

Variations in species and functional plant diversity along climatic and grazing gradients

Francesco de Bello, Jan Lepš and Maria-Teresa Sebastià

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Different components of biodiversity may vary independently of each other along environmental gradients giving insights into the mechanisms that regulate species coexistence. In particular, the functional diversity (FD) or the presence of rare or endemic species in natural assemblages do not necessarily increase with species diversity. We studied if different components of plant species diversity (species richness, Simpson diversity, evenness) varied similarly to FD (measured as a generalization of the Simpson index) and rarity along grazing intensity and climatic gradients. Plots under different sheep grazing regimes (high and low intensity, abandonment) were surveyed in five locations along a climatic gradient in north-eastern Spain, from semi-arid lowland to moist upland locations. Variation in species diversity, functional diversity and rarity followed different patterns. Species diversity was lowest in water-stressed environments (arid locations and southern aspects) and increased with grazing more markedly in humid locations. The FD was comparable between the most species-poor and species-rich locations and decreased with grazing in the moistest location, i.e. where species diversity markedly increased. The FD did not show a strong correlation with species richness nor with the Simpson index and less specious communities could show the highest functional diversity. The rarest species in the region were more frequently found in the abandoned areas, which held the lowest species diversity. Consequently, the mechanisms that enhance the diversity of species do not necessarily support a functional differentiation among those species or the maintenance of rare species in a region. We hypothesize that the degree of dependence of functional diversity on species diversity might be mostly related to the amplitude of the species' traits pool and on how species partition the niche space available.

F. de Bello (fradebello@ctfc.es) and M.-T. Sebastià, Laboratory of Plant Ecology and Forest Botany, Forestry and Technology Centre of Catalonia, ES-25280 Solsona, Spain. — J. Lepš, Dept of Botany, Faculty of Biological Sciences, Univ. of South Bohemia, CZ-370 05, České Budějovice, Czech Republic.

Although biodiversity can be defined using different components (Magurran 2004), species richness has been used as the main index in most studies linking biodiversity to ecosystem functioning (Loreau et al. 2002, Lepš 2004, Schmid and Hector 2004). The underlying hypothesis of this approach is that species diversity increases the space for the functional differences among species that regulate ecosystem processes (Petchey et al. 2004). The relationship between species and functional

diversity is thus central in identifying mechanisms of biodiversity effects (Diaz and Cabido 2001, Hooper et al. 2005, Mason et al. 2005).

The concept of functional diversity (FD) remains however rather complex because there are questions about how to define, measure and assess FD variability (Petchey and Gaston 2006). One approach that has gained currency considers the FD as the extent of functional trait variation among the species in a com-

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munity (Tilman 2001, Petchey and Gaston 2002). For example, two assemblages with a similar amount of species may be more or less functionally diverse depending on how similar/dissimilar the species' traits are among the species in the communities. The concept of trait dissimilarity (or "distance") among species has been thus introduced in order to avoid arbitrary decisions about the level at which interspecific differences among species are functionally significant (Mason et al. 2005, Petchey and Gaston 2006). When the species' dissimilarity in trait space is weighted by the species' abundance, as proposed here, the resulting FD index is then a generalization of the Simpson's index of species diversity (Rao 1982, Botta-Dukat 2005). This approach appears as a promising tool to analyse the relationship between species and functional diversity. Up to now, however, little efforts have been done in calculating this index with real species' traits matrices and for assemblages under different environmental conditions.

Whether species diversity covary with FD in different natural ecosystems is still an open question (Hooper et al. 2005). This relationship could be variable as different mechanisms are thought to support the coexistence of functionally similar and functionally distinct species along environmental gradients (Huston 1994). Aridity might, for example, decrease species diversity but also imply a wide range of possible adaptations to cope with water stress (Stubbs and Wilson 2004, Mason et al. 2005) and thus maintain the coexistence of species with a diversity of traits. Further, the heterogeneity in space (e.g. resource patches) and time (e.g. interannual climatic variability) of arid conditions provides heterogeneous niches for species with diverse traits (Chesson et al. 2004). In pasture systems, for example, rangelands in semi-arid climates are generally characterized by a heterogeneous structure (de Bello et al. in press) and by a high diversity of growth forms, compared with humid grasslands that have structurally simple and continuous swards (Vesk et al. 2004). In pastoral systems, livestock grazing might also decrease the FD

of a community, i.e. by filtering out species that lack traits, such as low stature and/or short life cycle, to persist in grazed habitats (Diaz et al. 2001).

