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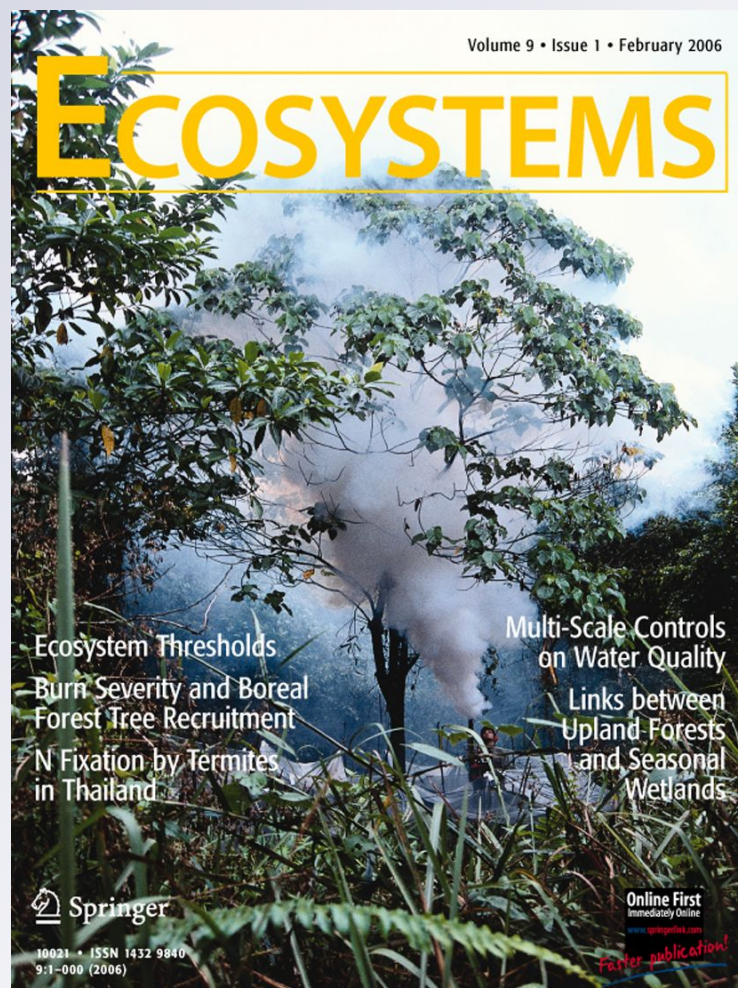
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# Assessing the Use of Functional Diversity as a Measure of Ecological Resilience in Arid Rangelands

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## ABSTRACT

It is becoming more apparent that species richness alone many not be sufficient to fully understand ecosystem resilience but that functional diversity (diversity of species having similar effects on an ecosystem process) may be more relevant. In particular, response diversity (diversity of species that respond differently to disturbance) within functional groups (FG) is suggested to be critical for resilience. We assess for the first time the use of response diversity as a measure of resilience in an empirical study. Our experimental design consisted of sites with three disturbance intensities during a grazing enclosure period and the same sites, 1 year later, after grazing. Plant FGs were identified based on effect traits related to nutrient cycling and soil retention, and species richness within groups was assessed during enclosure and after grazing. To assess if response diversity could predict loss of species richness (resilience analysis), response

diversity was calculated only during the enclosure period, based on traits related to grazing tolerance. We also assessed the contribution of richness to response diversity during enclosure (redundancy analysis). Response diversity was significantly and highly correlated with species richness within FGs during disturbance. That is, FGs with the lowest response diversity were the most affected, disappearing when disturbance appeared. Richness within FGs during enclosure was not significantly correlated with response diversity, showing that higher richness does not ensure resilience. We conclude that response diversity can be used to predict which FGs are more resilient, and hence, less vulnerable to future disturbance.

**Key words:** desertification; functional groups; Insurance Hypothesis; Monte Desert; resilience; rangeland management; response diversity.

## INTRODUCTION

Anthropogenic disturbances are causing rapid environmental changes, creating stress within

ecosystems all over the world. Among its consequences, species loss is of great importance due to its magnitude and links with ecosystem processes (Pimm and others 1995). Assessing and preventing the impacts of species loss on ecosystems is of critical importance for sustaining the services that ecosystems provide (Carpenter and others 2009). Many empirical and theoretical studies have revealed a positive relationship between biodiversity and ecosystem functioning, spanning a wide

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variety of ecosystems and functions (Hooper and others 2005; Balvanera and others 2006; Cardinale and others 2006; among many others). Current research needs to focus on linking this knowledge to an understanding of how ecosystems will respond to increasing environmental variability and land-use intensification to achieve management for sustainable development (Scheffer and others 2001; Carpenter and others 2009).

