

RESPONSE OF HERBACEOUS VEGETATION FUNCTIONAL DIVERSITY TO LAND USE CHANGE ACROSS FIVE SITES IN EUROPE AND ISRAEL

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ABSTRACT

Only a few studies have examined responses of grassland functional diversity to management and major environmental gradients, in order to address the question of whether grassland use can promote functional divergence. For five grassland sites in Israel, Portugal, the Czech Republic, Mediterranean France, and the French Alps, where traditional grassland management is being abandoned, we quantified community-weighted means (CWM) and functional divergence (FD_{vg}) for the three Leaf–Height–Seed (LHS) traits, individually and in combination. Responses of CWM and FD_{vg} to land use were analyzed by mixed linear models with aridity, phosphorus, fertility, and the fractions of grasses and annuals as covariates.

Responses of community-weighted traits to land use were consistent with current knowledge. More intense management favored plants with more rapid

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resource acquisition (high Specific Leaf Area, or SLA), whereas abandonment or less intense grassland management increased the dominance by tall plants with more conservative strategies (low SLA). Seed weight did not respond to land use. For the three traits and their combination, functional divergence decreased in response to land use change overall. Detailed responses, however, varied depending on sites and especially their climate. At the two French sites, traditional site management promoted functional divergence within communities by suppressing dominance by large perennial tussocks, whereas at the two Mediterranean sites it is likely that the drier climate promoted a functionally diverse pool of species tolerant to grazing.

This study demonstrates how simultaneous analyses of variations in community-mean traits and functional divergence for a focused set of traits offer promising avenues to understand mechanisms of community response to environmental change.

Keywords: plant functional trait, functional diversity, aridity gradient, grassland management, secondary succession, environmental filter, Leaf–Height–Seed

INTRODUCTION

Environmental changes such as climate and land use affect the functional composition of plant communities (reviewed by Lavorel et al., 2007). Recent syntheses on the mechanisms that link vegetation composition to ecosystem functioning and ecosystem services have highlighted the primary role of functional diversity, that is, the range and distribution of trait values within communities (Hooper et al., 2005; Díaz et al., 2006, 2007a). Functional diversity indices are designed to identify patterns of community structure reflecting complementarity of resource use among species or trait redundancy. Increasing functional divergence is thought to be conducive to increasing resource use efficiency (Mason et al., 2005) as well as ecosystem stability in the face of natural variability, extreme events, or disturbances (Hooper et al., 2005; Díaz et al., 2006). Patterns of functional divergence within communities have also received considerable attention in community ecology as a means to address mechanisms of community assembly, and whether coexisting species tend to have similar (convergent) or different (divergent) traits (Fukami et al., 2005; Grime, 2006; Ackerly and Cornwell, 2007; Pillar et al., 2009; Mouchet et al., 2010).

An increasing number of recent studies have examined patterns of variation in functional diversity in the field, including in response to land use (Flynn et al., 2009; Laliberté et al., 2010) and specifically to grazing (Hadar et al., 1999; Walker et al., 1999; de Bello et al., 2006, 2009; Cingolani et al., 2007; Pillar et al., 2009). These studies complement more numerous and advanced analyses of the response of community-level means to changing land use and other environmental conditions (reviewed by Lavorel et al., 2007; see also Pakeman et al., 2008, 2009), but still, little is known overall about how functional diversity changes in response to combined environmental gradients such as climate and disturbance (de Bello et al., 2006), making it difficult to project the future

structure and function of ecosystems. This question bears particular importance regarding grasslands, which are species- and functionally-diverse systems of primary importance to the global ecology, economy, and societies (Reid et al., 2005). We now review briefly evidence and knowledge gaps regarding the response of grassland functional diversity to management, with a special focus on European and Mediterranean regions.

Changes in life forms are a prominent feature of herbaceous vegetation response to land use (Díaz et al., 2007b). Globally, grazing favors annuals over perennials. Graminoids have predominantly neutral or negative responses to grazing, with a clear, positive response by stoloniferous graminoids and a negative response by tussock graminoids. Beyond these simple life form-based assessments, community mean functional responses to grassland management have been quantified using various traits. Among others, the LHS plant strategy scheme, based on Specific Leaf Area (SLA), plant height (**H**), and seed weight (**SW**), is a promising analytical framework because it captures key axes in the variation of plant structure and function (Westoby et al., 2002). Its relevance to grassland response to management has been confirmed (Kühner and Kleyer, 2008; Garnier et al., 2004a; Vesik et al., 2004; Moog et al., 2005; Golodets et al., 2009), but its applicability to secondary succession has, to our knowledge, been demonstrated only by one study (Castro et al., 2010). There is increasing evidence that SLA and other leaf traits associated with resource economy and in some, but not all cases, plant height respond to grassland management (Kahmen and Poschlod 2004; Louault et al., 2005; Díaz et al., 2007b; Garnier et al., 2007; Prach et al., 2007, and references therein). Seed weight responses, on the other hand, are inconsistent across sites (Pakeman, 2004; Pakeman et al., 2008). More intense management favors plants with more rapid resource acquisition (high SLA, low tissue and especially leaf density, high leaf nitrogen content), whereas abandonment or less intense management increases the dominance by more conservative strategies, and often, but not always, tall plants (Louault et al., 2005; Garnier et al., 2007). Recent results suggest that this response of SLA to management is associated with changes in nutrient availability (Gaucherand and Lavorel, 2007; Cruz et al., 2002; Quétier et al., 2007), although not always (Garnier et al., 2004b).

