Received: 2 September 2020 | Accepted: 26 January 2021

DOI: 10.1111/1365-2745.13622

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

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

M. Lucrecia Lipoma[1,2] | Diego A. Cabrol[1,3] | Aníbal Cuchietti[4] | Lucas Enrico[1,2] | Lucas D. Gorné[1,2] | Sandra Díaz[1,2]

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

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

[3]Departamento de Desarrollo Rural, Facultad de Ciencias Agropecuarias, Universidad Nacional de Córdoba, Córdoba, Argentina

[4]Ministerio de Ambiente y Desarrollo Sustentable (SAyDS), Dirección Nacional de Bosques, Ciudad Autónoma de Buenos Aires, Argentina

**Correspondence**
María Lucrecia Lipoma
Email: lucrecialipoma@gmail.com

**Funding information**
Inter-American Institute for Global Change Research, Grant/Award Number: SGP-HW 090; Secretaria de Ciencia y Tecnología, Universidad Nacional de Córdoba, Grant/Award Number: 33620180100767CB and PRIMAR Res 248/18; Fondo para la Investigación Científica y Tecnológica, Grant/Award Number: 11220130100103

**Handling Editor:** David Wardle

## 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

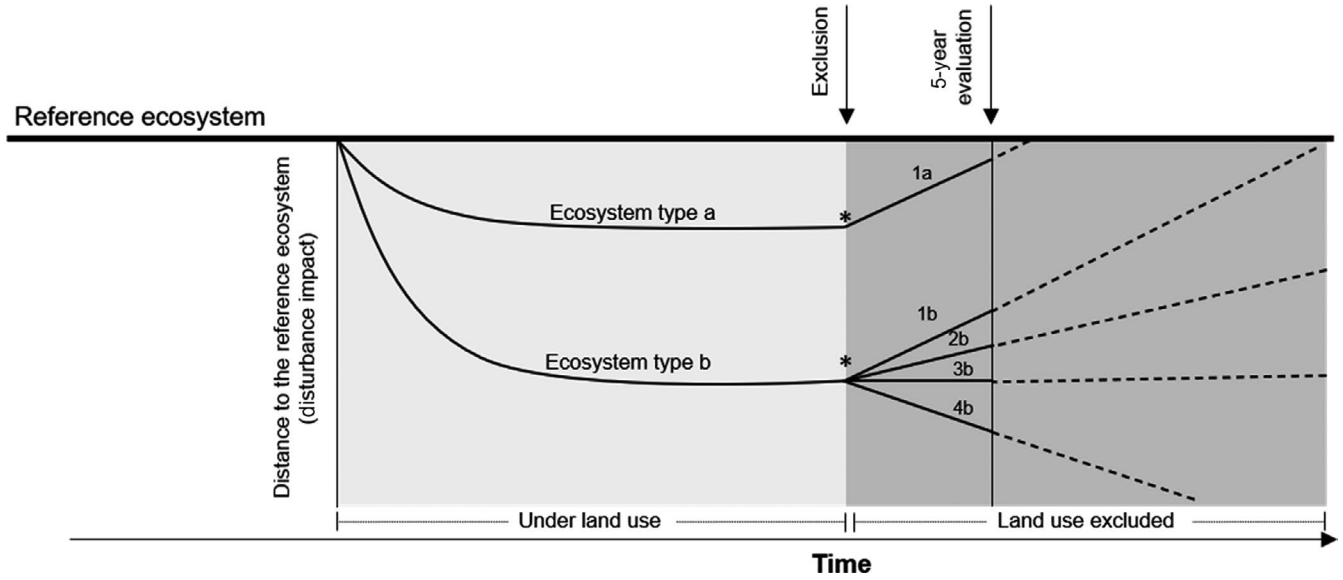



**FIGURE 1** Resilience evaluation of the Chaco forest ecosystem. The trajectory of different ecosystem types is represented with grey lines that are vertically more distant to the reference ecosystem as disturbance intensity increases (only two ecosystem types are represented for simplicity). After 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.

$$\mathrm{Resilience}(i,t) = \frac{\left(\mathit{fenced\ plot\ change}(i,t) - \mathit{unfenced\ plot\ change}(i,t)\right)}{2}, \quad (1)$$

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).

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

**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.

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

Where *FeDi (i,t)* is.

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

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.

