J. A., & Haefner, J. H. (1991). Seed entrapment in alpine ecosystems: Effects of soil particle size and diaspore morphology. *Ecology*, *72*(5), 1668–1677.

Chazdon, R. L. (2003). Tropical forest recovery: Legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*, *6*(1–2), 51–71. https://doi.org/10.1078/1433-8319-00042

Conti, G., & Díaz, S. (2013). Plant functional diversity and carbon storage – an empirical test in semi-arid forest ecosystems. *Journal of Ecology*, *101*, 18–28. https://doi.org/10.1111/1365-2745.12012

Conti, G., Kowaljow, E., Baptist, F., Rumpel, C., Cuchietti, A., Pérez Harguindeguy, N., & Díaz, S. (2016). Altered soil carbon dynamics under different land-use regimes in subtropical seasonally-dry forests of central Argentina. *Plant and Soil*, *403*(1–2), 374–387. https://doi.org/10.1007/s11104-016-2816-2

Corrià-Ainslie, R., Julio Camarero, J., & Toledo, M. (2015). Environmental heterogeneity and dispersal processes influence post-logging seedling establishment in a Chiquitano dry tropical forest. *Forest Ecology* *and Management*, *349*(11), 122–133. https://doi.org/10.1016/j.foreco.2015.03.033

Derroire, G., Coe, R., & Healey, J. R. (2016). Isolated trees as nuclei of regeneration in tropical pastures: Testing the importance of niche-based and landscape factors. *Journal of Vegetation Science*, *27*(4), 679–691. https://doi.org/10.1111/jvs.12404

Díaz, S., Acosta, A., & Cabido, M. (1992). Morphological analysis of herbaceous communities under different grazing regimes. *Journal of Vegetation Science*, *3*(5), 689–696. https://doi.org/10.2307/3235837

Díaz, S., Cabido, M., & Casanoves, F. (1998). Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science*, *9*(1), 113–122. https://doi.org/10.2307/3237229

Drake, D. R. (1998). Relationships among the seed rain, seed bank and vegetation of a Hawaiian forest. *Journal of Vegetation Science*, *9*(1), 103–112. https://doi.org/10.2307/3237228

Esmailzadeh, O., Hosseini, S. M., & Tabari, M. (2011). Relationship between soil seed bank and above-ground vegetation of a mixed-deciduous temperate forest in Northern Iran. *Journal of Agronomic Science and Technology*, *13*, 411–424.

Facelli, J. M., & Pickett, S. T. A. (1991). Plant litter: Its dynamics and effects on plant community structure. *The Botanical Review*, *57*(1), 1–32. https://doi.org/10.1007/BF02858763

Facelli, M., & Facelli, E. (1993). Interactions after death: Plant litter controls priority effects in successional plant community. *Oecologia*, *95*, 277–282.

Fenner, M. (Ed.) (2000). *Seeds, The ecology of regeneration in plant communities*. Wallingford, UK: CABI.

Funes, G., Díaz, S. M., & Venier, M. P. (2009). La temperatura como principal determinante de la germinación en especies del Chaco seco de Argentina. *Ecología Austral*, *19*, 129–138.

Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., … Zarovali, M. P. (2007). Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: A standardized methodology and lessons from an application to 11 European sites. *Annals of Botany*, *99*(5), 967–985. https://doi.org/10.1093/aob/mcl215

Gorgas, J., & Tassile, J. (2003). *Recursos naturales de la provincia de Córdoba. Los Suelos*. Manfredi, Córdoba: Agencia Córdoba Ambiente SE-INTA EEA.

Gross, C. L., & Vary, L. B. (2014). Arrested recovery in a sandy woodland correlates with a lack of heavy and long seeds in the seed bank. *Ecosphere*, *5*(6), 1–26. https://doi.org/10.1890/ES14-00020.1

Grubb, P. J. (1977). The maintenance ofspecies-richness in plant communities: The importance of the regeneration niche. *Biological Review*, *52*(1), 107–145. https://doi.org/10.1111/j.1469-185X.1977.tb01347.x

Gurvich, D. E., Enrico, L., & Cingolani, A. M. (2005). Linking plant functional traits with post-fire sprouting vigour in woody species in central Argentina. *Austral Ecology*, *30*(7), 789–796. https://doi.org/10.1111/j.1442-9993.2005.01522.x

Henderson, C. B., Petersen, K. E., & Redak, R. A. (1988). Spatial and temporal patterns in the seed bank and vegetation of a desert grassland community. *Journal of Ecology*, *76*(3), 717–728. https://doi.org/10.2307/2260569

Hille Ris Lambers, J., Clark James, S., & Lavine, M. (2005). Implications of seed banking for recruitment of southern Appalachian woody species. *Ecology*, *86*(1), 85–95.

