

Community assembly along a soil depth gradient: contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland

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Summary

1. Understanding how environmental factors drive plant community assembly remains a major challenge in community ecology. The strength of different assembly processes along environmental gradients, such as environmental filtering and functional niche differentiation, can be quantified by analysing trait distributions in communities. While environmental filtering affects species occurrence among communities, functional divergence or convergence is strongly related to species abundances within communities, which few studies have taken into account. We examine the trait-mediated effect of these two processes along a stress-resource gradient.

2. We measured species abundances and the distributions of eight traits related to vegetative and regenerative phases in plant communities along a gradient of soil depth and resource availability in Mediterranean rangelands. We quantified environmental filtering, defined as a local restriction of trait range, and trait divergence, based on abundance-weighted trait variance, using a two-step approach with specifically designed null models.

3. Communities presented a clear functional response to the soil gradient, as evidenced by strong trends in community-weighted trait means. We detected environmental filtering of different traits at both ends of the gradient, suggesting that, contrary to widespread expectations, trait filtering may not necessarily be the result of abiotic filtering under harsh conditions but could likely also result from biotic interactions in productive habitats.

4. We found marked shifts in trait abundance distributions within communities along the gradient. Vegetative traits (e.g. leaf dry matter content) diverged on shallow soils, reflecting the coexistence of distinct water- and nutrient-use strategies in these constrained habitats and converged with increasing soil resource availability. By contrast, regenerative traits (e.g. seed mass) tended to diverge towards deeper soils, while plant reproductive heights diverged all along the gradient.

5. *Synthesis:* Our study highlights how the combination of abundance data with traits capturing different functional niches is critical to the detection of complex functional responses of plant communities to environmental gradients. We demonstrate that patterns of trait divergence and filtering are strongly contingent on both trait and environment such that there can be no expectation of a simple trend of increasing or decreasing functional divergence along a gradient of resource availability.

Key-words: determinants of plant community diversity and structure, environmental filtering, functional community structure, functional convergence, functional divergence, null model, plant traits, soil resource gradient, trait–environment relationships

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Introduction

Understanding changes in vegetation patterns along environmental gradients is a long standing issue in ecology (Schimper 1903; Whittaker 1956), but predicting how environmental factors will drive community assembly still remains a major challenge (Grime 2006; Mayfield & Levine 2010). The assembly of species into local communities has been conceptualized as a series of filters selecting species according to their traits from a regional species pool into a local habitat (Keddy 1992). Focusing on traits rather than species identities has helped renew community ecology by increasing the potential for general principles to emerge, in that quantitative comparisons (e.g. trait–environment relationships) can be made among communities that may share few if any species (McGill *et al.* 2006; Messier, McGill & Lechowicz 2010). Despite substantial recent advances in trait-based community ecology, the relative importance of environmental filters is still hotly debated, particularly at small scales where stochastic dispersal and biotic interactions may prevail over abiotic environmental constraints (Bell 2005; Vellend 2010). The analysis of trait distributions within and among communities permits quantification of the strength of different filtering processes and constraints on community assembly along environmental gradients (Freschet *et al.* 2011; Violle *et al.* 2012). Competition is expected to create a divergent or ‘overdispersed’ distribution of trait values among locally co-occurring species, with coexistence contingent on limiting similarities in resource use among species (MacArthur & Levins 1967). Strong abiotic filters are expected to constrain the range of species trait values and to lead to convergent or ‘underdispersed’ local trait distributions (Weiher, Clarke & Keddy 1998; Cornwell, Schwilk & Ackerly 2006; Grime 2006).

Recently, an increasing number of studies have used traits to characterize community structure along environmental gradients (e.g. Cornwell & Ackerly 2009; Pakeman, Lennon & Brooker 2011; Ricotta & Moretti 2011; Katabuchi *et al.* 2012). Studies presenting rigorous quantification of trait–environment relationships are still relatively few (Weiher *et al.* 2011), and considerable uncertainty remains regarding which pattern of trait distribution (filtering, convergence or divergence) can be expected at different positions along environmental gradients, and for which traits (Grime 2006; Wilson 2007; Mayfield & Levine 2010). According to one line of reasoning, the strongest patterns of trait filtering and convergence are expected in harsh conditions (e.g. cold or dry) due to strong abiotic filtering (Weiher, Clarke & Keddy 1998; Cornwell, Schwilk & Ackerly 2006), while high trait divergence is expected in more competitive and productive habitats according to the limiting similarity hypothesis (MacArthur & Levins 1967; Wilson 2007; Wilson & Stubbs 2012). However, there are conflicting views regarding the existence of competition-driven trait divergence in plant communities (Grime 2006; Navas & Violle 2009). Some authors argue that a high level of competition may itself represent a strong filter, thereby leading to trait convergence through mechanisms of equalizing fitness for example (Chesson 2000;

Grime 2006). To some extent, considering multiple traits may allow these views to be reconciled: traits related to the use of a limiting resource may show more convergent patterns, while other traits related to regeneration may show more divergent patterns (Weiher & Keddy 1995; Grime 2006; Swenson & Enquist 2009; Grime & Pierce 2012). Despite the allure of these ideas, previous efforts for detecting trait assembly patterns have yielded sometimes inconclusive (e.g. Schamp, Chau & Aarssen 2008) and often contradictory results (e.g. Weiher, Clarke & Keddy 1998; Pakeman, Lennon & Brooker 2011; Mason *et al.* 2012).

Contradictory conclusions among studies may stem, in part, from aspects of methodology, such as studying gradients of different length (Weiher, Clarke & Keddy 1998; Cornwell & Ackerly 2009), with different traits (Spasojevic & Suding 2011; Wilson & Stubbs 2012), different analysis frameworks (Sonnier, Shipley & Navas 2010; Pakeman, Lennon & Brooker 2011) or the use of presence-absence versus abundance data (Cingolani *et al.* 2007; Thompson *et al.* 2010). Concerning the latter point, stronger trait–environment relationships may be observed when taking species abundances into account rather than simple presence/absence (Garnier *et al.* 2004; Cingolani *et al.* 2007), although few studies have specifically investigated this issue (but see Mouillot, Mason & Wilson 2007; Pakeman *et al.* 2008). In this paper, we combine all of these disparate aspects of earlier studies into a single, integrated analysis framework, which we use to investigate trait-based plant community structure among 12 communities along a steep soil moisture/depth gradient in calcareous rangelands of southern France. For eight traits representing both resource-use and regeneration strategies, we first characterize trends in community-weighted mean trait values along the gradient. We then use a two-step framework in which local trait distributions are analysed as the result of two distinct steps of community assembly (Fig. 1): (i) environmental filtering, defined here as the restriction of local species membership (i.e. presence/absence), which is manifested as a restriction of trait range compared with the regional pool of species and (ii) the determination of local species abundances via environment-dependent trait optima and/or interactions between species.