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

*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**

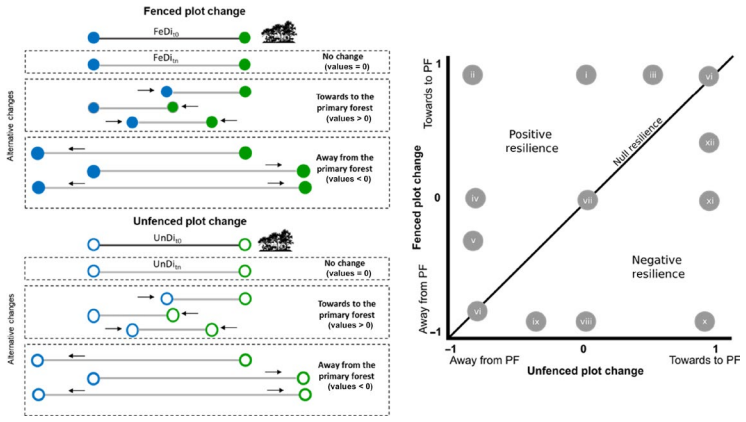
The ecosystem type did not recover because:

(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

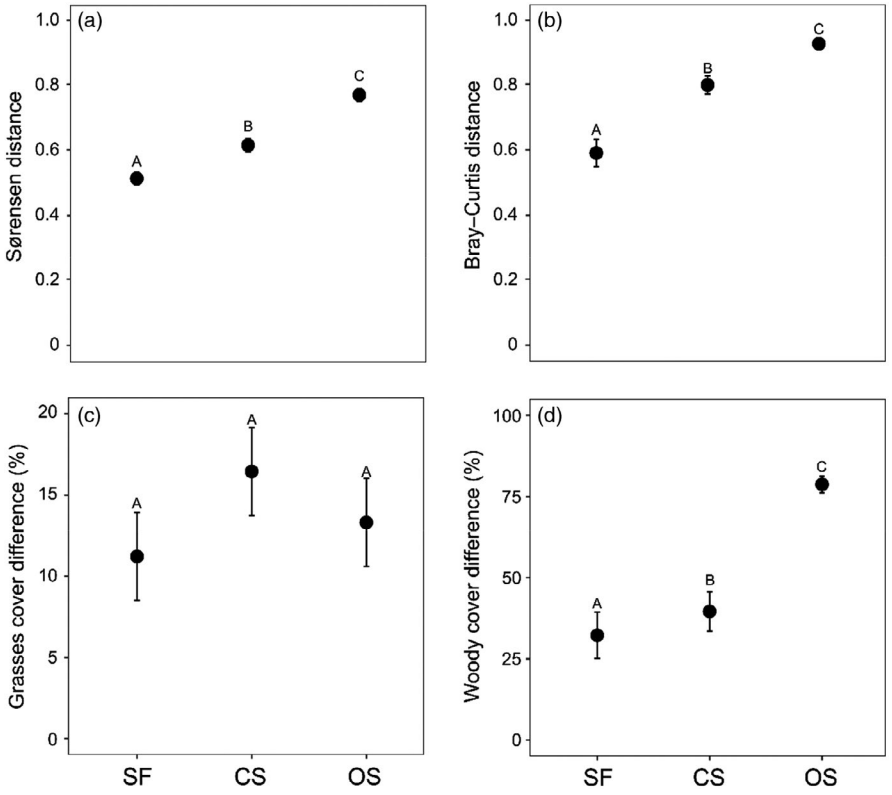



**FIGURE 2** Vegetation composition at the starting point for the different ecosystem types. Panels (a and b) show the Sørensen and Bray–Curtis distances to the primary forest for different ecosystem types at the beginning of the study. Panels (c and d) show aggregate grass and woody cover difference 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)