Another important implication of biodiversity indices, whether species or functional diversity are calculated, is that they do ignore the identity of the species in a community (Magurran 2004). The presence of endemic, rare or endangered species can be, for example, important for conservation and the measurements of diversity are not necessarily a good indicator of these components (Spitzer et al. 1993, Canals and Sebastià 2000, Pykälä et al. 2005).

In this context, the objective of the present study was to compare and contrast different measurements of diversity along environmental gradients. Although numerous studies have been conducted, there is still little evidence that different measurements are influenced in the same way by environmental factors (Canals and Sebastià 2000, Magurran 2004, Wilsey et al. 2005). This suggests that different components of community structure may change differently along environmental gradients giving insight into the mechanisms that regulate species coexistence. Specifically, the aim of the work was to ascertain whether indices of species diversity for a plant community (e.g. number of species, Simpson index, evenness) corresponds to measures describing 1) how different the species are in terms of their functional traits and 2) the number of species that are considered rare in a local flora. The potential effect of environmental constraints on these components of biodiversity were considered, by surveying communities under different grazing regimes and climatic conditions.

Methods

Study region

Five locations were selected along an altitudinal and climatic gradient in north-east Spain (Table 1), including the transition between the Mediterranean and the Boreo-alpine biographical regions. Climatic parameters

Table 1. Climate and vegetation of the study locations. Mean annual value provided for precipitation (P) and potential evapotranspiration (PET). AU stands for "animal units".

| Locations | Monegros 0°3'W, 41°21'N | Castellldans 0°45'E, 41°29'N | Vilamajor 0°45'E, 41°53'N | Boixols 1°9'E, 42°10'N | Alinyà 1°27'E, 42°12'N |
|--|---------------------------------------|---|---|---|---|
| Altitude (m a. s. l.) | 256 | 312 | 709 | 1354 | 2051 |
| Mean annual temp. (°C) | 15.2 | 14.7 | 12.8 | 9.2 | 7.1 |
| Precipitation (mm) | 325 | 392 | 461 | 783 | 952 |
| PET (mm) | 844 | 777 | 642 | 586 | 463 |
| Moisture index (P/PET) | 0.39 | 0.50 | 0.72 | 1.34 | 2.05 |
| Biome | garrigue with <i>P. halepensis</i> | from garrigue to evergreen <i>Q. ilex</i> forest | from evergreen <i>Q. ilex</i> to deciduous <i>Q. faginea</i> forest | <i>Q. humilis</i> and <i>P. sylvestris</i> forest | <i>P. mugo</i> subsp. <i>uncinata</i> forest |
| Max. stocking rates (AU ha ⁻¹ yr ⁻¹) | 0.2–0.25 | 0.2–0.3 | 0.3–0.4 | 0.3–0.4 | 0.3–0.4 |

covary along the gradient in such a way that selected locations ranged from semi-arid to sub-alpine humid conditions (Moisture index in Table 1; Anon. 1992) and each was placed in a different vegetation belt (Bolòs et al. 1993).

Local shepherds, farmers and technicians were interviewed in each location to identify areas along a gradient of grazing intensity. We limited our study to sheep-grazed systems, which is the most common traditional pasture system in the region. The selected areas were 1) abandoned for >10 yr, 2) with low or 3) high grazing intensity. These broad categories were used to allow comparisons among locations. The high-intensity grazing regime normally corresponds to 0.25 AU (animal units) ha⁻¹ yr⁻¹ in the most arid conditions and to 0.35 AU ha⁻¹ yr⁻¹ in more humid conditions (Table 1; de Bello et al. in press). Distance of areas from water points and corrals as well as evidences of fresh excrements were also taken into account in determining the grazing pressure. Recently burnt land and areas with rock outcrops were thus avoided as were areas abandoned because of their low productivity (see de Bello et al. 2005 for further details).

Four plots were established per grazing intensity (two replicates on south and two on north facing slopes). Only sloping areas have been included as, usually, flat areas are arable lands. The sampling protocol was based on a factorial design: 3 sheep grazing intensities × 5 localities × 2 aspects × 2 replicates = 60 plots. Slope inclination varied between 19° and 35°. Plots were placed in the approximate centre of a relatively homogeneous area and were surveyed at the time of the expected peak of vegetation development in the corresponding location. Vascular species composition and frequency were measured using 10 × 10 m plots, divided into 100 1 m² subplots. Each vascular species was characterized by its frequency, i.e. number of 1 m² subplots out of 100 where at least the aboveground parts of species were present. Nomenclature follows Bolòs et al. (1993).

