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Fire effects on the soil seed bank and post-fire resilience of a semi-arid shrubland in central Argentina

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Abstract Soil seed bank is an important source of resilience of plant communities who suffered disturbances. We analysed the effect of an intense fire in the soil seed bank of a semi-arid shrubland of Córdoba Argentina. We asked if the fire affected seed abundance, floristic and functional composition of the soil seed bank at two different layers (0–5 cm and 5–10 cm), and if fire could compromise the role of the soil seed bank as a source of resilience for the vegetation. We collected soil samples from a burned site and from a control site that had not burned. Samples were installed in a greenhouse under controlled conditions. During 12 months, we recorded all germinated seedlings. We compare soil seed bank with pre-fire vegetation in terms of floristic and functional composition. The high-intensity fire deeply affected the abundance of seeds in the soil, but it did not affect its floristic or functional composition. Floristic and functional composition of soil seed banks – at burned and unburned sites- differed markedly from that of the pre-fire vegetation, although a previous study at the same site indicated high resilience after fire of this plant community. Our results indicate that resilience of this system is not strongly dependent on direct germination from seeds buried in the soil. Other sources of resilience, like colonization from neighbouring vegetation patches and resprouting from underground organs appear to gain relevance after an intense fire.

Key words: Argentina, fire, plant functional types, propaguls colonization, resilience, shrubland, soil seed bank, underground meristems.

INTRODUCTION

Ecological resilience, defined here as the capacity of a system to return to its initial state after a perturbation (Holling 1973; Leps *et al.* 1982), depends on a number of ecosystem components or *sources of resilience*. Prominent among them is the soil seed bank (Thompson & Grime 1979; Leps *et al.* 1982; Garwood 1989; McDonald *et al.* 1996; Read *et al.* 2000; Augusto *et al.* 2001; Funes *et al.* 2001; Jankowska-Błaszczuk & Grubb 2006). Above-ground disturbances, such as fire, grazing or agriculture, can affect established vegetation, decreasing plant biomass, survival and seed production. In the long-term, this affects seed bank density and composition: species whose seeds are not replenished into the soil bank, either have other mechanisms to recover or could become increasingly likely to disappear from the community (Thompson & Grime 1979; Fenner & Thompson 2005; Vilá-Cabrera *et al.* 2008; Coop *et al.* 2010).

The effects of fire on soil seed banks have been extensively studied (Noble & Slatyer 1980; Keeley 1986; Segura *et al.* 1998; Odion & Davis 2000; Read *et al.* 2000; Auld & Denham 2006; de Andrade & Miranda 2014). It has been suggested, for example, that small-scale patterns of fire intensity and subsequent soil heating are determinants of spatial patterns of seed banks and seedling emergence after fire (Segura *et al.* 1998; Odion & Davis 2000). However, the vast majority of these studies deal with Mediterranean ecosystems where fire is considered an essential structuring force. The extent to which fires may deplete soil seed reserves in other ecosystems with shorter or less intense evolutionary history of fire is much less known (Auld & Denham 2006; Jaureguiberry & Díaz 2015).

After a fire, the regeneration of native vegetation depends on different mechanisms, such as resprouting from underground surviving organs (Noble & Slatyer 1980), germination of seeds that disperse into the burned areas (Bakker *et al.* 1996) or the survival of viable seeds in the soil seed bank (Rodrigo *et al.* 2012). Seeds of different species differ in their ability to respond to fire according to their distribution in the soil profile (Kwiatkowska-Falinska *et al.* 2014). Seeds that are buried in deeper soil layers should be less affected by fire because temperature sharply decreases with depth (Gill 1981; Bradstock & Auld 1995; Auld & Bradstock 1996; Ferrandis *et al.* 1999a,b; Williams *et al.* 2004; Auld & Denham 2006), although in some cases smoke, charred wood and/or nitrates can influence seeds′ germination at deep soil layers (Read *et al.* 2000). These seeds are expected to be an important component in the survival of plant populations after

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fire (Pake & Venable 1996; Facelli *et al.* 2005). Additionally, both taxonomic and functional identity of surviving seeds are critically important, because if species that recover after the fire share functional traits with species present before it, the normal functioning of the ecosystem can also recover. The existence of a similar proportion of different plant functional types (i.e. groups of plants that share similar functional traits, Diaz & Cabido 1997; Lavorel *et al.* 1997), in the soil seed bank and in the established vegetation, can therefore be a good predictor of the potential for re-establishment of the ecosystem properties after the disturbance, and therefore of resilience.

