

# Plant community resilience in the face of fire: experimental evidence from a semi-arid shrubland

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**Abstract** The ability of communities or ecosystems to recover their structure and function after a disturbance is known as resilience. According to different views, resilience can be influenced by the resource-use strategies of the plant functional types that dominate the community or by the existence of functional redundancy within plant functional types. We investigated how the dominance of different plant functional types and species affected the resilience of a mountain shrubland after an intense fire. We took advantage from a pre-existing long-term removal experiment in which either whole plant functional types (deciduous shrubs, graminoids, perennial forbs and annual forbs) or the dominant species within each plant functional type were removed for 10 years. We sampled species and plant functional types cover during the first growing season after the fire. First, to test whether functional redundancy increased resilience, we analyzed the existence of functional compensation inside plant functional types. Second, to test whether the dominance of plant functional types with different resource-use strategies affected recovery, we compared resilience at the levels of species, plant functional types and total cover, estimated on the basis of a change index and multivariate Euclidean distances. No compensation was observed in any of the plant functional types. At the level of species, we found that the assemblages dominated by conservative resource-use strategies were the ones showing higher resilience. This was due to the high recovery of the dominant species of shrubs plant functional type. The opposite (lowest recovery of conservative resource-use strategies) was found at the plant functional type and total cover-levels. Our study did not support the hypothesis of resilience by functional redundancy. Instead, regeneration by buried meristems from the pre-fire stage appeared to be the factor that most influenced recovery. Resource-use strategies explained resilience of vegetation cover, but not of floristic composition. Regeneration traits, rather than vegetative traits or mechanism of functional compensation, appeared as the most relevant to explain the response of this system after fire.

**Key words:** *Acacia caven*, Argentina, fire, functional redundancy, plant functional types, removal experiments, resilience, resource-use strategy.

## INTRODUCTION

The ways in which biological communities and ecosystems react to disturbances influence their dynamics, and thus the continuity of ecosystem processes and their derived social benefits (Pickett & Withe 1985; Grime 2001; Chapin *et al.* 2009). An essential component of ecosystem and community dynamics in the face of external drivers of change is resilience, or the capacity of a system to return to its initial state after a perturbation (Holling 1973; Leps *et al.* 1982). Resilience and resistance – the capacity of an ecosystem to avoid change in front of a perturbation (Leps *et al.* 1982) – are often seen as two different components of stability. The concept of resilience has become increasingly popular within the realms of both ecology (Leps *et al.* 1982; MacGillivray *et al.* 1995; Sankaran &

McNaughton 1999; Bellwood *et al.* 2006) and interdisciplinary science (Carpenter *et al.* 2001; Walker *et al.* 2002; Zell & Hubbart 2013). Studies quantitatively documenting it in the field, however, are much less common (e.g. MacGillivray *et al.* 1995; Sankaran & McNaughton 1999; Laliberté *et al.* 2010; López *et al.* 2013).

Resilience can be influenced by a number of community properties, which have been emphasized by different schools of thought. First, the existence of functional redundancy, that is, the presence in the community of different species showing the same effects on main ecosystem processes and, at the same time, different responses to a disturbance factor (response diversity, Walker *et al.* 1999; Díaz & Cabido 2001; Elmqvist *et al.* 2003) should enhance the capacity for recovery. In particular, a plant community can often be considered to be composed of different plant functional types (i.e. groups of plants that share similar traits, and therefore show similar responses to environmental constraints and/or similar effects on main ecosystem processes; Díaz & Cabido 1997; Lavorel *et al.* 1997). If each plant functional type consists of a single species, then there is no functional redundancy in the system, and the local

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extinction of the species automatically means the elimination of a whole plant functional type, with assumed consequences on ecosystem processes. The higher the number of species within each plant functional type, the higher the chances would be that at least one of them survives the perturbation, increases in abundance to compensate for the disappearance of the other members of the plant functional type and maintains the 'function' of the plant functional type (Walker 1995; Peterson *et al.* 1998; Walker *et al.* 1999; Díaz & Cabido 2001; Elmqvist *et al.* 2003; Suding *et al.* 2008). However, not all the species belonging to the same plant functional type have the same net influence on the rate at which ecosystem processes occur. Instead, it has been proposed that dominant species, because they represent most of the biomass and energy in the system, should be the main drivers of short-term ecosystem processes, and subordinate species should have an 'insurance effect', by replacing the dominant if it disappears (Grime 1998). This functional compensation within plant functional types is at the heart of the concept of increased resilience through functional redundancy (Walker *et al.* 1999; Gurvich 2005).