In social-ecological systems, management typically aims to keep a system within stable states to maintain desirable ecosystem goods and services (Resilience Alliance 2011). Within the framework of resilience thinking, resilience implies “the capacity of a system to absorb disturbance and reorganize while undergoing change so as to retain essentially the same function, structure, identity, and feedbacks” (Fischer and others 2009). There is a vast theoretical development around resilience and state shift in complex adaptive systems (Peterson and others 1998; Walker and others 1999; Carpenter and others 2001; Folke and others 2004; among many others). Results show that the relationship between diversity and stability is neither linear nor random, and extinction probabilities vary according to species traits (for example, trophic level, body size, and specialization), hence higher species richness does not always imply greater resilience (Elmqvist and others 2003). In response to this, different ways to assess resilience have been proposed, considering mainly the identification and modeling of driver feedback processes (Bennett and others 2005), determination of discontinuities and quantification of function within and across spatial scales (Allen and others 2005; Fischer and others 2007), identification of changes in system identity (Cumming and others 2005), and assessment of response diversity changes under increasing disturbance (Elmqvist and others 2003; Laliberté and others 2010). Despite all the knowledge and development around this topic, due to their complex nature, social-ecological systems defy our ability to accurately predict trajectories and prevent changes to undesirable states of the ecosystem (Anand and Desrochers 2004; Reynolds and others 2007; Fischer and others 2009).

The Insurance Hypothesis (Johnson and others 1996) suggests that an ecosystem containing species that perform similar functions, but that respond differently to environmental factors, can help to maintain its stability in response to environmental fluctuations (Yachi and Loreau 1999). When species have similar effects on a particular ecosystem process they can be grouped into functional groups (FG) (Díaz and Cabido 2001). Species richness within a

FG shows the number of species that have traits with similar effects on the ecosystem. Thus, higher species richness within a FG implies greater redundancy (more species performing similar functions) and this may provide insurance to the system if species show compensatory response to disturbance (Yachi and Loreau 1999; Allen and others 2005). For example, under grazing disturbance some species can be more affected than others for being more palatable or less tolerant to trampling, but yet, if they have similar functional roles the ecosystem function will not disappear because the reduction of one may be compensated by the increase of the other (Walker and others 1999). A similar compensatory effect due to different responses to disturbance of species with similar effect (on ecosystem process) traits has been observed in insect communities under fire disturbance (Moretti and others 2006). This variety of responses to disturbance within FGs has been referred to as “response diversity” (Elmqvist and others 2003). As species with the same function respond differently to disturbance, response diversity may allow that FGs remain available for renewal and reorganization after disturbance, which is important for ecosystem stability and sustainability. It has also been suggested to be critical for resilience (Elmqvist and others 2003; Folke and others 2004).

A decline in response diversity has been suggested to increase the vulnerability of FGs to disturbance (Elmqvist and others 2003). Nevertheless, to date only one study was able to quantify the effects of human-made disturbances on response diversity (Laliberté and others 2010). This study showed that land-use intensification significantly reduces response diversity across a wide variety of biomes, increasing the vulnerability of FGs to future disturbances, and consequently, diminishing resilience. However, if we aim to assess if response diversity values can predict the resilience of a system to a specific disturbance, it is necessary to analyze the response of the system over time (Carpenter and others 2001). We need to include the time component by quantifying response diversity before the occurrence of disturbance, and assess if those values predict the loss of species after disturbance. The number of FGs and the richness within them can give us an idea of the function, structure, and identity of the system. The loss of a FG (or richness within it) may imply the loss of traits that contribute to an ecosystem function or the loss of the function completely, increasing ecosystem vulnerability and potential shifts to undesirable states (Elmqvist and others 2003). If response diversity is critical to ecosystem resilience, then FGs with higher response diversity before disturbance should be the least af-

ected after disturbance. Although, theoretical and experimental approaches have linked functional diversity to ecosystem stability and state shifts including the time component (Yachi and Loreau 1999; Carpenter and Brock 2006), to the best of our knowledge, no studies have examined response diversity in this way.

