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RECONCILING RESILIENCE ACROSS ECOLOGICAL SYSTEMS, SPECIES AND SUBDISCIPLINES

Research Article

Low resilience at the early stages of recovery of the semi-arid Chaco forest—Evidence from a field experiment

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Abstract

1. Resilience—the capacity of an ecosystem to recover from disturbance—is a popular concept but quantitative empirical studies are still uncommon. This lack of empirical evidence is especially true for semi-arid ecosystems in the face of the combined and often confounding impacts of land use and climate changes.
2. We designed a methodology to disentangle vegetation responses to land-use exclusion and weather variability, and piloted it at the southern extreme of the Gran Chaco forest, the most extensive seasonally dry forest in South America. We established 16 pairs of neighbouring fenced and unfenced plots in four ecosystem types resulting from different long-term land-use regimes under the same climate and on highly similar soil parental material. From lower to higher land-use intensity, related with logging and livestock grazing and trampling, these types were: primary forest (no land use in the last 50 years), secondary forest, closed species-rich shrubland and open shrubland. In each plot we monitored plant species composition during the first 5 years following land-use exclusion, and evaluated the resilience as the rate of change of vegetation towards the primary forest, considered as the reference ecosystem.
3. We found that during the first 5 years of exclusion and despite the high rainfall, only grass cover in the secondary forest showed positive resilience (recovery towards the reference ecosystem). The rest of the variables in the other ecosystem types showed either no significant change (null resilience) or even transitioned away from the reference state (negative resilience).
4. *Synthesis*. The lack of detectable recovery after 5 years of exclusion suggests that (a) long-term land use, even at lower intensities, has affected the sources of resilience of this ecosystem; (b) rainy periods do not necessarily speed up recovery as suggested in the literature; and (c) study designs should incorporate the variation of the reference ecosystem in order to differentiate the effect of land use from other factors in a context of climate change. Although still confined to the early post-disturbance stages, our findings suggest that recovery of these systems may be slower and more complicated than predicted in the literature on the basis of space-for-time substitutions.

KEYWORDS

Argentina, Chaco, land-use change, passive restoration, resilience, seasonally dry forest

1 | INTRODUCTION

An essential component of ecosystem and community dynamics in the face of different drivers of change is resilience. Resilience has been defined in the literature as the capacity of a system to recover from disturbance (engineering resilience sensu Holling, 1996), and also as the capacity of a system to sustain its functioning in time despite facing some changes (ecological resilience, sensu Holling, 1973), although *engineering resilience* is the most commonly used when attempting to quantitatively evaluate resilience (Beisner, 2012). Resilience has become an increasingly popular concept in the past decades within the field of ecology (Bellwood et al., 2006; Isbell et al., 2015; Leps et al., 1982; Macgillivray & Grime, 1995; Sankaran & McNaughton, 1999; Wardle & Jonsson, 2014) and well beyond (Carpenter et al., 2001; Zell & Hubbart, 2013). Despite this growing interest, studies quantitatively documenting resilience in the field are still uncommon (e.g. López et al., 2013; Macgillivray & Grime, 1995; Sankaran & McNaughton, 1999). This lack of empirical evidence is especially true for arid and semi-arid woody ecosystems, where slow dynamics and high spatial heterogeneity make the study of temporal trends highly time-consuming, often exceeding the typical duration of research grants (Li et al., 2015; Lindenmayer et al., 2012; Meserve et al., 2003). Indeed, most existing studies in these systems are based on space-for-time substitution, that is, inferring the trajectory of deterioration and recovery on the basis of different situations that coexist in time (Pickett, 1989).

Ecosystem responses to disturbances are mediated by different community attributes or components that underpin the ecosystem's capacity to bounce back. Such 'sources of resilience' include for example the number of species (Tilman & Downing, 1994), functional composition (Leps et al., 1982; Lipoma et al., 2016; Macgillivray & Grime, 1995; Walker, 1992) and the existence of biological legacies such as persistent seed or seedling banks (Lipoma et al., 2019, 2020; Plieninger et al., 2011). The absence or the deterioration of one or more sources of resilience as a consequence of land-use change—one of the most important disturbance factors affecting ecosystems globally, (IPCC, 2019; IPBES, 2019) and particularly in arid and semi-arid ecosystems (Song et al. 2018)—can affect the capacity of ecosystems to recover after disturbance and maintain their functioning over time, or even push them to a different irreversible state (Folke et al., 2004).

Understanding how the resilience of ecosystems is affected by land use becomes particularly relevant in the context of adaptation to, and mitigation of climate change, where the safest and least costly path towards restoring forests, and thus sequestering carbon away from the atmosphere, is through passive natural regeneration, that is through 'harnessing' their natural resilience (Chazdon, 2003; Lewis et al., 2019).

In addition to land-use change, rainfall variability is another important driver of arid and semi-arid ecosystems (Holmgren et al., 2006). High-rainfall periods can trigger long-lasting shifts in vegetation, and thus have been presented as a window of opportunity for restoration (Anadon et al., 2014; Holmgren & Scheffer, 2001; Rietkerk et al., 1997). At the same time, they present a challenge for quantitative resilience evaluation because the response of the vegetation to land-use exclusion has to be disentangled from the responses to changes in rain conditions (de Bello et al., 2020; Ward et al., 2000).

The Gran Chaco forest—the most extensive seasonally dry forest in South America (Bucher, 1982)—has experienced significant land-use change throughout the 20th century and the beginning of the 21st century, with marked acceleration in the last few decades (Cabido et al., 1992; Fehlenberg et al., 2017; Hoyos et al., 2013). Although replacement of native ecosystems by industrial agriculture has been the predominant trend in the past three decades, slow but pervasive reconfiguration of native vegetation, as a consequence of logging, livestock farming and sometimes intentional burning, has been occurring for centuries, and continued without interruption to this day (Grau & Aide, 2008; Zak et al., 2008). Accordingly, the capacity to recover in the face of land use of the Gran Chaco, particularly in its drier extreme, has attracted interest for many decades and a considerable amount of work has been done on the basis of space-for-time substitutions (Adamoli et al., 1990; Cabido et al., 1992, 1994; Díaz et al., 1992; Morello, 1995; Morello & Adamoli, 1974). One key assumption of such studies is that vegetation at different stages of transformation in the Chaco forest, if released from disturbance, should be able to revert to the reference primary forest (shows engineering resilience), except in those cases where the topsoil layer has been lost.

