RESEARCH ARTICLE

Long-term and year-to-year stability and its drivers in a Mediterranean grassland

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Abstract

1. Understanding the mechanisms underlying community stability has become an urgent need to protect ecosystems from global change and resulting biodiversity loss. While community stability can be influenced by species richness, synchrony in annual fluctuations of species, species stability and functional traits, the relative contributions of these drivers to stability are still unclear. In semi-natural grasslands, land-use changes such as fertilization might affect stability by decreasing richness and influencing year-to-year fluctuations. In addition, they can promote long-term directional trends, shifting community composition and influencing grassland maintenance. Thus, it is important to consider how species and community stability vary year-to-year but also in the long term.

2. Using a 14-year vegetation time series of a species-rich semi-natural Mediterranean grassland, we studied the relative importance of richness, synchrony, species stability and functional traits on community stability. To assess land-use change effects on stability, we applied a fertilization treatment. To distinguish stability patterns produced by year-to-year fluctuations from those caused by long-term trends, we compared the results obtained using a detrending approach from those without detrending.

3. Independently of the treatment and approach applied, the most stable communities were those composed of asynchronous species with low specific leaf area. Fertilization decreased year-to-year and long-term community stability by increasing community-weighted mean of specific leaf area, decreasing species stability or also reducing richness in the case of year-to-year stability. Additionally, traits such as seed mass had an indirect effect on stability through synchrony. Long-term trends appeared in control and fertilized plots (due to fertilization), decreasing community and species stability and leading to differences in the relationships found between community stability and some of its drivers. This reflects the importance of accounting for the effect of temporal trends on community and species stability using both a long-term and a year-to-year approach.

4. *Synthesis.* Stability is influenced by richness, synchrony and functional traits. Fertilization decreases species and community stability by promoting long-term trends in species composition, favouring competitive species and decreasing richness. Studying stability at the community level and species level, and accounting for the effect of trends is essential to understand stability and its drivers more comprehensively.

1 | INTRODUCTION

The current global change and resulting biodiversity loss pose a threat to ecosystem functioning and highlight the need for a better understanding of the mechanisms underlying community stability (Craven et al., 2018; McCann, 2000; Sala et al., 2000). Community stability can be defined as the inverse of the variability in total community abundance over time (McCann, 2000; Tilman, 1999). For a long time, stability has been thought to be positively related to species diversity (Elton, 1958; Lepš et al., 2018; McCann, 2000; Tilman et al., 2006). In this sense, a higher number of species in a community might provide it with a wider range of responses to environmental changes, which will result in a more stable community (McCann, 2000). However, the actual pathways or processes explaining the stability–diversity relationship are still unclear, with a high number of studies suggesting different mechanisms to explain this relationship (Craven et al., 2018; Lepš, 2004; Loreau & de Mazancourt, 2013; McCann, 2000; Valencia, de Bello, Galland, et al., 2020).

Theory suggests three main driving components of stability in natural plant communities. The first component is the stability of individual species (Doak et al., 1998; Lepš et al., 2018; Thibaut & Connolly, 2013). The higher the stability in the abundance of individual species, the higher the stability of the total community. In this regard, dominant species, which tend to be highly stable (Roscher et al., 2011), are thought to play an important role in community stability (Valone & Balaban-Feld, 2018). However, community stability is also influenced by the degree of synchrony (i.e. concordance) in annual fluctuations of species (Blüthgen et al., 2016; Valencia, de Bello, Galland, et al., 2020). In this sense, it is often hypothesized that synchrony between species decreases community stability, while asynchrony (discordance) increases it. Synchrony can be due to similar responses of individual species to environmental fluctuations (mostly inter-annual weather fluctuations) (Lepš et al., 2018; Loreau & de Mazancourt, 2008), leading to concordant increases or decreases. In their sum, synchronously fluctuating populations of individual species will lead to higher variability of total community abundance. On the other hand, asynchrony can be due to slightly different responses to weather fluctuation, to demographic stochasticity or to competitive interactions (Lepš, Šmilauerová,

& Šmilauer, 2019; Loreau & de Mazancourt, 2008; Loreau & de Mazancourt, 2013). In this case, the decrease in the abundance of one species (e.g. due to competitive pressure) is compensated by the growth of other species, and the total abundance remains stable (i.e. compensatory dynamics; Lepš et al., 2018; Tilman, 1996; Gonzalez & Loreau, 2009). Related to this, species richness or diversity can be also an important driver of community stability. The insurance hypothesis argues that species richness increases the probability that communities contain species with different responses to environmental conditions and perturbations, leading to compensation (asynchrony) among species and thus, to an increase in community stability (Craven et al., 2018; McCann, 2000; Yachi & Loreau, 1999).

In addition to species richness, it has been found that other facets of diversity, in particular functional diversity, can influence community stability (Craven et al., 2018; Díaz & Cabido, 2001). Species with different functional strategies responding in different ways to similar weather fluctuations will promote asynchrony and enhance community stability (Lepš et al., 2018; Roscher et al., 2011). Nevertheless, asynchrony can also occur between pairs of functionally similar species due to competition (Lepš et al., 2018). In the same way, the functional composition, expressing the traits of the most abundant species in a community, can also influence stability (Craven et al., 2018; Díaz & Cabido, 2001; Polley et al., 2013). For example, it is hypothesized that conservative or 'slow' species with slow rates of growth, resource acquisition and tissue turnover tend to be more stable than exploitative or 'fast' species with opposite strategies (Craven et al., 2018; Májekova et al., 2014). The difference between slow and fast species is generally associated with the leaf economics spectrum (Reich, 2014; Wright et al., 2004), with high values of leaf dry matter content (LDMC) and low specific leaf area (SLA) representing slow species, and vice versa for fast species (Májekova et al., 2014; Polley et al., 2013). The leaf economics spectrum can be extended to a whole-plant economics spectrum (Reich, 2014), adding traits such as plant height and seed mass, related to life-history and reproductive strategies (Májekova et al., 2014; Westoby, 1998).

Not only biotic factors, but also abiotic factors such as changes in nutrient availability or environmental productivity might influence community stability, mostly indirectly via the aforementioned drivers (Lepš, 2004; Lepš et al., 2018; Zhang et al., 2016). In this regard, land-use changes such as fertilization are known to reduce species

diversity in semi-natural grasslands, negatively influencing the stability of plant communities and its functioning (Gazol et al., 2016; Lepš et al., 2018; Sala et al., 2000; Vitousek et al., 1997). Fertilization can also indirectly influence community stability by decreasing species stability and leading to changes in synchrony (Hautier et al., 2014; Lepš, 2004; Lepš et al., 2018; Zhang et al., 2016). In addition, fertilization may also lead to changes in both taxonomical and functional composition, favouring tall plants with large SLA and low LDMC (Gazol et al., 2016).