Diversity indices and data analysis

Various indices of diversity were calculated for each 10 × 10 m plot. The first group of indices were applied to measure components of the species diversity: a) species richness (S), defined as the number of species per plot; b) Simpson index of diversity (D), traditionally also defined as “heterogeneity” or “diversity”;

$$D = 1 - \sum_{i=1}^S p_i^2$$

c) Evenness according to Camargo (Ec);

$$Ec = 1 - \left(\sum_{i=1}^S \sum_{j=i+1}^S \left[\frac{p_i - p_j}{S} \right] \right)$$

where p_i is the proportion of the i_{th} species, i.e. $p_i = N_i/N$ and $N = \sum N_i$. Originally, N_i was used as the number of individuals of the i_{th} species. More recently, various quantitative characteristics of species representation in a sample have been used (Magurran 2004). We used species frequency in this study. See Magurran (2004) for references of all indices.

Two additional indices were calculated: d) rarity (R); and e) functional diversity (FD). Species rarity was defined as the number of species in each plot that are considered “extremely rare” in the study region (Bolòs et al. 1993). Rare species in the regional flora might not however be endangered in other regions. The index rather reflects the potential community contribution to the maintenance of diversity at the regional level (Pykälä et al. 2005). Thus the rarity index is not a measure of community diversity, but reflect components of community interest in terms of conservation.

The FD was based on the adaptation of an index of species dissimilarity (Rao 1982). Pairwise differences between species i and j are numerically given as the species distance d_{ij} (the function should fulfill $d_{ij} = d_{ji}$ and $d_{ii} = 0$):

$$FD = \sum_{i=1}^S \sum_{j=1}^S d_{ij} p_i p_j.$$

In this way, FD is the sum of the dissimilarity (or distance) in trait space among all possible pairs of species, weighted by the product of the species' relative abundance. Note that if all species are equally different, and substituting $d_{ij} = 1 (i \neq j)$, the Simpson diversity index (1-dominance) is obtained (Shimatani 2001). Therefore, it can be said that FD calculated in this way is a generalization of the Simpson index. As the distance scaled to have its maximum value = 1, if species do not share any common trait (see below), the Simpson index represents the maximum potential value that FD could reach.

Originally p was defined as the proportion of individuals in an infinite sample. Then, the index is the expected dissimilarity of two randomly chosen individuals. The formula has a similar meaning for p calculated on the basis of other quantitative characteristics but, instead of two randomly selected individuals, it refers to (less intuitively) the expected similarity of two species, when each species is selected with its probability p_i and each selection is independent (so that a species could be selected repeatably).

The species distances d_{ij} in this formula have been traditionally applied for species taxonomical differences (Warwick and Clarke 1998, Shimatani 2001, Bhat and Magurran 2006). Alternatively, it can be calculated on the basis of the species × traits matrix. We selected 9 traits (Table 2), available in existing Spanish floras and validated by field observations, for all 467 species found in the survey (de Bello et al. 2005). The calculated FD is

Table 2. Life history traits and their categories utilised in the species \times traits matrix. The variability of each category along the grazing intensity and climatic gradients is showed (in terms of the mean relative frequency): “+/-” indicate significant increase/decrease ($p < 0.05$ with general linear models; “ns” non significant variation) in grazed conditions (Graz.) or toward moister conditions along the climatic gradient (Moist.); “A+/-” and “M+/-” indicate variation with grazing only towards more arid (A) or humid (M) locations. The variability of functional diversity (FD) for each individual trait is shown.

| Trait | FD response (x single traits) | | Trait categories | Trait response (x category) | |
|----------------------|----------------------------------|--------|--|--------------------------------|------------------------------|
| | Graz. | Moist. | | Graz. | Moist. |
| 1. Growth form | ns | — | Grasses = grasses and sedges Forbs = non grassy herbs Subshrubs = chamaephytes (woody at least at the base) Shrubs = phanerophytes (perennial buds > 40 cm) | +A +A +M — | + + — — |
| 2. Life cycle | +A —M | — | Annual and biennial Herbaceous perennial Woody | + ns — | — + — |
| 3. Leguminosae | +M | | Legume/non legume | +M | ns |
| 4. Lateral spread | +A —M | + | Solitary = single shoot Tussock = caespitose Several stems = non caespitose with several stems Guerrilla = plant with elongated stolons or rhizome < 20 cm; 20–50 cm; 50–80 cm; 80–110 cm; > 110 cm | —M ns ns — | ns + — ns |
| 5. Shoot height | — | ns | < 0.5 cm; 0.5–2.5 cm; 2.5–5 cm; 5–10 cm; > 15 cm | —M | + |
| 6. Leaf length | +A | + | Presence/absence of thorns on leaves or stem | ns | ns |
| 7. Thorns | —A | — | Leaves regularly distributed along the stem Leaves in rosette or semirosette | — + | — + |
| 8. Leaf distribution | —M | — | Shoot scarcely foliated, stem and twigs assimilating Spring flowering shorter than 3 months Spring flowering longer than 3 months Summer flowering shorter than 3 months Summer flowering longer than 3 months Late or winter flowering | ns — ns +M + ns | — — ns + ns — |
| 9. Flowering period | ns | ns | | | |