In order to test this assumption directly, we established a network of exclosures in the field, on ecosystem types resulting from different long-term intensities of biomass removal caused by a combination of logging and livestock grazing and trampling, which represent the predominant land uses in the area during the past 5–10 decades. Even though all ecosystem types had suffered from different intensities of land use, they are initially derived from the same primary vegetation on similar substrate and under the same climate (Conti & Díaz, 2013). In this scenario we asked the following questions:

1. How do different intensities of land use affect the resilience of the semi-arid Chaco forest at the early stages of recovery?
2. Can the recovery of this ecosystem in response to land-use exclusion be distinguished from its natural response to rain variability?

We tested our empirical findings against the conceptual model of Figure 1. According to our model, different ecosystem types can show a trajectory towards the reference ecosystem that will depend on their distance from the latter (a consequence of the intensity of disturbance to which they were subjected) and also on the

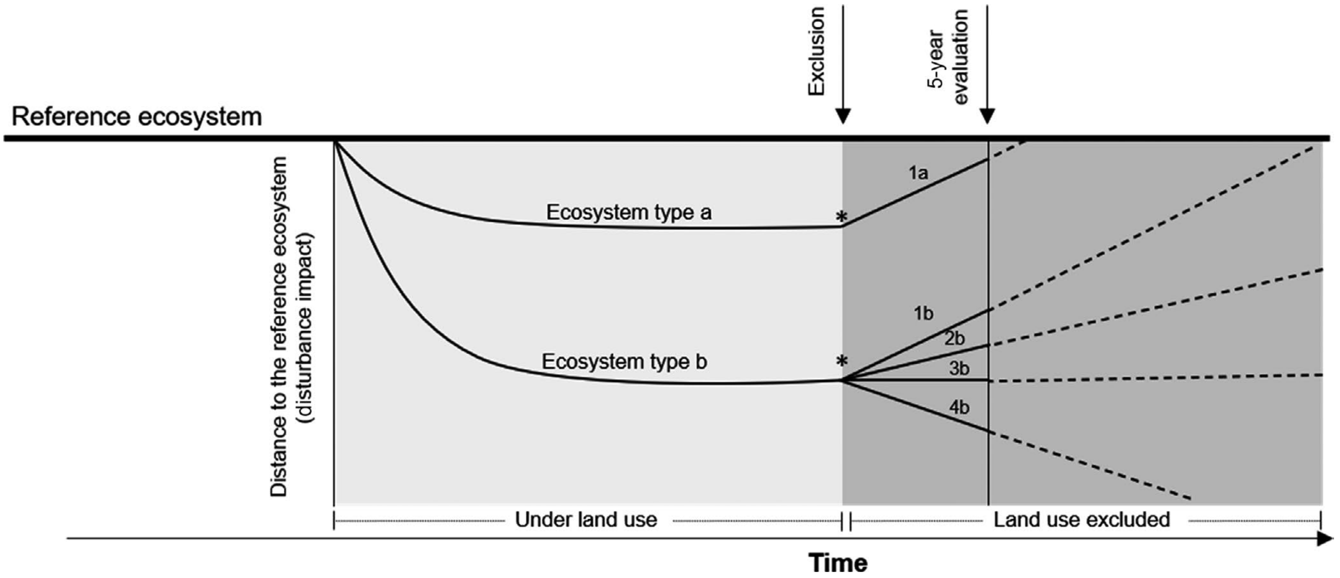


FIGURE 1 Resilience evaluation of the Chaco forest ecosystem. The trajectory of different ecosystem types is represented with grey lines that are vertically more distant to the reference ecosystem as disturbance intensity increases (only two ecosystem types are represented for simplicity). After land-use exclusion, these ecosystem types start their trajectory from different 'starting points' (*) and are expected to show resilience (*rate* of recovery towards the reference ecosystem) that will depend on how the different disturbances have affected the sources of resilience. If such sources of resilience have been affected to a similar degree, then the resilience of different ecosystem types should be similar (lines 1a and 1b), although ecosystem type b will take longer time to reach identity with the reference ecosystem, simply because it was pushed further from the reference ecosystem than ecosystem a. If, in contrast, the sources of resilience were affected differently by different land-use intensities, the two types will recover with different rates (lines 1a and 2b). If the sources of resilience were heavily affected and/or were overridden by other factors (e.g. climate), then there can be null resilience (line 3b) or a trajectory away from the reference ecosystem (line 4b). Note that the assessment presented in this work, done 5 years after the exclusion, informs about the rate of recovery (the slope of the curve during early succession) and not about the time required for each community to fully recover. Additionally, the trajectories of different ecosystem types were represented with straight lines to be consistent with the fact that a longer period of monitoring would be needed to model a different line shape, including hysteresis

preservation of their sources of resilience. If, independently of their distance from the reference ecosystem, different ecosystem types preserve their sources of resilience, they are expected to show similar resilience (a similar rate of change towards the reference ecosystem), although the absolute time needed for recovery will be longer for those that started their trajectory from a more distant point. Nevertheless, if the disturbance had significantly affected the sources of resilience, highly disturbed ecosystem types are expected to show slower or null recovery, or even a trajectory in a different direction.

2 | MATERIALS AND METHODS

2.1 | Study system and experimental set-up

The study was carried out at the southernmost and driest extreme of the Gran Chaco, in Chancani, 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 primary vegetation has been described by Cabido et al. (1992, 1994, 2018) as an open xerophytic forest with *Aspidosperma quebracho-blanco* as the canopy dominant and *Prosopis flexuosa* as the sub-canopy dominant. The shrub layer is dominated by *Mimozyganthus carinatus*, *Senegalia gilliesii*, *Celtis pallida* and *Larrea divaricata*. The herbaceous layer is dominated by *Deinacanthon urbanianum*, *Gouinia paraguayensis*, *Leptochloa pluriflora* and *Justicia squarrosa*. However, this vegetation, formerly fairly continuous, now occupies a very small proportion of the landscape, which is dominated by a rich mosaic of ecosystem types originally corresponding to the same ecosystem, and developed under the same climate, topography and on highly similar soil parental material, but now differentiated as a result of different combinations of historic and present livestock grazing and logging regimes (Cabido et al., 1994; Conti & Díaz, 2013; Zak et al., 2008). We selected four ecosystem types representative of this mosaic. The ecosystem types were as follows: (a) primary forest, with no significant logging or livestock grazing at least in the past seven decades and located at a State protected area; (b) secondary forest, with light selective logging and low cattle and goat stocking rates; (c) closed species-rich shrubland, with logging and cattle and goat stocking rates moderate at present, but historically (>2 decades) heavy; and lastly (d) open shrubland, strongly dominated by *L. divaricata*, and historically characterized by heavy logging and high cattle and goat stocking rates. There were no records or physical signs of fire, ploughing or application of soil fertilizer in any of the plots during the past few decades, and on the basis of historical sources, they were unlikely to have been tilled or cleared during at least the past 150 years.