All the above-mentioned processes can indirectly affect species and community stability at the scale of year-to-year fluctuations, but also in the long term. That is, species can also follow more long-term trajectories (Lepš, Götzenberger, et al., 2019) leading to changes in community structure and composition. Such long-term directional trends can be due to land-use changes, climate change or to succession after disturbance, among other processes, and are particularly frequent in grasslands (Lepš, Götzenberger, et al., 2019; Stevens et al., 2011; Valencia, de Bello, Lepš, et al., 2020). Land-use changes such as fertilization can lead to the presence of relatively long-term trends due to the legacy effects over time of past fertilization treatments and can modulate the impact of climate change (McIntyre et al., 2017). Long-term trends present a methodological and conceptual issue when studying synchrony and community stability (Lepš, Götzenberger, et al., 2019; Valencia, de Bello, Lepš, et al., 2020). Regarding synchrony, similar directional trends in two species can make these species appear to be synchronous, masking the actual signal of year-to-year fluctuations and leading to a misinterpretation of year-to-year synchrony. In the case of stability, opposite directional trends might have a stabilizing effect on the community, independently of year-to-year fluctuations. Two methods to remove the effect of long-term trends on synchrony and stability measures are using residuals of fitted species trends, or the three-term local quadrat variance (T3; Hill, 1973), by which the covariation between two species abundances is studied in three-year moving windows (Lepš, Götzenberger, et al., 2019). Despite their importance, there are still few temporal vegetation studies accounting for the effect of long-term trends on synchrony and stability (Lepš, Götzenberger, et al., 2019; Valencia, de Bello, Lepš, et al., 2020).

Here, we use a 14-year vegetation time series of a species-rich, semi-natural grassland to study (1) How the stability of individual species, synchrony and species richness influence community stability. (2) Whether both species and community stability are influenced by functional traits. (3) How changes in land-use (fertilization) influence each of these variables and their relationships. (4) Whether accounting for long-term trends influences our ability to quantify species and community stability and its drivers. In particular, we expect that (1) Community stability will increase with higher species stability and asynchrony, and higher species richness. (2) From a functional perspective, the most stable communities are expected to be those with higher functional diversity or dominated by conservative species (high LDMC and low SLA). (3) Fertilization reduces species stability and richness, and changes the degree of synchrony, finally decreasing community stability. (4) In addition, fertilization

creates long-term directional trends in species and community stability, apart from inducing year-to-year fluctuations.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

The study site is a semi-natural species-rich Mediterranean calcareous grassland (*Helianthemo italici-Aphyllanthion monspeliensis*) located near the village of Napal, 35 km east of Pamplona, Northern Spain (42°43′N, 1°13′W; 810 m a.s.l.). Average annual temperature is 12°C, ranging from 4°C in January to 21°C in August, and annual cumulative precipitation is 884 mm, ranging monthly from 38 mm in July to 99 mm in October (Gobierno de Navarra, 2021). Soils are developed over Eocenic marls on 5–15° south-facing slopes. Traditional management consisted of extensive sheep grazing, but it has markedly decreased in the last decades. The study site is located at the boundary between the Eurosiberian and Mediterranean regions (Moreno et al., 1990), which makes this grassland very species rich (with an average of 34 species of vascular plants per m²). The community is dominated by perennial herbs such as *Brachypodium retusum* and *Aphyllanthes monspeliensis*, accompanied by woody species (dwarf shrubs) such as *Dorycnium pentaphyllum* and *Genista scorpius*, and also by tiny annuals such as *Bupleurum baldense*. The small size of plant individuals also contributes to the high species richness in this grassland. Nomenclature follows Castroviejo (1986–2021).

In 2003, 12 plots of 15 × 5 m (hereafter called macro-plots) were established inside an area of 5500 m². Half of the macro-plots (six) were used as control plots and half were fertilized with sewage sludge in a single event in 2003, applying manually to the soil surface 5 kg m⁻² (see soil chemical characteristics of the plots in Table S1; for more details see Gazol et al., 2016). The sludge came from a municipal urban wastewater treatment plant located in Tudela (Navarra, Spain), and it was sludge previously dried to 28% dry matter by centrifugation. Plots were sufficiently separated from each other to avoid runoff and the movement of fertilizers between them. The 5500 m² area was fenced to avoid possible interferences in the experiment caused by differential grazing intensity between treatments (Gazol et al., 2016).

To accurately assess vegetation changes, a 1 × 1 m permanent plot was placed in the centre of each macro-plot. Every year for 14 consecutive years (from 2004 to 2017), at the end of June, vegetation was sampled by R. Ibáñez, who identified and recorded every vascular plant species present in each of the permanent plots (Table S2). The 1 × 1 m permanent plots were divided into 100 10 × 10 cm subplots to measure species abundance (frequency) by counting the number of 10 × 10 cm subplots in which the species was present (presence was recorded if shoots overlapped with the sampling unit/subplot, not exclusively if plants rooted). Fieldwork was carried out after obtaining the appropriate permit from Gobierno de Navarra, which is the owner of the land where the study took place.

2.2 | Richness, synchrony and stability measures

Species richness in each permanent plot was measured both as cumulative species richness, counting the number of species found at least once in a permanent plot during the 14 years of the study, and as mean species richness, averaging the number of species found in a permanent plot over the 14 years (Lepš et al., 2018). Community-level synchrony for each permanent plot was calculated using the log variance ratio index ('Logvar'), which is the log-transformation of the ratio of observed to expected variance (i.e. the ratio of variance of the total community abundance to the sum of variances of the abundance of each species; Lepš et al., 2018; Roscher et al., 2011). This is calculated as:

$$\text{logvar} = \log \left[\text{var} \left(\sum_{i=1}^{nsp} X_i \right) \Big/ \sum_{i=1}^{nsp} \text{var} \left(X_i \right) \right], \quad (1)$$

where nsp is the total number of species in the community and X_i is the abundance of species i (Lepš et al., 2018). This index has the advantage of expressing random fluctuations as 0, synchrony with positive and asynchrony with negative values (Lepš et al., 2018). Other synchrony indices were checked (e.g. abundance weighted 'Eta', 'Phi' and variance ratio index; Blüthgen et al., 2016; Loreau & de Mazancourt, 2008; Schluter, 1984), resulting in similar patterns. Stability at both the community level and the species level was calculated as the inverse of the coefficient of variation (CV^{-1}) across years of cumulative or individual species abundances in each permanent plot.