In this article, we examine a case study of response diversity and resilience in an arid rangeland in Argentina. Desertification is a major problem in this region (Villagra and others 2009), and is considered an important environmental change globally due to the loss of fertile soil in arid, semi-arid, and sub-humid lands as a consequence of resource overexploitation (Scheffer and others 2001; Reynolds and others 2007). Overgrazing is one of the main causes of this shift to an undesirable state of the ecosystem, with soil erosion and the loss of aboveground biomass and biodiversity being among the main consequences of desertification (Reynolds and others 2007). Here, we examine effect trait diversity in response to grazing disturbance, and FGs with traits related to soil and water retention, and litter formation, to assess whether response diversity can be used as a measure of ecosystem resilience. Our study aims to: (a) quantify response diversity as related to disturbance intensity (cattle grazing) within FGs; (b) assess the relationship between response diversity and species richness within FGs before and after disturbance (the time component). To assess the time component, we measured vegetation in paddocks with 1 year of grazing exclusion (before disturbance), and the same paddocks during cattle grazing (after disturbance). If response diversity within groups of species performing similar functions ensures higher resilience, then FGs with higher response diversity values will lose fewer species in response to future disturbance.

## METHODS

### Study Site Location and Sampling Design

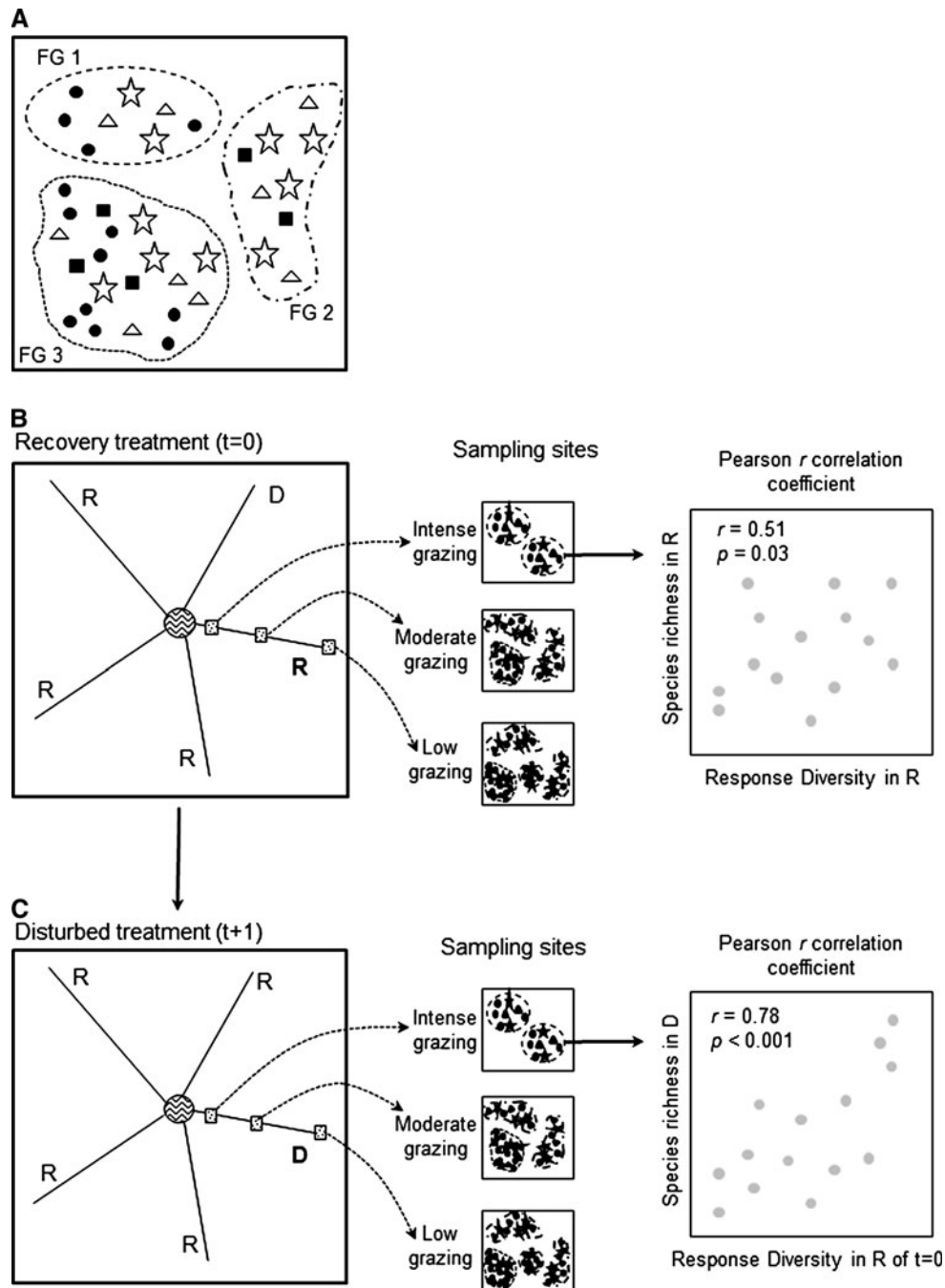
This study was conducted at El Divisadero Cattle and Range Experiment Station, approximately 200 km south-east Mendoza City, Argentina (33° 46' S, 67° 47' W). This region lies within the central temperate Monte Desert biome (Abraham and others 2009). The climate is semi-arid and markedly seasonal, with cold dry winters and hot wet summers. Mean annual rainfall for 1987–1998 was 303.4 mm (SD = 96.6) with nearly 85% occurring during the growing season (October–March). The vegetation is an open xerophytic savanna and shrubland, where grasses dominate the herbaceous