Fire is an important disturbance factor that affects semiarid Chaco forests in Argentina (Cabido & Zak 1999; Zak *et al.* 2004; Verzino *et al.* 2005; Renison *et al.* 2006; Giorgis *et al.* 2013). Although fire effects on Chaco forests have been studied before (Renison *et al.* 2002; Kunst *et al.* 2003; Gurvich *et al.* 2005; Bravo *et al.* 2010; Lipoma *et al.* 2016) there is no study analysing the relationship between fire effects on the soil seed bank and the resilience of plant communities in this system.

We assessed the effect of fire on the soil seed bank of a mountain shrubland in central Argentina, taking advantage of an accidental fire that occurred in 2009, when the established vegetation burned completely. Lipoma *et al.* (2016) studied the recovery of this vegetation after fire and asked whether different aspects of plant biodiversity had an effect on plant community resilience after the disturbance. While that study proved the importance of regeneration strategies in vegetation resilience, particularly that of dominant deciduous shrubs, it did not consider whether it recovered mainly by germination from the soil seed bank, resprouting from underground organs that survived the fire, or from the germination of seeds colonizing from neighbour sites that did not burned. By analysing soil seed banks from the burned site and from an adjacent unburned site, the present study answers these outstanding questions and thus provides further insight into the resilience of this plant community.

Specifically, we asked: (i) Does fire affect seed abundance and floristic composition of the soil seed bank? (ii) do these effects differ between the shallower (0–5 cm) and deeper (5–10 cm) soil layers? and (iii) can fire compromise the role of the soil seed bank as a source of resilience for the vegetation?

METHODOLOGY

Site description

The study was carried out in a mountain shrubland in Sierras de Córdoba (Argentina; 31° 30′ S, 64° 35′ W, 880 m a.s.l.). The historic mean annual rainfall is 720 mm (concentrated in the warm season) and annual mean temperature is 14.5°C (de Fina 1992). Soils are sandy, well-drained and shallow (Lithic Ustorthents Entisols) (Urcelay *et al.* 2009). Phytogeograpichally, this area belongs to the Mountain Chaco Forest (Cabrera 1976). The vegetation is dominated by the deciduous shrub *Acacia caven* (Fabaceae), the perennial forb *Cantinoa mutabilis* (Lamiaceae), the perennial C3 grass *Jarava ichu* (Poaceae), and the annual forb *Bidens pilosa* (Compositae). This type of vegetation, the most common in the Mountain Chaco Forest in Sierras de Córdoba, is the result of decades or perhaps centuries of logging, livestock grazing and fire (Cabido & Zak 1999; Zak *et al.* 2004).

The site was subjected to a long-term field removal experiment from 1998 until it burned in 2009. The experiment consisted in 10 different removal treatments where either a whole plant functional type or the most abundant species within a plant functional type were removed from the plot (see Urcelay *et al.* 2009 and Lipoma *et al.* 2016 for details). The removal treatments (described below) aimed to analyse the effect of the absence of a specific species or a complete plant functional type on ecosystem functioning, controlling the effects that removal per se could cause. Therefore, after 10 years of removal treatment, the absence by removal of a particular species or plant functional type was comparable with their true absence from the site. In this sense, if any difference were observed between burned plots subjected to removal treatments and unburned plots without the same species or plant functional type that was removed, it was more likely to be a consequence of the fire than that of the removal treatment carried out more than 10 years earlier.

In the winter of 2009, a widespread accidental fire burned the study site. This fire was of such intensity that homogeneously consumed all above-ground vegetation and carbonized the first centimetres of litter and soil in the experimental area (S. Díaz pers. comm. 2009).