As previously explained, both synchrony and stability can be influenced by the presence of long-term directional trends at the species level and community level. Having information about trends was crucial in our study, especially when one of the expected effects of fertilization was to promote the appearance of trends in the species and communities studied. However, to distinguish the patterns produced by long-term trends from those caused by year-to-year fluctuations, we also used the three-term local quadrat variance detrending method (T3; Hill, 1973) to remove the effect of long-term trends both on synchrony and stability indices (Lepš, Götzenberger, et al., 2019). This method consists in calculating the variance in 3-year time periods, as:

$$T3 = \frac{\sum_{i}^{n-2} \left(X_i - 2X_{i+1} + X_{i+2} \right)^2}{6 \left(n-2 \right)}. \quad (2)$$

where n is the number of years in the temporal series, and X_i is the abundance of a species in year i. Consequently, we calculated synchrony (log variance ratio) and stability (CV^{-1}) indices using both the non-detrending (hereafter 'long-term' synchrony and stability) and the T3-detrending approach (hereafter 'year-to-year' synchrony and stability) (Valencia, de Bello, Lepš, et al., 2020). The equation used to calculate year-to-year synchrony was similar to that used to calculate long-term synchrony (Equation 1), with the difference that the variance used in the equation was the T3 variance (Equation 2; Lepš,

Götzenberger, et al., 2019). All synchrony and stability indices were calculated using the *calc_sync* function of the package 'TEMPO' in R (Lepš, Götzenberger, et al., 2019).

2.3 | Plant functional traits and indices

We obtained data for five functional traits (plant height, leaf dry matter content or LDMC, specific leaf area or SLA, leaf area or LA and seed mass or SM; Table S3) for most of the species present in the 1×1 m permanent plots (data available for 98%, 78%, 84%, 98% and 85% of the species, respectively). Trait data were collected in-situ. Although the number of individuals measured for each trait varied, traits were measured following the protocols provided by Cornelissen et al. (2003). Missing data were obtained from BROT, a trait database for Mediterranean Basin species (Tavşanoğlu & Pausas, 2018; Tables S4 and S5), or from TRY database (Kattge et al., 2020; Tables S4 and S6). We presumed that there would not be important differences between direct measurements and data from databases, especially when using the Mediterranean BROT database. Moreover, interspecific variation is usually higher than intraspecific variation, and species ranking is known to be well conserved across data sources for the five traits used (Kazakou et al., 2014). Plant height was measured as the distance from ground to the highest photosynthetic tissue, and it is often associated with competitive vigour, whole-plant fecundity and with plant ability to establish between disturbances (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013). LDMC and SLA are inversely correlated with each other, with higher LDMC being related to a lower relative growth rate and productivity and to a longer life span, while higher SLA is associated with a higher growth rate and a shorter life span (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013). LA is the one-sided area of a leaf and it is negatively associated with drought stress, nutrient stress and disturbance (Pérez-Harguindeguy et al., 2013). Finally, SM is the oven-dry mass of a seed and is positively related to resource storage and survival in the face of environmental hazards (i.e. drought, deep shade) and negatively related to seed longevity in seedbanks. In addition, closely related taxa tend to have more similar SM (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013). Mean trait values and abundance data for each species were used to calculate community functional composition and functional diversity for the five traits studied. Functional composition was measured as the community-weighted mean (CWM; Garnier et al., 2004) and functional diversity as the Rao quadratic index (Rao, 1982), which is the sum of pairwise functional distances between species weighted by relative abundance (Mouchet et al., 2010). Changes in species richness are known to have spurious effects on Rao index, leading to wrong conclusions (Pavoine et al., 2013). However, the high species richness found in our plots (with an average of 34 species in control plots and 28 in fertilized plots) made the effects of changing richness negligible (Mason et al., 2013). To calculate these indices, we used the function *dbFD* of the 'FD' package in R (Laliberté et al., 2014; Laliberté & Legendre, 2010).

2.4 | Data analysis

One of our aims was to study how fertilization influenced stability, synchrony and species richness at the community level. In addition, we wanted to test whether the values displayed by these indices and their response to fertilization changed depending on the approach used to calculate them (e.g. long term or year to year). To test this, we carried out three multiple linear regression models using as response variables the stability, synchrony or species richness index in each plot, respectively. As explanatory variables we used the treatment applied in each plot (i.e. control or fertilized), the approach used to calculate de index (i.e. long-term or year-to-year stability and synchrony, and cumulative or mean species richness), and the interaction between both.

To discover the main drivers of community stability, we used different linear regression models to test for relationships between community stability (long term and year to year) and synchrony, richness, functional composition and diversity of the five traits studied and treatment. The explanatory variables were calculated in different ways depending on if we studied long-term or year-to-year stability so that the variables would as well reflect 'accumulated' or 'yearly' values. For long-term stability, we used long-term synchrony and cumulative species richness, and the functional composition and diversity indices were calculated using the cumulative abundance of each species across all years. By contrast, for year-to-year stability, we used year-to-year synchrony and mean species richness across years, and the functional composition and diversity were calculated separately for each plot and year and then averaged across all years. This way, the first type of models was more focused on detecting processes acting across years and promoting trends, while the second type was focused on year-to-year processes. We build linear regression models by first running simple regression models for each explanatory variable and then applied multiple regression models with synchrony, richness, treatment and the functional indices selected as significant or marginally significant in the simple models.

For a deeper understanding of the processes underlying community stability, we then studied stability at the species level. Species stability was averaged over control and over fertilized plots. As we found some extreme values corresponding to highly stable species (*Brachypodium retusum* and *Aphyllanthes monspeliensis*; Table S2, Figure S1), we log-transformed average species stability. We tested for relationships between log-transformed species stability (long term and year to year) and the five functional traits studied. We first used simple models for each trait and when a certain trait was significant we did multiple models using trait, treatment and the interaction between both as explanatory variables. On the other hand, we also studied how fertilization influenced species stability, checking if results changed when using the long-term or year-to-year approach. We calculated the Pearson's correlation coefficient and applied a paired *t*-test to test for differences in species stability between control and fertilized plots and between the long-term and year-to-year approach. All analyses were carried out with the *lm*, *cor.test* and *t.test* functions in R software (v. 4.0.3; R Core Team, 2020).