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, *4*(1), 1–23. https://doi.org/10.1146/annurev.es.04.110173.000245

Hopfensperger, K. N. (2007). A review of similarity between seed bank and standing vegetation across ecosystems. *Oikos*, *116*(9), 1438–1448. https://doi.org/10.1111/j.2007.0030-1299.15818.x

Hoyos, L. E., Cingolani, A. M., Zak, M. R., Vaieretti, M. V., Gorla, D. E., & Cabido, M. R. (2013). Deforestation and precipitation patterns in the arid Chaco forests of central Argentina. *Applied Vegetation Science*, *16*(2), 260–271. https://doi.org/10.1111/j.1654-109X.2012.01218.x

International Seed Testing Association. (2014). Biochemical test for viability: the topographical tetrazolium test. In *International Rules for Seed Testing* (6th edn, pp. 6–26).

Jaureguiberry, P., & Díaz, S. (2014). Post-burning regeneration of the Chaco seasonally dry forest: Germination response of dominant species to experimental heat shock. *Oecologia*, *177*(3), 689–699. https://doi.org/10.1007/s00442-014-3161-x

Jobbágy, E. G., Nosetto, M. D., Santoni, C. S., & Baldi, G. (2008). El desafío ecohidrológico de las transiciones entre sistemas leñosos y herbáceos en la llanura Chaco-Pampeana. *Ecologia Austral*, *18*, 305–322.

Khurana, E., & Singh, J. S. (2001). Ecology of seed and seedling growth for conservation and restoration of tropical dry forest: A review. *Environmentanl Conservation*, *28*(1), 39–52. https://doi.org/10.1017/S0376892901000042

Klimešová, J., & Klimeš, L. (2007). Bud banks and their role in vegetative regeneration - A literature review and proposal for simple classification and assessment. *Perspectives in Plant Ecology, Evolution and Systematics*, *8*(3), 115–129. https://doi.org/10.1016/j.ppees.2006.10.002

LalibertÃ©, E., Wells, J. A., DeClerck, F., Metcalfe, D. J., Catterall, C. P., Queiroz, C., … Mayfield, M. M. (2010). Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters*, *13*(1), 76–86. https://doi.org/10.1111/j.1461-0248.2009.01403.x

Leps, J., Osbornova-Kosinova, J., & Rejmanek, M. (1982). Community stability, complexity and species life history strategies. *Vegetatio*, *50*, 53–63. https://doi.org/10.1007/BF00120678

Lipoma, M. L. (2018). *Resiliencia ecológica antes distintos usos de la tierra en el bosque chaqueño del noroeste de Córdoba, Argentina*. Unpublished thesis, Córdoba, Argentina: Universidad Nacional de Córdoba.

Lipoma, M. L., Cuchietti, A., Gorne, L. D., & Díaz, S. M. (2019). Not gone with the wind: Vegetation complexity increases seed retention during windy periods in the Argentine Semiarid Chaco. *Journal of Vegetation Science*, *30*(3), 542–552. https://doi.org/10.1111/jvs.12747

Lipoma, M. L., Funes, G., & Díaz, S. (2018). Fire effects on the soil seed bank and post-fire resilience of a semi-arid shrubland in central Argentina. *Austral Ecology*, *43*(1), https://doi.org/10.1111/aec.12533

Lipoma, M. L., Gurvich, D. E., Urcelay, C., & Díaz, S. (2016). Plant community resilience in the face of fire: Experimental evidence from a semi-arid shrubland. *Austral Ecology*, https://doi.org/10.1111/aec.12336

Macgillivray, C. W., & Grime, J. P. (1995). Testing predictions of the resistance and resilience of vegetation subjected to extreme events. *Functional Ecology*, *9*(4), 640–649. https://doi.org/10.2307/2390156

Magliano, P. N., Fernández, R. J., Giménez, R., Marchesini, V. A., Páez, R. A., & Jobbágy, E. G. (2016). Cambios en la partición de flujos de agua en el Chaco Árido al reemplazar bosques por pasturas. *Ecología Austral*, *26*(2), 95–106.

Marchesini, V. A., Fernández, R. J., Reynolds, J. F., Sobrino, J. A., & Di Bella, C. M. (2015). Changes in evapotranspiration and phenology as consequences of shrub removal in dry forests of central Argentina. *Ecohydrology*, *8*(7), 1304–1311. https://doi.org/10.1002/eco.1583

Márquez, S., Funes, G., Cabido, M., & Pucheta, E. (2002). Efectos del pastoreo sobre el banco de semillas germinable y la vegetación establecida en pastizales de montaña del centro de Argentina Grazing effects on the germinable seed bank and standing vegetation in mountain grasslands from central Argentina El pa. *Revista Chilena De Historia Natural*, *75*(2), 327–337.

Martin, G. O., Nicosia, M. G., & Lagomarsino, E. D. (1997). Fenología foliar en leñosas nativas del Chaco Semiárido de Tucumán y algunas consideraciones para su aprovechamiento forrajero. *Revista Agronómica Del Noroeste Argentino*, *29*(1), 65–85.