Using this framework, we tested two overarching hypotheses from the literature:

1 Environmental filtering is associated with trait convergence and is strongest on shallower resource poor soils, while trait divergence is greatest in communities with higher soil resources and productivity.

2 Traits related to regeneration strategies tend to show divergent patterns, while traits related to vegetative growth tend to show convergent patterns in communities.

Alternatively, if patterns of convergence versus divergence are contingent both on the trait and the environment, then (i) both filtering and divergence are likely to occur at all positions on the gradient, depending on the trait and (ii) both regeneration and vegetative traits can show either convergent or divergent patterns, depending on gradient position. We will

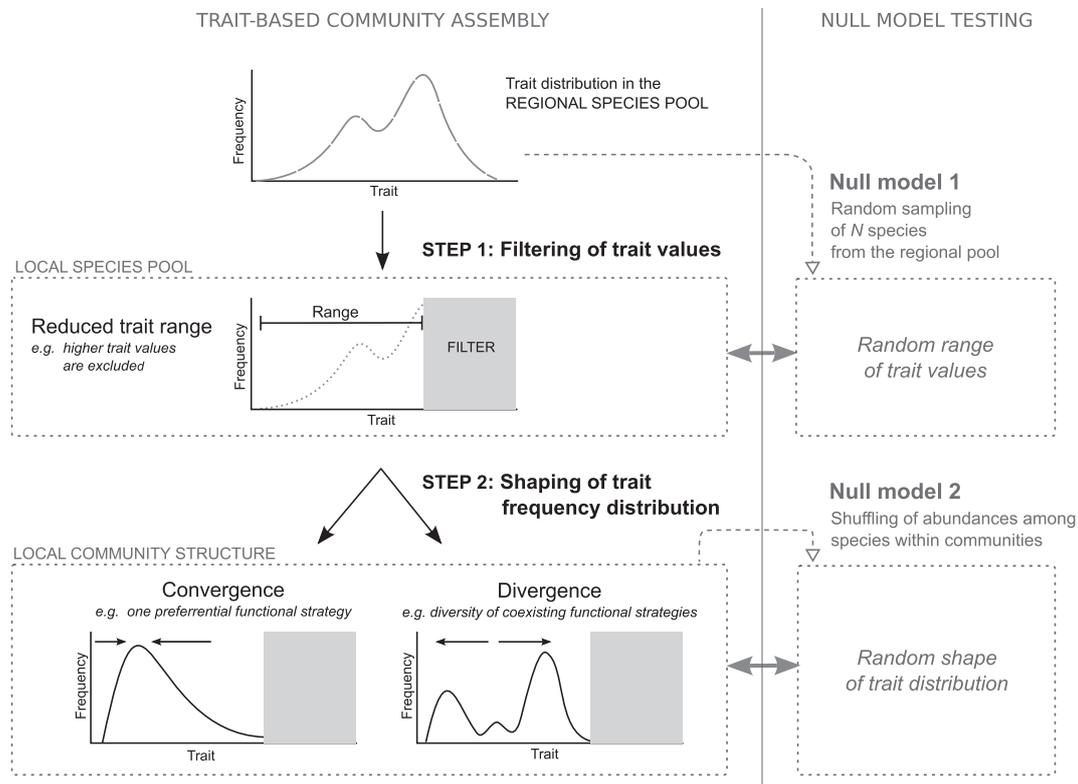


Fig. 1. Two-step conceptual framework for the analysis of trait-based community assembly. The distribution of trait values for a hypothetical trait is shown within the regional species pool (top panel), within a virtual transient community following environmental filtering (central panel), and in two examples of realized local communities (lower panels). Community assembly is conceived of as a two-step process. Step 1: Individuals from the regional species pool are dispersed to a local habitat, and trait filtering excludes individuals with unfit trait values. Step 2: Within the local species pool, trait values may influence performance, which may lead to patterns of trait convergence or divergence. Null model testing: null model 1 samples a given number of species randomly from the regional pool; null model 2 randomly shuffles abundances among species within communities.

demonstrate that several key conclusions depend on the combination of multiple components (i.e. including abundances, multiple traits, environmental gradient) that have not typically been combined in previous studies.

Material and methods

STUDY SITE

The study was carried out on dry calcareous rangelands in southern France, located on a limestone plateau (Larzac Causse) at the INRA La Fage experimental station (43°55'N, 3°05'E, 790 m a.s.l.). Climate on the plateau is subhumid with a Mediterranean influence. Cool and wet winters alternate with warm and very dry summers, with an annual mean precipitation of 1070 mm occurring mainly during spring and autumn. Mean monthly temperatures vary from 1 °C in January to 19 °C in August (data from 1973 to 2006; Fayolle 2008). Vegetation is dominated by perennial herbaceous species (*Bromus erectus* Huds., *Festuca christianii-bernardii* Kerguelen), along with loosely scattered shrubs and trees (e.g. *Buxus sempervirens* L., *Quercus pubescens* Willd.). For the past 35 years, the 280 ha of rangelands have been grazed by a sheep herd (Romane breed) raised outdoors year-round for meat production. A short growth period (spring and autumn) along with poor and shallow soils, accounts for the low productivity of the grasslands (average maximum standing biomass in spring of about 100 g m⁻²).

ENVIRONMENTAL GRADIENT AND STUDY DESIGN

Soils on the limestone plateau consist of dolomitic rendzinas arranged as a mosaic of different depths and textures. Twelve plots (6 × 9 m) up to 1.5 km apart were selected to span the widest possible range of soil types: from the shallow and dry soils of dolomitic sands to deeper, richer and moister soils. Soil characteristics, which appear to be primarily responsible for vegetation differences, were measured to quantitatively characterize the gradient (for further details, see Pérez-Ramos *et al.* 2012). Mean soil depth (ranging from 20 to 95 cm) was determined in each plot with 6–9 soil cores (5 cm wide) distributed randomly. Soil physico-chemical properties were assessed for three of these soil cores per plot. Five soil properties were determined using standard procedures (Afnor 1994): soil texture (clay, silt and sand gravimetric content), pH (in water), total organic carbon, available phosphorous (using the Olsen method) and the C/N ratio. To assess nitrogen limitation for plant growth, a nitrogen nutrition index (NNI) was calculated as the ratio between the actual nitrogen concentration of above-ground biomass (measured during spring 2009) and the critical nitrogen concentration (i.e. nitrogen concentrations allowing potential growth), as proposed by Lemaire (1997) (see also Garnier *et al.* 2007). Soil water content (SWC) was measured weekly during spring 2008 and 2009, using capacitance soil moisture probes (*DIVINER 2000*, Sentek Pty Ltd, Stepney, Australia), which provided a complete profile of soil humidity at three permanent locations in each plot. In each plot, average spring SWC was calculated and used as a variable representing soil water content during the peak of productivity (i.e. before summer drought).