3 | RESULTS

3.1 | Species richness and composition

The number of species recorded over the 14-year period (2004–2017) in the 12 plots was 129. From these, 96 species were found at least once in control plots, while 120 were found in fertilized plots. However, in terms of mean richness, control plots had 34 ± 3 species, while fertilized plots had 28 ± 4 species. Thus, cumulative richness was higher in fertilized plots, while mean richness was higher in control plots (Figure 1a). The most frequent species found in control plots were *Brachypodium retusum*, *Aphyllanthes monspeliensis*, *Carex flacca*, *Dorycnium pentaphyllum* and *Thymus vulgaris* subsp. *vulgaris*. The most frequent species in fertilized plots were *Brachypodium retusum*, *Dorycnium pentaphyllum*, *Aphyllanthes monspeliensis*, *Genista scorpius* and *Arrhenatherum elatius* subsp. *elatius* (Table S2). These most frequent species, apparently the dominant larger perennial species in the community, were also the most stable ones (Table S2).

3.2 | Synchrony and stability indices

Similarly to mean richness, both synchrony and stability were significantly lower in fertilized plots (Figures 1b,c). This negative effect of fertilization was consistent across approaches (long term and year to year), both for synchrony and stability. However, we found that the values of the indices changed from one approach to another. In the case of synchrony (Figure 1b), we found slightly higher values for year-to-year synchrony compared to long term, although these differences were not significant. Regarding stability, year-to-year stability was significantly higher than long-term stability (Figure 1c).

3.3 | Drivers of community stability

Simple regression models (Table 1) showed that long-term stability was not significantly influenced by long-term synchrony or cumulative species richness, but it was negatively influenced by fertilization (Figure 1c), high CWM of SLA and low CWM and diversity of SM. In contrast, in the multiple regression model long-term stability decreased with long-term synchrony and high CWM of SLA and SM (Table 1, Figure S2a).

On the other hand, year-to-year stability was negatively related to fertilization in simple regression models, in the same way as long-term stability, but it also had a significant and positive relationship with mean species richness (Table 1). Regarding community functioning, year-to-year stability decreased in communities with high CWM and diversity of SLA, not being influenced by SM. When putting all variables together in a multiple regression model (Table 1, Figure S2b), the results for year-to-year stability were almost similar to those of long-term stability: year-to-year stability decreased with year-to-year synchrony and high CWM of SLA, similarly to long-term stability, but also increased with mean species richness. We found
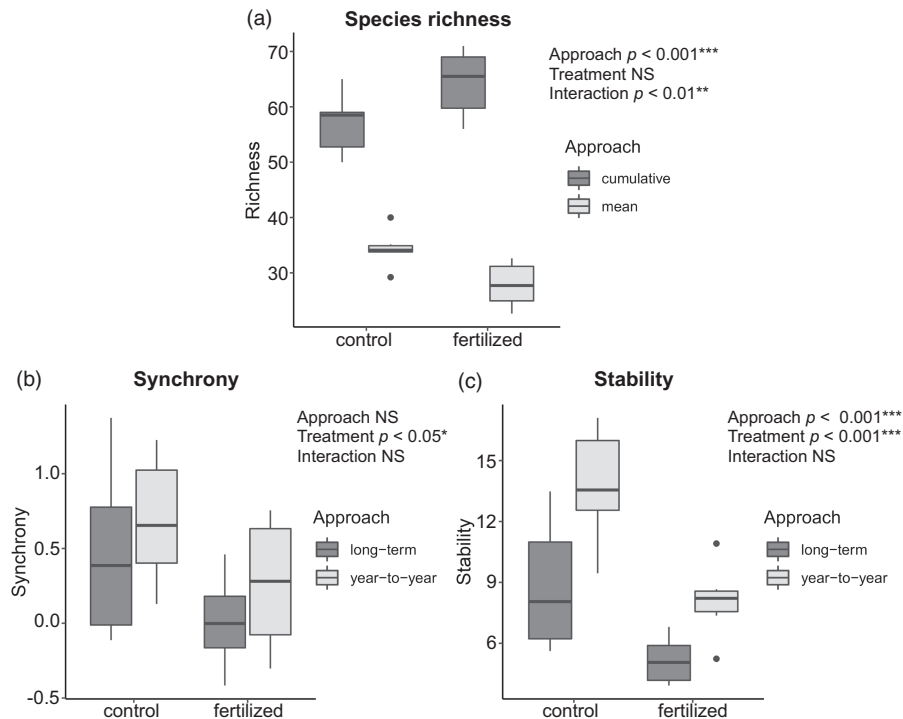
FIGURE 1 Boxplots showing the response of species richness (a), synchrony (b) and stability (c) to treatment, and the different results obtained when comparing long-term and year-to-year approach (in the case of species richness, calculated with cumulative and mean richness, respectively). Significance values (*p* values from the *F*-test) show the results of the multiple linear regression models testing for relationships between the respective index values and the approach used (long-term or year-to-year), treatment (control or fertilized) and their interaction. NS means not significant. The degrees of freedom are 20 in the three models

no significant effects of fertilization and functional diversity in multiple regression.

3.4 | Stability vs functional traits at the species level

Simple regression models showed that among the five traits studied, LDMC and SLA had a significant influence on both long-term and year-to-year stability at the species level (Table 2). In particular, the most stable species within the community were related to higher values of LDMC and lower values of SLA (Table 2).

When applying a multiple model to test for the effect of LDMC, treatment and the interaction between both on species stability, we found similar results (Table 2). The multiple regression models showed that both long-term and year-to-year species stability were significantly and positively related to higher values of LDMC (Table 2, Figure 2a,c), and this happened both in control and fertilized plots. In addition, long-term and year-to-year species stability were negatively related to fertilization (Table 2, Figures 2a,c).

When testing for the effect of SLA, treatment and the interaction between both in multiple regression models, we found similar results as in simple regression models (Table 2, Figures 2b,d). The most stable species both in the long term and year to year were those with lower values of SLA (e.g. *Brachypodium retusum*, *Aphyllanthes monspeliensis*, *Dorycnium pentaphyllum*, *Globularia vulgaris*; Table 2,

Figures 2b,d and Figure S1). However, the change in species stability in response to SLA depended on the treatment applied, according to the marginally significant interaction (Table 2, Figures 2b,d). In particular, the increase in species stability with lower values of SLA was stronger in control than in fertilized plots, as reflected in the slope of the regression line (Figures 2b,d). In addition, both long-term and year-to-year species stability were lower in fertilized plots.