On the other hand, the resilience of a community depends on the functional attributes related to life history and resource allocation strategy (also syndrome) of the dominant plant functional types, irrespective of the number of species that compose each of them (Leps *et al.* 1982; Holling 1992; MacGillivray *et al.* 1995; Grime 2001). According to this line of thought, plants with acquisitive traits (rapid acquisition of resources, preferential allocation to assimilation and growth and to the early production of numerous small seeds) are easy to damage but recover fast, while plants with conservative traits (slow acquisition of resources, preferential allocation to storage and defence, slow growth and low allocation to sexual reproduction) tend to be more resistant to damage, but once damaged, they are slower to recover (Grime 1974; Chapin 1980; Reich *et al.* 1997; Díaz *et al.* 2004; Wright *et al.* 2004). Therefore, assemblages dominated by acquisitive trait syndromes should have faster post-disturbance recovery than those dominated by conservative trait syndromes. It follows that functional trait identity of the dominant plants is at the heart of the concept of increased resilience through the dominance of acquisitive plants. Resilience through functional compensation and resilience mediated by the functional attributes of the dominant plants are not mutually exclusive mechanisms. However, to our knowledge, they have never been tested empirically in the same system.

In this study, we asked whether the dominance of different plant functional types with contrasting resource-use syndromes, or the presence of functional redundancy within plant functional types, affected the resilience of the whole plant community in a mountain shrubland in

central Argentina. To this end, we took advantage of a long-term removal experiment (Urcelay *et al.* 2009) that was burnt to the ground by an accidental fire approximately 10 years after its establishment. By focusing on how different components of plant community diversity affect resilience after a fire, the present study represents an opportunistic approach to that unexpected event.

The original field experiment was established in late 1998 in which experimental manipulations consisted of the removal of individual species or whole plant functional types in a number of plots. Some treatments involved the elimination of the dominant species of each of four contrasting plant functional types (deciduous shrubs, graminoids, perennial forbs and annual forbs), leaving the subordinate species in the plant functional type untouched. Other treatments consisted in the removal of one of the four plant functional types. Further details are given in Methods. In 2009, an accidental fire affected the whole experimental area, destroying all the aboveground biomass across all the plots, and thus offering the possibility of investigating how plots that have been dominated by different plant functional types and species configurations during the previous 10 years recovered from a disturbance that affected them homogeneously. Although its local evolutionary history is debatable (Díaz *et al.* 1999; Jaureguiberry *et al.* 2012), fire has been a major structuring factor in central Argentina for well over a century (Cabido & Zak 1999).

Our hypotheses and predictions were based on the two general, not mutually exclusive, bodies of theory summarized earlier. On the one hand, according to functional redundancy theory, we expected that the absence of a dominant species from the vegetation would be compensated for by functionally similar species. Therefore, we predicted that the cover of plant functional types whose dominant species were removed but whose subordinate species were left intact before the fire (no dominant treatments) would recover faster; they, therefore, would be similar after the fire to the cover of the same plant functional type in the plots that suffered no removal (control treatments), but higher than that in experimental plots subjected to the removal of the whole plant functional type (no plant functional type treatments), where no compensation could be possible.

On the other hand, according to resource-use strategy theory, we expected that the post-fire recovery of the vegetation of different plots should be predictable from the functional characteristics of the plant functional types that dominated them before the fire, being faster in plots dominated by acquisitive plants. Thus, we predicted that experimental plots dominated by more acquisitive species before the fire should be more similar – both in terms of cover and floristic composition – to the pre-fire situation than those dominated by more

conservative species before the fire. Specifically, resilience, in terms of similarity to the pre-fire situation, should be maximum in the no shrub treatments, minimum in the no annual forb treatments and intermediate in the no graminoid and no perennial forb treatments.

## METHODS

### Study area

The study was carried out in a mountain shrubland in Sierras Grandes de Córdoba (Argentina) located at 31° 30' S, 64° 35' W, at an altitude of 880 m, with a historic mean annual rainfall of 720 mm (concentrated in the warm season) and an annual mean temperature of 14.5°C (de Fina 1992). Soils are sandy, well drained and shallow (Lithic Ustorthents Entisols) (Urcelay *et al.* 2009). Until 2009, the vegetation at the site was dominated by the deciduous leguminous shrub *Acacia caven* (Fabaceae), the perennial forb *Cantinoa mutabilis* (Lamiaceae), the perennial C3 grass *Jarava ichu* (Poaceae) and the annual forb *Bidens pilosa* (Asteraceae). This type of vegetation is the result of decades or perhaps centuries of logging, livestock grazing and fire and is the most common in the Mountain Chaco Forest in Sierras de Córdoba (Cabido & Zak 1999).

