Interannual fluctuations in rainfall shift the functional structure of Mediterranean grasslands across gradients of productivity and disturbance

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ABSTRACT

Questions: How do interannual fluctuations in water availability affect the functional trait patterns along spatial gradients of resource availability and disturbance?

Location: Mediterranean grasslands in central Spain, near Madrid

Methods: We surveyed plant communities from 66 sites under different grazing regimes (from heavy grazing to grazing abandonment) in productive and unproductive habitats (corresponding to upper and lower topographic zones) in two years with contrasting rainfall conditions. Community weighted mean (CWM) and Rao quadratic entropy for three key plant ecology strategy traits (specific leaf area, height and seed mass) were calculated for each community. We used null models to estimate functional richness (FR) and functional divergence (FD), the two components of functional diversity with the highest power to detect changes in community assembly processes across environmental gradients.

Results: The patterns of CWM remained rather constant across years, with the only exception being seed mass, which experienced considerable temporal changes that suggested that heavy-seeded species are favored under stressful conditions. Marked and unchanging differences in FR between the two habitats revealed the existence of trait convergence -observed for vegetative traits in unproductive habitats and seed mass in productive ones- and divergence -seed mass in unproductive habitats and vegetative traits in productive ones- for different niche axes. In contrast, the patterns of FD of the vegetative traits changed considerably between years.

Conclusions: Increased water availability during the wet year had a greater impact on the functional structure of unproductive habitats. The appearance of taller species in unproductive habitats during the wet year suggested a relaxation of the abiotic filters. In addition, differences in the direction of the interannual changes of FD indicated that increased competition for light
can lead to increased niche partitioning in unproductive habitats, but also to the exclusion of weak competitors in undisturbed productive sites. Our results show that the temporal changes in the abundance of the species of Mediterranean grasslands largely depend on the species' traits, leading to great interannual changes in its functional structure, and that the patterns of trait convergence/divergence are, not only trait-dependent, but also depend on the complex interaction between productivity and disturbance.

**Keywords:** Annual plants; community assembly; dehesa; functional divergence; functional richness; grazing; productivity; species pool.

**Nomenclature:** Flora Europea (Tutin et al. 1964-1980)

**Running head:** Functional structure in Mediterranean grasslands

**INTRODUCTION**

Functional trait diversity is emerging as a powerful indicator of community assembly processes in plant communities (Mason *et al.* 2005, 2012a; Villeger *et al.* 2008; de Bello *et al.* 2010). Recent work has used functional diversity indices to reveal changes in assembly processes along spatial gradients of resource availability and disturbance (e.g. Cornwell & Ackerly 2009; Pakeman *et al.* 2011; Mason *et al.* 2011, 2012). However, it remains unclear how temporal variation in resource availability interacts with spatial gradients of stress and disturbance to influence assembly processes in plant communities. This study uses functional diversity for plant traits to explore how temporal and spatial variations in resource availability interact with grazing disturbance to influence assembly processes in Mediterranean grassland communities.

Limitations in resource availability reduce the range of vegetative trait values that are viable within a given site, favouring species adapted to the local conditions (Grime 2006). This may increase the likelihood of co-existence between species with trait values similar to the local
optimum (Mouillot et al. 2007; Mason et al. 2012; Spasojevic & Suding 2012), leading to reduced functional diversity (convergence; Grime 2006). On the other hand, the principle of limiting similarity (MacArthur & Levins 1967) predicts that competition will impose a limit to how similar coexisting species can be. According to this principle, the traits of coexisting species should be more different than expected at random (divergence; Mason et al. 2012; Spasojevic & Suding 2012). However, competition can also increase similarity among coexisting species by excluding species bearing traits associated with low competitive ability (Chesson 2000, Grime 2006, Mayfield and Levine 2010). Local increases in productivity produce a shift in the limiting factors for plant growth from soil resources to light, thus increasing the intensity of above-ground competition (Tilman 1988). For instance, low productivity selects for species with resource-retaining strategies (Cornwell & Ackerly 2009). Conversely, increased productivity, and hence increased competition for light, should enhance the abundance of fast-growing species, and lead to higher functional diversity for vegetative traits (Mason et al. 2011; Spasojevic & Suding 2012; Gross et al. 2013), although the latter may not be true when competition for light is very intense (e.g. Bernard-Verdier et al. 2012).

Grazing also plays an important role as a determinant of the functional structure of plant communities (Carmona et al. 2012). Plants deal with grazing adopting two main strategies: avoidance and tolerance (Anderson & Briske 2005; Cingolani et al. 2005). The avoidance strategy involves vegetative traits that allow plants to reduce its accessibility and palatability (such as short statures, small leaves or rosette growth forms). In contrast, grazing-tolerant plants, which have the capacity to regrow quickly after defoliation, have traits associated with high rates of resource capture relative to their size, such as a high specific leaf area or high concentrations of Nitrogen in the leaves. As a result, tolerant plants are highly palatable and selected by
herbivores, often leading to a positive feedback between grazing and plant quality (Cingolani et al. 2005). Nevertheless, traits associated to grazing tolerance also entail a less efficient conservation of resources, and therefore grazing tolerant responses are only expected to increase with grazing when there is a sufficient availability of resources (Cingolani et al. 2005). With respect to the distribution of trait values, disturbance has been considered as the most important source of trait divergence, because biomass removal should prevent the exclusion of weak competitors (Grime 2006; de Bello et al. 2013). However, recent studies have shown that disturbance can also result in trait convergence (Mason et al. 2011; Pakeman et al. 2011; Carmona et al. 2012; Laliberté et al. 2013), especially under harsh environmental conditions (Carmona et al. 2012).