There is little published information on how community trait responses to secondary succession may be affected by climate (Prach et al., 1997). In contrast, there is increasing support for the hypothesis that community responses to grazing depend on aridity (Milchunas et al., 1988). Differing responses to grazing with aridity may result from changed magnitude of the response of some traits and/or from the predominance of different types of strategies (Pakeman, 2004; de Bello et al., 2005). In systems with a long history of grazing, such as European and Mediterranean grasslands, morphological changes are expected to be less, but annuals would be more strongly promoted by grazing in drier than in more humid systems (Díaz et al., 2007b). An avoidance strategy can be promoted by grazing in dry (less productive) systems, while in humid (more productive) systems plants are expected to respond to grazing through increased growth (a tolerance strategy) (Herms and Mattson, 1992). The former would be achieved through phenological differentiation or, alternatively, through short size and tough (low SLA) leaves, while the latter would require fast nutrient acquisition, i.e., high SLA.

The response of functional divergence to grassland management has been far less studied than the response of community weighted means. The clearest hypothesis regarding trait functional divergence (FDvg henceforth) response to grassland management has been implicitly formulated by (Grime, 2006), stating that FDvg is promoted by disturbance, whereas abiotic gradients, and especially nutrient shortage, foster trait convergence. Consistent with this hypothesis, Fukami et al. (2005) observed that communities with a different initial floristic composition through sowing converged for functional composition after 9 years of secondary succession. Based on this, we would expect an overall decrease in FDvg in response to land use abandonment or decreasing management intensity. However, Walker et al. (1999) did not find any response of community-level mean traits to grazing intensity in semiarid Australian grasslands. They interpreted this result as an example of resilience through the reorganization of species of similar functional characteristics under the effects of grazing, implying that FDvg would be unchanged in response to grazing. In fact, the response of FDvg to grazing has been found to vary across traits, as well as to vary along an aridity gradient (de Bello et al., 2006). We might therefore expect variations in the response of FDvg to land use under different climatic conditions. The response of FDvg may also depend on the dominant species and life forms (de Bello et al., 2006).

In this study, we focus on the response of plant functional diversity to changing land use at five sites situated along a broad climate gradient across Europe and Israel. We compared the responses of community-level mean and functional divergence for specific leaf area, plant reproductive height, and seed weight. We asked the following questions:

- (1) Are there consistent responses in community-weighted mean and functional divergence for these traits across the five sites?
- (2) Can these responses and differences across sites be attributed to climate, fertility, and/or changes in the representation of life forms?

Results are interpreted in relation to the mechanisms that determine community structure and trait responses to land use, in the context of emerging theory on plant functional responses to environmental gradients (Grime, 2006; Lavorel et al., 2007; McGill et al., 2006).

METHODS

STUDY SITES

We used data from five sites where the effects of recent land use change on plant functional composition and ecosystem functioning in naturally unproductive herbaceous-dominated communities were quantified (Garnier et al., 2007). These five sites are distributed along the aridity gradient encompassed by the VISTA network across Europe and Israel (Garnier et al., 2007, Table 1). Climate was quantified by a compound index resulting from a PCA of climatic variables (mean annual temperature, total annual rain-

Table 1
 Geographic, climatic, land use and fertility characteristics of the five study sites

Site (country)	Site acronym	Coordinates Lat./Long.	Altitude (m)	Climate type	MAT (°C)	P (mm)	P/PET	Most used annuals, grass, PNI (%)	Least used annuals, grass, PNI (%)
Karei Deshe (Israel)	IS-KDE	32°55'N 32°35'E	150	Mediterranean, semiarid	19.6	572	0.47	Grazing 1.1 cow/ha/yr 90, 59, 94	Abandoned pasture, 20 years 56, 74, 117
Mertóla (Portugal)	PT-MER	37°40'N 8°00'W	100–150	Mediterranean	16.6	538	0.56	Grazing 0.99 sheep/ha/yr 96, 31, 94	Abandoned pasture, >10 years 41, 51, n.a.
Ohrazeni (Czech Republic)	CZ-OHR	48°57'N 14°36'E	510	Central-European temperate	8.2	583	1.20	Mown/ unfertilized 0, 63, 49	Unmown/ unfertilized 0, 67, 57
HautsGarrigues (France)	FR-HGM	43°51'N 3°56'E	100–160	Mediterranean sub-humid	13.2	994	1.16	Abandoned vineyard 2–5 years 74, 0, 109	Abandoned vineyard 25–45 years 2, 91, 90
Lautaret (France)	FR-LAU	45°02'N 6°21'E	1900–2100	Sub-alpine	3.0	902	2.94	Previously ploughed/ mown/manure 1, 37, 66	Never ploughed/ light summer grazing 0.8, 67, 51