For each ecosystem type we selected four sites (replicates). Sites were located at a distance of at least 1 km apart, and as interspersed as possible, in order to maximize independence.

In each of these 16 sites, we delimited a set of paired plots: a fenced plot of 36 m^2 to exclude disturbances related to logging and livestock grazing and trampling, and a neighbouring unfenced plot of the same size with a vegetation composition as similar as possible, which was considered the 'local control plot', in order to distinguish the response of the vegetation to land use from its response to other factors affecting the two plots, mainly variations in precipitation. During 6 years we carried out complete vegetation surveys in fenced and unfenced plots during each growing season.

Climatic variables during the study period showed an increase in precipitation above the historic mean recorded for the area, which corresponded with an ENSO event (National Meteorological Service; Supporting Information Appendix 1). Specifically, the season 2015–2016 showed the highest precipitation during the study (955.4 mm compared with an historic mean of 642.1 mm). Additionally, temperature during the study period did not differed from historic mean.

2.2 | Vegetation sampling

The analysis of resilience of the Chaco forest was performed through the evaluation of community properties related with plant diversity or vegetation structure because there is a large amount of evidence that plants play a key role in driving the rate and magnitude of most ecosystem processes (Díaz et al., 2004; Grime, 2006) and nature contributions to people (IPCC, 2019).

During each growing season between 2014 and 2019, we carried out two full plant species composition surveys in each of the plots (December and April), in order to maximize the chances to find both early- and late-season species, particularly in the herbaceous layer. We quantified the abundance of each woody or herbaceous species by estimating their cover inside a 16 m^2 area within each 36 m^2 fenced plot to avoid edge effects. The same estimation was carried out on the same day in the neighbouring unfenced plot. Cover was estimated at 5% intervals, following Cabido et al., (1993) and Díaz et al., (1998). Cover of each species was recorded as % cover. Therefore, total vegetation cover, including herbaceous and woody layers, could exceed 100% due to the overlapping canopies. Cover values were preferred over counts of adult individuals because they better represent how dominance is distributed between individuals of very different sizes (herbs vs. trees), and also because in many cases is difficult to tell individuals of the same species apart.

Given the variability due to the phenology of species during the growing season, especially in the case of herbs, values of cover corresponding to each plot on different dates during the same season were consolidated into a single inventory per plot, where each species was allocated the maximum cover value achieved during that season. Additionally, we calculated the aggregated cover of woody and grass growth forms, by pulling together the cover values of all species belonging to each of them (see Supporting Information Appendix 2 for floristic composition details).

2.3 | Data analysis

2.3.1 | Resilience measurements

To assess resilience we analysed the change in floristic composition and aggregate cover of different growth forms between each ecosystem type and the reference ecosystem (primary forest; Equation 1). We used the Sørensen (1948) and Bray and Curtis (1957) multidimensional dissimilarity indices to evaluate the change in floristic composition. To evaluate the change in the dominant growth forms, we used the difference in the aggregate cover of woody and grass species (Table 1). We always carried out comparisons between fenced plots and between unfenced plots in order to not incorporate possible side effects of fencing (e.g. involuntary exclusion of wild mammals, the use of poles as perches by birds that might disperse the seeds of particular plants) when estimating the change in unfenced plots. The value used for the reference ecosystem corresponded to a mean of the four replicates of the primary forest, one mean for the four fenced plots and another mean for the four unfenced plots. For example, to get the Sørensen or Bray–Curtis Index value of the fenced plot at a given site and at the reference ecosystem, we calculated first the distance of this specific site with each of the four fenced replicates of the primary forest and then we calculated the mean value of these distances. On the other hand, to get the difference in aggregated cover of grass or woody species with the fenced plot of the reference ecosystem, we calculated a mean of that cover for the four fenced replicates of the primary forest and then we calculated the difference with that mean for the fenced plot of each site. In Table 1 we present a detail of all variables that were analysed for each ecosystem type.

We quantified resilience of a given ecosystem type (i) at time (t) as.

$$\text{Resilience}(i,\,t) = \frac{(\textit{fenced plot change}(i,\,t) - \textit{unfenced plot change}(i,\,t))}{2}, \tag{1}$$

where *fenced plot change*(i,t) represents how much the vegetation of a given ecosystem type i changed after t years of exclusion with respect to the fenced primary forest (Equation 2), whereas *unfenced plot change*(i,t) represents the same change outside the exclosure (Equation 3) (Table 1).

$$\textit{Fenced plot change}(i,\,t) = \frac{\left|FeDi\,(i,\,t_n)\right| - \left|FeDi\,(i,\,t_0)\right|}{\left|FeDi\,(i,\,t_n)\right| + \left|FeDi\,(i,\,t_0)\right|} \times (-1), \tag{2}$$

TABLE 1 Variables used in the resilience analysis of the Chaco forest

Variable	Description	Notation
Vegetation composition variables		
Sørensen distance	Multivariate distance in species presence/absence between a given ecosystem type and the reference ecosystem	—
Bray–Curtis distance	Multivariate distance in species presence and their relative abundances between a given ecosystem type and the reference ecosystem	—
Difference in growth-form cover	Difference in the cover of a specific growth form (grass or woody) between a given ecosystem type and the reference ecosystem	—
State variables	Variables describing a given ecosystem type *i* at a specific time *t*.	
Vegetation composition at the 'starting point' at the fenced plot	The difference between the fenced plot of the reference ecosystem and the fenced plot of a given ecosystem type *i* at the beginning of the study (t_0)	$FeDi_{(i,t0)}$
Vegetation composition at the 'starting point' at the unfenced plot	The difference between the unfenced plot of the reference ecosystem and the unfenced plot of a given ecosystem type *i* at the beginning of the study (t_0)	$UnDi_{(i,t0)}$
Vegetation composition at time *n* at the fenced plot	The difference between the fenced plot of the reference ecosystem and the fenced plot of a given ecosystem type *i* at time *n* (t_n) after the exclusion	$FeDi_{(i,tn)}$
Vegetation composition at time *n* at the unfenced plot	The difference between the unfenced plot of the reference ecosystem and the unfenced plot of a given ecosystem type *i* at time *n* (t_n) after the exclusion	$UnDi_{(i,tn)}$
Change variables	Variables that denote change with time after exclusion between a given ecosystem type *i* and the reference ecosystem	
Fenced plot change(*i,t*)	Shows how much the fenced plot of a given ecosystem type *i* changed after exclusion (*t*) with reference to the primary forest	
Unfenced plot change(*i,t*)	Shows how much the unfenced plot of a given ecosystem type *i* changed after exclusion (*t*) with reference to the primary forest	
Resilience(*i,t*)	Shows how much a given ecosystem type *i* recovered the vegetation composition of the reference ecosystem after exclusion (*t*)	