Indeed, the predominant assembly processes can differ between niche axes; Grime (2006) suggested that, while divergence is common for reproductive traits, patterns of convergence predominate for vegetative traits. Traits related with the regeneration stage of plants, such as seed mass, play a crucial role in Mediterranean grasslands, where annual species are very abundant, accentuating the influence of the germination and establishment stages on the species composition of these systems (Espigares & Peco 1995). Seedlings coming from larger seeds are known to have higher survival rates (Metz et al. 2010), especially under stressful conditions, such as low availability of light and water (Moles & Westoby 2004). Therefore, high levels of productivity, associated with low light availability, should enhance the abundance of species with large seeds. On the other hand, small-seeded species produce greater numbers of seeds, which in turn result in a better capacity to colonise the gaps produced by livestock and leads to the increased abundance of such species under grazing conditions (Kohler et al. 2006; Peco et al. 2012; Dobarro et al. 2013).
In this context, temporal increases in water availability are very likely to alter the functional structure of annual plant communities, by selecting for species with higher growth rates over species that can tolerate low resource levels (Angert et al. 2009). Moreover, given that the effect of grazing is strongly mediated by resource availability (Díaz et al. 2007a; Carmona et al. 2012, 2013), increased water availability is also likely to affect the patterns of functional structure across grazing gradients, by enhancing the abundance of grazing-tolerant species along grazing gradients. In addition, temporal increases in water availability, and hence enhanced seedling survivorship, should result in increases in the abundance of small seeded species, especially considering that small seeds persist in the seed banks for longer periods (Thompson et al. 1993).

Mediterranean grasslands are an excellent system for testing whether or not spatial patterns in functional community structure are stable in the face of temporal fluctuation in resource availability. One of the main features of Mediterranean climate is the high level of interannual variability in rainfall, which generates a great variability in the productivity of Mediterranean grasslands. This translates into significant interannual differences in the productivity, species composition and diversity of these systems (Peco 1989; St. Clair et al. 2009; Fernández-Going et al. 2012; Péerez-Camacho et al. 2012; Carmona et al. 2012). In this paper, we examine the functional structure for three key plant traits (specific leaf area, height and seed mass; Westoby 1998) between two habitats differing in resource availability situated along a grazing intensity gradient, in a wet and a dry year. We test whether patterns in functional community structure across spatial gradients of resource availability and grazing vary between years of differing rainfall. We expect that interannual changes in rainfall will change the most successful functional strategies, resulting in changes in the functional structure patterns. Specifically, we hypothesize that: (1) increased water availability during the wet year should favour traits associated with
resource-acquiring strategies, such as high SLA or height; (2) these changes should be particularly evident in unproductive environments, because of the relaxation of the strong abiotic filters that impose a great constraint to trait values during the dry year; (3) because productivity modulates the effect of disturbance, interannual differences in water availability should alter the plant strategies selected by grazing, from grazing-avoidance strategies (characterised by low SLA values) in the dry year to grazing-tolerance strategies (characterised by high SLA values) in the wet year; (4) higher levels of water availability during the wet year should intensify competition for light leading to increased divergence in traits related with light use and acquisition; however, in productive habitats with little or no grazing, very intense competition for light may result in convergence by the exclusion of traits that confer weak competitive ability; (5) given that large-seeded species are more likely to overcome stressful germination and establishment conditions, enhanced conditions for small-seeded species during the wet year should be reflected in a reduction in average seed mass accompanied by an increase in the range of values of this trait (Table 1).

MATERIAL AND METHODS

Study area

The study area (5 × 4 km) is situated 35 km north of Madrid, in central Spain (40°38' N; 3°70' W; mean elevation 860 m). Climate is Mediterranean, with annual rainfall (average ca. 540 mm, with high interannual variability) concentrated mainly in spring and autumn, with very dry summers. Mean annual temperature is c. 13ºC. The landscape is characterised by moderate slopes, shallow acidic soils over a gneiss substratum and many rocky outcrops. Clearing of the original forest, where Quercus ilex subsp. ballota L. and Juniperus oxycedrus L. were the
dominant tree species, resulted in a typical “dehesa” landscape with c. 40 trees/ha over a
grassland understorey with a high proportion (ca. 70%) of annual species.