Nathan, R., & Muller-landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, *15*(7), 278–285. https://doi.org/10.1016/S0169-5347(00)01874-7

Oliver, T. H., Isaac, N. J. B., August, T. A., Woodcock, B. A., Roy, D. B., & Bullock, J. M. (2015). Declining resilience of ecosystem functions under biodiversity loss. *Nature Communications*, *6*, 1–8. https://doi.org/10.1038/ncomms10122

Paez, S. A., & Marco, D. E. (2000). Seedling habitat structure in dry Chaco forest (Argentina). *Journal of Arid Environments*, *46*(1), 57–68. https://doi.org/10.1006/jare.2000.0648

Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2016). R Core Team. nlme: linear and nonlinear mixed effects models. 2014. *R package version*, *3*, 1–78.

R Core Team. (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Ray, G. J., & Brown, B. J. (1995). Restoring Caribbean dry forests: Evaluation of tree propagation techniques. *Restoration Ecology*, *3*(2), 86–94. https://doi.org/10.1111/j.1526-100X.1995.tb00081.x

Ribbens, E., Silander, J. A., & Pacala, S. W. (1994). Seedling recruitment in forests: Calibrating models to predict patterns of tree seedling dispersion. *Ecology*, *75*(6), 1794–1806. https://doi.org/10.2307/1939638

Rotundo, J. L., & Aguiar, M. R. (2005). Litter effects on plant regeneration in arid lands: A complex balance between seed retention, seed longevity and soil-seed contact. *Journal of Ecology*, *93*(4), 829–838. https://doi.org/10.1111/j.1365-2745.2005.01022.x

Ruiz, M. A. (2009). El análisis de tetrazolio en el control de calidad de semillas. Caso de Estudio: Cebadilla Chaqueña. *EEA INTA Anguil Argentinca*, *77*, 1–19.

Sankaran, M., & McNaughton, S. J. (1999). Determinants of biodiversity regulate compositional stability of communities. *Nature*, *401*(6754), 691–693. https://doi.org/10.1038/44368

Seidl, R., Vigl, F., Rossler, G., Neumann, M., & Rammer, W. (2016). Assessing the resilience of Norway spruce forests through a model-based reanalysis of thinning trials. *Forest Ecology and Management*, *388*(11), 3–12. https://doi.org/10.1016/j.foreco.2016.11.030

Simpson, R. L., Leck, M. A., & Parker, V. T. (1989). Ecology of soil seed banks. *San Diego: Academic Press*, *1*(989), 149–209.

Thompson, K., Band, S. R., & Hodgson, J. G. (1993). Seed size and shape predict persistence in soil. *Functional Ecology*, *7*(2), 236. https://doi.org/10.2307/2389893

Thompson, K., & Grime, J. P. (1979). Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology*, *67*(3), 893–921. https://doi.org/10.2307/2259220

Török, P., Helm, A., Kiehl, K., Buisson, E., & Valkó, O. (2018). Beyond the species pool: Modification of species dispersal, establishment, and assembly by habitat restoration. *Restoration Ecology*, *26*(6), S65–S72. https://doi.org/10.1111/rec.12825

Velez, S., Chacoff, N. P., & Campos, C. M. (2018). Pre-dispersal seed loss in two *Prosopis* species (Fabacea: Mimosoidea) from the Monte Desert, Argentina. *Ecología Austral*, *28*(02), 361–373.

Vieira, D. L. M., Scariot, A., Sampaio, A. B., & Holl, K. D. (2006). Tropical dry-forest regeneration from root suckers in Central Brazil. *Journal of Tropical Ecology*, *22*(3), 353–357. https://doi.org/10.1017/S0266467405003135

Villagra, P. E. (2000). Aspectos ecológicos de los algarrobales argentinos. *Multequina*, *9*(2), 35–51.

Wijdeven, S. M. J., & Kuzee, M. E. (2000). Seed availability as a limiting factor in forest recovery processes in Costa Rica. *Restoration Ecology*, *8*(4), 414–424. https://doi.org/10.1046/j.1526-100x.2000.80056.x

Willis, K. J., Jeffers, E. S., & Tovar, C. (2018). What makes a terrestrial ecosystem resilient? *Science*, *359*(6379), 988–989.

Zak, M. R., Cabido, M., Cáceres, D., & Díaz, S. (2008). What drives accelerated land cover change in central Argentina? Synergistic consequences of climatic, socioeconomic, and technological factors. *Environmental Management*, *42*(2), 181–189. https://doi.org/10.1007/s00267-008-9101-y

Zuloaga, F. O. (1994). Catálogo de la familia Poaceae en la República Argentina. *Monographs in Systematic Botany from the Missouri Botanical Garden*, *47*, 1–178.

Zuloaga, F. O., & Morrone, O. (1996a). Catálogo de las plantas vasculares de la República Argentina. *Monographs in Systematic Botany from the Missouri Botanical Garden*, *60*, 1–323.

Zuloaga, F. O., & Morrone, O. (1996b). Catálogo de las plantas vasculares de la República Argentina. *Monographs in Systematic Botany from the Missouri Botanical Garden*, *74*, 1–1269.

How to cite this article: Lipoma ML, Fortunato V, Enrico L, Díaz S. Where does the forest come back from? Soil and litter seed banks and the juvenile bank as sources of vegetation resilience in a semiarid Neotropical forest. *J Veg Sci*. 2019;00:1–11. https://doi.org/10.1111/jvs.12842