MAT—mean annual temperature, P—total annual precipitation, P/PET—precipitation to potential evapotranspiration ratio over the growing season, %grass—relative abundance of grasses, %annuals—relative abundance of annuals, PNI—phosphorus nutrition index.

fall, Thornwaite's aridity index and the PET:precipitation ratio; see Garnier et al., 2007, for details). The first axis of the PCA (PCA1) was used to rank sites and was dominated by a gradient of decreasing aridity from Israel to the French Alps. Israel and Portugal were considered as more arid sites, the Czech Republic and Hautes Garrigues (Mediterranean France) sites were mesic, and the Lautaret site (French Alps) was wet.

At each site, we compared the most intensively used vs. the least intensively used land use treatment, while keeping levels as comparable as possible across sites. Details on land use types are described by Garnier et al. (2007). "Most used" was taken to correspond to "traditional use", usually associated with medium fertility and high biomass removal. "Least used" corresponded to cessation of these practices, resulting either in extensive grazing or abandonment. For abandoned sites, we chose to focus on comparable lengths of succession, using plots with intermediate duration of abandonment (>10 years) prior to dominance by woody species. These plots still had a predominant herbaceous component, except in Portugal, where we focused our analysis on the herbaceous stratum. The Israel data set excluded large hemicryptophytes (i.e., *Echinops* spp., *Ferula communis*, *Bituminaria bituminosa*) that make up a small fraction of the total biomass and do not respond to management (Sternberg et al., 2000), but included the dominant perennial grass *Hordeum bulbosum*.

Floristic surveys and trait measurements, including Specific Leaf Area, reproductive height, and seed weight were conducted within replicate plots for each land use treatment. In addition, nutrient (nitrogen and phosphorus) availability was quantified within each plot using nutrition indices that reflect availability for plant growth (Gastal and Lemaire, 2002; Jouany et al., 2004). The sampling designs and standardized methods for all measurements are described by Garnier et al. (2007). Additional details for different sites are found in Golodets et al. (2009) for Israel, Castro et al., (2010) for Portugal, Lepš (2004) for the Czech Republic, Garnier et al. (2004b) for Mediterranean France, and Quétier et al. (2007) for the French Alps.

QUANTIFYING FUNCTIONAL DIVERSITY

Dissimilarity can be defined either for a single trait, or for a combination of many traits. We quantified dissimilarity of individual traits taking into account both inter- and intra-specific trait variation using a modification of the Rao index (Lepš et al., 2006). If proportion of the i -th species in a community is p_i and dissimilarity of species i and j is d_{ij} , then:

$$FDvg = \sum_{i=1}^s \sum_{j=1}^s d_{ij} p_i p_j \quad (1)$$

where s is the number of species in the community. Proportion of a species (p_i) was estimated as its relative biomass within a bulked and hand-sorted sample of ca. 1 m², adjusted for representativity of local vegetation characteristics. If p_i is defined as the proportion of individuals in an infinitely large sample, FDvg can be defined as the expected value for the difference in trait values between two randomly chosen individuals.

Dissimilarity between two species for a given trait is estimated as one minus the overlap between the distributions of trait values within each species. These distributions are

assumed to be Gaussian, and the estimate of overlap is based on the mean and standard deviation of the trait value for each species in each land use treatment. The difference between species is scaled with respect to variability within species, and for combining traits, the same “currency” is used, the relative overlap within each trait. The dissimilarity for combined traits is then the average of dissimilarities for these traits. For single traits, this index has a parallel behavior across land use treatments to Mason’s functional divergence (Mason et al., 2005; Grigulis et al., unpubl.). Calculations were performed using an Excel macro (de Bello et al., 2009).

FDvg was calculated for SLA, reproductive height, seed weight, and for the combined traits. This overall FDvg index is equal to the average of FDvg values for each of these three traits and will be further referred to as LHS functional diversity ($FDvg_{LHS}$).

In addition, for each site we calculated the Simpson diversity index, given that at each site sampling was adjusted to capture the scale of variation of species diversity (Garnier et al., 2007), and that the Rao index of diversity is mathematically related to the Simpson index, i.e., the two quantities are fully comparable (Ricotta and Szeidl 2006).