### History of the site and pre-fire removal treatments

In late 1998, a long-term field removal experiment was established in the study area (Gurvich 2005; Urcelay *et al.* 2009). It consisted of 60 16-m<sup>2</sup> plots within a fenced area of about 1 ha. The area was divided into six topographically-defined blocks, and 10 plots were established in each block. All plots had to share a similar vegetation physiognomy and contain species from four different plant functional types, namely deciduous shrubs, graminoids (including grasses and sedges), perennial forbs and annual forbs. Each of the plots within each block was randomly allocated one of 10 possible removal treatments,

involving either the removal of a whole plant functional type or the most abundant species within a plant functional type (Table 1). Plant removal involved mostly mechanical, and in some cases, carefully-applied chemical procedures (addition of TogarBT: Picloram 3%–Triclo-pir 6%; Dow AgroSciences, Buenos Aires, Argentina, see Urcelay *et al.* 2009 for details), and in all cases, special care was taken in eliminating the target plants with minimum disturbance of remaining plants and soil. After the establishment of the experiment, visits continued periodically to make sure that plots remained free of target species until the fire of 2009, although with time, visits were required with increasingly lower frequency. Chemical removal of deciduous shrubs continued until the last 5 years before the fire, when they were interrupted because, on careful periodical inspections, shrubs were no longer present in the aboveground vegetation of the no shrub or no *Acacia caven* plots (see Appendix S3 where the complete species list is shown).

### Definition of plant functional types

We followed the definition of four plant functional types proposed by Gurvich (2005) and Urcelay *et al.* (2009), which in turn, were based on the multivariate-based classification of Díaz and Cabido (1997) and the general principles of Aerts and Chapin (2000), Grime (2001) and Díaz *et al.* (2004). These plant functional types differ in key traits related to stature, leaves, growth rate, longevity and reproduction, and represent a gradient from more acquisitive annual herbs to more conservative deciduous shrubs, with graminoids and perennial forbs at intermediate positions, and are expected to have different effects on ecosystem and community processes (Díaz & Cabido 1997, Díaz *et al.* 2004).

### Fire disturbance and post-fire sampling

In 2009 winter, all the plots at the study site were homogeneously affected by an accidental fire that is common

**Table 1.** Removal treatments applied to 60 experimental plots in the mountains of Sierras Grandes de Córdoba, Argentina between 1999 and 2009. For more details, see Urcelay *et al.* (2009)

	Treatments	Species removed
C	undisturbed control	None; soil and vegetation remained undisturbed
DC	disturbed control	None; mild soil and vegetation disturbance was applied to simulate physical disruption involved in the removal of plants
NS	no shrub	All deciduous shrubs
NAc	no <i>Acacia caven</i>	<i>Acacia caven</i> (dominant deciduous shrub)
NG	no graminoid	All graminoids
NJi	no <i>Jarava ichu</i>	<i>Jarava ichu</i> (dominant graminoid)
NF	no perennial forb	All perennial forbs
NCm	no <i>Cantinoa mutabilis</i>	<i>Cantinoa mutabilis</i> (dominant perennial forb)
NAn	no annual forb	All annual forbs
NBp	no <i>Bidens pilosa</i>	<i>Bidens pilosa</i> (dominant annual forb)

in central Argentina. This fire was of such intensity and severity that it homogeneously destroyed all aboveground vegetation and carbonized the first centimetres of litter and soil in all the experimental plots (S. Díaz pers. comm. Appendix S1). We did not have the opportunity to measure fire or soil temperature given the unpredictability of the event. However, some days after the field burned, no living above vegetation remnants were observed, the stems of all the woody plants, the herbaceous layer and the first few centimetres of the soil were almost completely carbonized.

During the first growing season after the fire (6 months after the disturbance, December 2009–April 2010), we recorded the cover of every species in each of the 60 plots at 15-day intervals. The cover estimations were carried out using the same method utilized by Gurvich (2005) to allow maximum comparability with the pre-fire records of the same plots. They consisted of detailed observation of ground cover of every single vascular plant species in each plot and subsequent classification in 5% interval classes. To minimize subjectivity in cover estimations, the operators involved in the pre-fire sampling participated in the new sampling and calibrated their estimations with those of the new operator.

Although the patterns observed in these early stages of recovery cannot be considered as representative of all the successional sequence, they are essential for understanding the full, often non-linear, trajectory of ecosystems subjects to perturbations (Purdie & Slatyer 1976; Bond & Wilgen 1996; Lloret & Vilà 2003; Cramer *et al.* 2007).

## Data analysis

Given the variability due to the turnover of species during the growing season, values of cover corresponding to each plot on different dates during the season were consolidated into a single inventory per plot, where each species was allocated the maximum cover value achieved during that season. This value was used to define the response variables used for the different analysis, that is, species cover (cover value of each individual species), plant functional type cover (sum of the cover values of all species belonging to a specific plant functional type) and total cover (sum of the cover values of all species in the same plot). We did the same with the data collected by Gurvich (2005) in 2003, the last year in which a full inventory of all species in all plots was carried out before the fire, in order to compare pre-fire and post-fire variables in both analyses.