Environmental variables (see Table S1 in Supporting Information) were analysed using a principal component analysis (PCA; Fig. S1). Importantly, most environmental variables were collinear, with a first axis of the PCA explaining over 67% of the variability: soils varied from shallow and dry with low nitrogen availability at one end of the axis, to deep and moist with high nitrogen availability at the other. The second axis, which explained only 12% of variance, captured mainly the variance caused by one outlier plot with unusually sandy soil (but not unusual vegetation). Hereafter, we refer to plot scores along the first PCA axis (PC1) as 'the soil gradient', values of which were used in all subsequent statistical analyses as a single variable representing soil conditions. Above-ground standing biomass, estimated from the total green above-ground biomass of two quadrats (1 × 1 m) per plot at the end of spring 2009, was also strongly collinear with PC1 (Fig. S1).

VEGETATION SURVEYS AND TRAIT MEASUREMENTS

In June 2009, the abundance of each species (77 species in total, see Table S2) was estimated in terms of the percentage covered in each of the 12 plots, using the point-intercept method along linear transects (Levy & Madden 1933). Five 3-m transects were distributed randomly in each plot. A 4-mm-diameter pin was inserted vertically every 10 cm along each transect, and the number of contacts of live organs per species at each pin-point was recorded.

Eight morphological, chemical and phenological plant traits (Table 1) were chosen to characterize the vegetative and regenerative phases. Five leaf traits were related to resource use, while seed mass and the onset of flowering depicted reproductive strategies. Reproductive height was chosen as a trait pertaining both to vegetative and reproductive strategies (Garnier & Navas 2012). For the 26 most abundant species (i.e. representing over 80% of cover; Pakeman *et al.* 2008), leaves were sampled in June 2009 on at least 12 individuals per species distributed across 4–12 plots. For each individual sample, leaf dry matter content (LDMC), specific leaf area, (SLA), leaf blade thickness (LT), leaf nitrogen content (LNC) and the carbon isotopic ratio ($\delta^{13}\text{C}$) were measured following standardized methods (Cornelissen *et al.* 2003; for leaf thickness, see Vile *et al.* 2005). For the same 26 species, mean reproductive height was

measured during summer 2010 on at least 40 individuals across the entire gradient.

For the less abundant species (representing 21–27 species according to traits; details in Table S2), leaf trait data and reproductive heights were collected from a previous study conducted on the same site (Fayolle 2008; Table S2), in which traits were measured using the same standardized methods, except for leaf thickness which was estimated from SLA and LDMC values according to the equation proposed by Vile *et al.* (2005). Linear regressions between trait values of species common to both our data and that of Fayolle (2008) indicated a very good comparability between data sets (for all traits, $r^2 > 0.90$, $P < 0.001$, slopes not significantly different from 1).

Seed mass data were also taken from Fayolle (2008), and completed for two species during the present study, using standardized protocols (Cornelissen *et al.* 2003). From March to November 2010, species phenology was monitored weekly in the 12 plots of the gradient, providing observations for the onset of flowering (OFL) of 62 species (see details in Table S2).

Average trait values were calculated for each species, as data in this study did not permit the analysis of intraspecific trait variability. Reproductive heights and seed masses were log-transformed to meet normality prior to all analyses.

ANALYSES

Defining the species pool

Defining the pool of species from which local communities theoretically assemble is a critical step in building null models (Gotelli & Graves 1996). In this study, the plant species found in each plot (6 × 9 m) represented local communities, while the regional species pool was defined as all the species observed across all 12 plots, and for which trait values were known. The small size (280-ha), even topography and mosaic nature of the study site at La Fage, plus the frequent movement of animals, suggest that dispersal limitation is unlikely to be a strong determinant of species absence from a given plot. Because of missing data for some traits, the regional species pool was not exactly the same for all traits (see Table S2). To test for

Table 1. Description of functional traits, related plant functions and associated phases of the plant life cycle, based on the literature*

Trait	Abb.	Description†	Related function*	Life-cycle phase
Specific leaf area	SLA	One-sided area of a fresh leaf divided by its oven-dry mass ($\text{m}^2 \text{kg}^{-1}$)	Photosynthetic rate, leaf longevity, relative growth rate	Vegetative growth
Leaf dry matter content	LDMC	Oven-dry mass of a leaf divided by its water saturated fresh mass (mg g^{-1})	Leaf tissue density, leaf physical resistance, stress tolerance	Vegetative growth
Leaf thickness	LT	Leaf blade thickness (μm)	Gas exchange, water retention	Vegetative growth
Leaf carbon isotopic ratio	$\delta^{13}\text{C}$	Deviation of the leaf $^{13}\text{C}/^{12}\text{C}$ isotopic ratio	Gas exchange, water-use efficiency	Vegetative growth
Leaf nitrogen concentration	LNC	Total amount of nitrogen per unit of leaf dry mass (mg g^{-1})	Light capture, photosynthetic rate	Vegetative growth
Reproductive height	Hrep	Shortest distance between the top of reproductive structures and ground level (cm)	Dispersal distance, light capture, above-ground competition	Regeneration and vegetative growth
Seed mass	SM	Air-dried mass of a seed (mg)	Dispersal and regeneration strategy, seedling competition	Regeneration
Onset of flowering	OFL	Day of the first flower observed (day of year; DOY)	Phenological and reproductive strategy	Regeneration

*Farquhar, Ehleringer & Hubick 1989; Grime *et al.* 1997; Weiher *et al.* 1999; McIntyre *et al.* 1999; Westoby *et al.* 2002; Cornelissen *et al.* 2003; Garnier & Navas 2012.