Note: The difference in vegetation composition between a given ecosystem type and the reference ecosystem was evaluated in terms of species presence (Sørensen distance), species presence and relative abundance (the Bray–Curtis distance) and aggregate cover of woody or grass growth forms. The value used for the reference ecosystem corresponded to a mean of the values of the four replicates of the primary forest, one mean for the fenced plots of the primary forest and another mean for the unfenced plots of the primary forest.

$$\mathit{Unfenced\ plot\ change}(i,t) = \frac{\left|UnDi\,(i,t_n)\right| - \left|UnDi\,(i,t_0)\right|}{\left|UnDi\,(i,t_n)\right| + \left|UnDi\,(i,t_0)\right|} \times (-1), \quad (3)$$

Where *FeDi (i,t)* is.

$$FeDi(i,t) = \left|\mathit{fenced\ plot}(i,t_n) - \mathit{reference\ fenced\ plot}(t_n)\right|, \quad (4)$$

the absolute difference in the vegetation variable between the fenced plot of a given ecosystem type *i* and the fenced plot of the reference ecosystem (calculated as the Sørensen or Bray–Curtis Indexes or as the difference in the aggregated cover) at the beginning of the study (t_0) or at time *n* (t_n) during the study.

Following the same rationale, *UnDi* (*i,t*) is the corresponding value for the unfenced plot, that is, under disturbances related to land use.

$$UnDi(i,t) = \left|\mathit{unfenced\ plot}(i,t_n) - \mathit{reference\ unfenced\ plot}(t_n)\right|. \quad (5)$$

FeDi (i,t_0) and *UnDi* (i,t_0) represent the starting point from which ecosystem types will respond after excluding land use. This starting point also indicates the impact of the difference intensities of land use on the vegetation. The values of fenced plot change and unfenced plot

BOX 1 Different categories of resilience as a result of the combination of the fenced and unfenced plot change indexes of a given ecosystem type. At the left side of the image the alternative changes of fenced and unfenced plots are illustrated. The initial distance between the fenced plot change of a given ecosystem type (filled blue circles) an that of the reference ecosystem (filled green circles) can show alternative changes from not changing at all, be reduced because the fenced plot of the ecosystem type approaches the primary forest, because the fenced plot of the primary forest approaches that of the ecosystem types or because both of them approach each other. The same alternative changes can be performed by the unfenced plot of a given ecosystem type (open blue circles) an that of the primary forest (open green circles). At the right side of the image the different categories of resilience are illustrated. Null resilience corresponds with the identity line. "Towards to PF" and "Away from PF" refer to the reference ecosystem (primary forest). Numbers are plotted in illustrative positions. This qualitative classification of resilience is adapted from Ingrisch and Bahn (2018). See the text for details

Positive resilience

The ecosystem type recovered because:

(i) the fenced plot moved towards the reference ecosystem and the unfenced plot did not change,
(ii) the fenced plot moved towards the reference ecosystem and the unfenced plot moved away,
(iii) both plots moved towards the reference ecosystem but the fenced plot got closer,
(iv) the unfenced plot moved away from the reference ecosystem and the fenced plot did not change, or
(v) because both plots moved away from the reference ecosystem but the unfenced plot got further.

Null resilience

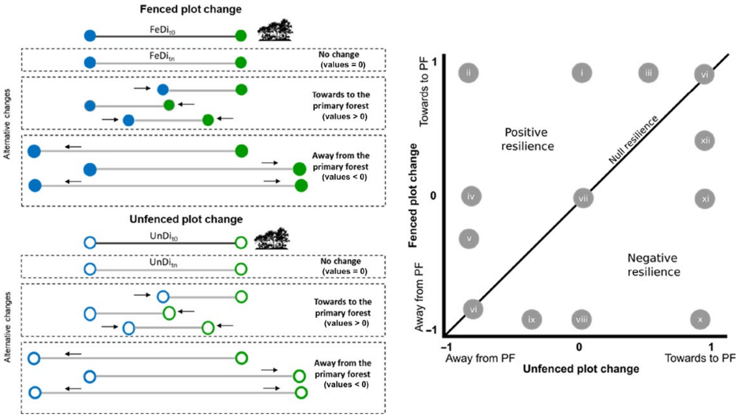
The ecosystem type did not recover because:

(i) both plots changed to a similar degree,in the same directions, cancelling each other, or
(ii) the fenced and unfenced plots did not change after exclusion.

Negative resilience

The ecosystem type became even more different because:

(i) the fenced plot moved away from the reference ecosystem and the unfenced plot did not change,
(ii) both plots moved away from the reference ecosystem but the fenced plot got further,
(iii) the fenced plot moved away from the reference ecosystem and the unfenced plot moved towards,
(iv) the unfenced plot moved towards and the fenced plot did not change, or finally,
(v) both plots moved towards the reference ecosystem but the unfenced plot got closer



Green circles represent the reference ecosystem (primary forest) and blue circles represent a given ecosystem type. Filled circles represent fenced plots and open circles represent unfenced plots. FeDit$_0$: The initial difference between the fenced plot of the reference ecosystem and the fenced plot of a given ecosystem type (black line), FeDit$_0$: the same difference 5 years after fencing (grey lines). UnDit$_0$: The initial difference between the unfenced plot of the reference ecosystem and the unfenced plot of a given ecosystem type (black line), UnDit$_0$: the same difference after five years (grey lines). Arrows indicate the direction of the change displayed by plots.

change vary between −1 and 1. Values >0 indicate a trajectory of plots towards the primary forest, with 1 indicating identical vegetation composition between the two plots. On the other hand, values <0 indicate that, after exclusion, the plots diverged from the primary forest vegetation, with values asymptotically approaching −1 indicating increasing divergence. Values indicating a trajectory towards or away from the forest can also be the result of a change of that particular variable in the primary forest, as the reference ecosystem can also show natural variation to changing conditions (Box1). We identified those cases and referred to them in the discussion section.

While in the unfenced plots the trajectory observed is attributable only to the 'climate effect' (changes mainly related with variations in precipitation, temperature, a combination of both or any external factor that affects the fenced and unfenced plots equally), the trajectory in the fenced plots is attributable to the combination of two effects, the 'climate effect' and the 'fencing effect' (changes related to the exclusion of land use). Therefore, we considered the difference between the changes observed in the fenced plot and those observed in the paired unfenced plot at the same sampling site, as the change induced by the release from land use. Therefore, this difference, defined as resilience in this paper, indicates how much the plant community composition of each ecosystem type recovered towards the reference ecosystem, irrespective of any change due to other factors (notably climate) that might be affecting both fenced and unfenced plots.