### *Assessing functional compensation*

In order to test for the existence of functional compensation within plant functional types, we compared the post-fire cover of each plant functional type in (i) the corresponding no plant functional type treatment (i.e. no shrub, no perennial forb, no graminoid or no annual forb), (ii) the corresponding no dominant species treatment (i.e. no *A. caven*, no *C. mutabilis*, no *J. ichu* and no *B. pilosa*); and (iii) the undisturbed control and disturbed control treatments. For this purpose, we developed a

two-way ANOVA with removal treatment and block as main effects. The interaction term (removal treatment \* block) was used as an error term because there was only one replicate per treatment per block. Differences among blocks, if present, were not considered in the results because they were not the focus of this study. Tuckey tests were applied *a posteriori* to locate the differences among treatment means. In those cases where the data did not meet the ANOVA assumptions, we ran Friedman non-parametric analyses (Sokal & Rohlf 1995).

We considered that there was functional compensation within a plant functional type when its post-fire cover was similar in the undisturbed control, disturbed control and no dominant species treatments, and at the same time, lower in the no plant functional type treatment. We assumed this was the result of subordinate species present in the no dominant treatment before fire increasing their cover after fire, and thus compensating for the absence of the removed dominant species belonging to the same plant functional type. Therefore, in order to assess whether plant functional type cover compensation was indeed due to subordinate species and not to the re-establishment of the removed dominant species, we also compared the proportional cover of subordinate and dominant species in the same no dominant and no plant functional type treatments in 2003 and 2010, using a Friedman non-parametric test.

### *Predicting resilience on the basis of resource-use strategies*

In order to assess the effect of the presence of different resource-use strategies on the resilience of the cover and floristic composition of the different plant assemblages, we carried out a two-way ANOVA and two detrended correspondence analyses (DCA; Hill & Gauch 1980, with PAST® software package; Hammer *et al.* 2001) on data obtained by the vegetation survey mentioned earlier, comparing control treatments and no plant functional type treatments only (36 pre-fire plots and 36 post-fire plots, excluding no dominants treatments from both seasons).

In order to analyze the response of the total cover (as an indicator of total vegetation biomass) to fire in different treatments, without considering floristic or plant functional type composition, we calculated a CI (change index) that quantifies how much the cover of each plot changed given the original cover value of the same plot before the fire.

$$\text{Change index (CI)} = (V_i - V_0)/(V_i + V_0)$$

where  $V_i$  is the value of the pre-fire cover, and  $V_0$  is the value of the post-fire cover. CI can take values between  $-1$  and  $1$  and indicates the variation of the cover after the fire with respect to the pre-fire cover.

We performed a two-way ANOVA on the basis of the CI values, with removal treatment and block as main effects and the interaction term as an error term.

We performed DCA at two different levels. The first DCA was at the level of species and was based on a 72 plots  $\times$  142 species matrix. The second DCA was at the level of plant

functional types and was based on a 72 plots  $\times$  4 plant functional type matrix. At species level, the identity of species in each plant functional type was a factor influencing the position of plots in the multidimensional plane, not so at plant functional type level, where only the plant functional type identity of the species mattered.

In both cases, each point on the ordination plane represented one plot either in 2003 or in 2010. The distance between plots in this plane was determined by both the taxonomic identity and the relative abundance of their species. Therefore, to measure the resilience of different treatments, we calculated a multivariate distance (Euclidean distance) between the two points corresponding to the same plot pre-fire and post-fire (Sankaran & McNaughton 1999, Brand & Jax 2007). We calculated Euclidean distance between two points  $P_{1_{2003}} = (p_{1_{2003} 1}, p_{1_{2003} 2}, \dots, p_{1_{2003} n})$  and  $P_{1_{2010}} = (p_{1_{2010} 1}, p_{1_{2010} 2}, \dots, p_{1_{2010} n})$  ( $P_{1_{2003}}$  representing plot 1 in the 2003 survey and  $P_{1_{2010}}$  representing plot 1 in the 2010 survey) located in the  $n$ -dimensional space ( $n$  corresponding to the species number or plant functional type number according to the level of analysis) as follows:

$$\begin{aligned} dE(P_{1_{2003}}, P_{1_{2010}}) = & \sqrt{(p_{1_{2003} 1} - p_{1_{2010} 1})^2} \\ & + (p_{1_{2003} 2} - p_{1_{2010} 2})^2 \\ & + \dots + (p_{1_{2003} n} - p_{1_{2010} n})^2. \end{aligned}$$

Resilience was then estimated as the inverse of the Euclidian distance between the position of a plot in 2003 and the same plot in 2010, determined by the cover and identity of species or plant functional type counted. To determine whether differences in Euclidian distances between treatments were statistically significant, we used a two-way ANOVA (at the species level), with removal treatment and block as main effects (the interaction term was used as an error term as explained earlier) and a non-parametric Friedman test (at the plant functional type level).

All statistical analyses were carried out with the INFOSTAT software package (Di Rienzo *et al.* 2012. InfoStat version 2012. InfoStat group, FCA, UNC, Argentina).

## RESULTS

### Species composition

Over the two sampling periods (2003 and 2010), we recorded a total of 142 vascular plant species belonging to 39 families, with 10 species corresponding to deciduous shrubs, 25 to graminoids, 29 to annuals forbs, 57 to perennial forbs and 21 to other minor groups (Appendixes S2, S3).