Extensive grazing has been the dominant use in the region for centuries, but currently there
is great spatial variability in grazing intensity, with intensification in some areas and
abandonment in others (Peco et al. 2006). In order to cover a wide range of situations, we
selected sites with four different levels of grazing intensity: (1) areas in which grazing has been
abandoned; (2) areas grazed only occasionally; (3) areas where livestock is permanently present,
but in which grazing pressure is moderate because they are distant from points of livestock
concentration such as water and feeding points; (4) areas under permanent high levels of grazing
because they are close to points of livestock concentration. We made sure that the grazing status
of all the selected areas has remained unchanged for at least 30 years. Two different habitat types
can be distinguished within each of the grazing intensity levels: (1) productive habitats, located
at the bottom of slopes, characterised by their deep soils, and that receive water and nutrient
inflows; (2) unproductive habitats, on the upper slopes with shallower soils, and nutrient and
water outflows. In each of these eight ‘habitat × grazing’ levels we selected eight or nine
independent sites, always situated in areas with slopes under 5% (total of 66 sites). In order to
guarantee the independency of our sampling units, we made sure that all sites were sufficiently
separated, with a minimum distance between adjacent sites of 45 m, and an average of 106 m.

The differing topographic positions of the two types of habitats have led to differences in
their levels of soil water availability, clay percentage, total nitrogen and soil organic matter (Peco
et al. 2006), which result in a much lower plant productivity of upper-slope habitats (Casado et
al. 1985). For instance, soil analyses in the same 66 sites have revealed that the two habitats
differ in Total N (0.39 g/100 g ± 0.03 in productive vs. 0.18 g/100 g ± 0.01 in unproductive
habitats) and organic matter contents (7.02 g/100 g ± 0.77 in productive vs. 2.68 g/100 g ± 0.16 in unproductive habitats), but not in P content (7.78 ppm ± 1.50 ppm in productive vs. 8.34 ppm ± 1.73 ppm in unproductive habitats; Navarro 2013). In order to corroborate the differences in soil water content between habitats, we collected and oven-dried a soil sample (5-cm cylinder of 98.17 cm³) from each site in April 2012. We defined the water content of these soil samples as the ratio of the mass of water to the dry weight of the sample. As expected, we found significant differences between the mean soil water contents of productive (33.04% ± 1.39% SE) and unproductive habitats (14.60% ± 1.09%). Accordingly, total plant cover in lower-slope habitats is substantially higher than in upper-slope ones (ca. 82% vs 62%; Carmona et al. 2013).

Vegetation and functional traits sampling

At each site we set up three sampling quadrats (20 × 20 cm), always in the same relative positions (1 m N, E and W from the site centre). We surveyed these quadrats twice, in the spring of 2009 (dry year, with 315 mm of precipitation between October and June, which is ca. 65% of the long term average during that period) and 2010 (wet year, with 575 mm of precipitation, ca. 119% of the average precipitation between October and June). Interannual differences in precipitation have an important effect on the productivity of grasslands, especially of those situated in dry environments such as the studied ones (Yang et al. 2008; St. Clair et al. 2009). We estimated the abundance of each species in each quadrat, using six cover classes: (0) absent; (1) cover <1%; (2) 1% < cover ≤ 12%; (3) 12% < cover ≤ 25%; (4) 25% < cover ≤ 50%; and (5) cover >50%. Subsequently, we assigned to each species the median value of its cover class, and transformed these covers, by ensuring that the sum of all the covers of the species at each quadrat was always 1.
We found a total of 177 species in the surveys (Appendix S1). For each species we collected data on three functional traits – height, specific leaf area (SLA) and seed mass – related to species’ strategies in response to disturbance and productivity. Data on SLA and height were taken from Peco et al. (2005) or measured in the cases in which such information was not available. Plant height (distance between the plant base and the highest photosynthetic leaf) was measured on 10 non-grazed mature individuals of each species, at least 25 m from each other, in the areas where the species was more abundant. Height regulates plant responses to resource availability and disturbance and can be interpreted as an indicator of successional status and response to grazing (Westoby et al. 2002; Díaz et al. 2007a). Specific leaf area (SLA; mm²/mg) was measured on the same individuals, dividing the leaf area by its oven-dried mass. SLA is an indicator of resource-use strategies, with low SLA values being associated with long-lived leaves, low relative growth rates and long residence times of nutrients (Westoby et al. 2002). Seed mass was obtained in most cases from Azcárate et al. (2002), and new measurements were taken for the species not included in that paper, following the same protocol (30 dry seeds per species). Seed mass influences seedling survival -large-seeded species produce large seedlings that survive better under difficult conditions such as shade, drought or defoliation- as well as the colonisation capacity of species -species with large seed produce smaller numbers of seeds per unit of mass (Westoby 1998; Moles & Westoby 2004). The three traits were independent, as revealed by Mantel tests (9,999 permutations) performed between the respective matrices of trait distances between species (SLA-Height: r = -0.006, p = 0.495; SLA-Seed mass: r = -0.007, p=0.423; Height-Seed mass: r = 0.02, p=0.249)

**Functional structure calculation**
The study of the variation in community functional structure along ecological gradients requires the combined use of indicators of shifts in the functional composition and in the patterns of trait convergence and divergence (Spasojevic & Suding 2012; Bernard-Verdier et al. 2012). Changes in the functional composition of communities can be detected by analysing the patterns of community average trait values (Pakeman et al. 2011; Mason et al. 2012). On the other hand, functional diversity reveals the changes in the patterns of trait convergence/divergence associated to changes in community assembly. Among the different components of functional diversity, we analysed functional richness and functional divergence. Functional richness, an indicator of the amount of niche space occupied by the species in a community (Mason et al. 2005), reveals the influence of trait-based assembly processes on species’ occurrence. Additionally, functional divergence, an indicator of the degree of trait divergence between the most abundant species, can reveal effects of trait-based assembly processes on species’ relative abundances (Mason et al. 2012, 2013). While limiting similarity is associated with high functional richness and divergence, abiotic filters reduce the values of these indicators (Mouchet et al. 2010; Mason et al. 2012).