Resilience is, according to Equation 1, dimensionless and its value is bounded between 1 and −1, as a result of the values of fenced and unfenced plot change indexes, with values higher than 0 indicating **positive resilience**, lower than 0 indicating **negative resilience** and values of 0 indicating **null resilience** (Box 1).

2.3.2 | Model structure

We used linear mixed models (LMMs) to evaluate the effect of different intensities of land use (independent variable; low in the secondary forest, intermediate in the closed shrubland and high in the open shrubland) on the vegetation composition of the semi-arid Chaco forest (using the Sørensen Index, Bray–Curtis Index and the difference in aggregate cover of grasses and woody plants as response variables). The first sampling date (t_0) was considered the 'Starting point' value of a given variable for each ecosystem type. For this model, both fenced and unfenced plots at a given site were considered sub-replicates, as the exclosure was assumed to have no effect at t_0. A random factor was included to model the lack of independence between the two sub-replicates of each site. Models were analysed to meet the assumptions of normal distribution and homogeneous variance. In the cases of lack of homogeneous variance, we included a variance correction function in the model (varPower, varExp, varIdent or a combination of them). We used the Akaike Information Criterion (AIC) to evaluate the model fit (Burnham & Anderson, 2004; Johnson & Omland, 2004). Then, we used the Di Rienzo a-posteriori test (Di Rienzo & Romero, 2010) to analyse differences between ecosystem types.

A visual evaluation was performed to analyse the variations of the different vegetation composition variables of both fenced and unfenced plots from each ecosystem type, along all the years where the study was developed.

Resilience of each variable was evaluated for the different ecosystem types (secondary forest, closed shrubland and open shrubland) through a Linear Model where the intercept was removed in order to assess if the resilience value was different from zero. Models were analysed to meet the assumptions of normal distribution and homogeneous variance and, if needed, corrections were implemented as for the previous model. The components of resilience (fenced plot change and unfenced plot change) were evaluated in order to identify the 'resilience category' (positive, null, negative, see Box 1) for each case.

Analyses were carried out in R (version 3.3.1, R Core Team, 2015). Models were developed using the 'lm', 'lme' and 'gls' functions from the NLME package (Pinheiro et al., 2020).

3 | RESULTS

3.1 | How is land use affecting plant communities in the Chaco forest?

Disturbances related to land use affected the vegetation composition of the Chaco forest ecosystem (Figure 2; Table S3; Figure S4). At the starting point (t_0), ecosystem types differed in their similarity to the reference ecosystem (primary forest) in terms of both the species present and their relative abundances (Figure 2a,b) and the aggregate grass and woody cover (Figure 2c,d). See Supporting Information Appendix 2 for a complete list of species.

After 5 years of exclusion, vegetation composition variables of fenced and unfenced plots within each ecosystem type showed different trajectories (Figure 3; Figure S5). Fenced and unfenced plots showed a weak trajectory towards the primary forest in terms of species relative abundances, but not in terms of species presence (Figure 3a–f). Difference in grass cover with the primary forest increased with time in the open and closed shrublands, while it showed almost no change in the secondary forest (Figure 3g–i). Difference in woody cover with the primary forest increased substantially in the open shrubland, but also slightly in the fenced plots of the closed shrubland and the secondary forest (Figure 3j–l). These changes in growth-form cover where mainly driven by an increase in grass cover in the open and closed shrubland and an increase in woody cover in the primary forest, not equally reflected in the other ecosystem types (Figure S6).

3.2 | Is the Chaco forest resilient to different intensities of land use?

After 5 years of land-use exclusion, floristic composition showed null resilience in all the ecosystem types (Figure 4a,b) despite experiencing some changes with time, as shown above. Grass cover

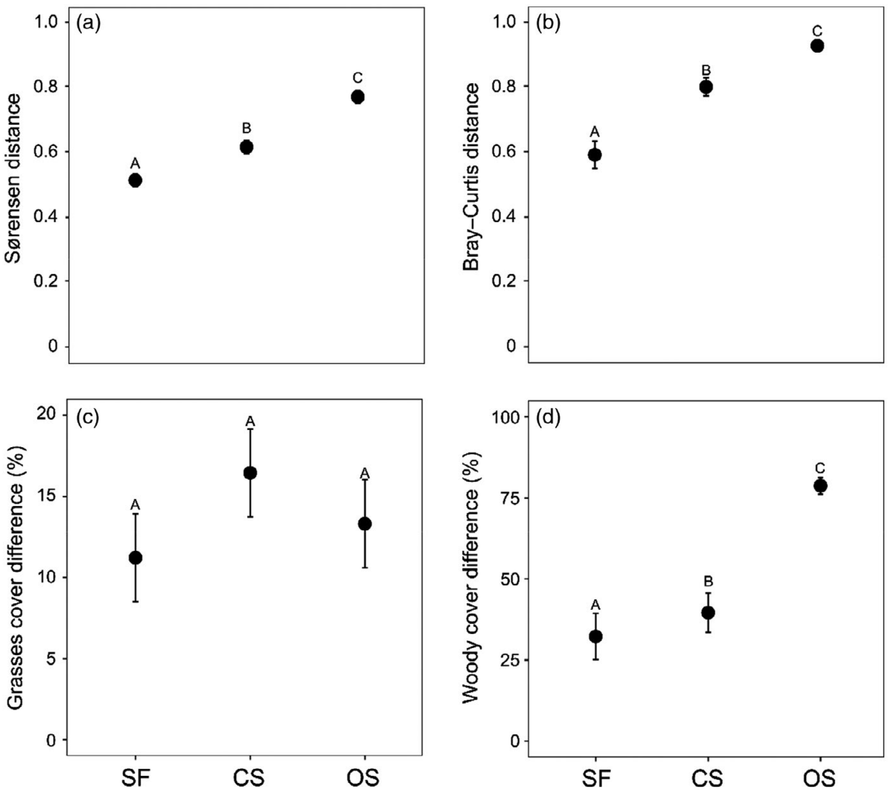


FIGURE 2 Vegetation composition at the starting point for the different ecosystem types. Panels (a and b) show the Sørensen and Bray–Curtis distances to the primary forest for different ecosystem types at the beginning of the study. Panels (c and d) show aggregate grass and woody cover difference with that of the primary forest (%) for the different ecosystem types at the beginning of the study. Ecosystem types SF: secondary forest, CS: closed shrubland and OS: open shrubland. Values show mean and standard errors. Different letters indicate significant differences between ecosystem types ($p < 0.05$, Di Rienzo a-posteriori test)