### Functional compensation

We found no evidence of functional compensation in any of the plant functional types analyzed (Fig. 1). With the exception of deciduous shrubs, differences in post-

fire total cover between controls, no dominant and no plant functional type treatments were not significant (Fig. 1a,b,c). The fact that the no dominant treatments did not differ significantly from the no plant functional type treatments suggests the existence of other mechanisms underpinning the recovery of the vegetation after fire, not necessary the compensation by subordinate species. Even though these mechanisms appear not to be the same, species within deciduous shrubs, annuals forbs and perennial forbs plant functional types and principally their dominants showed some ability to recolonize the area (Fig. 1b,c,d). Graminoids was the plant functional type that recovered the least after the fire (with a cover reaching 22% of the total area before the fire and only 8% after it; data not shown).

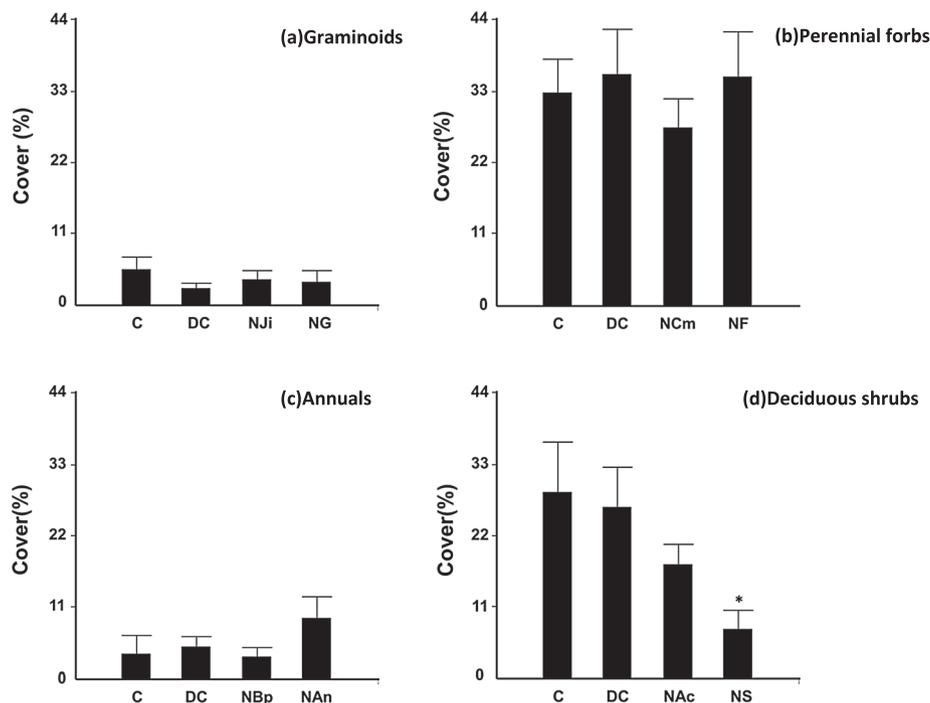
The fact that the post-fire cover reached by deciduous shrubs in the no *A. caven* treatment (Fig. 1d) did not differ from those of controls, and was significantly higher than that of the no shrub treatment, at first sight appeared consistent with the hypothesis of functional compensation. However, closer inspection of the proportion of cover represented by dominant and subordinate species (Table 2) revealed that this compensation was only apparent.

In the no *A. caven* treatment, we found that the proportion of subordinate species of deciduous shrubs did not differ significantly between 2003 and 2010 (Table 2). In contrast, the proportion of the dominant species of the plant functional type (*A. caven*) in the same plots significantly increased after the fire. This indicates that the apparent functional compensation of deciduous shrubs observed in the first analysis was actually due to the recovery of the dominant species in the plots from which it had been absent from the aboveground vegetation for years. This was due to resprouting from underground organs (indicated by the absence of cotyledons), presumably stimulated by the fire.

The same analysis for the no shrub treatment showed significant increase of proportion of cover for both subordinate and dominant species, also by resprouting. Therefore, the resprouting capacity of *A. caven* and the subordinate species appear to be the main cause of the remarkable recovery of this plant functional type after fire.

### Resource-use syndromes

To analyze the influence of resource-use syndromes in the vegetation resilience under the different treatments, we compared the vegetation cover and floristic composition of plots under each treatment before and after the fire. We expected differences in these variables to be smaller in a plot dominated by acquisitive plant functional types before the fire. In order to distinguish patterns at three different levels – total vegetation cover, species composition and plant functional types – we carried out three separate ANOVAs: one on the basis of CI



**Fig. 1.** Cover of different plant functional types in plots under different treatments (expressed as % of total ground cover by each species belonging to the same plant functional type) measured in the first growth period after fire. C: Control, DC: disturbed control, NJI: No *Jarava ichu*, NG: no graminoid, NHm: no *Hiptys mutabilis*, NF: no perennial forb, NBp: no *Bidens pilosa*, NAn: no annuals forb, NAc: no *Acacia caven* and NS: no shrub. Asterisk indicates differences significant at  $P < 0.05$ .