layer. Woody vegetation consists of only three tree species (*Prosopis flexuosa*, *Geoffrea decorticans*, and *Bulnesia retama*), and over 24 species of shrubs and subshrubs (mainly *P. alpataco*, *Junellia seriphioides*, *Larrea* sp., *Lycium* sp., *Fabiana pequi*, and *Aloysia gratissima*). The herbaceous layer consists of more than 40 species of grasses and forbs, and is dominated by *Panicum urvilleanum*, *Setaria leucopila*, *Aristida inversa*, *Pappophorum caespitosum*, *Chloris castilloniana*, *Cottea pappophoroides*, *A. mendocina*, *Baccharis* sp., *Solanum* sp., and *Portulaca* sp. This desert ecosystem is also characterized by fast recovery of the herbaceous layer mainly due to the rapid responses of annual plant assemblages to changes in rainfall conditions (Holmgren and Scheffer 2001; 2006; Sassi and others 2009).

Vegetation sampling was conducted within a grazing system of rest-rotation (Guevara and others 2009). The rest-rotational grazing strategy design involves paddocks radiating from a central watering point. Cattle are rotated between paddocks, and each paddock goes through 12 months of grazing exclusion, where fast vegetation growth allows recovery of the herbaceous layer (recovery treatment); followed by 4 months of intense grazing (disturbed treatment). Thus, different treatments are the same sites but at a different time periods, where the disturbance conditions are different. We sampled vegetation at five transects in the recovery treatment ( $n = 5$ ), and five transects in the disturbed treatment ( $n = 5$ ). Each transect consisted of three sites at varying distances from the watering point, where distances were chosen to reflect three different grazing intensities: intense, moderate, and low (Figure 1). Within each site (grazing intensities), we measured percentage of cover per plant species in 50 randomly distributed plots of 1 m<sup>2</sup>. Samples were taken during the growing season of the years 2008–2010.

### Selection of Functional Traits

A key methodological aspect was to choose the most accurate plant traits for our objectives. Plant functional traits can be classified into effect and response. Functional effect traits are those that influence a specific function of the ecosystem (for example, primary productivity, nutrient cycling); whereas functional response traits are those that respond to the environment (for example, climate variations, disturbance) (Díaz and Cabido 2001). As we mentioned before, FGs are comprised of species with similar effects on a particular ecosystem function. Thus, effect traits are used to group these species. As desertification is the state shift that we