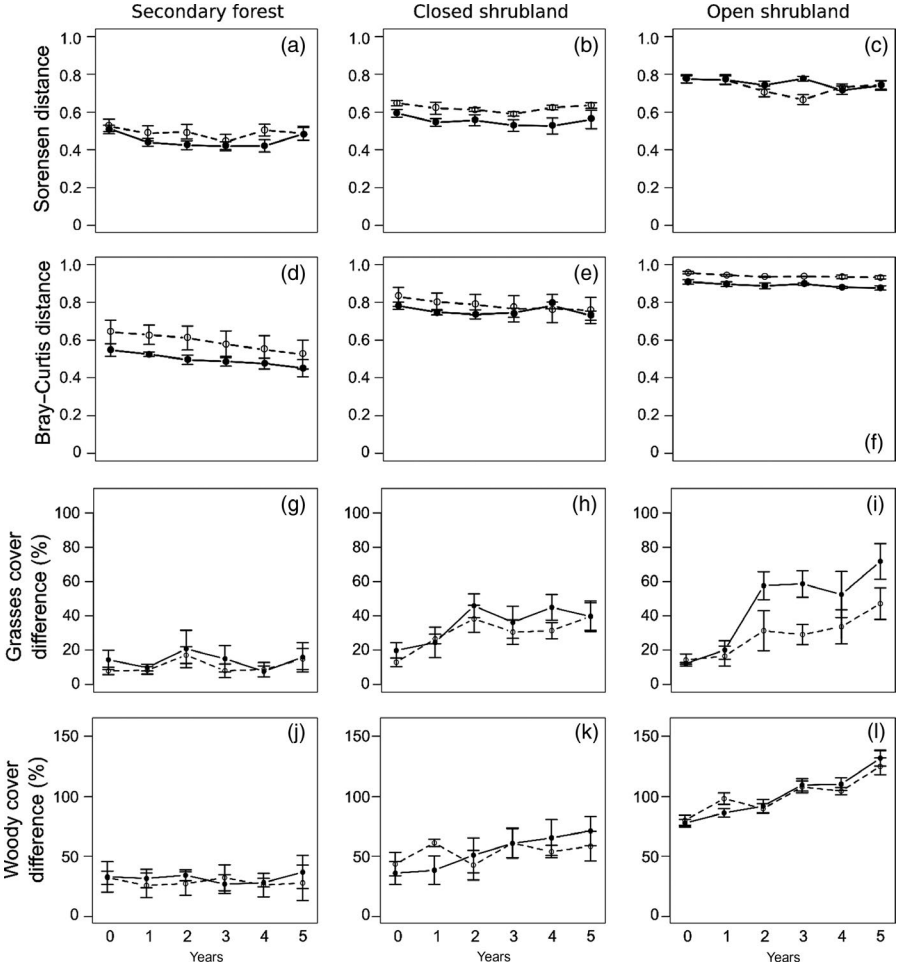



**FIGURE 3** Change in vegetation composition variables with time. Year number '0'" indicates the beginning of the study (starting point), while number '5' indicates the last measurement. Circles indicate the mean value and standard error for fenced (full circles) and unfenced (open circles) plots. Lines 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,l,l)

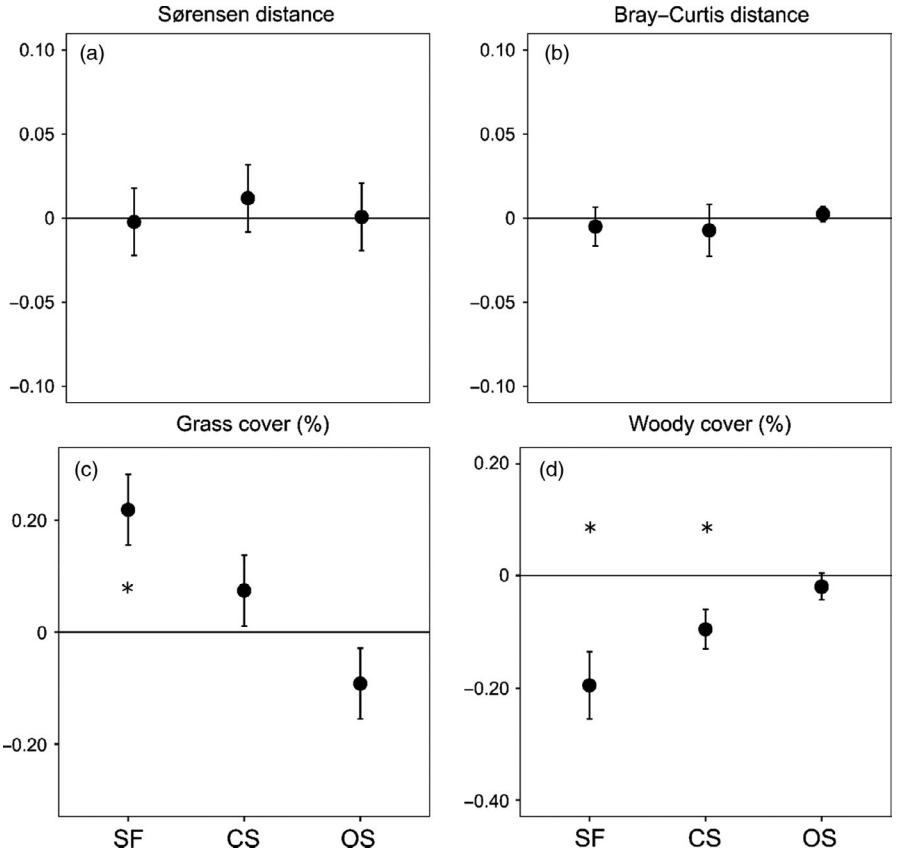



**FIGURE 4** Resilience of floristic composition (a, b), grass cover (c) and woody cover (d) within each ecosystem type (SF: secondary forest, CS: closed shrubland and OS: open shrubland). Values of resilience close to 0 indicate null resilience (horizontal line), while positive values indicate positive 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 ($p < 0.05$)