always one of many possible ones (see discussion in Mason et al. 2005, Petchey and Gaston 2006). The number of traits used to calculate the index of FD can, for example, affect the values of the index (Petchey and Gaston 2002). We thus calculated the FD diversity for all the individual 9 traits alone (in Table 2) and also calculated FD indices based on the combination of 4, 7 and 9 traits. Correlations among traits are often inherent. As it has been noticed that non-orthogonality of traits affects the calculation of species distances (at least in the index by Petchey and Gaston 2002), we minimized as far as possible such correlations in the selection of traits. This was done by reducing the number of original traits in de Bello et al. (2005) from 23 to 9 and then, within these 9, by calculating a PCA on the base of a species \times trait matrix (not shown). In this way, for the index calculated with 4 traits we used traits number 1,3,4, and 6 from Table 2 and for the 7-trait index we used traits from 1 to 7. We then focused in particular our analysis on the variation 7-trait FD index, as further justified in the results and because traits 8 and 9 in Table 2 (leaf distribution and flowering period) were partly correlated at the species level to other traits in the matrix (i.e. to growth form and life cycle).

Differences between pairs of species (d_{ij}) were computed as the number of characteristics that did not coincide, divided by the total number of traits examined (i.e. 1-simple matching coefficient; in this way, the difference of species differing in all traits equals 1). For

example: if two species are equal in all characteristics apart from two traits (e.g. shoot height and life cycle), their distance will be equal to 2/7 (i.e. 0.28), if considering 7 traits and 2/4 (i.e. 0.50), if considering 4 traits. All traits were treated as categorical variables (categories used in de Bello et al. 2005 have been also slightly broaden for introducing all species found in the sampling and for limiting the number of categories for each trait, i.e. the more categories are chosen the higher is the potential dissimilarity for a given trait).

Indeed, the functional dissimilarity among species has to be based on some set of species traits. There is always the question to which extent the traits used for characterizing species similarity are functional. This is particularly true for studies using large number of species (our study is based on 467 species), where the trait set is limited to those available in databases or published sources. However, easily measurable traits (“soft” traits) are considered reasonable surrogates for more functional, but difficult to measure, traits (“hard” traits; McIntyre et al. 1999). We are aware that detailed and specific information on more species’ functional traits would be of great relevance but this data are yet greatly dispersed, unpublished or simply not available for the Mediterranean flora (as for many other eco systems). The selected traits relate to several components of plant strategies (i.e. relative growth rate, strategy in the occupation of space, nitrogen fixation, biomass,

palatability, resource capturing) linked to ecosystem processes.

Three-way ANOVA was used to test the effect of grazing regime, location and aspect on the diversity indices. The second order interaction (grazing \times aspect \times location) was based on a low number of replicates ($n=2$), and would yield rather weak results. Consequently, only the main effects and first order interactions were included in the ANOVA models, and the second order interaction was included in the error term (to increase the denominator degrees of freedom and power of the test for the first order interactions and main effects). At first, slope was included as covariate in the ANOVA model but later removed for never being significant.

Results

In the combined data set (i.e. the 60 plots), the indices of species diversity (richness, Simpson and evenness) were robustly correlated among them, with the exception of evenness, which was weakly correlated to richness (Table 3). Different indices of FD (calculated by taking into account a different number of traits) were significantly correlated among them (Table 3). Only the FD index that takes into account 7 traits presented a significant, but weak, correlation with richness ($r=0.40$; $p>0.05$) and the Simpson index ($r=0.29$; $p<0.05$; Table 3 and Fig. 1). Consequently most analyses and discussion were particularly focused on this index. This enabled us to show that even the index that correlates significantly with Simpson diversity can show quite different environmental response from it. The FD calculated with 4 and 9 traits was also slightly negatively correlated to species evenness (Table 3). Within each location, only in Vilamajor there was a significant positive correlation of FD with richness and the Simpson index ($p<0.05$) while in all other locations, the relationship was not significant ($p>0.05$). FD did not increase consistently with species richness or the Simpson index and least species rich-diverse community