To calculate these indices, we first log-transformed and standardised the SLA, height, and seed mass values to a 0–1 scale. For each quadrat \( j \) we calculated the community weighted mean (Díaz et al. 2007b) of each trait (\( CWM_{SLA} \), \( CWM_{Height} \) and \( CWM_{Seed} \)). Additionally, we calculated, for each trait, a matrix of Euclidean distances between all possible species-pairs. In order to have an indication of functional richness and functional divergence, we calculated the Rao quadratic entropy (henceforth “Rao”; Rao 1982; de Bello et al. 2010) for each trait in each quadrat and year. The Rao Index can be expressed as:
\[ Rao = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} p_i p_j , \]

where \( d_{ij} \) expresses the dissimilarity between each pair of coexisting species \( i \) and \( j \) and varies from 0 (two species with exactly the same trait values) and 1 (two species with completely different traits). \( p_i \) and \( p_j \) indicate the relative abundances (in this case relative cover) of species \( i \) and \( j \). Rao is a combination of both functional richness and functional divergence (Mouchet et al. 2010). We chose Rao because it has been found to be a reliable index when analysing changes in assembly processes across gradients of stress (Mason et al. 2012, 2013) and can take species’ relative abundances into account (de Bello et al. 2010). For each quadrat and year we calculated two Rao values. The first one was calculated taking into account species’ covers (“Raoab”). For the second Rao value we took into account only species' presences (i.e. assigning the same abundance value to all the species in a quadrat; “Rao_{pr}”).

Both raw Rao values may be influenced by species richness (i.e. may be correlated with species richness even in randomly generated data), especially when using presence/absence data (Pavoine et al. 2013). Consequently, relationships between Rao and environmental gradients can arise simply due to variation in species richness. To remove spurious effects of species richness on Rao values, we compared observed Rao values with two different null models. First, we compared the observed Rao_{pr} of each quadrat with null values generated using a matrix-swap null model (using 2000 initial swaps and 2000 swaps between calculation of each null value) based on the species presence-absence matrix (177 species x 198 quadrats; Manly 1995). Given the reduced geographical extension of our study area, we considered a common species pool for all quadrats. Comparisons of observed Rao_{pr} values with null values obtained following this procedure are a powerful method to detect the effects of ecological processes on species'
occurrences, and are good estimators of functional richness (Mason et al. 2013). Second, we compared observed Rao_ab with null values generated by randomising abundances across species but within quadrats (Hardy 2008; Mason et al. 2012). This procedure preserves all the processes that led to the observed composition, except those determining the abundances of species (Mason et al. 2012). Comparing the observed Rao_ab values with the Rao_ab obtained in this second type of randomisation provides a pure estimation of functional divergence. Simulation studies indicate that these indices collectively provide a high level of power to detect changes in assembly processes along environmental gradients (Mason et al. 2013). This method has been used before in field-based studies (Mason et al. 2011, 2012), showing its reliability to detect changes along gradients.

We performed 10,000 randomisations of each null-model in order to calculate the standardised effect size (SESRao = [observed Rao – mean of simulated Rao]/standard deviation of simulated Rao; Gotelli & McCabe 2002). Subsequently, we averaged the values of the three quadrats of each site, thus obtaining two SESRao values per site: SESRao_pr (observed Rao_pr compared with the matrix-swap null model) and SESRao_ab, (observed Rao_ab compared with the null model randomising abundances across species but within 20 cm x 20 cm sampling quadrats). For convenience, we refer to them respectively as FR and FD henceforth.

**Statistical analyses**

We examined the influence of grazing intensity, habitat type and year on the CWM, FR and FD of the three studied traits by means of mixed effects models, with site as a random factor (Table 1). Given that in many occasions the variability between the groups was not uniform, we fitted 7 different models for each response variable: one model with no different spread per stratum and 6 models in which we allowed the variance to vary within groups. Such groups were
defined as the levels of each of the studied factors (grazing intensity, habitat type and year), as well as their pairwise combinations. Subsequently, for each response variable, we selected the model with the lowest AIC value (Zuur et al. 2009). We checked for spatial autocorrelation in the residuals of the models using Mantel tests. Because our models included two observations of each site (two different years), we performed two Mantel test for each model, with the matrix of distances of the residuals of the dry and of the wet year, respectively, and the matrix of spatial distances. Finally, for each model, we performed Bonferroni-corrected pairwise comparisons to detect differences between grazing intensities within habitat types and year as well as interannual changes within sites (differences between years within habitat types and grazing intensities). All analyses were performed using R (R Development Core Team 2013).

RESULTS

For CWM and FD, AIC values indicated that the models that considered different variances within groups were generally more parsimonious than those that assumed equal variance across strata. In contrast, the models with the lowest AIC scores for FR were those that did not considered differences in variance among groups (Appendix S2). In addition, the Mantel tests performed for each year and model revealed that there was not spatial autocorrelation in the residuals of the models (Appendix S3).