3.5 | Stability of individual species

The results obtained from comparing species stability between treatments showed that both for long-term and year-to-year species stability there was a significant and positive correlation between control and fertilized plots (long term: $r = 0.62$, $p < 0.001$, $df = 85$, Figure 3a; year to year: $r = 0.61$, $p < 0.001$, $df = 85$, Figure 3b). On the other hand, the results from the paired *t*-test showed that both long-term and year-to-year species stability were significantly higher in control plots than in fertilized plots (long term: mean of the differences = 0.134, $p < 0.001$, $df = 86$; year to year: mean of the differences = 0.115, $p < 0.01$, $df = 86$). This is visually reflected in Figure 3a,b by the fact that most points lie below the 1:1 line.

When testing the effect of long-term trends on species stability, we found similar results for control and fertilized plots (Figures 3c,d). There was a significant and positive correlation between long-term and year-to-year species stability, both in control ($r = 0.95$, $p < 0.001$,

TABLE 1 Results of simple (left side) and multiple (right side) linear regression models testing for relationships between community stability (long term and year to year) and richness, synchrony, treatment and functional composition (CWM) and diversity (Rao) of the five traits studied (plant height, leaf dry matter content, specific leaf area, leaf area and seed mass). The values presented in the table are the estimate with the standard error (SE), the F value, the p value associated with the F-test and the degrees of freedom of each model (df). Each variable was calculated in a different way depending on the model used, accounting for long-term trends or not. The variables used in multiple models were richness, synchrony, treatment and the functional indices selected as significant or marginally significant in the simple models. Significant or marginally significant relationships are highlighted in bold (significance codes: 0 <'***' ≤ 0.001<'**' ≤ 0.01<'*' ≤0.05<'.' ≤ 0.1). Degrees of freedom are not shown in the simple linear regression because it is always 10

Simple linear regression models

	Estimate ± SE	F value	p value (F-test)
Long-term stability			
Richness (cumulative)	−0.167 ± 0.128	1.689	0.223
Synchrony (long-term)	−0.485 ± 1.836	0.070	0.797
Treatment	−3.648 ± 1.393	6.859	**0.026***
Single traits (cumulative)			
CWM			
Plant height	−0.181 ± 0.262	0.475	0.506
LDMC	0.038 ± 0.088	0.190	0.672
SLA	−1.029 ± 0.392	6.883	**0.025***
LA	−0.759 ± 1.416	0.288	0.604
SM	1.502 ± 0.634	5.606	**0.039***
Rao			
Plant height	−14.771 ± 12.954	1.300	0.281
LDMC	−6.911 ± 8.454	0.668	0.433
SLA	−5.167 ± 3.663	1.990	0.189
LA	−3.328 ± 6.723	0.245	0.631
SM	34.819 ± 14.144	6.060	**0.034***
Year-to-year stability			
Richness (mean)	0.481 ± 0.185	6.763	**0.027***
Synchrony (year-to-year)	1.575 ± 2.452	0.412	0.535
Treatment	−5.676 ± 1.383	16.849	**0.002****
Single traits (mean)			
CWM			
Plant height	−0.270 ± 0.308	0.767	0.402

Multiple linear regression model (richness + synchrony + treatment + CWM + Rao)

	Estimate ± SE	F value	p value (F-test)	df
Long-term stability				
Richness + Synchrony + Treatment + CWM + Rao				5
Richness (cumulative)	0.056 ± 0.097	0.037	0.856	
Synchrony (long-term)	−5.402 ± 1.569	24.680	**0.004****	
Treatment	−0.762 ± 2.419	0.099	0.766	
CWMSLA (cumulative)	−1.875 ± 0.779	24.560	**0.004****	
CWMSM (cumulative)	−2.107 ± 2.658	5.274	**0.070.**	
RaoSM (cumulative)	52.079 ± 57.118	0.591	0.477	
Year-to-year stability				
Richness + Synchrony + Treatment + CWM + Rao				6
Richness (mean)	0.336 ± 0.108	8.470	**0.027***	
Synchrony (year-to-year)	−4.143 ± 1.046	19.948	**0.004****	
Treatment	−0.817 ± 1.586	0.265	0.625	

TABLE 1 (Continued)

Simple linear regression models	Estimate ± SE	F value	p value (F-test)	Multiple linear regression model (richness + synchrony + treatment + CWM + Rao)	Estimate ± SE	F value	p value (F-test)	df
LDMC	0.043 ± 0.107	0.157	0.700					
SLA	−1.774 ± 0.386	21.143	0.001***	CWMSLA (mean)	−1.967 ± 0.933	80.774	0.0001***	
LA	1.610 ± 1.768	0.829	0.384					
SM	0.394 ± 1.044	0.143	0.714					
Rao								
Plant height	−22.059 ± 17.811	1.534	0.244					
LDMC	3.248 ± 12.433	0.068	0.799					
SLA	−12.200 ± 5.397	5.110	0.047*	RaoSLA (mean)	2.555 ± 6.543	3.522	0.110	
LA	10.189 ± 7.756	1.726	0.218					
SM	16.520 ± 22.980	0.517	0.489					

$df = 94$) and in fertilized plots ($r = 0.89$, $p < 0.001$, $df = 118$). On the other hand, the paired t-test showed that year-to-year species stability was significantly higher than long-term species stability both in control (mean of the differences $= −0.151$, $p < 0.001$, $df = 95$; Figure 3c) and in fertilized plots (mean of the differences $= −0.151$, $p < 0.001$, $df = 119$; Figure 3d).

4 | DISCUSSION

The results obtained support our first hypothesis indicating that community stability will increase with higher species richness and asynchrony, and also showed that accounting for long-term trends influenced these relationships. As expected in our second hypothesis, both species and community stability were influenced by functional traits, finding higher stability in communities dominated by conservative species (e.g. with lower SLA). Finally, our results were consistent with our hypotheses about the negative effect of fertilization on species and community stability, and about the presence of long-term trends, which decreased stability at both the community level and the species level, and which led to differences in the relationships found between community stability and some of its drivers.