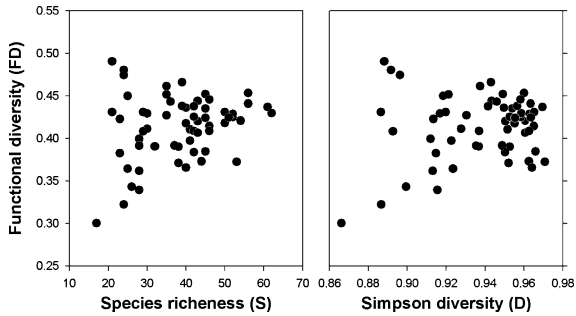


Fig. 1. Relationship between functional diversity (calculated with 7 plant traits) and species richness (left), and the Simpson index of diversity (right). Values calculated for 60 communities along grazing and climatic gradients.

could show the greatest FD (Fig. 1, for the 7-trait FD index).

The environmental factors considered explained a large portion of variability of the studied indices (adjusted $R^2 \geq 0.57$ for all indices; Table 4). However, the variation in species diversity, functional diversity and rarity followed different patterns along the considered environmental gradients (the importance of individual effects in the ANOVA models varied among the indices; F values in Table 4).

In particular, species diversity, functional diversity and rarity varied differently along the grazing intensity gradient. Species diversity indices (richness, Simpson and evenness) increased with grazing more markedly in more humid locations (Fig. 2; not shown for evenness). Nevertheless, the location \times grazing interaction was not significant for richness and Simpson index ($p>0.05$; Table 4) indicating a general increase of these indices with grazing in the study region, independently of the location. The FD decreased with grazing in the most humid upland location (i.e. where the positive effect of grazing on species diversity was marked) and increased with grazing intensity in two out of the three locations in the Mediterranean region (Fig. 2, for the 7-trait FD index). The rarest species in the region were more frequently found in the abandoned areas ($p<0.05$

Table 3. Pearson correlations among the considered diversity measurements (S = species richness; D = Simpson diversity; Ec = Camargo evenness; R = rarity; FD = functional diversity). Four measurements of functional diversity were calculated, by taking into account a different number of traits for each measurement (considering 1 trait, i.e. growth form, 4, 7 and 9; see Methods). Values in bold indicate a significant ($p<0.05$) correlation.

| | S | D | Ec | R | FD (1-trait) | FD (4) | FD (7) | FD (9) |
|--------|-------------|-------------|--------------|-------------|--------------|--------------|-------------|--------------|
| S | | 0.88 | 0.32 | 0.31 | 0.20 | 0.23 | 0.40 | 0.25 |
| D | 0.88 | | 0.64 | 0.33 | 0.11 | 0.02 | 0.29 | 0.13 |
| Ec | 0.32 | 0.64 | | -0.03 | -0.22 | -0.38 | -0.16 | -0.26 |
| R | 0.31 | 0.33 | -0.03 | | 0.11 | -0.86 | 0.21 | 0.19 |
| FD (1) | 0.20 | 0.11 | -0.22 | 0.11 | | 0.31 | 0.67 | 0.54 |
| FD (4) | 0.23 | 0.02 | -0.38 | -0.86 | 0.31 | | 0.67 | 0.55 |
| FD (7) | 0.40 | 0.29 | -0.16 | 0.21 | 0.67 | 0.67 | | 0.95 |
| FD (9) | 0.25 | 0.13 | -0.26 | 0.19 | 0.54 | 0.54 | 0.95 | |

Table 4. Results of 3-way AN OVA for each diversity index considered (the FD shown here refers to the index calculated with 7 plant traits). Adjusted R-square is shown. Rarity refers to the number of very rare species in the region according to the local flora by Bolòs et al. (1993).