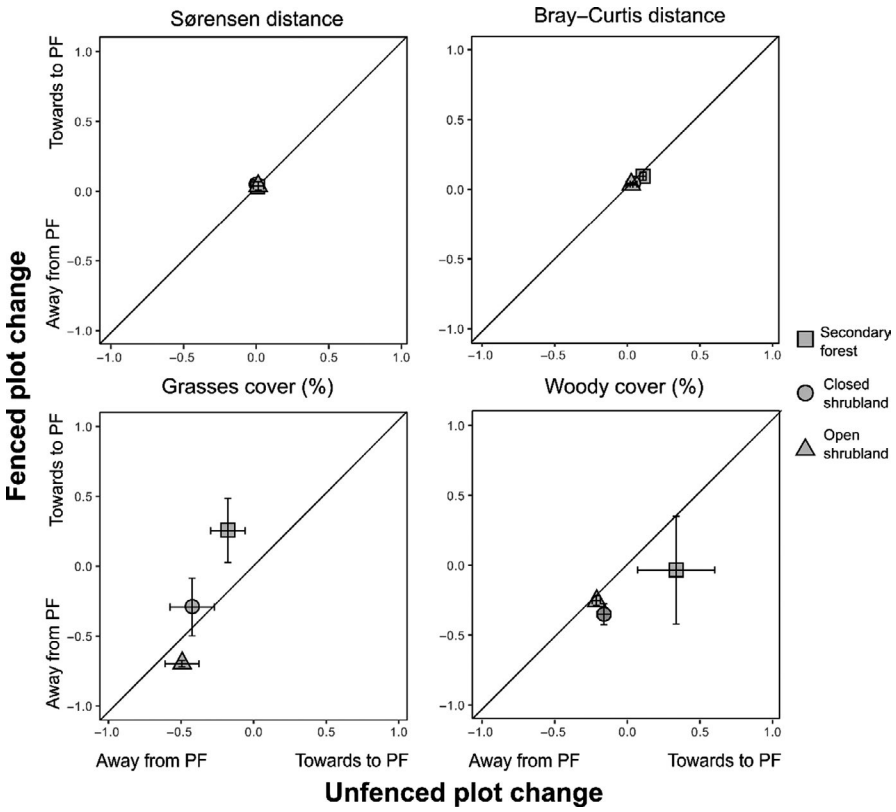



**FIGURE 5** Trajectory of fenced and unfenced plot within each ecosystem type in relation to the reference vegetation. Each point shows the value of fenced and unfenced plot change of the different variables for the different ecosystem types (Secondary forest, Closed shrubland and Open shrubland). Values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

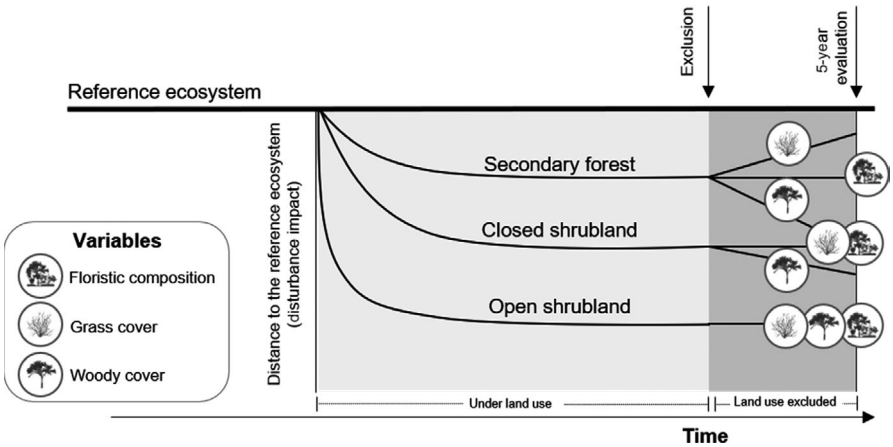



**FIGURE 6** Summary resilience evaluation of different ecosystem types in the semi-arid Chaco. Before exclusion, lines are more distant to the reference ecosystem as the disturbance impact increases. Five years after exclusion, floristic composition (weighed or not by abundance) showed null resilience 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.