4.1 | Drivers of community stability

Focusing on the results from multiple regression models, the significant negative effect of synchrony on long-term stability is consistent with theory suggesting that asynchronous or compensatory dynamics between the species of the community decrease total variability and enhance community stability (Gonzalez & Loreau, 2009; Kigel et al., 2021; Valencia, de Bello, Galland, et al., 2020; Wilcox et al., 2017; Yang et al., 2012). The negative effect of a high CWM of SLA on long-term community stability suggests that communities dominated by species with more acquisitive traits are less stable than communities dominated by conservative species, as has been found in other studies (Májeková et al., 2014; Polley et al., 2013). This also reflects the impact that highly abundant species can have on community functional composition and community stability (Polley et al., 2013; Valone & Balaban-Feld, 2018), which is due to the fact that the indices used to calculate functional composition (CWM) and stability (CV^{-1}) account for species abundance, in such a way that abundant species contribute more to these indices than rare species. In accordance with the marginally significant effect of CWM of SM on long-term stability, certain characteristics related to seed mass (SM) such as seed dormancy (Pérez-Harguindeguy et al., 2013) have been found to determine the coexistence of different annual plant species and the survival of annuals in unfavourable periods, which might contribute to community stability (Chesson et al., 2004).

These results contrast with the lack of significant influence of cumulative richness, which appears to contradict previous studies showing a positive relationship between species richness and

TABLE 2 Results of simple (left side) and multiple (right side) linear regression models testing for relationships between species stability (long term and year to year) and the values of the five traits studied (plant height, leaf dry matter content, specific leaf area, leaf area and seed mass). The values presented in the table are the estimate with the standard error (SE), the F value, the p value associated with the F-test and the degrees of freedom of each model (df). The variables used in multiple models were the traits selected as significant in the simple models (LDMC or SLA), treatment (control and fertilized), and the interaction between treatment and the trait studied. Significant or marginally significant relationships are highlighted in bold (significance codes: $0 < '{***}' \leq 0.001 < '{**}' \leq 0.01 < '{*}' \leq 0.05 < '.' \leq 0.1$)

Simple linear regression models

	Estimate ± SE	F value	p value (F-test)	df
Long-term stability				
Plant height	0.001 ± 0.001	1.994	0.159	210
LDMC	0.001 ± 0.0002	12.374	**0.001***	163
SLA	−0.014 ± 0.002	30.349	**1.26e-07***	177
LA	3.408e-05 ± 1.064e-03	0.001	0.974	210
SM	−4.686e-05 ± 1.198e-04	0.153	0.696	179
Year-to-year stability				
Plant height	0.002 ± 0.001	2.391	0.124	210
LDMC	0.001 ± 0.0003	11.383	**0.001***	163
SLA	−0.017 ± 0.003	26.472	**7.05e-07***	177
LA	−0.001 ± 0.001	0.423	0.516	210
SM	−6.357e-05 ± 1.638e-04	0.151	0.698	179

Multiple linear regression models (trait + treatment + interaction trait:treatment)

	Estimate ± SE	F value	p value (F-test)	df
Long-term stability				
LDMC + Treatment + Interaction				
LDMC	0.001 ± 0.0003	13.157	**0.0004***	161
Treatment	−0.206 ± 0.132	12.114	**0.001***	
Interaction	0.0002 ± 0.0005	0.193	0.661	
SLA + Treatment + Interaction				
SLA	−0.018 ± 0.004	32.898	**4.186e-08***	175
Treatment	−0.288 ± 0.087	13.258	**0.0004***	
Interaction	0.009 ± 0.005	3.612	**0.059.**	
Year-to-year stability				
LDMC + Treatment + Interaction				
LDMC	0.001 ± 0.0005	11.768	**0.001***	161
Treatment	−0.328 ± 0.179	6.412	**0.012***	
Interaction	0.001 ± 0.001	1.109	0.294	
SLA + Treatment + Interaction				
SLA	−0.023 ± 0.005	27.810	**3.912e-07***	175
Treatment	−0.340 ± 0.120	7.713	**0.006****	
Interaction	0.012 ± 0.007	3.238	**0.074.**	

FIGURE 2 Relationship between species stability (long term and year to year, log-transformed) and two functional traits (leaf dry matter content in (a) and (c), and specific leaf area in (b) and (d)) in control and fertilized plots, based on multiple linear regression models. Significance values (p values from the F-test) show the results of the multiple linear regression models testing for relationships between stability and the trait studied, treatment (control or fertilized) and the interaction between trait and treatment. NS means not significant. The degrees of freedom are 161 for (a) and (c), and 175 for (b) and (d). species are represented as circles ($n = 165$ in (a) and (c), $n = 179$ in (b) and (d)). The names of the most stable species are signalled near their corresponding circle. Black regression lines show significant relationships between species stability and the trait studied. In the case of a significant trait and treatment interaction (at a significance level of $p < 0.1$), different colours of regression lines (green and red) are signalling a different response depending on the treatment applied

community stability (de Mazancourt et al., 2013; Gross et al., 2014; Lepš et al., 2018; Tilman, 1996). In addition, there was a lack of effect of treatment and SM diversity in multiple regression models, compared to their significant effect in simple regression models. To explain this, if we tentatively construct a structural equation model (SEM) with the variables studied to better understand the interactions between variables within the system, we find that the SEM indicates certain indirect effects of fertilization and SM diversity, although it should be taken with caution due to the low number of samples (Figure S3a). In particular, SM diversity appears to indirectly influence stability mainly through its effect on synchrony. As seed mass is related to the establishing phase of seedlings and persistence, among other aspects of plant ecology (Kazakou et al., 2014; Peco et al., 2009; Westoby, 1998), it seems consistent that a diversity in strategies through different seed masses could lead to asynchronous dynamics and to higher