Within each site the direction of the response of FDvg of single traits was compared to the response of their weighted mean (CWM) (Garnier et al., 2004b), calculated for each trait \times site \times treatment combination as:

$$CWM = \sum_i p_i \cdot t_i \quad (2)$$

where p_i is proportion of the i -th species, t_i is the trait value of the i -th species.

The fraction of community abundance encompassed by annuals (%ANN) and by grasses (%GRASS) were calculated in the same way, based on species life history and life form classifications, respectively.

Calculations of both FDvg and weighted means considered only the most dominant species within each community (Garnier et al., 2004b). Together, these represented over 80% of the total community biomass (5–20 species per plot). By construction of these two indices, the contribution of rare species traits is low; consequently, the exclusion of less abundant species is justified and usually does not affect response patterns (Garnier et al., 2004b, but see Pakeman and Queded, 2007). FDvg and weighted means hence reflect the differentiation and response of the most abundant species (see also Lavorel et al., 2008, for discussion).

DATA ANALYSIS

The responses of FDvg, Simpson species diversity, and trait-weighted means to land use, and their co-variation with climate, were analyzed using mixed effect linear models fitted with Restricted Maximum Likelihood methods (REML) with the statistical package GenStat® 10. In these analyses, “site” was used as a random term, and we tested the effects of land use (categorical variable with two levels), climate (continuous variable represented by the first axis of the PCA on climatic variables, PCA1 (Garnier et al., 2007)), fertility indices, fractions of grasses and annuals, and their interactions taken as fixed additive terms. Fractions of grasses and annuals were included in the analyses based on the knowledge that different functional groups tend to differ in their traits re-

ardless of management, grasses tending to have denser leaves and therefore lower SLA than forbs (Cruz et al., 2002—for the opposite relationship for LDMC, which is negatively correlated with SLA), and annuals tending to have a shorter stature and especially greater SLA than perennials (Garnier et al., 1997) (see also the meta-analysis by Poorter et al., 2009). Preliminary analyses showed that phosphorus, rather than nitrogen fertility was relevant to functional diversity responses, and we will hence report only results on effect of the phosphorus nutrition index (PNI). Differences across land use treatments within each site were further analyzed by one-way ANOVAs, conducted for each site separately. Dependencies among explanatory variables were analyzed using REML with “site” as a random term.

RESULTS

DEPENDENCIES AMONG LAND USE, ARIDITY, NUTRIENT AVAILABILITY, AND FRACTIONS OF GRASSES AND ANNUALS

Results of the analyses of relationships among explanatory variables are presented in Table 2. Decreased land use significantly increased the representation of grasses and decreased that of annuals. Aridity increased the representation of annuals, and was also associated with increased phosphorus fertility. PNI was also negatively affected by the abundance of grasses. Finally, there was a symmetric negative relationship among the fractions of annuals and grasses.

RESPONSE OF SINGLE TRAIT WEIGHTED MEANS AND FUNCTIONAL DIVERGENCE

The REML analyses of joint effects of land use, abiotic covariates, and community life form composition on trait community weighted means (CWM) and FD_vg for the different traits are presented in Table 3.

Overall aridity did not influence community-weighted means or functional divergence for single traits (Table 3), nor was there any interaction between land use and aridity responses (data not shown). SLA was the single exception, with an increase in

Table 2

REML analysis of relationships among land use, abiotic variables, and life form representation. Climate was represented by the first axis of the PCA on climatic variables (PCA1, Garnier et al., 2007), reflecting increasing aridity. PNI (%)—Phosphorus nutrition index, %GRASS—relative abundance of grasses, %ANN—relative abundance of annuals. The table presents *p*-values in bold for the significant variables retained in mixed models

Response variable	Explanatory variables				
	LU	PCA1	PNI	%GRASS	%ANN
PNI	0.643	0.012	–	0.066	0.019
%GRASS	<0.001	0.962	0.220	–	<0.001
%ANN	<0.001	<0.001	0.054	<0.001	–

Table 3

REML analysis of land use effects (LU), climate, fertility, and life form representation on community-weighted mean traits (CWM-trait) and functional divergence (FDvg-trait). Climate was represented by the first axis of the PCA on climatic variables (PCA1, Garnier et al., 2007), reflecting increasing aridity. PNI (%) — Phosphorus nutrition index, %GRASS — relative abundance of grasses, %ANN — relative abundance of annuals. The table presents *p*-values for each of the variables for the full model and for the final, most parsimonious model (AIC criterion)