#### ACKNOWLEDGEMENTS

We are grateful to land dwellers, owners and managers for allowing us to work on their properties, and to the Secretaría de Ambiente de Córdoba and staff of the Reserva Natural Chancaní, specially to José González. We also thank all those who kindly helped during the

experiments and monitoring (in particular, G. Conti and G. Bertone), the four anonymous reviewers and to the Senior and Associated Editors for their insightful comments on this manuscript. This study was supported by FONCyT, CONICET (PIP 11220130100103), SECyT-Universidad Nacional de Córdoba (33620180100767CB and PRIMAR Res 248/18), the Newton fund (NERC-UK and CONICET-Argentina) and the Inter-American Institute for Global Change Research (IAI) SGP-HW 090.

## 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

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13622.

## DATA AVAILABILITY STATEMENT

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

## ORCID

*M. Lucrecia Lipoma* https://orcid.org/0000-0001-7409-6015
*Diego A. Cabrol* https://orcid.org/0000-0003-2400-5757
*Aníbal Cuchietti* https://orcid.org/0000-0002-5916-0418
*Lucas Enrico* https://orcid.org/0000-0002-8932-0144
*Lucas D. Gorné* https://orcid.org/0000-0003-1940-1755
*Sandra Díaz* https://orcid.org/0000-0003-0012-4612

## REFERENCES

Adamoli, J., Sennhauser, E., Acero, J. M., & Rescia, A. (1990). Stress and disturbance: Vegetation dynamics in the dry Chaco region of Argentina. *Journal of Biogeography*, *17*(4), 491–500.

Anadon, J. D., Sala, O. E., & Maestre, F. T. (2014). Climate change will increase savannas at the expense of forests and treeless vegetation in tropical and subtropical Americas. *Journal of Ecology*, *102*(6), 1363–1373. https://doi.org/10.1111/1365-2745.12325

Angerer, J. P., Reid, R. S., Khishigbayar, J., Fern, M. E., Chantsallkham, J., Baasandorj, Y., & Zumberelmaa, D. (2015). Mongolian rangelands at a tipping point? Biomass and cover are stable but composition shifts and richness declines after 20 years of grazing and increasing temperatures. *Journal of Arid Environment*, *115*(September), 100–112. https://doi.org/10.1016/j.jaridenv.2015.01.007

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

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

Barchuk, A., Iglesias, M. D. R., & Oviedo, C. (2006). Rebrote basal de Aspidosperma quebracho-blanco en estado de plántula: Mecanismo de persistencia en el Chaco Árido. *Ecologia Austral*, *16*(2), 197–205.

Beisner, B. E. (2012). The shifting states of resilience: Easier to define than to measure. *Ideas in Ecology and Evolution*, *5*. https://doi.org/10.4033/iee.2012.5.13.c

Bellwood, D. R., Hoey, A. S., Ackerman, J. L., & Depczynski, M. (2006). Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology*, *12*(9), 1587–1594. https://doi.org/10.1111/j.1365-2486.2006.01204.x

Bestelmeyer, B. T., Duniway, M. C., James, D. K., Burkett, L. M., & Havstad, K. M. (2013). A test of critical thresholds and their indicators in a desertification-prone ecosystem: More resilience than we thought. *Ecology Letters*, *16*(3), 339–345. https://doi.org/10.1111/ele.12045

Bray, J. R., & Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, *27*(4), 325–349. https://doi.org/10.2307/1942268

Bucher, E. H. (1982). Chaco and Caatinga—South American arid savannas, woodlands and thickets. In B. J. Huntley, & B. H. Walker (Eds.), *Ecology of tropical savannas* (Vol. *42*, pp. 48–79). Ecological Studies (Analysis and Synthesis). Springer.

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research*, *33*(2), 261–304. https://doi.org/10.1177/0049124104268644

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

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

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

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

Carpenter, S., Walker, B., Anderies, J. M., & Abel, N. (2001). From metaphor to measurement: Resilience of what to what? *Ecosystems*, *4*(8), 765–781. https://doi.org/10.1007/s10021-001-0045-9

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

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

Conti, G., Enrico, L., Jaureguiberry, P., Cuchietti, A., Lipoma, M. L., & Cabrol, D. (2018). El rol de la diversidad funcional en la provisión de múltiples servicios ecosistémicos: Un análisis empírico en el Chaco seco de Córdoba, Argentina central. *Ecosistemas*, *27*(3), 60–74. https://doi.org/10.7818/ECOS.1491

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

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

Cotroneo, S. M., Jacobo, E. J., Brassiolo, M. M., & Golluscio, R. A. (2018). Restoration ability of seasonal exclosures under different woodland degradation stages in semiarid Chaco rangelands of Argentina.