†Standardized definitions from the *Trait Thesaurus* (Laporte, Mougenot & Garnier 2012).

possible differences due to unequal species sampling, we re-ran all analyses using only the 42 species for which data was available for all traits and found overall the same trends (results not shown).

Species diversity and composition along the gradient

To provide context for our trait-based analyses, we quantified species diversity and composition within and across plots. Species diversity was characterized by computing in each plot species richness (SR) and species evenness with the Gini-Simpson diversity index (Simpson 1949). Similarity in species composition between communities was calculated using the Sørensen index (Sørensen 1948; Legendre & Legendre 1998). A distance–decay curve representing the turn-over of species along the gradient was built by comparing pairwise Sørensen similarities between plots against pairwise Euclidean distances in environmental conditions (scores on PCA1 – see above); significance of the correlation was assessed with a Mantel test (Legendre & Legendre 1998).

Environmental filtering

Environmental filtering was assessed by calculating the range of trait values observed in each plot (max–min) and comparing it to the range expected given the regional pool and the local species richness (Weiher, Clarke & Keddy 1998; Cornwell & Ackerly 2009; Fig. 1). A null model of community assembly (NM1) was built to test the following specific null hypothesis: species occurrences are distributed among plots randomly with respect to traits or environment. For a given plot i with an observed number of species S_i , NM1 makes repeated random draws (without replacement) of S_i species from the regional species pool (Lawlor 1980; Gotelli & Graves 1996; Cornwell, Schwillk & Ackerly 2006), with each species' probability of being chosen proportional to its regional abundance. Thus, NM1 assumes that a species ability to colonize a plot is proportional to its abundance in the species pool (Kraft & Ackerly 2010). We interpreted a smaller range than expected as an indicator of trait filtering. A larger range than expected could not consistently be interpreted as trait over-dispersion, given the sensitivity of range measures to extreme values and outliers (Cornwell & Ackerly 2009).

Community trait distributions

To characterize trait distributions in communities, we investigated both the mean and the variance of trait values, weighted by species abundances. The community-weighted mean (CWM) for each trait t was calculated as the mean of species trait values, t_i , of the S species in each plot, with each species, i , weighted by its relative abundance, p_i (Garnier *et al.* 2004; Violle *et al.* 2007):

$$\text{CWM} = \sum_{i=1}^S p_i \times t_i \quad \text{eqn 1}$$

Community-weighted trait variances (CWV) were computed for each trait in each plot as follows (Sonnier, Shipley & Navas 2010):

$$\text{CWV} = \sum_{i=1}^S p_i \times (t_i - \text{CWM})^2 \quad \text{eqn 2}$$

This formulation of trait variance is close to Mason *et al.*'s (2003) FDvar and to Rao's quadratic entropy calculated with Euclidian dissimilarities (Rao 1982; De Bello *et al.* 2009), which both yielded similar results to CWV (results not shown).

We first tested for correlations between the CWM of each trait and the soil gradient. Next, to test for nonrandom patterns in the CWV values, a second null model (NM2) was constructed to test the following null hypothesis: species abundances within a plot are distributed randomly with respect to trait values. In NM2, the list of observed species in each local community (and their associated traits) remained unchanged, but the abundance values were shuffled randomly among them (see also Mason *et al.* 2008). This randomization broke any relationship between trait values and abundances, while maintaining the same richness and evenness of abundances within plots. We interpret a lower observed CWV than expected as evidence of convergence towards a common trait value, while a larger CWV than expected represented a divergent trait distribution (Fig. 1 bottom panels). A CWV close to the null expectation indicated a random dispersion of abundances among local species trait values.

Null model testing

Null model testing permits to quantify as an 'effect size' the extent to which the observed value of a metric is different from its expected distribution under a well-defined null hypothesis. For each trait and community, the observed value of a given metric (i.e. trait range or CWV) was compared with the distribution generated by 9999 runs of the appropriate null model (NM1 or NM2). An effect size (ES) was calculated based on the probability for the observed value to be lower than expected by chance (i.e. the quantile of the null distribution in which the observed value is found; Kelt, Taper & Meserve 1995; Chase *et al.* 2011; see calculations in Appendix S1). ES values were re-scaled to vary from -1 to 1 , with negative values indicating a lower observed value than expected, and vice versa; values close to zero indicate observed values close to the median of the null distribution. This standardization of effects was preferred to the often-used Standardized Effect Size (SES; e.g. Swenson & Enquist 2009; Kraft & Ackerly 2010; Jung *et al.* 2010), which is expressed in units of standard deviations from the mean, due to the asymmetrical or otherwise non-normal shape of most null distributions in our study.

STATISTICAL ANALYSES

Two types of statistical analyses were carried out on the ES values for each trait and each metric. First, we tried to detect general patterns of community structure (i.e. range restriction, divergence) that may be present in all communities, regardless of the soil gradient. To do this, we tested if ES values were overall different from zero (either positive or negative) using a two-tailed Wilcoxon signed-ranks test (Sokal & Rohlf 1995). Second, because different processes may be driving assembly along the gradient, we investigated the variations in community structure along the soil gradient. To do this, we plotted ES values against the soil gradient (i.e. plot scores along the first axis of the PCA on environmental parameters; Fig. S1) and tested for significant trends using nonparametric Spearman's rank correlations. All analyses including null models testing were performed using R (R Development Core Team 2010).

Results

SPECIES DIVERSITY AND TURNOVER ALONG THE GRADIENT

We found 15–33 species per plot, and no trend in species richness along the gradient (Pearson correlation: $r = -0.07$,

$P = 0.59$). However, there was a significant negative correlation of the Gini-Simpson diversity index with the soil gradient ($r = 0.76$, $P < 0.001$), indicating a steep decrease in species evenness towards the deeper soils where a single dominant species, the perennial grass *B. erectus*, represented 60–80% of aboveground biomass. By contrast, on shallow soils the dominant species, the perennial grass *F. christianii-bernardii*, represented only from 25% to 42% of biomass. Standing biomass also increased from *c.* 50 g m⁻² on the shallow soils (with 10% bare ground) to *c.* 250 g m⁻² on the deeper soils (no bare ground). There was a clear turnover of species along the soil gradient, as shown by the strong negative correlation between Sørensen similarities and differences in soil conditions (plot scores on PC1; Mantel $r = 0.7$, $P < 0.001$; see Fig. S2). Annual species were mainly present in the five shallowest-soil plots, in which they represented 3–15% of the biomass, and mostly absent from the intermediate to deeper-soil plots (see Fig. S3).