**Figure 1.** Schematic representation of the methodological approach. **A** Representation of a sample site and classifications made. FG 1, 2, and 3 are functional groups. Within each FG the total number of symbols represents species richness (functional redundancy); and different symbols represent different responses to disturbance (response diversity). **B** Redundancy analysis. Lines are replicate transects around the watering point (*center circle*). “R” are transects with cattle exclusion (recovery treatment) and “D” is transect with cattle (disturbed treatment). Each transect contains three grazing intensities indicated by *squares* at different distances from the *center circle*. To assess if richness within FGs was related to response diversity values, we calculated the Pearson correlation coefficient ( $r$ ) between both variables in transect R. **C** Resilience analysis. This treatment is considered  $t + 1$  because it represents the same transect but when the disturbance reappeared. Representations are the same as **B**. To assess if response diversity values during the recovering treatment (in R of  $t = 0$ ) were related to richness inside FGs when the disturbance reappeared (in D of  $t + 1$ ) we calculated  $r$  between both variables.

want to avoid, we chose eight effect traits related to primary production, litter formation, nutrient cycling, and soil retention (Table 1). For example, life cycle may influence litter formation and nutrient cycling by the speed at which dead matter enters the system. Different growth forms and lateral spread gives different vertical structure and soil cover, influencing primary production, soil, and litter retention. Different main root systems influ-

**Table 1.** Plant Functional Effects (E) and Response (R) Traits used for the Analysis

| Trait  | Trait categories        | Type |
|--|-------------------------|------|
| Growth form                                  | Grasses                 | E    |
|  | Forbs                   |      |
|  | Subshrubs               |      |
|  | Shrubs and trees        |      |
| Life cycle                                   | Annual                  | E    |
|  | Deciduous               |      |
|  | Evergreen               |      |
| Nitrogen fixer                               | Yes/no                  | E    |
| Leaf length                                  | Small (<0.5 cm)         | E    |
|  | Medium (0.5–2.5 cm)     |      |
|  | Large (>2.5 cm)         |      |
| Root main system                             | Taproot                 | E    |
|  | Fibrous                 |      |
| Lateral spread                               | Single shoot            | E    |
|  | Tussock                 |      |
|  | Several stems           |      |
|  | Stolons                 |      |
| Storage organs                               | Yes/no                  | E    |
| Leaf texture                                 | No leaf                 | E    |
|  | Coriaceous              |      |
|  | Intermediate            |      |
|  | Membranous              |      |
| Trend in abundance<br>Along grazing gradient | Increasing trend        | R    |
|  | Decreasing trend        |      |
|  | Medial trend            |      |
|  | Extremist trend         |      |
|  | No trend                |      |
| Raunkiaer                                    | Phanaerophytes          | R    |
|  | Chamaephytes            |      |
|  | Hemicryptophytes        |      |
|  | Geophytes               |      |
|  | Therophytes             |      |
| Vegetative reproduction                      | Yes/no                  | R    |
| Palatability                                 | Non-palatable           | R    |
|  | Palatable not preferred |      |
|  | Palatable preferred     |      |
| Thorns                                       | Yes/no                  | R    |
| Dispersal syndrome                           | Adhesion                | R    |
|  | Ingestion               |      |
|  | Wind or mobile          |      |
|  | Undefined               |      |

*Effects traits were used for the conformation of functional groups and response traits were used to quantify response diversity.*

ence soil retention (for example, fibrous root) and nutrient cycling (for example, taproot) (Cornelissen and others 2003). We chose those traits for which there is available information in publications and/or herbaria to make the methodology easy to apply for local managers.

To accurately measure response diversity in our study system, we chose six response traits related to grazing tolerance, with low or no intraspecific variation (Table 1) (Cornelissen and others 2003; Díaz and others 2007). Almost all trait values were recorded from published sources and/or herbarium information, except for the “trends in abundance” trait which we measured in the field. Particularly, trends in abundance along the grazing gradient were assessed using species frequency as the dependent variable and distance from water as the independent variable (ten different distances from the watering point). Then, we fit regressions describing a set of hypothesized trends (increasing trend, decreasing trend, convex unimodal trend, concave unimodal trend, and no-trend) (see Landsberg and others 2003 for more details).

### Classification of FGs and Quantification of Response Diversity

Following the process of producing functional classifications suggested by Petchey and Gaston (2006), we classified species into FGs using the Unweighted Pair Group Method (UPGM) clustering on the Gower dissimilarity species × effect-traits matrix. The number of groups was determined by performing a randomization test of 10,000 permutation bootstrap resampling. This method tests the null hypothesis that the clusters in the bootstrap samples are random samples of their most similar corresponding clusters in the observed data. The resulting probability indicates if the groups in the classification are sharp enough to reappear consistently in resampling (Pillar 1999). This method is useful to avoid subjective grouping classification. Analyses were performed using MULTIV software (Pillar 2006).