*Journal of Arid Environments*, *158*, 28–34. https://doi.org/10.1016/j.jaridenv.2018.08.002

Cramer, V., Hobbs, R., & Standish, R. (2007). What's new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology & Evolution*, *23*(2), 104–112. https://doi.org/10.1016/j.tree.2007.10.005

Cuchietti, A., Marcotti, E., Conti, G., Casanoves, F., Mazzarino, M. J., Vaieretti, M. V., Díaz, S., & Pérez-Harguindeguy, N. (2017). Uso de la tierra y ambiente local de descomposición en el Chaco Semiárido de Córdoba, Argentina. *Ecología Austral*, *27*(3), 326–339. https://doi.org/10.25260/EA.17.27.3.0.434

de Bello, F., Valencia, E., Ward, D., & Hallett, L. (2020). Why we still need permanent plots for vegetation science. *Journal of Vegetation Science*, *31*(5), 679–685.

de Noir, F. A., Bravo, S., & Abdala, R. (2002). Mecanismos de dispersión de algunas especies de leñosas nativas del Chaco Occidental y Serrano. *Quebracho*, 140–150.

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

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

Díaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., Montserrat-Marti, G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S., Castro-Diez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Perez-Harguindeguy, N., Perez-Rontome, M. C., … Zak, M. R. (2004). The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*, *15*(3), 295–304. https://doi.org/10.1658/1100-9233(2004)015[0295:TPTTDE]2.0.CO;2

Di Rienzo, J. A., & Romero, M. C. (2010). *lsmeans. An R library for the calculation of least square means form lm, gls and lme models*. R-Forge repository. install.packages "lsmeans", repos= http://R-Forge.R-project.org

Fehlenberg, V., Baumann, M., Gasparri, N. I., Piquer-Rodriguez, M., Gavier-Pizarro, G., & Kuemmerle, T. (2017). The role of soybean production as an underlying driver of deforestation in the South American Chaco. *Global Environmental Change*, *45*, 24–34. https://doi.org/10.1016/j.gloenvcha.2017.05.001

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., & Holling, C. S. (2004). Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics*, *35*(1), 557–581. https://doi.org/10.1146/annurev.ecolsys.35.021103.105711

Gardner, S. M., Cabido, M., Valladares, G. R., & Díaz, S. (1995). The influence of habitat structure on arthropod diversity in Argentine semiarid Chaco forest. *Journal of Vegetation Science*, *6*(Lawton, 1987), 349–356. https://doi.org/10.2307/3236234

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

Grau, H. R., & Aide, M. (2008). Globalization and land-use transitions in Latin America. *Ecology and Society*, *13*(2). https://doi.org/10.5751/ES-02559-130216

Grime, J. P. (2006). *Plant strategies, vegetation processes, and ecosystem properties*. John Wiley & Sons.

Hillebrand, H., & Kunze, C. (2020). Meta-analysis on pulse disturbances reveals differences in functional and compositional recovery across ecosystems. *Ecology Letters*, *23*(3), 575–585. https://doi.org/10.1111/ele.13457

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, *4*, 1–23.

Holling, C. S. (1996). Surprise for Science, Resilience for Ecosystems, and Incentives for People. *Ecological Applications*, *6*(3), 733–735. https://doi.org/10.2307/2269475

Holmgren, M., López, B. C., Gutiérrez, J. R., & Squeo, F. A. (2006). Herbivory and plant growth rate determine the success of El Niño Southern Oscillation-driven tree establishment in semiarid South America. *Global Change Biology*, *12*(12), 2263–2271. https://doi.org/10.1111/j.1365-2486.2006.01261.x

Holmgren, M., & Scheffer, M. (2001). El Niño as a window of opportunity for the restoration of degraded arid ecosystems. *Ecosystems*, *4*(2), 151–159. https://doi.org/10.1007/s100210000065

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

IPBES. (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. S. Díaz, J. Settele, E. S. Brondízio, H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A. Pfaff, S. Polasky, A. Purvis, J. Razzaque, B. Reyers, R. Roy Chowdhury, Y. J. Shin, I. J. Visseren-Hamakers, K. J. Willis, & C. N. Zayas (Eds.). IPBES secretariat. 56 p.

IPCC. (2019). Summary for policymakers. In H.-O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, & N. M. Weyer (Eds.), *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*. In press.