**Table 2.** Comparison of the proportion of the cover of *A. caven* and subordinated species belonging to the plant functional type deciduous shrubs in no shrub (NS) and no *A. caven* (NAc) treatments between 2003 (before fire) and 2010 (after fire)

Treatments	Proportion of cover of <i>Acacia caven</i>		Proportion of cover of subordinate species	
	2003	2010	2003	2010
NS	0	0.46*	0	0.54*
NAc	0	0.25*	1	0.75

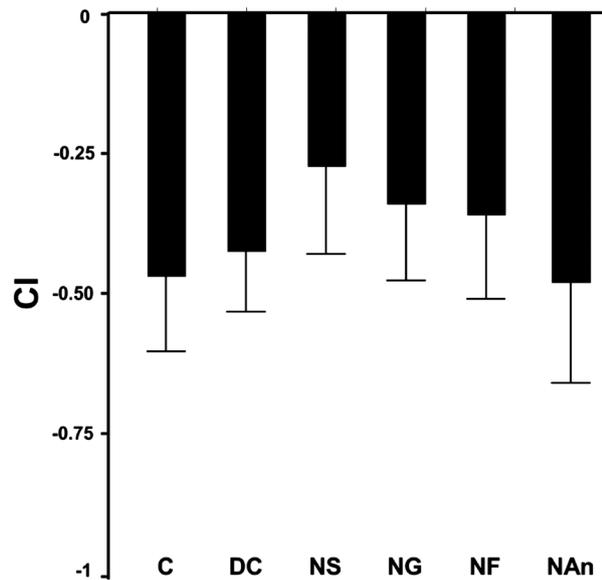
Asterisk indicates differences significant at  $P < 0.05$  between 2003 and 2010.

(total vegetation cover) and two on the basis of the Euclidean distances between two points representing the same plot before and after the fire. These Euclidean distances were in turn obtained from two separate DCAs, one based on the floristic composition and the other on the plant functional type composition (Appendixes S4, S5). We found no difference in CI or in post-fire resilience (measured as the inverse of the Euclidean distance in species and plant functional type levels) between any of the treatments. This was probably due to the great heterogeneity among replicate plots, which is a common feature of field experiments based on naturally-occurring communities (Díaz *et al.* 2003). However,

we found some clear trends, which differed between the three levels of analysis (Figs. 2 and 3).

Predictably, in all treatments, total vegetation cover in the growing season after the fire was lower than before it (as indicated by negative CI, Fig. 2). Although no significant difference was observed, the no shrub treatment (dominated by the more acquisitive plant functional types) showed the smallest change, while the no annual forb treatment (dominated by the more conservative plant functional types) showed the greatest change.

At the species level, DCA (Fig. 3a) revealed that plots dominated by more acquisitive species (no shrub and no graminoid treatment) showed the lowest resilience (largest Euclidean distance) between the pre-fire and post-fire situations. This was mostly due to the fact that many of the species that appeared after the fire were different from the ones that grew in the plots before it, although they showed similar resource-use strategy. This resulted in strong differences in species composition (high Euclidean distance) between the same plots before and after the fire. On the other hand, plots dominated by more conservative species (no annual forb treatment) showed the highest resilience (smallest Euclidean distance), mainly because there was very little change in the identity of the species present before and after the fire, with most of the recovery accounted for by the resprouting of shrubs.



**Fig. 2.** CI (change index) of vegetation cover between 2003 and 2010 (mean + SE) of different treatments: C: control, DC: disturbed control, NS: no shrub, NG: no graminoid, NF: no perennial forb and NAn: no annuals forb. See the text for CI values' explanation.

At the level of plant functional types, the trend was opposite to that at the level of species, but similar to the total vegetation cover analysis (Fig. 3b). Resilience of cover was highest in the no shrub treatment, where the great recovery of the annual forbs plant functional type as a whole resulted in small Euclidean distance between pre-fire and post-fire plots. On the other hand, resilience in the no annual forb treatment was the lowest, mostly because the most conservative plant functional type, deciduous shrubs, could not reach its pre-fire cover, despite the fact that most individuals resprouted (shrubs covered 80% of the ground surface in 2003 and only 30% in 2010 in some plots; data not shown).