Sampling

On April 2012, 3 years after the fire, 12 soil samples were collected in the burned site and 12 in the control unburned site (an adjacent shrubland of similar condition that did not burn). In the unburned site, six samples were taken from under shrubs and six from open space between shrubs. In the burned site, samples were obtained from two of the ten treatments developed during the removal experiment before the fire to compare with the unburned site. These treatments consisted of (i) the removal of all shrubs inside a 4 × 4 m plot without affecting other

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plants (comparable with samples taken from open space in unburned site); and (ii) no removal at all (comparable with samples taken from under shrubs in unburned site). Samples from each site were considered as replicates in order to account for the heterogeneity of the vegetation structure. Because this was an opportunistic study taking advantage of the unique combination between long-term experimental removals and an accidental event, there is no interspersion between the burned and unburned samples. The possible drawbacks from this were statistically controlled (see section on data analysis).

Samples were collected with a 5 cm-diameter bore, removing the litter layer present in the soil surface. Sampling was carried out immediately after the community had set seeds; therefore, the seed bank included elements of the transient and persistent seed bank (sensu Thompson & Grime 1979). In order to differentiate superficial and deeper seed banks, two soil depths were sampled: 0–5 and 5–10 cm.

Soil samples were sieved through 2 mm-mesh sieves to eliminate plant fragments and stones (Ter Heerdt *et al.* 1996; Funes *et al.* 2003) and then chilled in a refrigerator at low temperate for a month in order to break seed dormancy (Houle & Phillips 1988; Kaoru & Tilman 1996; McDonald *et al.* 1996). Samples were then spread over a 2 cm-thick layer of sterilized sand in 15 × 20 cm plastic trays. All trays were placed under control conditions in a greenhouse, at 27°C, and watered daily at field capacity. Eight additional trays containing sterilized soil were used to control for contamination from exogenous seeds.

Using the seedling emergence method (Thompson & Grime 1979), we estimated number and identity of the seeds present in the soil bank in each tray during 12 months. Whenever possible, seedlings were identified at an early stage and removed from trays. If flowers were needed for identification, seedlings were transplanted to separate pots within the same greenhouse. Although some degree of underestimation is to be expected, the germination rate with this methodology varies between the 80 and 100% of the viable seeds in the soil (Ter Heerdt *et al.* 1996) and is a well-established indirect method for assessing the functional significance of soil seed banks (Gross 1990; Pierce & Cowling 1991). In this sense, if seeds present in the soil are not able to germinate after the fire, because they are dead or absent or because they need different cues, they should not be able to re-establish the community immediately after the fire either. If a particular species needs a particular requirement (like coat scarification), we could also find that species germinating in the greenhouse if that requirement was fulfilled previously in the field, in that case that individual would be capable to grow and establish after the fire.

Nomenclature and species classification

Species (whose nomenclature follows Zuloaga (1994) and Zuloaga and Morrone (1996a,b,c)) were classified into four plants functional types following the classification proposed by Gurvich (2005) and Urcelay *et al.* (2009), namely deciduous shrubs, graminoids (including grasses and sedges), perennial forbs and annual forbs. This classification is based on the multivariate-based classification of (Diaz & Cabido 1997) and the general principles of Aerts and Chapin (2000), Grime (2001) and Díaz *et al.* (2004). These four plants functional types differ in key attributes related to stature, leaves, relative growth rate, longevity and reproduction. They represent a gradient from more acquisitive annual forbs, to more conservative deciduous shrubs, with graminoids and perennial forbs at intermediate positions, and they are expected to have different effects on ecosystem and community processes, as well as to respond differently to environmental factors (Diaz & Cabido 1997; Díaz *et al.* 2004).

Established vegetation

In order to answer the question about the potential role of the soil seed bank on the resilience of the plant community after the fire, both, the species composition and the proportion of each plant functional type in soil seed bank was compared with that of established vegetation. Plant functional type composition was used together with the analysis of similarity in species composition because we were interested in analysing the ability of the soil seed bank to provide individuals that sustain the function of the system after the fire. To this end, we took advantage of detailed vegetation surveys carried out in the burned site before the fire (Gurvich 2005; Lipoma *et al.* 2016), and compared them with burned and unburned soil seed banks (see Gurvich 2005 and Lipoma *et al.* 2016 for details). Since the fire was accidental, there was no information about the soil seed bank of this community before the event; the adjacent unburned site was thus selected to represent the ¨pre-fire¨ condition of the soil seed bank. Pre-fire census on established vegetation were developed in all experimental plots, but for the present study we only use data from treatments where soil samples were collected after fire (removal of all shrubs and no removal at all).