community stability (Lepš et al., 2018; Roscher et al., 2011). In this sense, in the area and period studied, opposite long-term trends were found between different plant functional groups (i.e. annuals and perennials; Valerio et al., unpublished data). In particular, annuals, with smaller and lighter seeds, tended to decrease their abundance over time, while perennials, with larger seeds, tended to increase (Funk et al., 2016; Leishman et al., 2000). This is an interesting result, as case studies reporting an indirect effect of functional diversity through synchrony are scarce for plants, while some can be found for animals (Klink et al., 2019). On the other hand, regarding the effect of treatment, the SEMs indicate that fertilization might indirectly decrease long-term community stability by increasing CWM of SLA, favouring the dominance of more productive, fast-growing species with acquisitive traits, that are advantageous in favourable conditions (Gazol et al., 2016; Pérez-Harguindeguy et al., 2013).
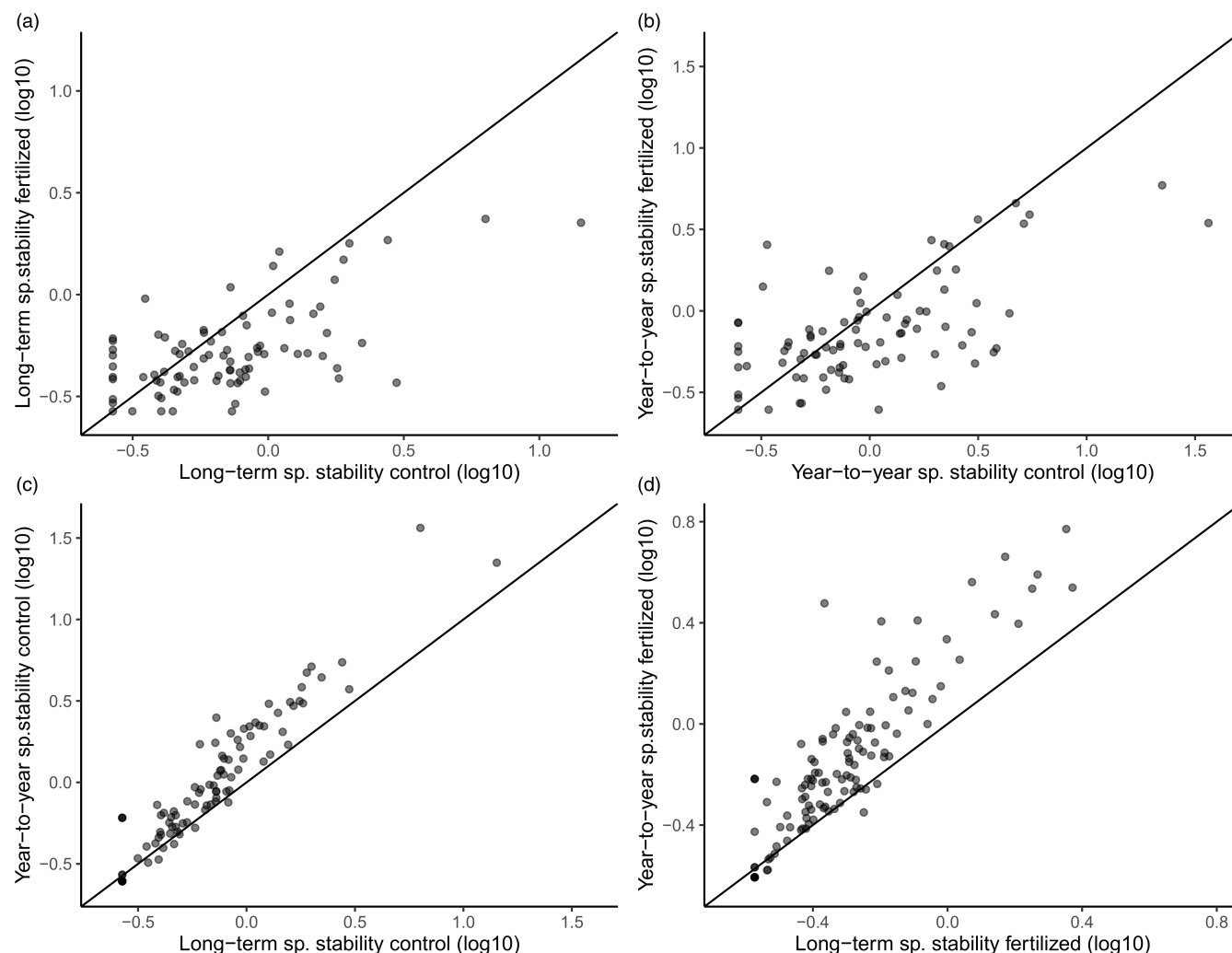
FIGURE 3 Effects of treatment and long-term trends on species stability (log-transformed). Each circle represents a species (a, b: 87 species present both in control and fertilized plots; c: 96 species in control plots; d: 120 species in fertilized plots). The solid line represents a 1:1 relationship above which species stability would be higher in fertilized plots than in control plots (a, b), or year-to-year species stability would be higher than long-term stability (c, d)

Regarding year-to-year community stability, multiple regression models showed that there was a significantly positive relationship between mean richness and stability, as predicted by theory and shown in previous studies (Craven et al., 2018; Hautier et al., 2015; Tilman et al., 2006; Yang et al., 2012). Similarly to long-term stability, synchrony showed a significant negative relationship with year-to-year stability (Craven et al., 2018; Kigel et al., 2021; Yang et al., 2012). In terms of functional composition and diversity, the positive effect of CWM of SLA on year-to-year stability indicates that the most stable communities are those dominated by species with low values of SLA (i.e. conservative strategies). When looking at the SEMs to understand the lack of influence of treatment and SLA diversity on year-to-year community stability (Figure S3b), we find that SLA diversity acts indirectly on community stability by increasing the CWM of SLA, which is consistent with other studies showing a higher explanatory power for functional composition than for functional diversity (Polley et al., 2013). Fertilization indirectly affects year-to-year stability mainly by increasing the CWM of SLA,

as found for long-term stability, but in this case also by decreasing mean species richness, in accordance with previous studies (Hautier et al., 2015; Yang et al., 2012; Figure S3b).

4.2 | Species stability and its dependence on traits

The results obtained from simple and multiple regression models for both long-term and year-to-year species stability confirmed what we found in the models at the community level. In terms of functional traits, as expected, slow-growing species with conservative traits (i.e. high LDMC and low SLA) were more stable than fast-growing species with acquisitive traits (i.e. low LDMC and high SLA; Májekova et al., 2014; Polley et al., 2013), as we found for *Brachypodium retusum*, *Aphyllanthes monspeliensis*, *Dorycnium pentaphyllum* and *Globularia vulgaris*, the most stable species in our study. In addition, these stable species were the most abundant perennials in the community, supporting the connection described in previous

studies between dominance and stability (Roscher et al., 2011). However, even within perennials the most stable species also tended to be those with higher LDMC and lower SLA values (although the relationship was only marginally significant: $p < 0.1$ for LDMC in long-term stability and for SLA in both long-term and year-to-year stability). In any case, it would be interesting for future studies to test stability and its drivers between and within life forms. On the other hand, the fact that the strength of the relationship between SLA and species stability (both long term and year to year) decreased with fertilization, while finding non-significant interactions between LDMC and treatment, indicates that the predictive power of LDMC is independent of fertilization, while the predictive power of SLA for species stability might vary under different experimental conditions, decreasing with fertilization (Májekova et al., 2014). When comparing species stability between treatments, the positive correlation between species stability in control and fertilized plots suggests that the most stable species in control plots are also the most stable in fertilized plots. However, although the relative stability of each species remained the same among treatments, fertilization promoted an overall decrease in both the long-term and year-to-year stability of the species present in the community. This suggests that fertilization decreases community stability through a decrease in species stability, as found in previous studies (Lepš, 2004; Zhang et al., 2016).