Response diversity was defined as the variety of responses to disturbance within FGs. Thus, within each FG we calculated the diversity of response traits using Rao's coefficient. This index is a generalization of the Simpson index (Botta-Dukát 2005). As we aim to evaluate if response diversity values can be used to assess which FG is less or more resilient (loses more or less species after disturbance), response diversity was always calculated in the recovery treatment (before the reappearance of the disturbance) (Figure 1A).

## Relationship between Response Diversity and Species Richness

Higher species richness does not always ensure higher functional richness or higher response diversity (Díaz and Cabido 2001; Elmqvist and others 2003; Laliberté and others 2010). Thus, to assess if response diversity values depend on richness within FGs (redundancy analysis) (Laliberté and others 2010), we tested the relationship between these two variables in recovered sites (Figure 1B). For the resilience analysis, we wanted to assess if response diversity values predict the loss of species under future disturbance. For this, we evaluated the relationship between response diversity (calculated before the disturbance) and richness within FGs after disturbance (the time component) (Figure 1C). If a positive correlation is found, then higher response diversity implies higher resilience.

To assess the above-mentioned relationship between response diversity and species richness (for both, redundancy and resilience analysis), we tested the null hypothesis that there is no relationship between these two variables, and our criterion test was Pearson's correlation coefficient. We tested the significance of the correlation using a permutation test of 10,000 iterations and generated a null distribution of response diversity values. For this, within each FG and for each replicate the null distribution was created by randomly selecting species, but keeping constant the number of species. Response diversity values were always calculated in the recovered sites (before disturbance), but species richness was calculated before and after disturbance. Thus, for the redundancy analysis we correlated the null distribution of response diversity values against species richness before disturbance. For the resilience analysis, the null distribution of response diversity values was correlated with species richness after disturbance. If the observed response diversity value (for each FG) was lower than the null distribution of  $\alpha = 0.01$ , the correlation was significantly different from the null distribution. These analyses were performed using MULTIV software. Also, to evaluate if there were significant differences in species richness between treatments (recovery and disturbed) and between grazing intensities (intense, moderate, and low) we performed a Kruskal–Wallis test.

## RESULTS

A total of six FGs were identified, mainly grouped by life cycle, lateral spread, and root system traits (Table 2). In both treatments, richness within

**Table 2.** Main Trait Categories Found Inside Each Functional Group (FG)

| FG | Growth form  | Life cycle            | Nitrogen fixer | Leaf size      | Root system       | Lateral spread   | Storage organs | Leaf texture              |
|----|--------------|-----------------------|----------------|----------------|-------------------|------------------|----------------|---------------------------|
| 1  | Grass (forb) | Deciduous (annual)    | No             | Medium (large) | Fibrous           | Tussock (stolon) | No (yes)       | Intermediate              |
| 2  | Shrub (tree) | Deciduous (evergreen) | No (yes)       | Medium (small) | Taproot           | Single shoot     | No             | Coriaceous (intermediate) |
| 3  | Shrub (tree) | Deciduous             | Yes            | Small (medium) | Taproot           | Stolon           | No             | Coriaceous (intermediate) |
| 4  | Forb         | Annual                | No             | Medium (large) | Fibrous (taproot) | Single shoot     | No             | Membranous (intermediate) |
| 5  | Subshrub     | Evergreen             | No             | No leaf        | Taproot           | Single shoot     | Yes            | No leaf                   |
| 6  | Forb         | Deciduous             | No             | Large (medium) | Fibrous (taproot) | Single shoot     | Yes            | Membranous (intermediate) |

Categories shown between brackets were important but less significant in the classification.