Data analysis

We compared abundance of seeds between burned and unburned sites using a Poisson Generalized Linear Mixed Model, with site (burned and unburned)

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and soil depth (0–5 and 5–10 cm) as main effects and site x depth as interaction term. To model the lack of independence of samples we included two random factors, ¨block¨, because of the clustered nature of burned and unburned samples, and "replicate" as each soil sample was divided into two different depths. *P* values for each factor were calculated trough a randomization of the response variable and the comparison of the ¨F¨ parameter obtained by the randomization and the ¨F¨ parameter obtained by the original model.

Changes in floristic composition between soils seed banks from burned and unburned sites and between them and established vegetation were analysed through the Sørensen Index (Sørensen 1948) based on presence and absence data.

We carried out a Detrended Correspondence Analyses (Hill & Gauch 1980) based on a Euclidean distance matrix of plant functional types X plots to visually analyse the distribution of plots in the space delimited by the proportion of the four plant functional types. Additionally, the proportion of each plant functional type in each site was analysed statistically through the development of a Generalized Linear Mixed Model for each plant functional type (annuals, forbs, graminoids and shrubs). The "compartment" (i.e. burned seed bank, unburned seed bank, or pre-fire established vegetation) was taken as a fixed factor and "block" as a random factor (to model the lack of independence of samples from burned seed bank and pre-fire vegetation plots). *P* values for each factor were calculated trough a randomization as explained above. Although the proportion of different plant functional types in the soil seed bank was calculated from abundance data and that in the established vegetation from cover data, we considered them comparable in terms of representation of each plant functional type in each compartment.

Statistical analysis were carried out in RStudio (Version 0.98.983 R Development Core Team 2011), with GLMMs and fitted by the function glmer and lmer of the package "lme4" (R core team 2015; Bates *et al.* 2014).

RESULTS

We identified 831 individual plants belonging to 48 species germinating from the seed banks (Appendix S1). Seedlings of 15 distinct species died before identification was possible, but they accounted for less than the 10% of all recorded seedling. These unidentified seedlings were only used for abundance analysis and were excluded from floristic composition analysis. The dominant plant family in both burned and unburned sites was Asteraceae, representing 40% of all individuals.

Fire effect on soil seed bank abundance and species composition

Fire strongly affected seed abundance in the soil. Mean seed number at the burned site (4.79 ± 0.89 seeds per sample) was c. 6 times lower than that at the unburned site (29.79 ± 6.08 seeds per sample). This trend was observed both at shallower (0–5 cm) and deeper (5–10 cm) soil layers (Fig. 1). No significant effect was detected in the case of depth or the interaction term (site x depth), indicating that the position of seeds in the soil profile did not prevent them from being affected. For that reason, we did not distinguish between soil layers in subsequent analysis.

The Sørensen Index showed a similarity of 55% between the floristic composition of seed banks from burned and unburned sites. The most abundant species present in the seed bank from the unburned site, (*Scoparia montevidensis, Galium richardium* and *Gamochaeta* sp.) were also present in the seed bank from the burned site, although with much lower abundance. The same happened with the most abundant species from the burned site (*Bidens subalternans* and *Oxalis conoriza*) (Appendix S1).

Floristic and functional composition in established vegetation and soil seed banks

We found low similarity between the floristic (species) composition of the established vegetation and those of the soil seed banks (17% similarity with burned and 25% with unburned sites, Sørensen Index). The functional composition (proportion of

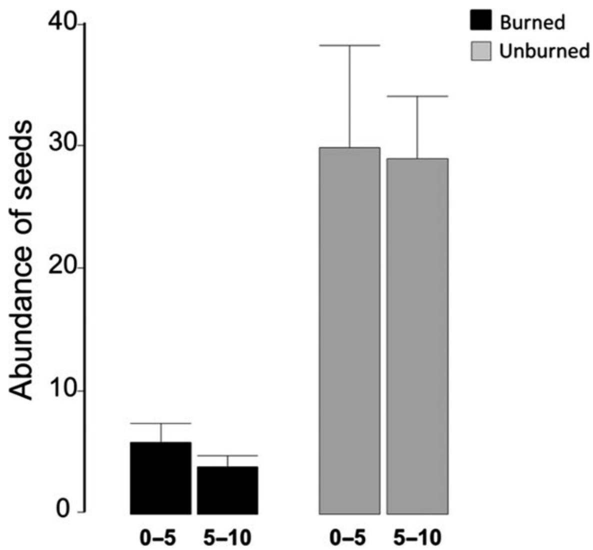

Fig. 1. Mean seed's abundance in the soil bank at the burned and unburned sites at two depths (0–5 and 5–10 cm). Error bars indicate SE.