4.3 | Long-term vs. year-to-year approach to estimate community and species stability

Although we found a similar influence of synchrony and CWM of SLA on both long-term and year-to-year community stability, in line with other studies (Valencia, de Bello, Lepš, et al., 2020), our results showed that certain relationships found between community stability and its drivers (species stability, synchrony, richness and functional traits), as well as the effect of fertilization on them, changed depending on the approach used in the study. This might have important implications in the interpretation of the results and in the conclusions obtained (Lepš, Götzenberger, et al., 2019; Valencia, de Bello, Lepš, et al., 2020). However, most studies focused on stability do not make this differentiation between long-term directional trends and year-to-year fluctuations (according to Valencia, de Bello, Lepš, et al., 2020), although certain exceptions can be found (i.e. Craven et al., 2018; Song & Yu, 2015; Tilman et al., 2006).

Regarding the effect of treatment, fertilization increased cumulative richness and decreased mean richness. This seems consistent, as fertilization might promote the growth of certain fast native colonizers (e.g. *Arrhenatherum elatius* subsp. *elatius*, *Bromus sterilis*, *Genista scorpius*; Table S2, Figure S1) that can outcompete and replace other native conservative species (e.g. *Brachypodium retusum*, *Carex flacca*, *Globularia vulgaris*; Table S2, Figure S1), increasing species turnover (related to cumulative richness), but decreasing the number of species on average (Bobbink et al., 2010; Lepš, 2004; Stevens et al., 2004; Yang et al., 2012). Contrary to Lepš et al. (2018), our study showed opposed results depending on the type of richness

used. As most current studies focus on mean richness, we suggest that future studies on community stability could make use of the approach used here, to enable a more comprehensive comparison and interpretation of the results obtained.

Synchrony values tended to decrease with fertilization and in the presence of long-term trends (probably due to opposite trends among species), in line to what we expected and to what was found in previous studies (Lepš et al., 2018; Lepš, Götzenberger, et al., 2019; Valencia, de Bello, Lepš, et al., 2020).

Regarding stability both at the community level and at the species level, the type of approach used significantly influenced community and species stability values, although it did not affect their response to treatment. The increase in year-to-year community and species stability values compared to long-term stability is consistent with previous studies (Valencia, de Bello, Lepš, et al., 2020), and indicates that both in control and fertilized plots there might be some long-term directional trends that are decreasing community and species stability. In control plots, the cause of these trends could be shrub encroachment and succession after grazing exclusion (i.e. recovery of larger and more palatable plants according to Kigel et al., 2021, or increase in exotics in Bobbink et al., 2010), as indicated by the temporal increase in frequency of shrubs such as *Dorycnium pentaphyllum* and *Thymus vulgaris* subsp. *vulgaris* (Figure S1). In fertilized plots, this could be also due to the effect of fertilization (Lepš, Götzenberger, et al., 2019; Valencia, de Bello, Lepš, et al., 2020), as was the case for *Arrhenatherum elatius* subsp. *elatius*, *Bromus sterilis* or *Genista scorpius*, among others (Figure S1).

It is important to note that the decision to use one approach or the other might depend on what the objectives of the study are and what aspect of stability is targeted. For studies aiming to reflect the influence of factors or processes promoting directional trends on the community (i.e. land-use changes, climate change), and to consider these long-term trends as part of stability, the long-term approach seems the more reasonable option (Lepš, Götzenberger, et al., 2019). On the other hand, for studies focused on biological patterns and their generating processes more internal to the community, such as the functioning of its species and the influence of species dynamics or year-to-year fluctuations on stability, the year-to-year approach appears more interesting (Lepš, Götzenberger, et al., 2019; Valencia, de Bello, Lepš, et al., 2020). In this regard, an additional aspect to consider when studying stability would be to study it both at the community level and at the species level. Although the approach used might be selected according to the focus of the study, we suggest that combining both approaches would be a useful method for acquiring a more comprehensive understanding of the mechanisms and processes underlying community stability (Lepš, Götzenberger, et al., 2019; Valencia, de Bello, Lepš, et al., 2020). However, it is important to consider that variables are calculated in different ways for each approach and that each approach gives different information, at different time scales, to not draw biased conclusions. In this sense, future studies testing for combinations of long-term and year-to-year variables will shed light on the best way to distinguish long-term and year-to-year processes.

5 | CONCLUSIONS

Our study shows that long-term directional trends do appear in the Mediterranean grassland studied, as a result of shrub encroachment and succession in response to fertilization. The presence of these trends reduces stability values, both at the community level and at the species level, which highlights the need for accounting for the effect of these trends on stability using both a long-term and a year-to-year approach. The presence of conservative and non-competitive species with asynchronous dynamics is the most important driver of community stability. In addition, having a higher number of coexisting species is better for community stability than having a higher species turnover. In this sense, fertilization reduces community stability by favouring acquisitive species which increase competition, reducing the number of coexisting species, and decreasing the stability of the remaining species. This study contributes to the understanding of the mechanisms driving community stability in Mediterranean grasslands, at the same time demonstrating the influence of long-term directional trends on the results and conclusions obtained.

CONFLICT OF INTEREST

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

AUTHORS' CONTRIBUTIONS

L.G., R.I. and A.G. conceived the ideas and designed the methodology; R.I. and M.V. collected the data; M.V. analysed the data; M.V. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.8pk0p2npt (Valerio et al., 2022). Data of species abundance over time available upon request in LOTVS database: https://lotvs.csic.es/ (Napal dataset). Voucher information for the species studied available from GBIF: https://doi.org/10.15470/pxktos (Ibáñez et al., 2022).

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