| | DF | Species richness (S) | | Simpson diversity (D) | | Camargo evenness (Ec) | | Functional diversity (FD) | | Rarity (R) | |
|--------------------|----|----------------------------|------------------|----------------------------|------------------|----------------------------|------------------|----------------------------|------------------|----------------------------|------------------|
| | | F | p | F | p | F | p | F | p | F | p |
| Location | 4 | 16.10 | <0.001 | 33.07 | <0.001 | 13.33 | <0.001 | 7.88 | 0.001 | 10.49 | <0.001 |
| Aspect | 1 | 4.75 | 0.036 | 5.27 | 0.027 | 2.81 | 0.102 | 7.09 | 0.011 | 0.31 | 0.576 |
| Grazing intensity | 2 | 4.91 | 0.013 | 5.82 | 0.006 | 7.28 | 0.002 | 0.86 | 0.430 | 3.93 | 0.028 |
| Aspect × location | 4 | 3.18 | 0.024 | 2.91 | 0.034 | 1.17 | 0.339 | 11.82 | <0.001 | 2.09 | 0.101 |
| Aspect × grazing | 2 | 0.47 | 0.631 | 1.20 | 0.311 | 0.79 | 0.461 | 1.32 | 0.281 | 4.57 | 0.017 |
| Location × grazing | 8 | 1.90 | 0.110 | 2.06 | 0.065 | 2.82 | 0.015 | 3.92 | 0.002 | 4.78 | <0.001 |
| Error | 38 | | | | | | | | | | |
| | | adj. R ² = 0.59 | | adj. R ² = 0.73 | | adj. R ² = 0.57 | | adj. R ² = 0.63 | | adj. R ² = 0.57 | |

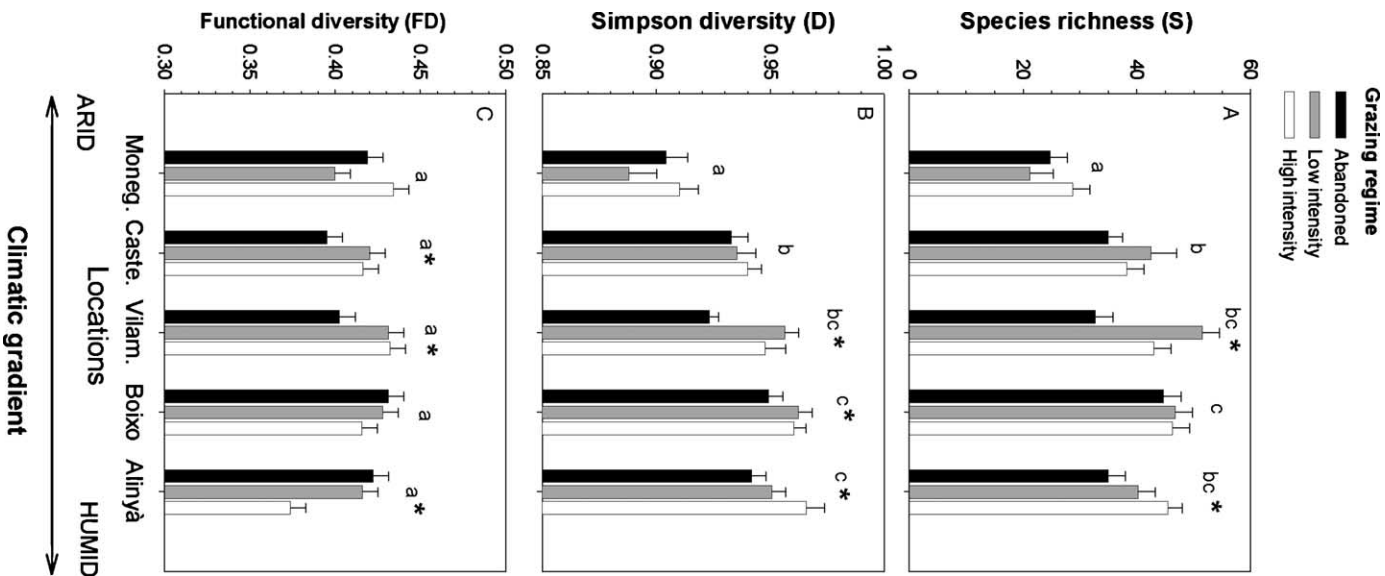


Fig. 2. Changes in (A) species richness, (B) species diversity and (C) functional diversity, (calculated with 7 plant traits), under different grazing regimes and in various locations along a moisture-altitudinal gradient. The error bars denote ± 1 SE. Results of the ANOVA are in Table 4. Different letters indicate significant differences among locations (Tukey's test, $p < 0.05$) and asterisks denote a variation of the diversity indices with grazing within a given location (Tukey's test, $p < 0.05$).

Tukey's post-hoc test), which held the lowest species diversity.

Along the climatic gradient, species diversity indices were highest in the moistest locations, while FD did not follow the same pattern (Fig. 2). For example, high species-rich and diverse humid grasslands did not show a different FD than the more species-poor rangelands in semi-arid locations. North-facing slopes generally had higher species diversity than south-facing ones ($p < 0.05$, least significant differences; no effect of aspect was noted for evenness). This pattern was generally more marked in most arid areas (for indices for which aspect \times location was significant; Table 4). The variation of functional diversity with aspect orientation was markedly different in different locations (Table 4): FD was lower in north-facing slopes in moistest locations and higher in the most arid ones (not shown).