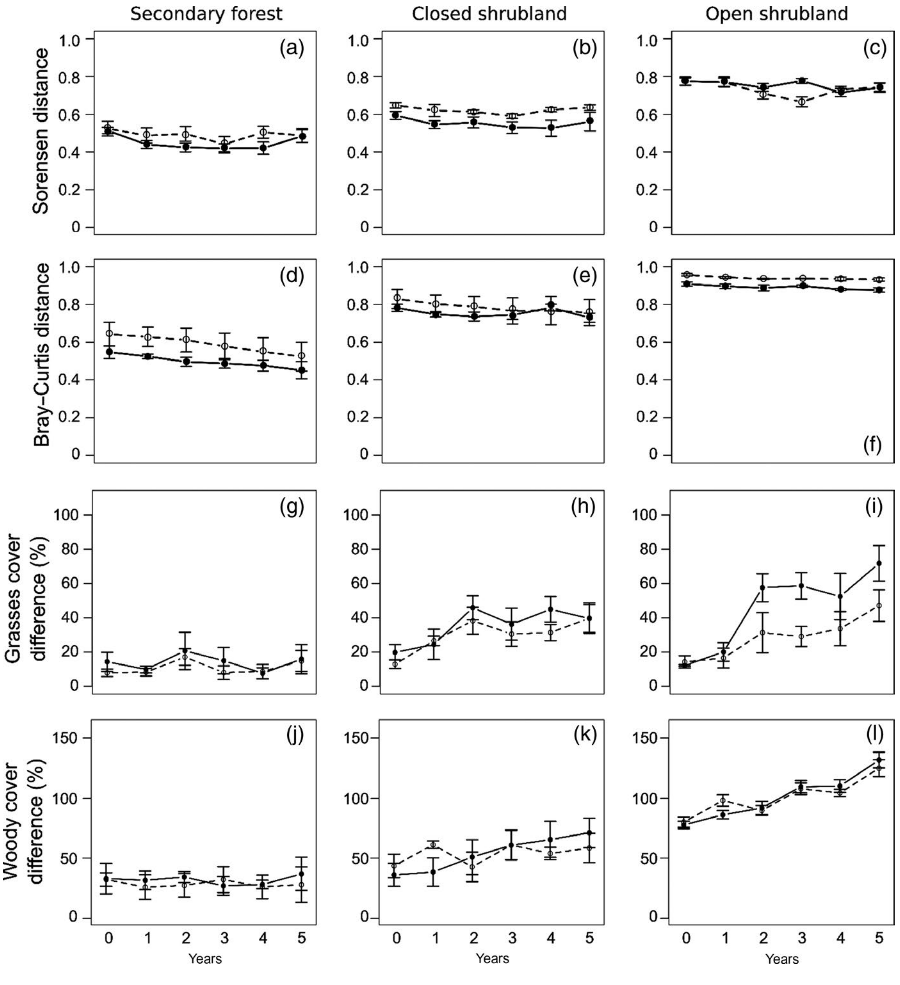


FIGURE 3 Change in vegetation composition variables with time. Year number ‘0’” indicates the beginning of the study (starting point), while number ‘5’ indicates the last measurement. Circles indicate the mean value and standard error for fenced (full circles) and unfenced (open circles) plots. Lines indicate the trajectory of fenced (solid line) and unfenced (dotted lines) plots within different ecosystem types: secondary forest (a,d,g,j), closed shrubland and (b,e,h,k) and open shrubland (c,f,I,l)

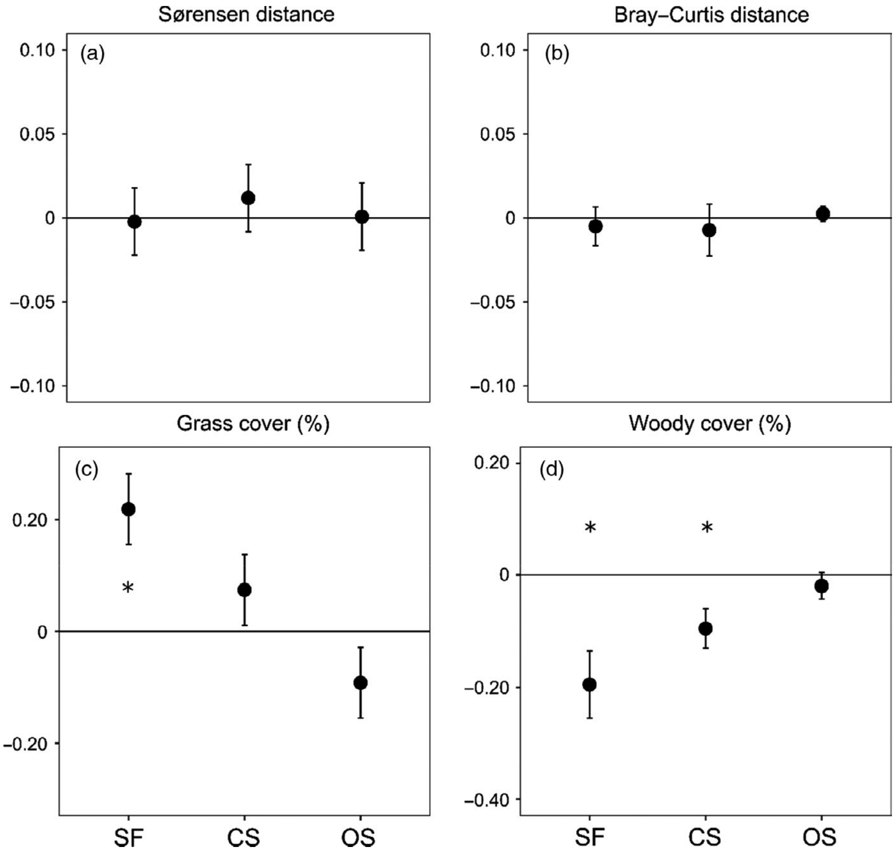


FIGURE 4 Resilience of floristic composition (a, b), grass cover (c) and woody cover (d) within each ecosystem type (SF: secondary forest, CS: closed shrubland and OS: open shrubland). Values of resilience close to 0 indicate null resilience (horizontal line), while positive values indicate positive resilience and negative values indicate negative resilience. Values represent the mean and standard errors. Asterisks indicate when the value of resilience is different from zero ($p < 0.05$)