VARIATION IN COMMUNITY TRAIT MEANS ALONG THE GRADIENT

Community-weighted means (CWM) showed significant trends along the gradient for all traits except $\delta^{13}\text{C}$ (Fig. 2).

The CWM of leaf dry matter content and leaf thickness decreased, while those of specific leaf area and leaf nitrogen content increased significantly from shallow to deep soils (linear regressions on Fig. 2). We also observed a significant increase in CWM for reproductive height, onset of flowering, and seed mass along the gradient.

TRAIT FILTERING ALONG THE GRADIENT

Trait filtering was detected when trait ranges were narrower than expected with NM1. We found no evidence for overall reductions in trait range when considering all plots collectively (non-significant Wilcoxon test towards lower values; Fig. 3). However, significant trends in the standardized effect of trait range were found along the soil gradient for six of the eight traits (Fig. 3). The trait ranges of leaf dry matter content, leaf $\delta^{13}\text{C}$ and seed mass were generally greater than expected on shallow soils and less than expected on deeper soils, while the opposite was true for leaf nitrogen content, plant height and leaf thickness. Wider ranges than expected were found across the entire gradient for the onset of flowering (Wilcoxon test; Fig. 3), indicating the existence of both early and late flowering species in all communities.

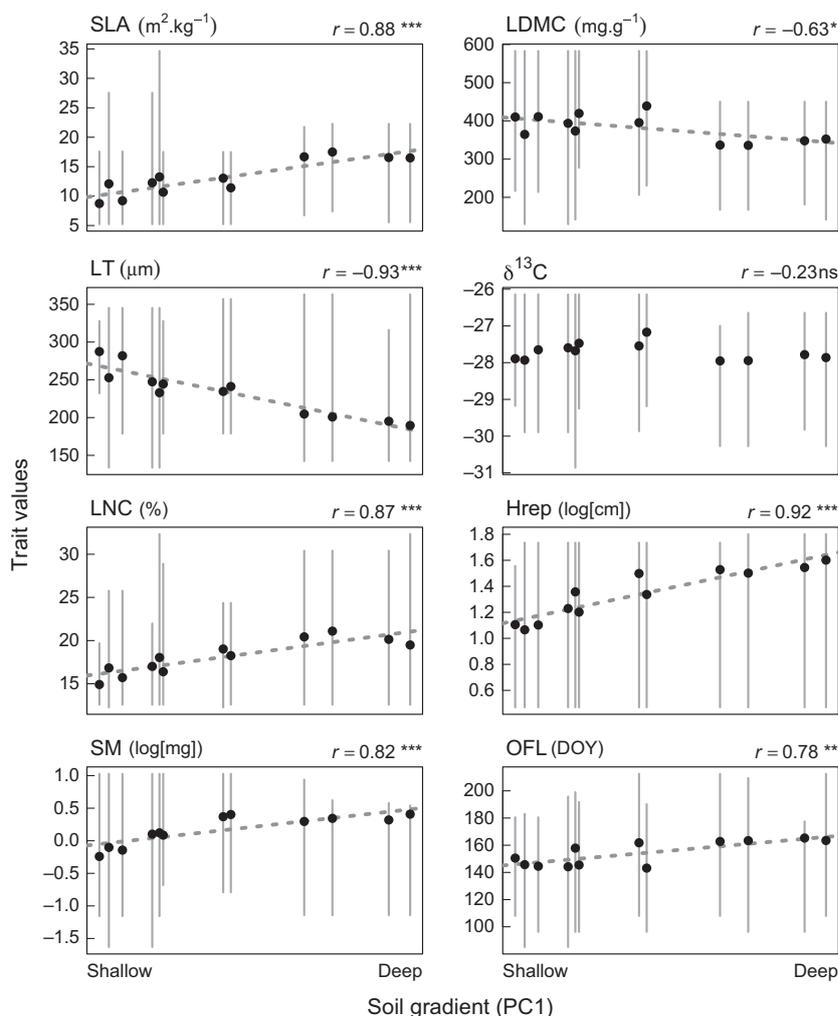


Fig. 2. Trait ranges and abundance-weighted means (CWM) in communities along the soil gradient for eight functional traits. Vertical grey segments represent the range of trait values observed in each community, from the minimum to the maximum value. CWM (black bullets) were tested along PC1 of the soil gradient (cf. Fig. 2) using a linear regression (statistics in the top right corner of panels). Dashed grey lines represent significant regressions (n.s.: $P > 0.5$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

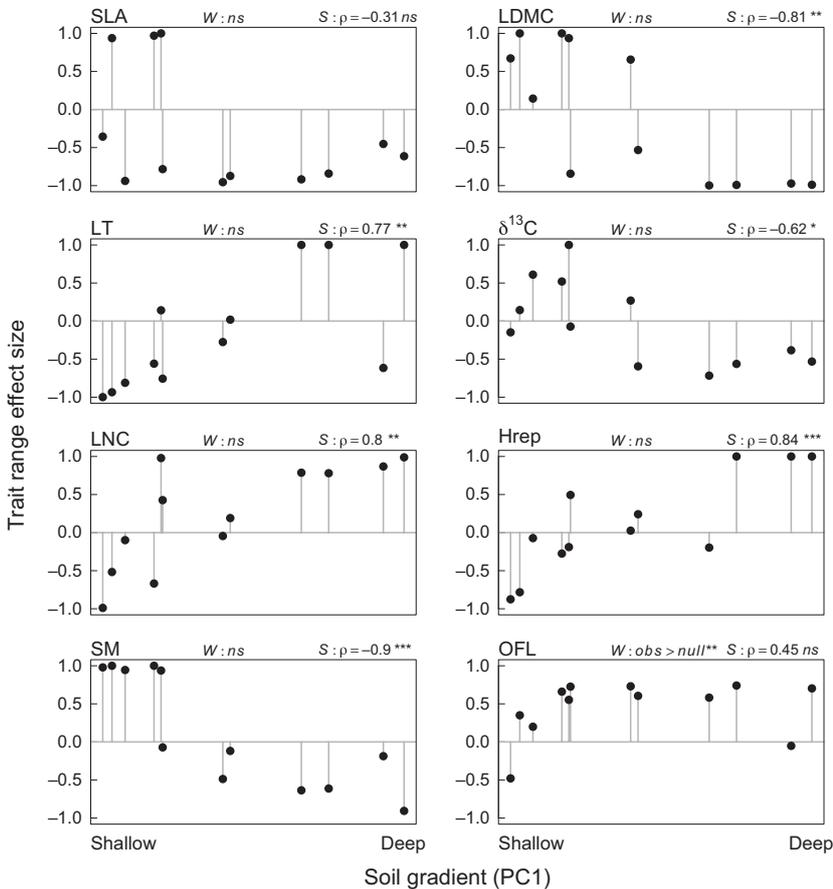


Fig. 3. Variation in community trait range along the soil gradient. Effect sizes (ES) of trait range were calculated relative to a null model of random assembly (NM1; see methods). Negative ES indicate a narrower trait range than expected, suggesting environmental filtering. The solid horizontal line corresponds to the null expectation (ES = 0). Statistics for one-sided Wilcoxon tests (W) and Spearman's rank correlations (S) are indicated above panels. (n.s.: $P > 0.5$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