Variable	Model	LU	PCA1	PNI	%GRASS	%ANN	%variance
CWM-SLA	Full model	<0.001	<0.001	0.005	0.334	0.046	
	-LU + PCA1 + PNI + %ANN	<0.001	<0.001	0.005	—	0.030	27
FD-SLA	Full model						
	-LU + PNI — %GRASS	0.033 0.025	0.683 —	0.039 0.040	0.003 0.002	0.952 —	40
CWM-H	Full model						
	+LU	<0.001 <0.001	0.743 —	0.181 —	0.131 —	0.099 —	30
FD-H	Full model						
	-LU + PNI — %GRASS	<0.001 <0.001	0.932 —	<0.001 <0.001	<0.001 —<0.001	0.349 —	19
CWM-SW	Full model						
	+PNI + %ANN	0.337 —	0.427 —	0.008 0.004	0.047 —	0.025 0.016	6
FD-SW	Full model						
	-LU + PNI — %GRASS	<0.001 <0.001	0.499 —	0.001 <0.001	0.002 0.001	0.523 —	27
Simpson	Full model						
	-LU + PNI — %GRASS	<0.001 —	0.548 —	0.057 0.047	0.015 0.011	0.816 —	33
FD-LHS	Full model						
	-LU + PNI — %GRASS	<0.001 <0.001	0.713 —	0.001 0.002	<0.001 <0.001	0.998 —	27

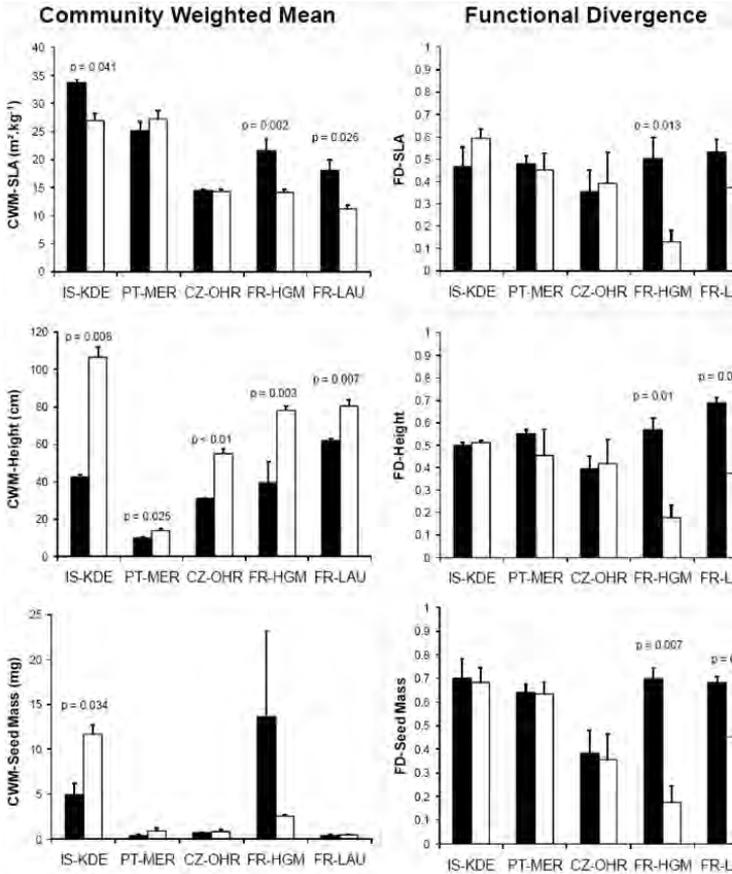


Fig. 1. Effect of land use change on functional diversity at the five VISTA sites (identified in Table 1). Community-weighted mean value (CWM, left column) and functional divergence (FD, right column) for SLA, height, and seed mass are presented. P-values for significant differences between most-used (dark bar) and least-used (open bars) treatments within each site are displayed when one-way ANOVA was significant. Overall statistics are summarized in Table 3.

CWM-SLA with increasing aridity (Israel and Portugal) (Fig. 1). This effect resulted from the dominance at drier sites, including in the most used treatments, by annual species (Table 1), which have higher SLA than perennials (Garnier et al., 1997). Across sites CWM-SLA decreased in response to land use change, with significant responses at the Israel, Hautes-Garrigues, and Lautaret sites (Fig. 1). CWM-SLA was enhanced in most used plots by increased representation of annuals. It was further increased by phosphorus fertility (PNI).

Community plant height increased consistently across sites in response to land use change (Fig. 1), with no further effects of abiotic or life form variables (Table 3). In

contrast, community seed weight did not change in response to land use overall (Fig. 1). It increased with land use change at the Israel site, but showed no significant response at the other sites (Fig. 1, one-way ANOVAs). Instead, CWM-SW was increased by phosphorus fertility and the abundance of annuals (Table 3), although the statistical model captured little of the total variance in CWM-SW across plots.