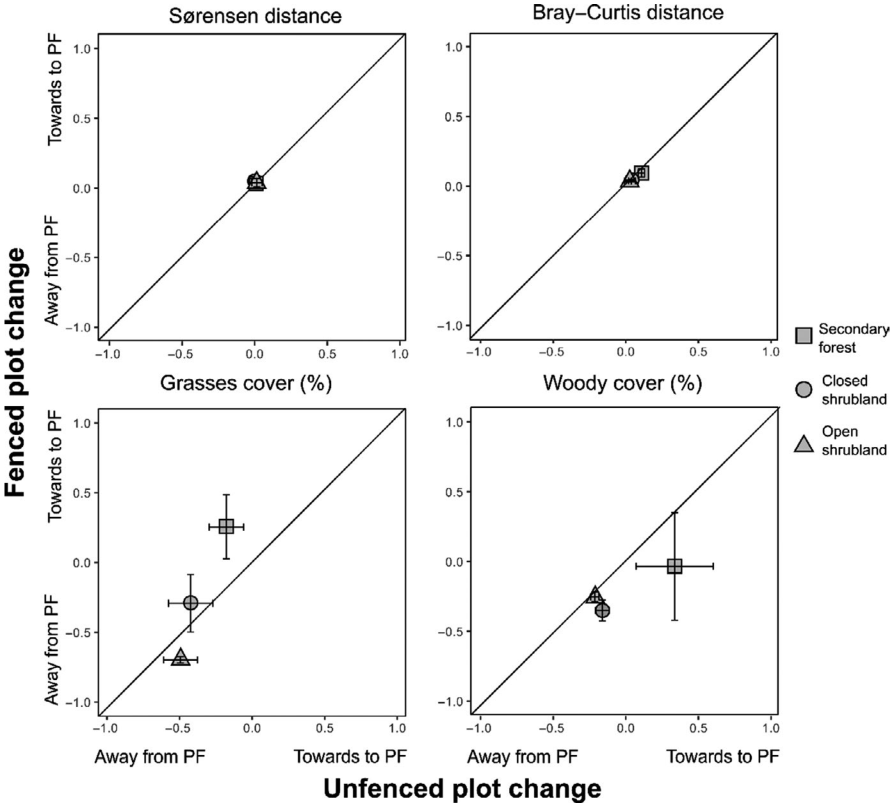


FIGURE 5 Trajectory of fenced and unfenced plot within each ecosystem type in relation to the reference vegetation. Each point shows the value of fenced and unfenced plot change of the different variables for the different ecosystem types (Secondary forest, Closed shrubland and Open shrubland). Values represent the mean and confidence intervals for a 95% of confidence

showed positive resilience only in the secondary forest (Figure 4c; Table S7), whereas woody cover showed negative resilience in the secondary forest and in the closed shrubland (Figure 4d).

Fenced and unfenced plot changes were analysed in order to identify how these different indices influenced values of resilience (Figure 5). Null values of resilience of floristic composition in all ecosystem types were the result of very low values of both fenced and unfenced plot change during the period analysed (Figure 5a,b; Table S7). The positive value for the resilience of grass cover in the secondary forest was the result of a trajectory towards the primary forest in the case of the fenced plot and away from it in the case of the unfenced plot (Figure 5c; Table S7), resulting in a positive effect of the exclosure in this ecosystem type. On the contrary, fenced and unfenced plots of the other ecosystem types showed similar trajectories away from the reference ecosystem, resulting in null resilience (Figure 5c; Table S7). The negative value for the resilience of aggregate woody cover in the secondary forest was the result of a trajectory towards the reference ecosystem of the unfenced plot, and no change in the fenced plot (Figure 5d; Table S7). In the case of the closed shrubland, negative resilience was observed as a result of a prominent trajectory of the fenced plot away from the reference ecosystem (Figure 5d; Table S7). The open shrubland showed similar trajectories away from the reference ecosystem for both plots, resulting in null resilience (Figure 5d; Table S7).

4 | DISCUSSION

What was the resilience (capacity to transition back towards a reference ecosystem) of different ecosystem types after 5 years? Based on a methodology that allowed us to disentangle the effects of the release from disturbance from changes related to year-to-year variations in climatic conditions, we found that, in general, vegetation composition did not revert during the first 5 years following the exclusion of land use. Only grass cover showed positive resilience in the ecosystem type previously subjected to the lower land-use intensity (secondary forest). Other aspects of plant community composition either did not change significantly (null resilience) or even transitioned away from the reference state (negative resilience; Figure 6).

None of the ecosystem types showed resilience of floristic composition—weighed or not by relative abundance of species (Figure 6). Very few new species were recorded (10 out of a total of 112) and very few disappeared (7 species) from different plots during the study (Supporting Information Appendix 2). In both cases, these species were very rare, so they did not influence the compositional distance to the primary forest. Additionally, although fluctuations in species relative abundance occurred, they did not differ between fenced and unfenced plots, resulting in null values of resilience, which is consistent with the literature that shows that the floristic composition tends to exhibit a slower recovery than productivity or biomass (Hillebrand & Kunze, 2020; Sansevero et al., 2017).

Negative values of resilience of the woody cover were observed in the secondary forest and the closed shrubland (Figure 6). In the first case, the woody cover in the fenced plot did not change with respect to the primary forest (it increased in both, Figure S6) while the unfenced plot showed a trajectory towards the primary forest, an unexpected effect of the exclosure for which so far, we do not have a full explanation. In the closed shrubland, the woody cover in the fenced plots increased its distance with that of the primary forest, also an unexpected effect of the exclosure. These different responses were mostly driven by the increase in cover of woody species in the primary forest, especially of *A. quebracho-blanco*, the dominant species of this ecosystem type (Figure S6). This species has shown higher recruitment in protected areas and under shrubs where abiotic conditions are ameliorated, and can resprout after being damaged (Barchuk & Del Pilar Díaz, 1999; Barchuk et al., 2006; de Noir et al., 2002; Tálamo et al., 2015). This gain in cover in the primary forest could have been associated with an increased in rainfall (see Supporting Information Appendix 1), but the fact that it was not equally observed in the ecosystem types under land use suggests that conditions at these sites may not be as suitable as in the primary forest or the response may have a time lag.