Some patterns of trait range were due to the presence on shallow soils of a few rare annual species (see Fig. S3), which had the highest SLA values and the lowest seed masses. Interestingly, when examining perennials only, patterns of trait filtering remained the same for all traits except for SLA and SM. SLA ranges were found to be reduced in all communities along the gradient (Wilcoxon towards lower values: $P < 0.001$; see Fig. S4), while SM ranges of perennials showed no sign of filtering. Results for community-weighted means and variances remained entirely unchanged with or without annuals, given the very low abundances of these annual species.

TRAIT DIVERGENCE ALONG THE GRADIENT

Trait divergence emerges from the analysis of community-weighted variance (CWV) and its related null model (NM2; Fig. 4). Overall, communities displayed a higher CWV in reproductive height (Hrep) than expected, indicating that abundant species tended to have dissimilar reproductive heights all along the gradient. The variance of $\delta^{13}\text{C}$ and leaf nitrogen concentration decreased significantly, while the variance of seed mass and onset of flowering tended to increase towards the deeper soils. Results for LDMC show a shift in CWV along the gradient: LDMC tended to be divergent in shallow to intermediate plots (positive effect sizes), and then abundant tended to converge in the deeper plots (Fig. 4).

CWV of SLA presented a non-linear trend along the gradient: SLA values diverged strongly at intermediate soil depths, while they tended to be randomly distributed or even to converge towards both ends of the gradient. Leaf thickness followed a somewhat similar pattern of variance as SLA, although it diverged only in two intermediate plots.

Discussion

In these Mediterranean rangeland communities, we detected a clear turnover of species in response to a gradient in soil, water and nutrient availability, which was associated with changes in functional community structure. Our approach shows how taking into account environmental gradients in community assembly studies can reveal contrasting patterns of assembly that would remain otherwise undetected (summarized schematically in Fig. 5). We show that strong but sometimes opposite functional patterns of assembly can exist at each end of an environmental gradient, which may cancel each other out in a 'global' analysis ignoring the gradient. By analysing independently a wide array of functional traits, we uncovered different patterns of trait response to the gradient, depending on the functional dimensions captured by traits. Moreover, the two-step approach we used allowed us to show that a trait could locally be both limited in range by environmental factors and still have a divergent distribution of values within the community. By explicitly including spe-

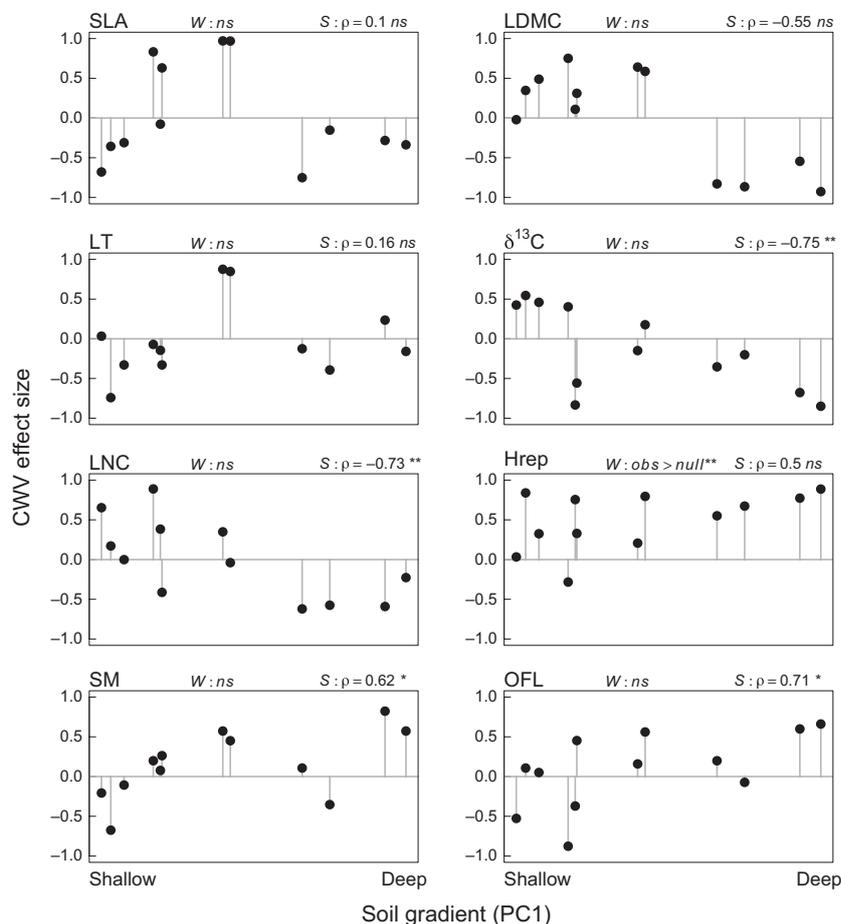


Fig. 4. Community-weighted trait variance (CWV) along the soil gradient. Effect sizes (ES) of CWV were calculated by comparing observed CWV to a null distribution obtained by randomly shuffling abundances among species in each community (NM2; see Methods). Negative (respectively positive) ES represent a lower (larger) CWV than expected, suggesting a tendency for trait convergence (divergence). The solid horizontal line corresponds to the null expectation ($ES = 0$). Statistics for one-sided Wilcoxon tests (W) and Spearman's rank correlations (S) are indicated above panels. (n.s.: $P > 0.5$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

cies abundances in our analyses instead of using presence-absence data, we were able to detect significant patterns of divergence or convergence for most traits on some point of the gradient.