FDvg-SLA was low to moderate for all sites, with different responses to land use change depending on sites (Fig. 1). Likewise FDvg-Height and FDvg-Seed weight did not respond to management at the Israel, Portuguese, and Czech sites, but decreased at the Hautes-Garrigues and Lautaret sites (Fig. 1, one-way ANOVAs). Nevertheless, across-sites functional divergence for all three traits decreased significantly in response to land use change, with a common explanatory model structure for each trait (i.e., Land Use + PNI – %GRASS). Decrease in FDvg was strongly driven by increased representation of grasses, but was less strong when phosphorus fertility was higher (Table 3).

RESPONSE OF MULTI-TRAIT FUNCTIONAL DIVERGENCE TO LAND USE CHANGE ACROSS SITES

FDvg_{LHS} followed closely variations in Simpson diversity ($R^2 = 0.896$, $p < 0.001$), suggesting that FDvg_{LHS} was dominated by changes in species abundances (Fig. 2). Consistent with trends observed for the three traits, FDvg_{LHS} decreased in response to decreased land use but did not respond significantly to aridity (Table 3). FDvg_{LHS} was unchanged at the Israel, Portugal, and Czech sites and decreased in response to decreased land use at the two French sites (Fig. 2, ANOVA results). Across the five sites, the response of functional divergence for the three traits considered in combination (LHS) was consistent with responses for single traits (see Table 3 and Results, above).

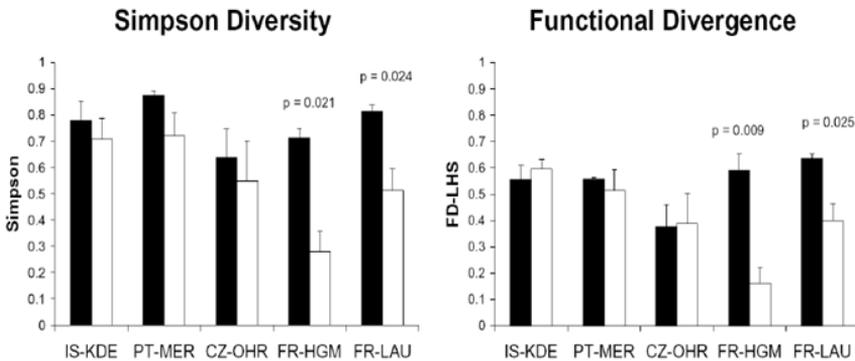


Fig. 2. Effect of land use change on overall species and functional diversity at the five VISTA sites. Simpson diversity (left column) and combined functional divergence for SLA, height, and seed mass (FD-LHS, right column) are presented. P-values for significant differences between most-used (dark bar) and least-used (open bars) treatments within each site are displayed when one-way ANOVA was significant. Overall statistics are summarized in Table 3.

DISCUSSION

RESPONSE OF COMMUNITY-WEIGHTED MEAN TRAITS TO LAND USE ALONG AN ARIDITY GRADIENT

Consistent with Díaz et al. (2007b) and the wider gradient formed by the eleven VISTA sites overall (Garnier et al., 2007), we found that grazing or other forms of grassland management (e.g., mowing) favored short plants, wherever the location. The magnitude of variation of CWM-height with land use was comparable across sites, contrary to the expectation of a stronger response at more humid sites (Milchunas et al., 1988; Vesk et al., 2004; Díaz et al., 2007b). CWM-SLA was higher on average at more arid sites and, as across the eleven VISTA sites (Garnier et al., 2007), increased under more intensive management. This response was magnified by the dominance of annuals at drier sites, and their decrease in least-used plots. More disturbed communities were dominated at all sites by tolerant species with a shorter stature and higher SLA (i.e., softer) leaves, and in Mediterranean floras, more annuals than in least-disturbed communities. This lack of evidence for a shift from tolerance to avoidance strategies in drier climates may reflect the limited species pool available at dry Mediterranean sites with a long grazing history, where fast-growing annuals rather than tough grasses or spiny sub-shrubs get promoted by grazing (Noy-Meir et al., 1989; Hadar et al., 1999; Osem et al., 2004). Alternatively, our climate gradient may not span into dry enough situations to encompass these strategies expected under arid or semiarid climates, and observed in other parts of the Mediterranean basin (Jauffret and Lavorel, 2003).

The colonization by grasses, mostly perennial, rather than woody species within 20 years after abandonment, except at the Portuguese site, may reflect limited propagule availability for colonization in long-grazed landscapes (e.g., Landsberg et al., 1999) and/or slow change under limiting abiotic conditions (Hulme et al., 1999). Our results contrast with other studies that have focused on sites with strong shrub colonization after grazing abandonment (de Bello et al., 2005), illustrating that growth form replacement after changes in grassland management can drive the response of functional composition (McIntyre et al., 1999).