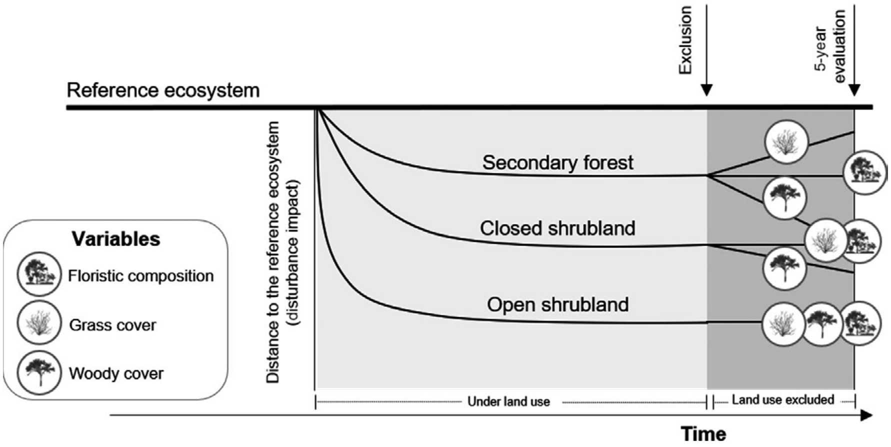


FIGURE 6 Summary resilience evaluation of different ecosystem types in the semi-arid Chaco. Before exclusion, lines are more distant to the reference ecosystem as the disturbance impact increases. Five years after exclusion, floristic composition (weighed or not by abundance) showed null resilience in all ecosystem types, grass cover showed positive resilience only in the secondary forest and woody cover showed negative resilience in the secondary forest and in the closed shrubland (with a higher negative value for the former). Curves are qualitative and not scaled proportionally to data

Finally, the secondary forest was the only ecosystem type that showed positive resilience, that is, a trajectory getting closer to the reference ecosystem after 5 years of disturbance release, but only in terms of grass cover (Figure 6). Grass species are not dominant in the primary forest, as most of them are not shade tolerant (Cabido et al., 1992, 1994); a trajectory towards the primary forest in this case thus indicates the reduction of the grass cover in the fenced plot of the secondary forest, possibly associated with the generalized increased in the cover of woody species which decreases light availability in the understorey. On the other hand, in the closed and open shrublands, grass cover increased in both unfenced and fenced plots, resulting in null resilience (Figure 6). Grass species are very well represented in the soil seed bank of the Chaco forest, and can respond fast to higher rainfall when enough light is available (Adamoli et al., 1990; Kunst et al., 2012). Nevertheless, the grass species increasing in the closed and open shrubland were functionally very different. Taller and more palatable tussock species (like *Leptochloa pluriflora* and *Setaria parviflora*, Díaz et al., 2004), more typical of the primary forest (Cabido et al., 1994; Morello et al., 1985) increased their cover in closed shrublands, while shorter and tougher species typical of open areas (like *Aristida mendocina*, *Neobouteloua lophostachya and Pappophorum* sp) increased in open shrublands. This difference suggests that these two ecosystem types are at the initial stages of what will turn to be different trajectories in the next years, the closed shrublands increasingly converging (in this sense) with the primary forest by incorporating some species that, although not dominant, are also found in the reference ecosystem, and the open shrubland increasingly diverging from it. However, longer periods under climatically favourable conditions are needed to truly analyse this nonlinear trajectory (Cotroneo et al., 2018; Cramer et al., 2007).

The open shrubland did not show resilience for any of the variables (Figure 6). These results, based on direct measurements over time, are in line with what was proposed by Cabido et al. (1992, 1994), based on a space-for-time substitution, and suggest that the ecosystem type subjected to the highest intensities of land use cannot respond upon release of disturbance, at least within the timeframe of this study. According to our general model (Figure 1), the results of this study suggest that disturbances related to land use could have affected the sources of resilience preventing the recovery after land use ended. Several studies have shown that various sources of resilience decrease in the Chaco forest under high land-use intensity, including seed availability and retention (Corrià-Ainslie et al., 2015; Lipoma et al., 2019; Nathan & Muller-landau, 2000; Wijdeven & Kuzee, 2000), and the recruitment and establishment of new individuals (Corrià-Ainslie et al., 2015; Khurana & Singh, 2001; Lipoma et al., 2019; Paez & Marco, 2000; Rotundo & Aguiar, 2005). Nevertheless, changes observed in grass aggregate cover suggest that some other regeneration mechanisms are responding to changing conditions.

Although the patterns observed in these early stages of land-use exclusion clearly cannot be considered representative of the whole recovery sequence, they are essential for understanding the full, often nonlinear, trajectory of ecosystems released from disturbance, which would not be evident from studies that substitute space for time. A good understanding of these nonlinear trajectories, including the often-erratic early stages; are fundamental for restoration or rehabilitation programs that intend to harness ecosystems natural resilience when this is high enough, or assist recovery as soon as possible when it is not (Bakker et al., 1996; Cramer et al., 2007; Lewis et al., 2019).

4.1 | Testing resilience apart from other drivers

Can the recovery trajectories of these ecosystems following land-use exclusion be disentangled from their natural responses to rain variability? Our resilience index allowed the explicit incorporation of the reference ecosystem (primary forest in our case) and the natural variation of this reference state during the period of analysis. The analysis of the recovery towards a reference state is sometimes limited because such reference system is difficult to define, because it is constantly changing (shifting baseline), or it does not even exist (Mumby et al., 2014; Pimm, 1984; Thrush et al., 2009). In general, studies use a ‘fixed’ pre-disturbance state as reference, ignoring its natural variation (Angerer et al., 2015; Bestelmeyer et al., 2013; Rudolphi et al., 2014). The variation observed in the reference ecosystem in our study highlights the need for designs that incorporate the reference system as a ‘moving target’ (i.e. including its natural variation) in order to differentiate the effect of disturbance release from those of other drivers, such as an increased in precipitation in our study.

Additionally, our index included not only different intensities of present and past land use (represented as the different ecosystem types), but also the variation of these ecosystem types in time, through a local control. These control plots enabled us to assess the impact of different intensities of land use, confirming the general findings of previous studies (Conti & Díaz, 2013; Conti et al., 2016, 2018; Cuchietti et al., 2017; Gardner et al., 1995; Lipoma et al., 2019), and also to identify changes in vegetation composition that were the result of factors different from exclusion, principally variation in precipitation (Supporting Information Appendix 1). High-rainfall periods in the ecosystem of the Chaco forest are supposed to have a synergistic effect with exclusion from grazing (Adamoli et al., 1990; Cabido et al., 1992, 1994; Cotroneo et al., 2018) and it has been suggested that the restoration of degraded arid ecosystems might be achieved in an efficient way by adjusting stocking rates to the occurrence of temporal windows of opportunity (Holmgren & Scheffer, 2001; Meserve et al., 2003). The lack of resilience observed in this study seems to cast doubt about this idea and suggests that longer and well-designed monitoring of permanent plots is crucial for the evaluation of the resilience of arid and semi-arid ecosystems.

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AUTHORS' CONTRIBUTIONS

M.L.L. and S.D. conceived the idea and designed the methodology; M.L.L., D.A.C., A.C., L.E. and L.D.G. collected the data and discussed the data analysis; M.L.L. analysed the data; M.L.L. wrote the manuscript, with input from S.D. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data from this study are available from Zenodo https://doi.org/10.5281/zenodo.4502630 (Lipoma, 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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