Patterns in the functional structure of vegetative traits

Species with high SLA and low stature were more abundant under higher grazing intensities, regardless of the year or habitat type (Table 2a; Fig. 1; Appendix S4). The communities of productive habitats were composed of taller plants with lower SLA values than those of unproductive habitats (Table 2a; Fig. 1). Although the patterns of average values of the studied traits across grazing intensities and habitat types were consistent across years, the CWM_{SLA} of
the communities sited in unproductive habitats experienced significant interannual variations (Table 2; Appendix S4). Importantly, the direction of this change was modulated by grazing intensity, resulting in increased SLA values during the wet year in the most intensively grazed areas and the opposite pattern in the less intensively grazed areas (Fig. 1a). In contrast, CWM_{Height} was rather constant across years in both habitat types across the whole grazing gradient (Fig. 1b; Appendix S4).

High grazing pressures reduced the range of height values in unproductive habitats in both years, but did not have any effect on productive habitats (Table 2b; Fig. 2b). In contrast, FR_{SLA} was not affected by grazing in any of the studied scenarios (habitats and years). Again, habitat type played a very important role (Table 2b), with higher FR values in productive than in unproductive habitats, for both SLA and height, during both years (Fig. 2b; Appendix S4). With the exception of FR_{Height} in unproductive habitats, which generally increased during the wet year, the temporal variability in FR within habitats and grazing intensities was minor compared to the differences between habitats (Fig. 2b).

On the contrary, the values of FD for vegetative traits experienced a much higher degree of interannual variability. For instance, the effect of grazing on FD_{SLA} contrasted markedly between years, regardless of habitat type, with grazing having a significant and generally negative effect on FD_{SLA} during the dry year, and no effect during the wet year (Fig. 3). Interestingly, the interannual variability in FD_{SLA} within sites was contingent on habitat type: during the wet year FD_{SLA} increased in unproductive habitats throughout the grazing gradient, whereas it underwent an important decrease in the communities of the productive habitats where grazing had been abandoned (Fig. 3a). The high within-site temporal variability of FD_{SLA} contrasted with the temporal constancy observed in FD_{Height} (Fig. 3a; Appendix S4).
The average values of seed mass displayed a very complex response to grazing and productivity. During the dry year, CWM\textsubscript{Seed} was higher in unproductive than in productive habitats, but that relationship reversed during the wet year, especially in the most intensively grazed sites, that experienced great interannual increases (in productive habitats) or reductions (in unproductive habitats) in seed mass (Fig. 1c; Appendix S4). Seed mass decreased with grazing, but only during the dry year in productive habitats and during the wet year in unproductive ones (Fig. 1c).

The lack of any effect of grazing on the functional richness of seed mass contrasted with the remarkable differences between habitats in this parameter. FR\textsubscript{Seed} was much higher in unproductive than in productive habitats, a tendency that became even more evident during the wet year (Fig. 2c; Appendix S4). Finally, none of the studied factors affected FD\textsubscript{Seed} or its temporal variability (Table 2b and Fig. 3c).

**DISCUSSION**

Temporal and spatial variations in resource availability interact with disturbance in complex ways, altering the functional structure of plant communities. Our results show that temporal fluctuations can drive considerable variation in the functional trait patterns across gradients. As we expected, the functional structure of unproductive habitats experienced greater interannual variations than that of productive habitats (Hypothesis 2). Interannual changes in unproductive habitats indicated a relaxation of the strength of abiotic filters during the wet year. The habitat-dependent direction of the interannual changes in functional divergence patterns suggested that the outcome of competition for light depend on its intensity (Hypothesis 4). Grazing selected for tolerance strategies more strongly during the wet year in unproductive environments, confirming...
the role of productivity as a modulator of the effects of grazing on plant communities

(Hypothesis 3). Below, we discuss our main results in more detail, focussing successively on the different traits considered.

**Patterns in vegetative traits**

Average SLA increased with grazing in all but the less productive scenario -unproductive environments, dry year-, showing that grazing selects for tolerance strategies when there is sufficient resource availability (Eskelinen et al. 2012). In addition, higher mean SLA values during the wet year in the most intensively grazed sites of unproductive habitats was consistent with the expected shift towards grazing-tolerance strategies when water availability increased (Hypothesis 3). This shift can be mediated by a few abundant species; for instance, the abundance of *Poa bulbosa*, a species with fast growth rates and a relatively high SLA value, increased remarkably during the wet year (Appendix S5; Fig. A1). This increase is probably related to the high sensitivity of *P. bulbosa* to water deficits (Mamolos et al. 2001) and with its increased tolerance to grazing under high-resource-availability conditions (Staalduin et al. 2010). Simultaneously, the abundances of species with rosette form and intermediate SLA values, such as *Leontodon taraxacoides* or *Hypochaeris glabra*, decreased in unproductive habitats during the wet year, suggesting that dry conditions favour grazing-avoidance strategies, whereas more humid conditions favour grazing-tolerance strategies (Diaz et al. 2007a). On the contrary, mean SLA decreased in the non-grazed sites during the wet year (Fig. 1a), suggesting that within-site interannual changes in the most successful resource-use strategies are mediated by the disturbance regime.