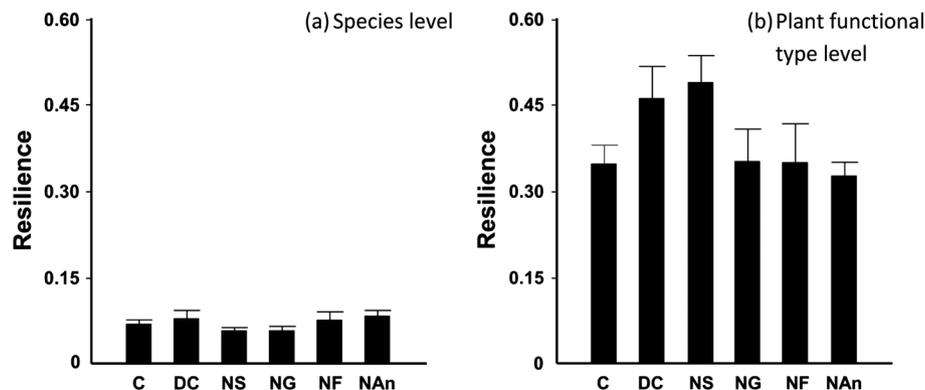
Plant assemblages under the no perennial forb treatment showed an intermediate pattern, appearing as more resilient than the no shrub and no graminoid treatments at the species level and less resilient at the plant functional type level (Fig. 3a,b, respectively), presumably because of the presence in these plots of the plant functional types with the most contrasting contributions to resilience, annual forbs and deciduous shrubs.

## DISCUSSION

### Functional compensation by members of the same plant functional type

Our results indicate that no functional compensation could be demonstrated in any of the plant functional types analyzed. That is, during the first year of recovery after the fire, the presence of subordinate species before the fire in each of the plant functional types did not improve the resilience of the plant community. Of all plant functional types, graminoids was the one that recovered the least. This result is very different from those found by other authors in similar systems, where this growth form is strongly promoted by fire (Anderies *et al.* 2002; Lloret & Vilà 2003; Kuenzi *et al.* 2008). Other studies have found that fire can be detrimental to grasses if frequency and intensity are very high (Boer & Staffor Smith 2003), making the recovery from seeds or meristems difficult, at least during the first years after the disturbance.

The rest of the plant functional types showed a high post-fire recovery, which is consistent with the results of other studies (Quintanilla Pérez & Castro Ríos 1998; Lloret & Vilà 2003 for annual and perennial forbs and Renison *et al.* 2002; Gurvich *et al.* 2005; Verzino *et al.* 2005 for deciduous shrubs). The fact that functional compensation was not observed is mainly the result of the important recovery of the dominant species of



**Fig. 3.** Post fire resilience measured as the inverse of the Euclidean distance (mean + SE) at (a) species level; and (b) Plant functional type level of different treatments: C: control, DC: disturbed control, NS: no shrub, NG: no graminoid, NF: no perennial forb and NAn: no annuals forb. Note that in figure a, small differences between treatments is the result of the small contribution of every single species in the position of each plot in the multidimensional space.

these groups (*C. mutabilis*, *B. pilosa* and *A. caven*) both in control plots and in plots where they were completely absent from the aboveground vegetation for years before the fire.

The comparison of proportion of cover of subordinate and dominant species of deciduous shrubs showed the high capacity of this plant functional type to recover after fire. Not only *A. caven* but other species – mainly *Aloysia gratissima* (Verbenaceae) and *Celtis ehrenbergiana* (Celtidaceae) – were detected in plots where they had been completely absent from the aboveground vegetation before the fire. We suspect that fire could have stimulated underground meristems that remained dormant during the entire time since the first removal treatments were applied. The high resprouting ability of the shrubs and especially of *A. caven* has been documented by several authors (Gurvich *et al.* 2005; Verzino *et al.* 2005; Jaureguiberry *et al.* 2012; Torres *et al.* 2013); however, there are few studies that have reported resprouting from underground roots (Kraus *et al.* 2003; Wright & Clarke 2007; Clarke *et al.* 2012), and we found none that documented regrowth from underground long-time dormant meristems for these species. Nevertheless, this recovery behaviour has been described for species of *Solidago* (Morrow & Olfelt 2003) where ‘phoenix’ clones of one individual plant appear aboveground after 2–10 years of being ‘dead’, from underground dormant buds that are activated when the aboveground bud is killed by clipping. In addition, Kraus *et al.* (2003) reported that *A. caven* has the capacity to develop underground adventitious buds when aboveground buds are killed, generating clones that can be easily misidentified as different individuals. In either situation (sudden belowground meristem activation after several years of absence from the aboveground vegetation or clonal regrowth of individuals growing outside the no-shrub plots burned during the fire), it was not functional compensation but the ability of dominant species to resprout from belowground what defined the recovery of aboveground shrub cover after the fire.

Other studies have also found no evidence of functional compensation in post-fire recovery. Kuenzi *et al.* (2008) found that communities whose biomass had been removed before a fire showed a cover response more related to the fire intensity than to the treatments themselves. The importance of past vegetation ‘memory’ or ‘legacy’ embodied in a persistent seed or meristem bank has been recognized since the early days of ecology (Clements 1916) and also by contemporary authors (Bakker *et al.* 1996; Bond & Midgley 2001; Pliening *et al.* 2011). In our case, both the intensity of disturbance (e.g. in the case of graminoids) and the existence of a ‘legacy’ (persistent meristem bank in the case of deciduous shrubs, especially *A. caven* and a seed bank in the case of forbs) appear as significant factors determining community resilience.