Discussion

Our data show that environmental factors, such as climate and disturbance, account for a large proportion of the variance of different components of biodiversity. The measurements of species diversity (richness, Simpson, evenness), however, did not vary similarly to other components of biodiversity (such as the functional diversity or the number of rare species in a community) along the considered environmental gradients.

In particular, the increased species diversity with increased grazing intensity or moisture was not followed by similar trajectories for functional diversity. The FD, for example, did not differ between the most species-poor semi-arid locations and the most species-rich humid ones (Fig. 2). Semi-arid rangelands, despite their relatively lower species diversity, showed a more even composition in different growth forms and life cycles than the species diverse humid grasslands, which were composed mainly by herbaceous perennials (Table 2, Fig. 3), as hypothesised by Veski et al. (2004). This shows that the functional differentiation among species' and species richness can vary rather independently to each other. It has been noted that environmental filters might limit species composition to a given range of functional characteristics (species-traits pool; Diaz and Cabido 2001) thus limiting the degree of variation of functional diversity with respect to species diversity (Grime 2001, Hooper et al. 2005). The increased species richness within a more homogenous pool of traits thus might lead to a finer division of the available niche space among similar species rather than to a greater functional diversity (Diaz and Cabido 2001). Results also suggests that drought, for some plant traits, might imply the coexistence of functionally dissimilar species (Mason et al. 2005), resulting probably in complementary uses of resources (Stubbs and Wilson 2004).

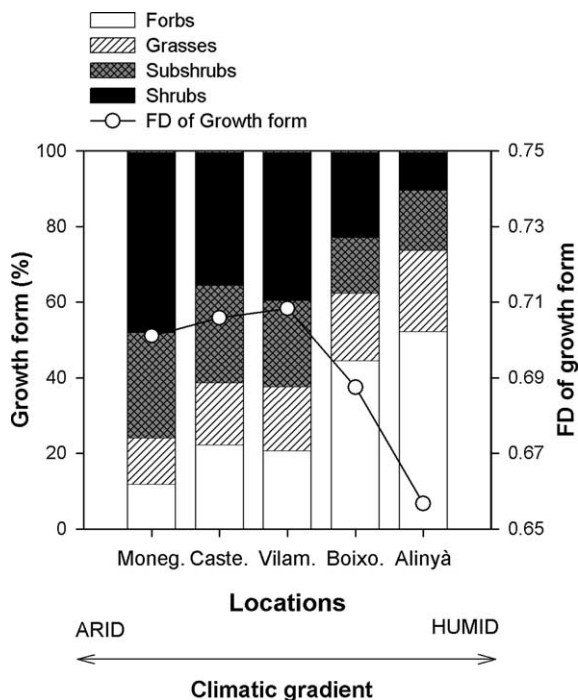


Fig. 3. Example of shifts in trait composition in different locations along the climatic gradient: change in the relative frequency of different growth forms (i.e. the first trait in Table 2). Subshrubs = woody Chamaephytes, small shrubs with average height lower than 40 cm. The line refers to the value of functional diversity calculated with respect of growth form trait (FD GF).

The indices of species and functional diversity varied also differently in response to sheep grazing regime (Fig. 2). The stronger positive effect of grazing intensity on species diversity in humid conditions in comparison with arid ones is generally consistent with the prediction that competitive exclusion in the absence of disturbance would be faster in productive environments (Huston 1994, Dupre and Diekmann 2001, Lepš 2005, Cingolani et al. 2005, Bakker et al. 2006, Petru et al. 2006). In the location where species diversity markedly increased with grazing (i.e. the subalpine Alinyà site) FD presented the opposite pattern and decreased with grazing (Fig. 2). The decrease of FD might confirm that livestock act by removing species that lack set of traits for persisting under grazed conditions, i.e. to avoid or tolerate defoliation (Diaz et al. 2001). This selection of traits should thus decrease the overall dissimilarity among species. However, the effect of grazing on FD tended also to be positive in more arid locations (Fig. 2). This could depend on the fact that, in more patchy vegetation (as in more arid locations; de Bello et al. in press), grazing might also increase heterogeneity in resource distribution (i.e. to a wider niche space Adler et al. 2001) and promote the coexistence of species with dissimilar resource acquisition strategies (i.e. different traits Stubbs

and Wilson 2004) through an increase of aggregation patterns (Pugnaire et al. 2004). The potential link between species spatial distribution and dissimilarity of their traits (Stubbs and Wilson 2004) opens up field for further research. The role of grazer's characteristics and size (Cingolani et al. 2005, Bakker et al. 2006) might also exert an influence on FD variation: animal selective effects on species' traits might be less marked in sheep grazing systems than in cattle grazing ones, as cattle are normally more generalists in their consumption.