There were important differences between habitats in the patterns of functional richness for SLA, which were much higher in productive than in unproductive habitats. In contrast, habitat
type did not stand out as the main determinant of the patterns of functional divergence of SLA (Table 2c). According to Hypothesis 4, we expected to observe trait convergence among the most abundant species under low water availability and increased divergence under higher water availability. The generalised increase in the divergence of SLA in unproductive habitats during the wet year partially confirmed these predictions. The enhanced abundance of *Vulpia myuros*, a graminoid with a much lower SLA value than the dominant *P. bulbosa*, contributed decisively to this increase (Fig. 3a and Appendix S5; Fig. A2). In contrast, we also observed a great decrease in the functional divergence of SLA during the wet year in the grazing-abandoned productive habitats' communities (Fig. 3a and Appendix S5; Fig. A3). Apparently, under conditions that favor strong competition for light (i.e. wet year, productive habitats and no grazing disturbance), large differences in competitive abilities led to the preeminence of equalizing fitness mechanisms and, as a consequence, to trait convergence (Chesson 2000; Grime 2006; Mayfield & Levine 2010). Our results suggest that functional divergence for SLA peaks at intermediate productivity levels, a pattern similar to that reported by Bernard-Verdier et al. (2012) in Mediterranean rangelands.

Unproductive habitats had, on average, shorter species than productive ones, which suggests that the importance of competition for light increased with higher resource availability (Bernard-Verdier et al. 2012; Spasojevic & Suding 2012). In addition, grazing decreased average height, in agreement with the results of previous studies (Peco et al. 2005; de Bello et al. 2005; Diaz et al. 2007a). Again, habitat type was the main driver of FR$_{\text{Height}}$, with higher functional richness in productive than in unproductive environments. This result, along with the above-mentioned for FR$_{\text{SLA}}$, corroborates that environmental filters impose significant restrictions to the range of vegetative trait values present at a given site (Hypothesis 2; Grime 2006). This was further
confirmed by the increase in FR\textsubscript{Height} in unproductive habitats during the wet year (Fig. 2b), where reduced water stress increased the occurrences of tall species. However, the enhanced presence of these species was not accompanied by great increases in their abundances, as suggested by the temporal consistency of mean height. Additionally, high grazing intensities reinforced the effects of aridity, further reducing the small FR\textsubscript{Height} values in unproductive habitats (Cingolani et al. 2005; Carmona et al. 2012). These results provide support for the notion of disturbance as a force that leads to convergence in trait patterns (Mason et al. 2011; Pakeman et al. 2011; Laliberté et al. 2013).

In general, the patterns of vegetative traits across the grazing gradient depended strongly on rainfall conditions. Functional divergence decreased with grazing during the dry year, with the only exception of height in productive habitats. However, the non-significant effect of grazing on functional divergence observed during the wet year (Fig. 3) confirms that the effects of grazing are highly influenced by the productivity level (Milchunas et al. 1988, de Bello et al. 2006; Carmona et al. 2012). Future studies including a wider range of productivity conditions would help to discern the conditions in which disturbance acts as a driver of trait divergence (Grime 2006) or convergence.

**Seed mass**

As expected, grazing reduced mean seed size (Peco et al; 2005; Kohler et al. 2006; Dobarro et al. 2013), but these reductions were highly context-dependent. Interannual differences in mean seed size increased with grazing intensity, but the direction of this change depended on habitat type. As a result, average seed size was higher in unproductive habitats during the dry year, whereas it maximized in productive habitats during the wet year (Fig. 1c). These results, which are in agreement with Hypothesis 5, suggest that increased stress levels, manifested as increased
shading in productive habitats during the wet year, and as severe constraints on water availability in unproductive habitats during the dry year, select for large-seeded species with higher survivorship rates in stressed conditions (Moles & Westoby 2004). In addition, the increase in average seed mass experienced by the most intensively grazed productive sites during the wet year is consistent with a reduction in the availability of regeneration gaps -of which small seeded species take advantage (Kohler et al. 2006)- caused by livestock trampling and defoliation.

Between-habitat differences in productivity played a major role determining the functional richness of seed mass, which was greater in unproductive than in productive habitats. These differences further increased during the wet year (Table 2b), associated with the aforementioned reduction in average seed mass in unproductive habitats and the increase in productive habitats. For instance, in unproductive habitats, we observed increased presence and abundance of small-seeded species (e.g. Tuberaria guttata, Spergula arvensis or Vulpia myuros) during the wet year, combined with a decline of species with heavy seeds (e.g. Biserrula pelecinus, Brassica barrelieri or Erodium cicutarium). The functional richness of seed size displayed the opposite pattern in productive habitats (Appendix S5; Fig. A4). The interannual changes observed for FRSeed can be caused by the capacity of small seeds to persist in the seed bank for longer times than large seeds (Thompson et al. 1993). Thus, small-seeded species present in the seed bank probably experienced buffered population growth (Chesson 2000), i.e. enhanced germination and seedling survivorship under less stressful environmental conditions (higher water availability in unproductive habitats during the wet year and higher light availability in productive habitats during the dry year, respectively). The appearance of small-seeded species along with the presence of large-seeded ones in the communities regardless of water availability would therefore explain the increase in FRSeed values under favourable conditions.
Finally, the lack of effect of any of the studied factors on the functional divergence of seed mass is in line with previous results (Viard-Crétat et al. 2011). In this sense, it is important to note that patterns of divergence or convergence in seed size would indicate a great importance of seedling-seedling interactions, which rarely occur in natural or experimental conditions (Peco & Espigares 1994; Moles & Westoby 2004; Ben-Hur et al. 2012).