## Resilience and resource-use syndromes

At the level of individual species, our results contradicted the hypothesis that assemblages dominated by more acquisitive plants would recover faster than those dominated by more conservative plants. The assemblages under the no shrub treatment – with the most acquisitive remaining vegetation – showed the lowest resilience, whereas those under the no annual forb treatment – with the most conservative remaining vegetation – showed the highest resilience. The low resilience of the assemblages under the no shrub treatment was explained by the high species turnover of forbs, particularly annuals. This compositional change of annual forbs, although not representing a large change in cover or in resource-use strategy, involved 19 species, and thus could be explained by the colonization of different species that were present in the seed bank or in neighbouring areas. Maarel and Sykes (1993) described the species turnover of a species rich community as a ‘carousel model’ where the colonization of a site does not necessarily respond to niche differentiation but mostly to seed availability in the area. In contrast, the higher resilience shown by the no annual forb treatment was related to the little post-disturbance shift in species composition because of the remarkable recovery of the deciduous shrub species – especially *A. caven*, but also *A. gratissima* and *C. ehrenbergiana*. Vegetative reproduction has been repeatedly mentioned as an important mechanism of persistence of woody species in frequently disturbed sites (e.g. Noble & Slatyer 1980; García-Núñez & Azócar 2004; Gurvich *et al.* 2005; Torres *et al.* 2013). The opposite tendency was observed both at the total cover and plant functional type-levels, where the assemblages dominated by more acquisitive syndromes showed higher resilience than those dominated by more conservative ones, as predicted by resource-use strategy theory.

Together, these findings indicate that community resilience is influenced by aspects not initially included in our study, particularly life history characteristics of individual species. Resilience of vegetation cover was best explained by resource-use syndromes; acquisitive species quickly recovered their collective cover after disturbance likely because of their fast rates of resource acquisition, with the opposite being true for conservative species (Leps *et al.* 1982; MacGillivray *et al.* 1995; Díaz *et al.* 2004). Resilience of floristic composition, in contrast, was best explained by the regenerative strategies of particular species, which in this case were the high-resprouting capacities of the relatively conservative deciduous shrubs, in particular, *A. caven*. The importance of regeneration strategies in community responses to disturbance, as a relatively independent dimension from resource-use syndromes, was proposed by the regeneration niche model of Grubb (1977) and has been

repeatedly documented in the literature (Thompson *et al.* 1996; Symstad & Tilmund, 2001). Here, the resprouting of deciduous shrubs involves a regeneration strategy different from that dependent on the seed bank and can be analyzed in the context of the persistence niche proposed by Bond and Midgley (2001). Both the regeneration niche, in the form of regeneration from seeds, and the persistence niche, in the form of belowground meristems, are part of the legacy of this system, expressed in the recovery process 1 year after the fire.

Other studies have referred to the importance of the regeneration of the first months after disturbances by different mechanisms and mention that during the re-establishment of the mature vegetation, the majority of the species, which gain dominance, are present during the first few years after disturbance (Purdie & Slatyer 1976; Bond & Midgley 2001), supporting the idea of legacies of past vegetation as major factor of resilience.

## CONCLUSIONS

We analyzed the influence of different aspects of plant community composition on resilience at the first stages of post-fire recovery. We found no evidence of enhanced resilience because of functional compensation by members of the same plant functional type, and therefore rejected the hypothesis of functional redundancy as a source of resilience in this system. We found evidence of an impact of dominant resource-use syndromes on resilience of the total cover and that of plant functional types, but not on resilience of community floristic composition, providing partial support to community resilience being driven by resource-use syndrome of the dominant species. Regeneration strategies of individual species appeared as an important factor explaining resilience of these communities, in accordance to the regeneration and the persistence niche models, and highlighting the need to include these aspects as well as established-phase syndromes in resilience studies. It should be stressed once again that the patterns described here correspond only to the early stages of post-fire vegetation recovery. Although these are fundamental to understand the full shape of post-disturbance trends (MacGillivray *et al.* 1995; Lloret & Vilà 2003), they do not represent the full trajectory of recovery, which in shrublands, may take several years, even decades.

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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.** Pictures of the study site, Sierras Grandes, before and after the fire.

**Appendix S2.** Species, families, plant functional types (PFTs) and their average covers of each species per treatment in the first growing season after fire (2010).

**Appendix S3.** Species, families, plant functional types (PFTs) and their average covers of each species per treatment before fire (2003).

**Appendix S4.** DCA ordination of the species X treatments matrix.

**Appendix S5.** DCA ordination of the plant functional types X treatments matrix.