Ingrisch, J., & Bahn, M. (2018). Towards a comparable quantification of resilience. *Trends in Ecology & Evolution*, *33*(4), 251–259. https://doi.org/10.1016/j.tree.2018.01.013

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T. M., Bonin, C., Bruelheide, H., de Luca, E., Ebeling, A., Griffin, J. N., Guo, Q., Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., … Eisenhauer, N. (2015). Biodiversity Increases the Resistance of Ecosystem Productivity to Climate Extremes. *Nature*, *526*, 574–577. https://doi.org/10.1038/nature15374

Johnson, J. B., & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology & Evolution*, *19*(2), 101–108. https://doi.org/10.1016/j.tree.2003.10.013

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

Kunst, C., Ledesma, R., Bravo, S., Albanesi, A., Anriquez, A., van Meer, H., & Godoy, J. (2012). Disrupting woody steady states in the Chaco region (Argentina): Responses to combined disturbance treatments. *Ecological Engineering*, *42*, 42–53. https://doi.org/10.1016/j.ecoleng.2012.01.025

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

Lewis, S. L., Wheeler, C. E., Mitchard, E. T. A., & Koch, A. (2019). Regenerate natural forests to store carbon. *Nature*, *568*(7750), 25–28. https://doi.org/10.1038/d41586-019-01026-8

Li, B., Parr, T., & Rozzi, R. (2015). Geographical and thematic distribution of publications generated at the International Long-Term Ecological Research Network (ILTER) Sites. In *Earth Stewardship* (pp. 195–216). Springer. https://doi.org/10.1007/978-3-319-12133-8_13

Lindenmayer, D. B., Likens, G. E., Andersen, A., Bowman, D., Bull, C. M., Burns, E., Dickman, C. R., Hoffmann, A. A., Keith, D. A., & Liddell, M. J. (2012). Value of long-term ecological studies. *Austral Ecology*, *37*(7), 745–757. https://doi.org/10.1111/j.1442-9993.2011.02351.x

Lipoma, M. L. (2021). Species abundances Chacoforest. *Zenodo*, https://doi.org/10.5281/zenodo.4502630

Lipoma, M. L., Cuchietti, A., Gorne, L. D., & Díaz, S. (2019). Not gone with the wind: Vegetation complexity increases seed retention during

windy periods in the Argentine Semiarid Chaco. *Journal of Vegetation Science*, (February), 1–11. https://doi.org/10.1111/jvs.12747

Lipoma, M. L., Fortunato, V., Enrico, L., & Díaz, S. (2020). Where does the forest come back from? Soil and litter seed banks and the juvenile bank as sources of vegetation resilience in a semiarid Neotropical forest. *Journal of Vegetation Science*. https://doi.org/10.1111/jvs.12842

Lipoma, M. L., Gurvich, D. E., Urcelay, C., & Díaz, S. (2016). Plant community resilience in the face of fire: Experimental evidence from a semi-arid shrubland. *Austral Ecology*, *41*(5). https://doi.org/10.1111/aec.12336

López, D. R., Brizuela, M. A., Willems, P., Aguiar, M. R., Siffredi, G., & Bran, D. (2013). Linking ecosystem resistance, resilience, and stability in steppes of North Patagonia. *Ecological Indicators*, *24*, 1–11. https://doi.org/10.1016/j.ecolind.2012.05.014

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

Meserve, P. L., Kelt, D. A., Milstead, W. B., & Gutiérrez, J. R. (2003). Thirteen years of shifting top-down and bottom-up control. *BioScience*, *53*(7), 633–646. https://doi.org/10.1641/0006-3568(2003)053[0633:TYOSTA]2.0.CO;2

Morello, J. (1995). Grandes ecosistemas de Sudamérica. In G. Gallopín (Ed.), *El futuro ecológico de un continente*. Editorial de la Universidad de las Naciones Unidas/Fondo de Cultura Económica (FCE).

Morello, J., & Adamoli, J. (1974). *Las grandes unidades de vegetación y ambiente del Chaco Argentino: Vegetación y ambiente de la provincia del Chaco*. Instituto Nacional de Tecnología Agropecuaria Secretaría de Estado de la Nación.

Morello, J. H., Protomastro, J., Sancholuz, L., & Blanco, C. (1985). *Estudio macroecológico de los Llanos de La Rioja*. APN, Administración de Parques Nacionales, Secretariat de Agricultura, Ganadería y Pesca, Ministerio de Economía.