**Concluding remarks**

Our results suggest that wet years foster trait diversity in unproductive habitats, while dry years allow resource-retaining species, which are poor competitors for light, to remain in the communities. Therefore, resource fluctuations seem to promote the diversity of trait values, playing an important role in the maintenance of diversity (Chesson et al. 2004). The present study provides support for the consideration of disturbance as a driver of functional convergence (e.g. Pakeman et al. 2011), rather than a source of trait divergence (Grime 2006).

The application of an approach similar to the one presented here can help to reduce the number and importance of possible confounding factors, opening a new and promising venue for the study of changes in patterns of trait convergence/divergence associated to shifts in resource availability or disturbance. However, we are aware of the potential confounding effects of factors other than the total amount of rainfall, which are likely to have changed between years. For example, small-seeded species are favored in years with early autumn rains, whereas large-seeded species are more abundant after dry autumns (Peco et al. 2009). Another possible caveat of our study is the lack of consideration of dispersal limitation, which might reduce the functional pool available at each site (Myers & Harms 2009), and have a confounding effect on our FR analyses. Finally, we want to stress that we only considered a single average trait value per species regardless of the year. Therefore, our study only considers differences in functional
structure caused by changes in species composition, but not those due to within-species variability (Lepš et al. 2011). Among the studied traits, height is the most likely to experience within-species variation associated to environmental changes (Garnier et al. 2007), a feature that can be behind the lack of interannual changes in mean height values. Studies using a similar research framework, but including a higher number of years, as well as considering the possible effects of dispersal limitation and within-species variability in trait values, are needed in order to adequately describe the role of temporal variation in resource availability.

The temporal consistency and the importance of the differences in average trait values and functional richness between habitats indicate that long-term and sustained differences, such as the ones produced by the different topographical positions between unproductive and productive habitats, have a great influence on these values through trait-mediated changes in the species pool. This contrasted with the great interannual changes observed for the functional divergence of the vegetative traits, particularly for SLA. Interannual changes in functional divergence show that the temporal fluctuations in the abundance of the species of Mediterranean grasslands largely depend on the species' traits. Our results illustrate that the patterns of trait convergence/divergence are, not only trait-dependent, but also depend on the complex interaction between productivity and disturbance. Most importantly, we provide evidence showing that the conclusions drawn from studies analysing the trait patterns across ecological gradients can be substantially modified by temporal fluctuations in resource availability. Our findings indicate that the results derived from a single year should be considered with caution. Consequently, we recommend that future studies analysing these patterns should take into account the temporal fluctuations in resource availability, especially in plant communities dominated by annual species.
ACKNOWLEDGEMENTS

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REFERENCES


**Supporting Information**

**Appendix S1.** Species recorded in the study.

**Appendix S2.** AIC values of the different linear mixed effects models.

**Appendix S3.** Results of the Mantel tests performed to check for spatial autocorrelation in the residuals of the models

**Appendix S4.** Mean values of the different indicators of functional structure for each functional trait and combination of grazing, habitat productivity and year.

**Appendix S5.** Additional figures.
Table 1 Main hypotheses tested, reasoning for each and expected results.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Reasoning</th>
<th>Expected results</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Higher SLA or Height during the wet year.</td>
<td>Increased water availability favours resource-acquiring strategies.</td>
<td>Significant Year effect.</td>
</tr>
<tr>
<td>2. Greater increases in SLA or Height in unproductive habitats.</td>
<td>The constraint to trait values imposed during dry years is greater in unproductive habitats.</td>
<td>Significant Year x Habitat interaction.</td>
</tr>
<tr>
<td>3. Plant strategies selected by grazing differ among years.</td>
<td>Productivity modulates the effect of grazing.</td>
<td>Significant Year x Grazing interaction.</td>
</tr>
<tr>
<td>4. Higher FD for traits related with light acquisition during the wet year; especially in unproductive habitats or ungrazed and productive sites.</td>
<td>Intensified competition for light during the wet year may leave to greater trait divergence, but can also increase dominance in undisturbed productive environments.</td>
<td>Significant Year x Grazing x Habitat interaction.</td>
</tr>
<tr>
<td>5. Smaller seeds, and greater FRSeed during the wet year.</td>
<td>Enhanced conditions for small-seeded species during the wet year, but no reason for heavy seeds to dissapear.</td>
<td>Significant Year effect.</td>
</tr>
</tbody>
</table>
Table 2 Results of the linear mixed models analysing the values of the community weighted mean (CWM), functional richness (FR) and functional divergence (FD) for each functional trait. Grazing intensity, habitat type and year as well as their interactions were used as fixed-effects explanatory variables. Site was used as a random factor. P-values are shown in brackets. Significant results ($P < 0.05$) are in bold.