TRAIT-ENVIRONMENT RELATIONSHIPS

There was a clear functional response of grassland communities to the soil gradient, as evidenced by the strong trends in community-weighted means observed for seven of the eight traits (Fig. 2). As expected, leaf traits related to the resource-use and acquisition/conservation trade-off known as the leaf economics spectrum (Wright *et al.* 2004), and other leaf traits related to leaf functioning such as leaf thickness (Garnier & Salager 1999) and leaf dry matter content (Wilson, Thompson & Hodgson 1999) presented strong responses to the soil gradient: they revealed a gradual change in successful resource-use strategies from slow-growing and nutrient conservative species on shallow soils to fast-growing and less efficient species on the deeper and more fertile soils (Grime 1977; Garnier & Navas 2012). Furthermore, the functional response of communities also involved shifts in plant stature and regeneration strategies, dominants becoming taller, with larger seed masses and later onset of flowering towards the deeper soils. The increase in mean reproductive heights suggested that higher competitive ability for above-ground resources (e.g. light;

Gaudet & Keddy 1988; Violle *et al.* 2009) and/or higher dispersal distances (Thomson *et al.* 2011) were advantageous towards the deeper soils. Larger seeds have been interpreted as a successful regeneration trait under dense covers where seedling competition may arise and light may be limiting (Murray *et al.* 2005). By contrast, plants with smaller seeds, mostly early flowering and annual species, are often more abundant in dry and less productive Mediterranean grasslands (Azcarate *et al.* 2002), which is consistent with annual species only occurring on the drier shallow soils in our study. The larger seed output and greater longevity in the seed bank associated with small seeded species (Bekker *et al.* 1998) can be advantageous under unpredictable inter-annual variations in perturbations such as severe summer drought (Thompson 2000).

ENVIRONMENTAL FILTERING OF DIFFERENT TRAITS ALONG THE GRADIENT

Our results clearly support the hypothesis that trait filtering may occur at both ends of a gradient in resource availabilities. However, the detection of filtering patterns depended critically on the type of trait considered: different traits, pertaining to different aspects of plant strategies, were filtered at each end of the gradient (summarized in Fig. 5). SLA was the only trait to be filtered all along the gradient, highlighting the key

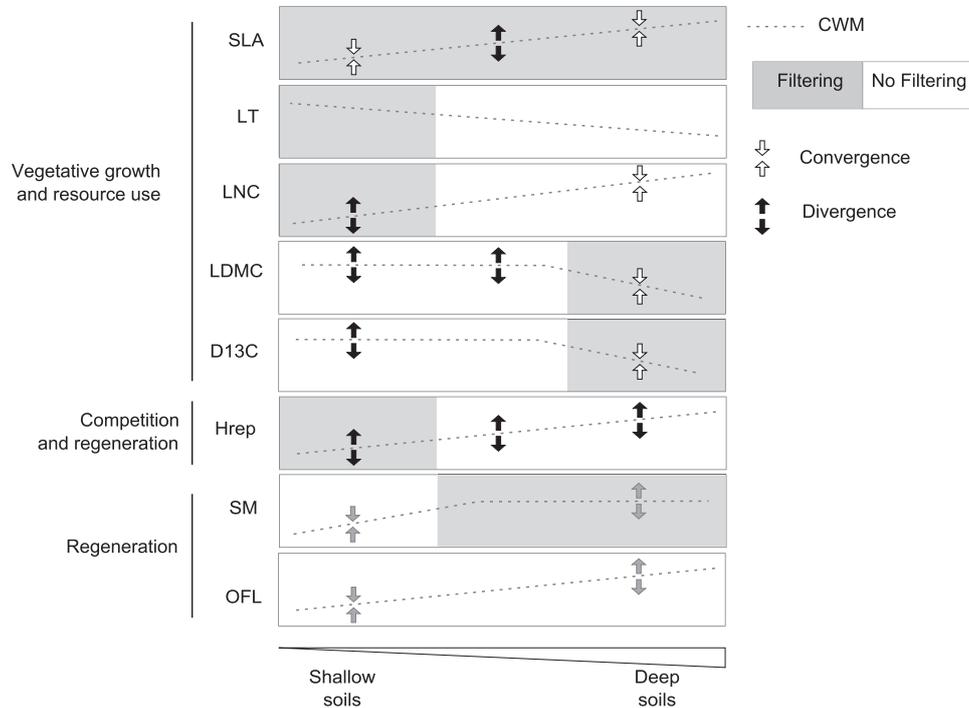


Fig. 5. Schematic interpretation of the trends in functional community structure observed for eight functional traits along the soil depth gradient. Results of the study discussed in the main text are summarized schematically at three points along the axis of the gradient: shallow, intermediate and deep soils. Dotted lines represent trends in community-weighted means (CWM); greyed areas highlight the regions of the gradient in which a restricted trait range (i.e. environmental filtering) was found compared with null model 1; arrows illustrate the patterns of trait divergence (diverging black arrows) or convergence (converging white arrows) in plots compared with null model 2, with grey arrows indicating weaker trends ($0.01 < P < 0.05$) combined with smaller CWM effect sizes ($-0.5 < ES < 0.5$; Fig. 4). No arrows were represented when trait variance in plots was close to random.

role of SLA in discriminating the physiological strategies able to persist or not in different habitats (see also Cornwell & Ackerly 2009; Jung *et al.* 2010). On shallow soils, plants with rapid growth and nutrient acquisition strategies (i.e. ‘Competitors’ *sensu* Grime 1977) were filtered out, as revealed by the reduced range of height and leaf traits related to the leaf economics spectrum (Fig. 3). Only conservative and stress-tolerant strategies (small plants with thin leaves, low SLA and low LNC; Grime 1977; Wright *et al.* 2004) seemed to be able to persist and cope with local nutrient and water shortages, except for the rare annual species whose early and short life cycles ended before the onset of summer drought.

Trait range reduction detected towards the deeper soils supports the hypothesis that trait filtering may also exist in more favourable and productive habitats. Slow-growing and water-conservative strategies, as well as annual species, were excluded from deeper soils. As predicted by Grime (1977, 2006) and Keddy (1990), these more productive deep soils selected for competitive strategies of nutrient acquisition, by creating both filtering and convergence of the ‘productivity-related’ traits LDMC, $\delta^{13}\text{C}$, and SLA on deeper soils (Figs 3 and 4). Strong above-ground competition for space and light in the dense cover of these productive grasslands, as well as below-ground depletion of nutrients and water by neighbours (Tilman 1982; Violle *et al.* 2009), may account for this type of filtering and convergence through mechanisms of strong asymmetrical competitive exclusion, linked for example with

the strong dominance by *B. erectus*, or through equalizing fitness (Chesson 2000; see also Spasojevic & Suding 2011). In sum, our findings support the hypothesis recently proposed by Mayfield & Levine (2010) that ecological filtering can occur at both ends of an environmental gradient. Importantly, we extended this hypothesis originally developed for phylogenetic dispersion within communities by showing that this is due to the differential filtering of different traits along the gradient.