**Table 3.** Mean Values (and Standard Deviation) of Species Richness within Each Functional Group (FG 1–6) in Recovered and Disturbed Treatment, in Three Different Grazing Intensities (Intense, Moderate, and Low)

|      | Intense    |            | Moderate    |            | Low         |             |
|------|------------|------------|-------------|------------|-------------|-------------|
|      | Recovered  | Disturbed  | Recovered   | Disturbed  | Recovered   | Disturbed   |
| FG 1 | 6.8 (2.3)  | 3.7 (2.93) | 11.9 (2.41) | 9.4 (1.71) | 12.6 (5.59) | 11.3 (1.91) |
| FG 2 | 6.1 (2.21) | 5.7 (2.8)  | 11.7 (0.9)  | 11 (1.68)  | 13.2 (1.77) | 12.8 (1.82) |
| FG 3 | 0.2 (0.45) | 0.2 (0.45) | 1.6 (0.45)  | 1.2 (0.49) | 1.4 (0.45)  | 0.8 (0.53)  |
| FG 4 | 2.6 (1.81) | 0 (0)      | 4.2 (2.28)  | 2.4 (1.6)  | 6.6 (2.51)  | 2.8 (2.61)  |
| FG 5 | 0 (0)      | 0 (0)      | 0.6 (0.55)  | 0 (0)      | 0.6 (0.55)  | 0.4 (0.55)  |
| FG 6 | 2.4 (1.51) | 0 (0)      | 2.4 (1.67)  | 0 (0)      | 4 (0.71)    | 0.8 (0.45)  |

**Table 4.** Mean Values (and Standard Deviation) of Response Diversity within Each Functional Group (FG 1–6) in Recovered Treatment, in Three Different Grazing Intensities (Intense, Moderate, and Low)

|      | Intense       | Moderate      | Low           |
|------|---------------|---------------|---------------|
| FG 1 | 0.036 (0.015) | 0.045 (0.008) | 0.065 (0.004) |
| FG 2 | 0.091 (0.052) | 0.137 (0.081) | 0.146 (0.089) |
| FG 3 | 0 (0)         | 0.062 (0.002) | 0.003 (0)     |
| FG 4 | 0.002 (0)     | 0.003 (0.01)  | 0.001 (0)     |
| FG 5 | 0 (0)         | 0.049 (0.005) | 0.083 (0.076) |
| FG 6 | 0 (0)         | 0 (0)         | 0 (0)         |

most FGs declined with increasing disturbance intensity (Table 3). Under intense and moderate grazing intensities, the recovery treatment had significantly higher species richness than the disturbed one ( $K = 5.88$ ,  $P = 0.01$ ;  $K = 3.87$ ,  $P = 0.04$ , respectively). Under low grazing intensity, there was no significant difference between treatments ( $K = 1.53$ ,  $P = 0.108$ ). During the grazing exclusion period (recovery treatment) intense grazing sites showed significantly lower richness than low grazing ( $K = 8.23$ ,  $P < 0.001$ ), but there was no difference when compared to moderate grazing ( $K = 2.62$ ,  $P = 0.07$ ). Also, moderate and low grazing intensities did not differ in richness ( $K = 1.16$ ,  $P = 0.28$ ). When cattle disturbance reappeared (disturbed treatment), species richness in intense grazing was significantly lower than in both moderate and low grazing intensities ( $K = 3.71$ ,  $P = 0.04$ ;  $K = 10.94$ ,  $P < 0.001$ , respectively). As in the recovery treatment, moderate and low grazing intensities did not differ in species richness ( $K = 1.91$ ,  $P = 0.17$ ).

Response diversity values ranged from 0 (no diversity in the response) to 0.146 (Table 4). This maximum value of response diversity is low, but FGs with higher values of response diversity in the

recovery treatment were the least affected by the reoccurrence of disturbance (Tables 3, 4). In the redundancy analysis, values of response diversity were not significantly correlated with species richness within FGs during the recovery treatment ( $r = 0.51$ ,  $P = 0.03$ ; Figure 1B), although the correlation value was high. By contrast, in the resilience analysis we found that species richness within FGs in disturbed treatments was significantly and highly correlated with response diversity ( $r = 0.78$ ,  $P < 0.001$ ; Figure 1C).

## DISCUSSION

Our results show that when response diversity within FGs is measured before disturbance, it can be used to predict which FGs are more resilient, and hence, less vulnerable to be affected after the occurrence of the disturbance. This can be seen in the positive and significant relationship between response diversity within FGs before disturbance (exclusion period), and species richness with the reappearance of the disturbance (grazing period). We examined both intensity of disturbance as well as a temporal component of disturbance, to show that groups with the lowest response diversity values were the most affected, losing species or even disappearing entirely when the disturbance reoccurred or became more intense. By assessing response diversity changes along a grazing gradient (spatial variation of disturbance intensity), our results confirm those of Laliberté and others (2010) who, using a meta-analysis showed that land-use intensification negatively affected the value of response diversity. However, as there was no time scale considered in that study (that is, before and after disturbance), these results could not examine the potential of response diversity as a quantitative measure to predict responses to environmental changes. Our study shows that response diversity is

sensitive to short-term (that is, 1 year) temporal changes in ecosystems under disturbance and thus could be an effective tool to assess and evaluate the degree of ecological resilience. Future studies with longer time scales than the one used in this study, and different kinds of disturbance regimes could use the general approach outlined here.