<table>
<thead>
<tr>
<th></th>
<th>SLA</th>
<th>Height</th>
<th>Seed mass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>$F$</td>
<td>df</td>
</tr>
<tr>
<td>a) CWM</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grazing intensity</td>
<td>3</td>
<td>19.88 ($&lt;0.001)$</td>
<td>65.02 ($&lt;0.001)$</td>
</tr>
<tr>
<td>Habitat</td>
<td>1</td>
<td>109.64 ($&lt;0.001)$</td>
<td>208.73 ($&lt;0.001)$</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>&lt;0.001 (0.989)</td>
<td>0.02 (0.877)</td>
</tr>
<tr>
<td>Grazing × Habitat</td>
<td>3</td>
<td>3.39 (0.012)</td>
<td>3.21 (0.029)</td>
</tr>
<tr>
<td>Grazing × Year</td>
<td>3</td>
<td>9.93 ($&lt;0.001$)</td>
<td>1.31 (0.279)</td>
</tr>
<tr>
<td>Habitat × Year</td>
<td>1</td>
<td>10.96 (0.002)</td>
<td>1.31 (0.257)</td>
</tr>
<tr>
<td>Grazing × Habitat × Year</td>
<td>3</td>
<td>0.39 (0.764)</td>
<td>1.39 (0.253)</td>
</tr>
<tr>
<td>b) FR</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grazing intensity</td>
<td>3</td>
<td>0.57 (0.639)</td>
<td>7.28 ($&lt;0.001$)</td>
</tr>
<tr>
<td>Habitat</td>
<td>1</td>
<td>122.75 ($&lt;0.001$)</td>
<td>128.78 ($&lt;0.001$)</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>0.93 (0.338)</td>
<td>3.36 (0.072)</td>
</tr>
<tr>
<td>Grazing × Habitat</td>
<td>3</td>
<td>0.23 (0.873)</td>
<td>14.94 ($&lt;0.001$)</td>
</tr>
<tr>
<td>Grazing × Year</td>
<td>3</td>
<td>0.72 (0.546)</td>
<td>1.82 (0.154)</td>
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<tr>
<td>Habitat × Year</td>
<td>1</td>
<td>0.20 (0.660)</td>
<td>14.46 ($&lt;0.001$)</td>
</tr>
<tr>
<td>Grazing × Habitat × Year</td>
<td>3</td>
<td>2.28 (0.089)</td>
<td>0.485 (0.694)</td>
</tr>
<tr>
<td>c) FD</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grazing intensity</td>
<td>3</td>
<td>5.21 (0.003)</td>
<td>3.93 (0.013)</td>
</tr>
<tr>
<td>Habitat</td>
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<td>5.28 (0.025)</td>
<td>26.21 ($&lt;0.001$)</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>17.32 ($&lt;0.001$)</td>
<td>6.60 (0.013)</td>
</tr>
<tr>
<td>Grazing × Habitat</td>
<td>3</td>
<td>1.64 (0.191)</td>
<td>2.25 (0.093)</td>
</tr>
<tr>
<td>Grazing × Year</td>
<td>3</td>
<td>3.24 (0.028)</td>
<td>0.97 (0.414)</td>
</tr>
<tr>
<td>Habitat × Year</td>
<td>1</td>
<td>49.70 ($&lt;0.001$)</td>
<td>0.219 (0.641)</td>
</tr>
<tr>
<td>Grazing × Habitat × Year</td>
<td>3</td>
<td>5.21 (0.003)</td>
<td>5.36 (0.003)</td>
</tr>
</tbody>
</table>
FIGURE LEGENDS

Figure 1. Boxplots showing the effect of grazing intensity (1: abandoned; 2: grazed occasionally; 3: grazed moderately; 4: overgrazed) and year (dry and wet) on the community weighted mean values of the different functional traits for each grazing intensity level and year, in productive (left) and unproductive (right) habitats. When the effect of grazing is significant, different letters for each year (lower case for the dry year and upper case for the wet year) indicate significant differences between grazing intensity levels. Similarly, asterisks show significant differences between years for a given habitat type and grazing intensity level. Outliers are not shown to improve the clarity of the figures.

Figure 2. Boxplots showing the effect of grazing intensity (1: abandoned; 2: grazed occasionally; 3: grazed moderately; 4: overgrazed) and year (dry and wet) on functional richness (FR; SESRaopr) values of the different functional traits for each grazing intensity level and year, in productive (left) and unproductive (right) habitats. Interpretation of the statistical results is as in Fig. 1. Outliers are not shown to improve the clarity of the figures.

Figure 3. Boxplots showing the effect of grazing intensity (1: abandoned; 2: grazed occasionally; 3: grazed moderately; 4: overgrazed) and year (dry and wet) on functional divergence (FD; SESRaoab) values of the different functional traits for each grazing intensity level and year, in productive (left) and unproductive (right) habitats. Interpretation of the statistical results is as in Fig. 1. Outliers are not shown to improve the clarity of the figures.
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Figure 2. Boxplots showing the effect of grazing intensity and year on functional richness (FR; SESRaop) values of the different functional traits for each grazing intensity level and year, in productive (left) and unproductive (right) habitats. Interpretation of the statistical results is as in Fig. 1. Outliers are not shown to improve the clarity of the figures.
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