RESPONSE TO LAND USE OF FUNCTIONAL DIVERGENCE FOR SINGLE TRAITS

Overall, functional divergence within most-used plots reflected the high diversity of plant strategies represented in traditionally managed European grasslands (Austrheim et al., 1999; Moog et al., 2005). When considering the five sites overall, functional divergence for each of the three traits examined individually (SLA, height, seed weight) decreased in response to land use change, increasing grass dominance and decreasing phosphorus availability (Table 3, Fig. 3). The combination of these three effects meant that functional divergence decreased significantly in least-used plots only at the Hautes-Garrigues and Lautaret sites. At these sites, decreased land use or abandonment lead to strong dominance by “colonial” tussock grasses (*Brachypodium phoenicoides* and *Festuca paniculata* at FR-HGM and FR-LAU, respectively). Less-used grassland or secondary successional communities have a simplified structure due to the strong light

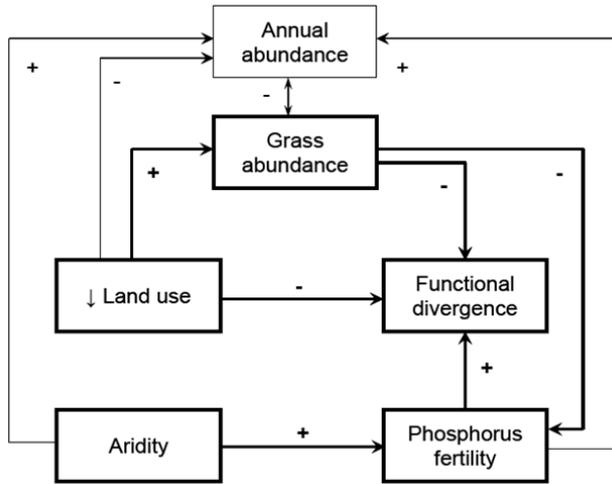


Fig. 3. Summary of statistical relationships among land use change, climate (PCA1 ~ aridity), phosphorus fertility (PNI), life form representation (grass abundance, annual abundance) and functional divergence for SLA, reproductive height, and seed mass. Boxes and arrows in bold represent the core model explaining variations in FDvg. Direction of relationships are given by the sign of the mean effect. Additional boxes and arrows picture additional relationships among explanatory variables. Statistical significance for the relationships is found in Tables 2 and 3.

competition exerted by this functional group. Dominance by large unpalatable tussocks has been noted in secondary succession on poor soils (Clément and Touffet, 1990), especially under humid conditions (*Brachypodium pinnatum*, Liancourt et al., 2005). Their strong dominance leads to a collapse in functional diversity. Similarly, Louault et al. (2005) reported coexistence of species with diverse functional syndromes in more intensively used montane pastures, whereas decreased use led to the dominance of a single grass functional type.

At the drier sites (Israel and Portugal) the negative effect of grass dominance on functional diversity was offset by the positive effects of annual abundance (including among grasses) and high phosphorus availability (Table 1), leading to no net change. Grazed plots were dominated by short annuals with high SLA, whereas abandonment promoted taller grasses with lower SLA (e.g., *Avena sterilis*, *Hordeum bulbosum* in Israel) without leading to a collapse in species diversity (Fig. 2) or functional divergence (Fig. 1).

In spite of these differences, our analyses were not able to capture a climate signal across sites in the responses of functional divergence to land use. First, with only five independent observations for climate, the power of the test of the aridity effect was low. Second, differences in responses across sites were accounted for directly by changes in representation of life forms (annuals and grasses) and in fertility (phosphorus availability, PNI) across sites. Both of these were shown to vary with site aridity (Table 2),

although in the case of PNI this may be more coincidence than a climatic response (the three Mediterranean-climate sites had higher PNI). Overall, positive effects of phosphorus availability on functional diversity (as well as on species diversity) reflect the fact that at all sites, even the most intensive land use treatments can still be considered as of intermediate intensity, so that patterns of diversity response to fertility fall to the left hand-side (increasing) part of the bell-shaped response.

RESPONSE OF FUNCTIONAL DIVERGENCE ACROSS PLANT STRATEGIES (LHS)

Results for FD_{LHS} were partly consistent with a similar analysis in NE Spain, where functional divergence for seven traits was stable along an aridity gradient and varied either positively (at more arid locations) or negatively (at moister locations) in response to grazing, resulting in no overall significant response to land use (de Bello et al., 2006).

FD_{LHS} tracked closely variations in Simpson diversity, and was therefore strongly driven by changes in species dominance, especially in least-used plots at the more humid sites. The convergence to Simpson diversity of FD_{LHS} calculated for increasing numbers of traits may reflect the fact that ultimately individual species present unique trait combinations. De Bello et al. (2006) did not find robust proofs of this effect, even with seven traits, but this could be due to their using species frequencies rather than biomass as species abundance weights, and thereby overrepresenting the effects of less abundant species (see Lavorel et al., 2008, and Poos et al., 2009, for discussion). Nevertheless, our results suggest that, consistent with the Leaf–Height–Seed scheme (Westoby, 1998), species tend to represent unique combinations of SLA, height, and seed weight. We recommend, therefore, analyzing FD of single traits rather than combining traits to approach mechanisms of community response to changing environments.