It has been suggested that species richness is not always equivalent to functional richness (Díaz and Cabido 2001), and in particular to response diversity (Elmqvist and others 2003). Indeed, we found no significant correlation between species richness and response diversity in recovery sites (although a trend could be inferred). As an example, FG 1 and 2 have similar mean richness in moderate and low disturbance intensities (in recovery treatment), but their response diversity values are very different. For FG 1, the response diversity value is similar to the one of FG 5, which has much lower mean richness. Although, the statistical test was not significant, the correlation value was high, and this demands further attention. This is related to the debate of whether biodiversity ensures the stability of ecosystem functions (McCann 2000). Most studies were done with experimental or modeled communities, and proved that in most cases, higher diversity leads to the stability of communities by increasing the function or decreasing its variance (Tilman and others 2006; Isbell and others 2009). In addition, as the Insurance Hypothesis states, biodiversity insures ecosystem functioning if higher species richness guarantees that some will maintain the function when others disappear (Yachi and Loreau 1999). It had been suggested that response diversity can be high even with low values of species richness if the remaining species are widely dispersed in the response trait space (Elmqvist and others 2003; Laliberté and others 2010). Although, our results do not allow us to further explore this debate, we believe that both mechanisms are important. What we can suggest is that in our study site, species richness is not to be ignored, but on its own, it does not ensure resilience; rather response diversity is more important in this regard.

The quantification of response diversity within FGs before disturbance provides a clue to determine which groups are more vulnerable to future disturbance. Furthermore, when analyzing the traits that define the FG, we can get an idea of the contribution of the group to an ecosystem function. In our case study, the most affected FGs (with lower values of response diversity) were those with traits related to litter formation and soil retention (mainly forbs, annual or deciduous, and fibrous as main root system). The loss of these effect traits

may favor the shift to a more desertified state of the ecosystem. To avoid such shifts, recent research suggested that the identification of rising variance in the ecosystem (that is, increasing standard deviation) along time series may signal forthcoming shifts (Carpenter and Brock 2006). Nevertheless, as such changes may occur once a regime shift is initiated, researchers call for the need for detecting critical indicator levels of response variables rather than simply changes in the variable values (Biggs and others 2009). The local scale analysis that we propose here, comparing response diversity values among FGs and the traits that characterize the groups, may give us information about critical indicator values. For example, we were able to determine the most vulnerable groups and the disturbance intensity at which they lose resilience. Ultimately, this information can be used to implement strategies and specific policies to manage biodiversity with enough insurance to cope with future changes, and implement management strategies with specific priorities of conservation in production systems (Folke and others 2002; Elmqvist and others 2003).

It is important to consider that when FGs are assessed according to a specific function (Petchey and Gaston 2006) and response diversity is assessed regarding a specific disturbance factor (Elmqvist and others 2003) the strength of the prediction will be higher and more reliable for management strategies. It is also important to consider that ecosystems perform multiple functions, and greater biodiversity is needed to preserve this multifunctionality (Hector and Bagchi 2007). In our study, we assessed the resilience of the plant community using traits related to a specific ecosystem function (nutrient cycling and soil retention), thus further research is needed to assess the use of this resilience indicator for multiple ecosystem functions. Furthermore, we note that our results show only a partial functional response of the community to disturbance, only focusing on vegetation. How these responses at the primary producer level will reverberate across the whole community assemblage is also of interest and yet to be determined. Further research is also needed to assess the use of this resilience surrogate in other types of ecosystems, disturbances, processes, and time scales. With the increased availability of information about plant traits through global initiatives such as TRY (Kattge and others 2011), this should become an increasingly feasible task. This information will be useful to evaluate the potential generalization of response diversity as an indicator of ecosystem vulnerability and potential shifts in ecosystem states under environmental fluctuations.

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