Mumby, P. J., Chollett, I., Bozec, Y. M., & Wolff, N. H. (2014). Ecological resilience, robustness and vulnerability: How do these concepts benefit ecosystem management? *Current Opinion in Environmental Sustainability*, *7*, 22–27. https://doi.org/10.1016/j.cosust.2013.11.021

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

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

Pickett, S. T. A. (1989). Space-for-time substitution as an alternative to long-term studies. In G. E. Likens (Ed.), *Long-term studies in ecology* (pp. 110–135). Springer.

Pimm, S. L. (1984). The complexity and stability of ecosystems. *Nature*, *307*, 321–326. https://doi.org/10.1038/307321a0

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2020). *{nlme}: Linear and nonlinear mixed effects models*. R package version 3.1-148.

Plieninger, T., Schaich, H., & Kizos, T. (2011). Land-use legacies in the forest structure of silvopastoral oak woodlands in the Eastern Mediterranean. *Regional Environmental Change*, *11*(3), 603–615. https://doi.org/10.1007/s10113-010-0192-7

R Core Team. (2015). *R: A language and environment for statistical computing [Internet]*. R Foundation for Statistical Computing; 2014.

Rietkerk, M., van den Bosh, F., & van de Koppel, J. (1997). Site-specific propoerties and irreversible vegetation changes in semi-arid grazing systems. *Oikos*, *80*, 241–252.

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

Rudolphi, J., Jönsson, M. T., & Gustafsson, L. (2014). Biological legacies buffer local species extinction after logging. *Journal of Applied Ecology*, *51*(1), 53–62. https://doi.org/10.1111/1365-2664.12187

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

Sansevero, J. B. B., Prieto, P. V., Sánchez-Tapia, A., Braga, J. M. A., & Rodrigues, P. J. F. P. (2017). Past land-use and ecological resilience in a lowland Brazilian Atlantic Forest: Implications for passive restoration. *New Forests*, *48*(5), 573–586. https://doi.org/10.1007/s11056-017-9586-4

Song, X. P., Hansen, M. C., Stehman, S. V., Potapov, P. V., Tyukavina, A., Vermote, E. F., & Townshend, J. R. (2018). Global land change from 1982 to 2016. *Nature*, *560*(7720), 639–643. https://doi.org/10.1038/s41586-018-0411-9

Sørensen, T. (1948). A method of establishing groups of equal amplitude in plant sociology based on similarity of species and its application to analyses of the vegetation on Danish commons. *Biologiske Skrifter*, *5*, 1–34.

Tálamo, A., Barchuk, A. H., Garibaldi, L. A., Trucco, C. E., Cardozo, S., & Mohr, F. (2015). Disentangling the effects of shrubs and herbivores on tree regeneration in a dry Chaco forest (Argentina). *Oecologia*, *178*(3), 847–854. https://doi.org/10.1007/s00442-015-3269-7

Thrush, S. F., Hewitt, J. E., Dayton, P. K., Coco, G., Lohrer, A. M., Norkko, A., Norkko, J., & Chiantore, M. (2009). Forecasting the limits of resilience: Integrating empirical research with theory. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1671), 3209–3217. https://doi.org/10.1098/rspb.2009.0661

Tilman, D., & Downing, J. A. (1994). Biodiversity andstability in grasslands. *Nature*, *367*(27), 363–365. https://doi.org/10.1038/367363a0

Walker, B. H. (1992). Biodiversity and ecological redundancy. *Conservation Biology*, *6*(1), 18–23. https://doi.org/10.1046/j.1523-1739.1992.610018.x

Ward, D., Saltz, D., & Olsvig-Whittaker, L. (2000). Distinguishing signal from noise: Long-term studies of vegetation in Makhtesh Ramon erosion cirque, Negev desert, Israel. *Plant Ecology*, *150*(1–2), 27–36. https://doi.org/10.1023/A:1026529126729

Wardle, D. A., & Jonsson, M. (2014). Long-term resilience of above-and belowground ecosystem components among contrasting ecosystems. *Ecology*, *95*(7), 1836–1849. https://doi.org/10.1890/13-1666.1

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

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

Zell, C., & Hubbart, J. A. (2013). Interdisciplinary linkages of biophysical processes and resilience theory: Pursuing predictability. *Ecological Modelling*, *248*, 1–10. https://doi.org/10.1016/j.ecolmodel.2012.09.021

## SUPPORTING INFORMATION

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

**How to cite this article:** Lipoma ML, Cabrol DA, Cuchietti A, Enrico L, Gorné LD, Díaz S. Low resilience at the early stages of recovery of the semi-arid Chaco forest—Evidence from a field experiment. *J Ecol*. 2021;00:1–14. https://doi.org/10.1111/1365-2745.13622