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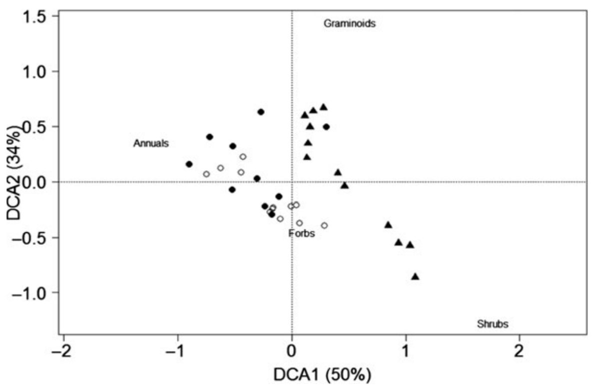

Fig. 2. DCA ordination of the proportion of the plant functional types X plots matrix. ● = soil seed bank from burned site, ○ = soil seed bank from unburned and ▲ = established vegetation before the fire.

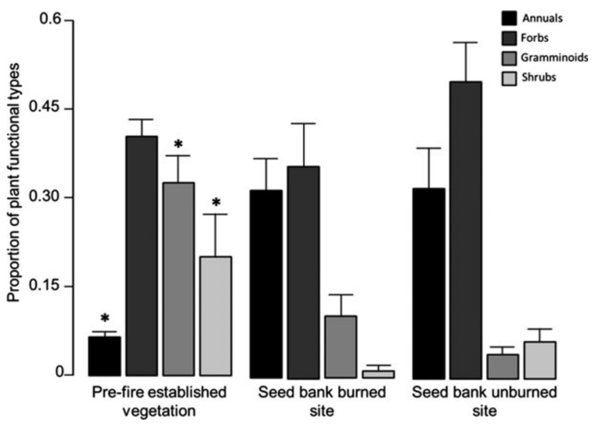

Fig. 3. Proportion of each plant functional type in the established vegetation before the fire, and in the soil seed bank (0–10 cm) at burned sites and unburned sites after the fire. Asterisk indicates significant difference ($P < 0.05$) between sites for each plant functional type; error bars indicate SE.

different plant functional types) in the soil seed banks and in the established vegetation showed similar patterns (Fig. 2): a clear differentiation was observed between the established vegetation, strongly associated to graminoids and shrubs, and the soil seed banks (both from burned and unburned sites), more associated with annuals. Forbs showed association with the three situations.

These trends were reinforced by the analysis of the proportion of each plant functional type in each compartment (Fig. 3). In comparison with the soil seed bank, established vegetation showed different proportions for three of the four plant functional types, while all plant functional types were similarly represented in soils seed banks from burned and unburned sites. Perennial forbs were the plant functional type best represented in all three compartments. Deciduous shrubs and graminoids showed a high proportion in the established vegetation, but they were not as well represented in the soil seed banks. In contrast, annuals were the least represented plant functional type in the established vegetation but it was very well-represented in the soil seed banks.