MECHANISMS OF RESPONSE OF COMMUNITY FUNCTIONAL DIVERSITY TO LAND USE AND CLIMATE

To interpret the combined effects of climate and land use on functional divergence we need to consider the effects of different environmental filters, climate, and land use (including disturbance and fertility), and of filtering by biotic interactions (Huston, 1994, Díaz et al., 1999).

Management is a strong filter that at high intensity removes from the regional pool species with traits associated with disturbance intolerance, such as low SLA and tall stature (e.g., Olff and Ritchie, 1998; Grime, 2006). Management at intermediate intensity allows coexistence of a diversity of co-dominant species, and hence promotes high FD_{LHS} locally (Grime, 2006). In southern France and the French Alps, less intense management favored a few dominants with strong competitive ability, and hence decreased FD_{LHS} -SLA and FD_{LHS} -H. In contrast, little change in FD_{LHS} -SLA and FD_{LHS} -H was observed in response to management in Israel and Portugal, where, due to convergent evolution with drought response, grazing may be a less strong filter on leaf trait values than at more humid sites (Herms and Mattson, 1992).

Our results suggest that community rearrangements after land use change might combine changes in the dominance of certain traits (i.e., average at the community level)

as well as in the dissimilarity across species for this trait (i.e., functional divergence; Grime, 2006). For example, changed CWM with stable FDvg (SLA and height in Israel and Portugal) indicate that land use change induces a turnover in dominants, but that within the dominants for each land use level there is a filtered, constant dissimilarity in trait values (Grime, 2006), as would be expected when aridity selects a trait pool that is tolerant of grazing through convergent evolution (Landsberg et al., 1999). The response of seed weight at the drier sites followed a similar pattern, but with high FDvg across land uses, reflecting species coexistence through regeneration niche differentiation within communities (Chesson et al., 2004).

Changed CWM associated with a decrease in FDvg (height and SLA at Hautes-Garrigues and Lautaret) indicate that decreased land use strongly selects for a single (or very few) dominant strategy. Our results on the effect of phosphorus fertility concur with current evidence that decreasing nutrient availability is a key factor in functional responses to decreased grassland management intensity in semi-natural grasslands (Cruz et al., 2002; Louault et al., 2005; Gaucherand and Lavorel, 2007; Quétier et al., 2007) although this may not apply to secondary succession (Garnier et al., 2004b). Conditions of intermediate fertility and disturbance associated with “traditional” grassland management promote coexistence of a greater diversity of species and strategies (Grime, 2006). For example, tall and short dominant grasses may coexist due to differential tolerances to shading (Westoby et al., 2002; Gross et al., 2007a), and species with high or low SLA may coexist through complementarity in nutrient use (Gross et al., 2007b). Moderate levels of disturbance also promote coexistence between grasses and forbs (Grubb, 1986; Quétier et al., 2007), thereby leading to combinations of dominants with lower and higher SLA, respectively. In grazed grasslands, patchy grazing of intermediate intensity may also promote coexistence of species with more attractive, tender leaves (high SLA and associated nitrogen content) with less palatable species (low SLA and associated high toughness) (Loucougaray et al., 2004; Louault et al., 2005). The response of seed weight at the Hautes-Garrigues and Lautaret sites followed a similar pattern, though CWM did not change significantly across land use intensities. Dominance by large tussock grasses with small seeds following decreased land use was strong, in contrast to the wide range of seed weight values present under more intensive use. Such seed weight diversity may promote species coexistence through regeneration niche differentiation (Grubb, 1986; Rees, 1993).

CONCLUSION

We quantified variations of functional divergence (*sensu* Mason et al., 2005) using the three traits of the LHS scheme, examined individually and in combination. While confirming the relevance of the LHS to describe community responses to land use, our analyses highlighted that single-trait analyses may be most appropriate to access mechanisms of community response to changing land use and climate.

Results supported current hypotheses on community-mean trait responses to land use and especially grazing. We observed a greater magnitude of response of functional

divergence to land use at the two moister sites for the three traits examined, reflecting the dominance by large perennial tussocks under changing land use. Our results may be generalizable only to sites with a dominant herbaceous component, since we analyzed the replacement and functional differentiation operating within and across herbaceous growth forms (grasses and forbs).

Simultaneous analyses of variations in community-mean trait values and functional divergence for a focused set of traits, taken one at a time, offer promising avenues to understand mechanisms of community response to environmental change.

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