FUNCTIONAL DIVERGENCE AT BOTH ENDS OF THE GRADIENT

Our results support the hypothesis that trait divergence may be found in both productive and harsh habitats alike, and that patterns of trait divergence may be unrelated to patterns of environmental filtering (Fig. 5). The ubiquitous divergence of reproductive heights all along the gradient (Fig. 4), representing both vertical partitioning of above-ground resource capture (Vojtech *et al.* 2008) and differences in dispersal distances (Thomson *et al.* 2011), provides strong support for the existence of niche differentiation processes in grasslands (Wilson 2007), although specific mechanisms (e.g. limiting similarity, facilitation) cannot be inferred here.

Towards deeper soils, seed mass and flowering time tended to be divergent in communities (Fig. 4), suggesting a spatial and temporal partitioning of regeneration and growth. The

coexistence of multiple 'regeneration niches' (Grubb 1977; Moles & Westoby 2004) might be a general structuring pattern in plant communities, as suggested by the recent observations of seed size over-dispersion in various systems (Cornwell & Ackerly 2009; Swenson & Enquist 2009; Wolkovich & Cleland 2011; Viard-Cr  tat *et al.* 2011). By contrast, the temporal partitioning of flowering in communities has often been hypothesized (e.g. Wolkovich & Cleland 2011), but rarely demonstrated (e.g. Ashton 1988), especially at the community level (Pleasants 1990). The dispersion of the onset of flowering may also be related in these communities to a partitioning of vegetative growth throughout the growing season (Grubb 1977), and points to the need for further investigation on the reproductive and vegetative phenology of grasslands.

Surprisingly, at the other end of the gradient, despite the strong filtering of leaf trait ranges on shallow soils, abiotic constraints did not lead to a strong convergence in leaf functioning. On the contrary, although abundant species did tend to share an overall nutrient conservative strategy (tendency for SLA to converge towards low values; Figs 2 and 4), at least two contrasting strategies of resistance to water and nutrient shortages coexisted successfully, as revealed by the divergence observed in LDMC, $\delta^{13}\text{C}$, and LNC (Fig. 4). Abundant species on shallow soils were either perennial grasses with high LDMC, low LNC and tough water-efficient leaves, which limited water losses and tolerated tissue desiccation (e.g. *F. christinaii-bernardii*; Larcher 2001), or small woody chamaephytes with long tap roots, low LDMC, low water-use efficiency, and leaves which shrivelled under extreme drought (e.g. *Helianthemum canum* (L.) Baumg.; Proctor 1956). This diversity of water-use strategies in water-limited habitats confirms that functional divergence can exist under strong abiotic constraints (Cornwell & Ackerly 2009; Spasojevic & Suding 2011) possibly as a consequence of below-ground resource partitioning between coexisting species (Chesson 2000), or facilitating mechanisms between complementary plant strategies (Callaway *et al.* 2002).

Interestingly, only at intermediate soil depths was there no trait convergence, with all traits either diverging or randomly distributed (Fig. 5). We can speculate that a relaxation of both abiotic and biotic constraints allowed for the coexistence of a wide array of functional strategies, in accordance with theories of maximum diversity at intermediate levels of disturbance (Grime 1973), productivity or competition importance (Navas & Violle 2009).

BEYOND THE REGENERATIVE VERSUS VEGETATIVE TRAITS DICHOTOMY

Our results tend to support the hypothesis stating that both 'regeneration-related traits' and 'productivity-related traits' (*sensu* Grime 2006) can be either convergent or divergent within communities depending on environmental conditions (Fig. 5). Grime and colleagues (Grime 2006; Grime & Pierce 2012) recently proposed a 'twin-filter model', in which convergence is expected for traits associated with life-history and core metabolism (CSR-related; Grime 1977) due to a first

'Competition, Stress, and Disturbance' (CSD) filter. A second 'proximal filter' is predicted to cause divergence of traits that are not entrained in the CSR axes (e.g. regenerative traits), thereby allowing local species coexistence. Although this 'twin-filter model' shares some similarity with the two-step framework presented in this study (Fig. 1), our framework differs in that it does not specify *a priori* particular categories of traits that should show divergence or convergence, and it allows for the possibility of traits being simultaneously filtered (restricted range) and divergent (within the restricted range). While our results are consistent with Grime & Pierce's hypothesis in the deeper and more productive plots (e.g. SLA and LDMC converge, but seed mass and flowering onset diverge), opposite patterns were observed in the intermediate to shallow soils (e.g. seed mass converges, while LDMC and SLA diverge). Thus, it seems that the regeneration- versus productivity-related traits dichotomy observed in a number of previous studies (Thompson *et al.* 1996; Swenson & Enquist 2009) may exist within productive communities, but may not hold when abiotic constraints increase or productivity decreases (e.g. Pakeman, Lennon & Brooker 2011).

Conclusion

Our results reveal that community assembly is strongly driven by environmental conditions, which affect both species occurrence among communities as well as species abundance within communities. We clearly demonstrate that patterns of trait divergence and filtering are strongly contingent on both trait and environment, such that there is no expectation of a general trend of increasing or decreasing functional divergence along a gradient of resource availability. Higher resource availability appears to have driven a strong functional convergence towards competitive strategies of resource-use but allowed for the divergence of regeneration strategies. By contrast, water and nutrient limitations allowed for the coexistence of distinct resource-use strategies. This multiplicity of functional responses could not have been captured by a single multivariate index of functional diversity. Moreover, taking environmental gradients into account—rather than testing only for 'global' signatures of trait convergence/divergence—combined with multiple traits and species abundances, all together confer greater power to detect the complex patterns and underlying processes of community assembly, not only in Mediterranean rangelands but possibly in many other systems and biomes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Principal component analysis on soil parameters.

Figure S2. Turnover of species along the soil gradient.

Figure S3. Relative abundance of annual species in communities.

Figure S4. Filtering of SLA for perennial species only.

Table S1. Environmental parameters in each plot.

Table S2. Species trait values and regional abundances.

Appendix S1. Description of null models and effect size calculation.

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