DISCUSSION

Seed number and species composition in soil seed bank

Three years after an intense fire event in a mountain shrubland in central Argentina, abundance of seeds present in the soil at the burned site was significantly lower than in a neighbouring, otherwise strongly similar, unburned site. Contrary with our initial expectations, this pattern was no different between soil depths (0–5 and 5–10 cm). Other studies have found similar decreases at burned sites (Pierce & Cowling 1991; Ferrandis *et al.* 1999a,b) in shallow soil but these effects are not reported for seeds buried relatively deep in the soil. The difference often found between soil layers is likely associated to the fact that soil temperature during wild fires in semiarid shrublands can reach nearly 700°C at the surface level depending on fire intensity and weather conditions (Beadle & Beadle 1940; Woodmansee & Wallach 1981; Rundel 1983; DeBano *et al.* 1991; Neary *et al.* 1999), but decreases sharply with soil depth (Miranda *et al.* 1993; Auld & Bradstock 1996; Scott *et al.* 2010). However, studies in ecosystems with high fuel accumulation, and fires occurring during the dry season (Beadle & Beadle 1940; Ferrandis *et al.* 1999a,b; Neary *et al.* 1999; DeBano 1991), as was our case, have reported temperatures of 150°C at 5–10 cm or deeper. Moreover, studies of exposure of seeds to different temperatures suggest a threshold between 120 and 130°C, beyond which seeds of different species do not seem to survive (e.g. Beadle & Beadle 1940 for deciduous shrubs; Martin *et al.* 1975 for legumes; Keeley & Keeley 1987 for monocots and perennial forbs; Overbeck *et al.* 2006; for forbs; Reyes & Trabaud 2009 for woody and herbaceous Mediterranean species; Jaureguiberry & Díaz 2015 for shrubs and graminoids of the Argentine Chaco; O'Loughlin *et al.* 2014; for various growth forms in Mediterranean Australia). Other studies have reported a non-destructive effect of fire on soil seed bank, although the majority of them were developed in fire prone ecosystem composed by species with germination cues related to fire exposure (Valbuena & Trabaud 2001; Scott & Morgan 2012; Santana *et al.* 2014) or have analysed the effect of prescribed

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fires with much less severity (de Andrade & Miranda 2014). Alternatively, there are studies that have reported a depletion of the soil seed bank after a fire not as a consequence of seeds mortality, but of the great germination of some seeds after the fire (Kunst *et al.* 2003; Auld & Denham 2006). In the case of our study, the effect of fire in above-ground conditions could have promoted indirectly the germination of seeds that survived, diminishing the abundance of seeds in soil after the fire. Nevertheless, the big difference between abundance of seeds from burned and unburned sites and the low cover of vegetation during the first growing season after fire (even though some plant functional types showed some degree of recovery, as reported by Lipoma *et al.* 2016) indicates that fire should have had an important effect diminishing the soil seed bank.

In the present study, high fire intensity and dry soil condition during the burning event, and the lack of any evident pre-adaptation to high temperature of species from this ecosystem, probably acted together to achieve soil temperatures that were high enough, even deeper than 5 cm, to seriously compromise seed survival.

Seeds buried deep in the soil are generally associated with persistent strategies in temperate mesic ecosystems, i.e. they persist for more than a year after dispersion (Thompson & Grime 1979; Simpson *et al.* 1989) and are considered to play an important role in vegetation resilience after severe above-ground disturbances, particularly those associated with agriculture (Pake & Venable 1996; Facelli *et al.* 2005; Hopfensperger 2007). The role of deeply buried seeds is less clear in drier, less intensively managed ecosystems (Funes *et al.* 1999). Whatever their role, our findings strongly suggest that high-intensity fires can seriously compromise them.

Despite the strong effect of fire on seed abundance, the species composition was relatively similar between the burned and unburned plots, as suggested by the Sørensen index. This similarity after fire between the soil banks of burned and unburned sites could be the result of two different processes: (i) the replenishment of the soil seed bank through recolonization by the same species after the fire; or, alternatively, (ii) the survival of some individuals of almost all species due to a non-selective effect of fire on the soil seed bank. Although seed rain from neighbouring vegetated patches can be an important source of resilience of the vegetation after disturbances (Noble & Slatyer 1980; Rodrigo *et al.* 2012; Davies *et al.* 2013), a full replenishment of the soil seed bank is a relatively slow and complex processes (Ferrandis *et al.* 1999a,b). Not all species that reach the soil are readily buried in deep layers. Very small, quasi-spherical seeds get buried relatively quickly, but burial is much more difficult for larger and more irregularly shaped seeds (Thompson & Grime 1979; Grime *et al.* 1997), which are common in the local flora (Funes *et al.* 1999). Therefore, and although colonization by new individuals from adjacent areas almost certainly played a role (see below) our results are more compatible with the idea of a non-selective effect of severe fire on the seed bank. In ecosystems with low selective pressure from fire, such as the one in this study, species show different tolerances to temperature, but in general, they do not increase germination or even survive at temperatures higher than 120°C (Jaureguiberry & Díaz 2015). Hence, this intense fire appears to have affected all species present in the soil, suggesting that the ones that were recorded after the fire were the few that survived it, representing a reduced version of the original bank.

Vegetation recovery and soil seed bank

The composition of soil seed banks -both burned and unburned- showed very little similarity with that of the established vegetation, either in terms of species or plant functional types. Deciduous shrubs and graminoids, which were abundant in the pre-fire established vegetation, were much less represented in the soil seed banks. Low similarity between seed bank and vegetation composition is common in mesic temperate and tropical woody ecosystems (Valbuena & Trabaud 2001; Hopfensperger 2007; Scott & Morgan 2012; Davies *et al.* 2013), but this relation is less clear for semiarid woody ecosystems with some degree of disturbance. The present study therefore suggests that the established vegetation of this semiarid shrubland cannot readily re-establish itself from the soil seed bank after a very intense fire.

Studying the established vegetation in the same system, Lipoma *et al.* (2016) found a very fast recovery of annuals, perennials and shrubs plant functional types, but not of graminoids after the fire. Our results suggest that the recovery of the above-ground vegetation one year after fire could not have been fully explained by the soil seed bank, as its abundance was severely reduced by the fire, and especially its floristic and functional composition was very different from that of the established vegetation. How then can the fast recovery of the vegetation observed by Lipoma *et al.* (2016) and these new results be interpreted jointly, and shed light on the overall resilience of this system? Together, these two studies reinforce the idea that regenerative strategies (sensu Grubb 1977) other than recruitment from the soil seed bank, are crucial in the process of recovery of this vegetation. Such strategies may include resprouting from surviving underground vegetative organs and the arrival and immediate germination of seeds from neighbouring unburned patches after the

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disturbance. Dominant woody species are known to be conspicuously absent in soil seed banks, instead, this plant functional type tends to recover through vegetative persistence and resprouting (Keeley 1991; Williams *et al.* 2004; Gurvich *et al.* 2005; Scott *et al.* 2010; de Andrade & Miranda 2014; O'Loughlin *et al.* 2014). This also seems to be the case of shrubs from this site that recovered almost exclusively from resprouting from surviving organs after the fire (Lipoma *et al.* 2016). On the other hand, seed rain from neighbouring vegetated patches may play an important role in established vegetation regeneration (although not in the replenishment of the soil seed bank) during the first few years after a fire (Russell-Smith & Setterfield 2006; Daïnou *et al.* 2011; Rodrigo *et al.* 2012). Graminoids, which were almost absent in the soil seed bank and did not show signals of resprouting after the fire, seem to depend exclusively on external colonization to recover, although this can take several seasons. Finally, annuals and perennial forbs could recover either from the soil seed bank or through external colonization, but the depletion of the soil seed bank after the fire suggests that these plant functional types depend heavily on external colonization after a severe fire. Although the re-establishment of these plant functional types often involves turnover in species composition (van der Maarel & Sykes 1993; Lipoma *et al.* 2016), it ensures the recovery of the general functional composition of the system.

Our findings together with previous analyses of the same site (Lipoma *et al.* 2016), suggest that both the survival of underground organs and the persistence of patches conserving different components of the original pool of species and plant functional types in the landscape, are key sources of resilience for these plant communities, as they are in other systems (Clements 1916; Bakker *et al.* 1996; Turner *et al.* 1998; Bond & Midgley 2001; Bengtsson *et al.* 2003; Plieninger *et al.* 2011).

CONCLUSION

The present study asked about the effect of fire on the soil seed bank and its implications for the resilience of the established vegetation in a mountain shrubland of Córdoba, Argentina. We found that high-intensity fire deeply affects the abundance of seeds in the soil bank, at both shallow and deep layers but it appears not to substantially affect its floristic or functional composition. We also found that the composition of soil seed banks –both burned and unburned- differs markedly from that of the established vegetation.

This indicates that the resilience of this system, expressed as recovery of the established vegetation after an intense fire, is not strongly dependent on direct germination from seeds buried in the soil. Other sources of resilience, like colonization from neighbouring vegetation patches and notably resprouting of dominants from underground organs appear to play a much more important role.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Complete list of species found in the soil seed bank.

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