Our study showed an overall low covariation between species and functional diversity (Fig 1 and 2), indicating that the mechanisms that support the coexistence of many species not necessarily support the functional differentiation among those species (Huston 1994, Fukami et al. 2005). This implies that the diversity of species need not capture consistently the functional differences among species that regulate ecosystem processes. If we assume that ecosystem functioning is mainly dependent on functional diversity, because functional diversity is a link between species traits and ecosystem processes (Loreau et al. 2002, Petchey and Gaston 2006), then the link between species diversity and ecosystem functioning might be context dependent. As discussed above, the degree of dependence of functional diversity on species diversity might be mostly related to the amplitude of the species' traits pool and on how species divide into the niche space available. This is a potential ground for understating the mechanism that regulate the functioning of biodiversity under different environmental constraints (Schmid and Hector 2004). The development of new indices of FD, such as the functional generalization of the Rao index, will also help testing whether the increase of FD reflects higher degrees of niche differentiation, lower resource competition and more efficient resource use (Mason et al. 2005).

It has been noted that functional diversity has different components (Mason et al. 2005), mostly depending on the definition of functional diversity itself and on the ecosystem function intended to reflect (Lavorel and Garnier 2002). Petchey and Gaston (2006) differentiated, for example, the use of "functional diversity" when species distance in trait space is weighted by species abundance (as for the Rao index), and "functional richness" when species abundance is not taken into account. It should be noted that the Rao index allows for the potential biological effect of a decrease in functional diversity with an increase of species richness (such as an increase in redundancy Stevens et al. 2003). It is difficult to conclude that increased species richness can decrease functional diversity as long as species abundance is ignored (Petchey and Gaston 2006). In this sense, the abundance of the species is of primary importance in linking species diversity with ecosystem functioning (Wilsey et al. 2005). Resilience

might be influenced by the traits of the less abundant species (Walker et al. 1999) while other ecosystem functions (e.g. stability, productivity) could be more dependent on the dominant species' traits (Grime 2001, Lepš 2005) and on the evenness of species (Petchey and Gaston 2006).

The Rao index is a mathematical generalization of the Simpson index, where the Simpson index is the upper limit for its values. Consequently, purely mathematically, we cannot expect that these two values will be independent. However, how closely they are related to each other depends mostly on properties of the data set and the biological communities considered. Probably, an important issue is how the variability of the Simpson index compares with the variability of the functional diversity index (Table 4 and Fig. 2). Another important topic is how the FD compares between species rich vs species poor communities (Fig. 2). As Simpson is a generalization of the Rao index, it has little meaning to statistically test the null hypothesis about their independence. On the contrary, if we observe that the relationship is very weak (Table 3, Fig 1 and 2), we can conclude that the functional diversity is a component of biodiversity not captured by the variation of species diversity.

Our data (Fig. 1) confirms also the results of previous simulations showing that least specious community can show the greatest functional diversity (Petchey and Gaston 2006). Often, the Rao index shows a convergence to intermediate values with increasing richness or diversity and a wider variation at lower richness/diversity level (Warwick and Clarke 1998, Shimatani 2001, Bhat and Magurran 2006). This mathematical property suggests also that the introduction/removal of a species in a rich community is expected to affect less the dissimilarity among dominant species than in a poor species assemblage (e.g. conferring, in a poorer community, either a positive or negative effect according to the traits of the dominant species).

In general, this study confirms that different components of diversity may vary independently of each other (Magurran 2004). This clearly implies that single indicators (i.e. species richness) could be incomplete surrogates of biodiversity, and that its various components have to be considered together (Wilsey et al. 2005). In our study, species that are catalogued by local floras as "very rare" were related principally to ungrazed habitats (at least in all but the driest locations), which were generally less species diverse (Fig. 2). Thus, the species diversity needs not be a good indicator of the potential contribution of communities to the maintenance of diversity at the regional level (Pykälä et al. 2005). As disturbance may promote ruderal species, with generally a low conservation interest (Spitzer et al. 1993, Canals and Sebastià 2000), the increase of the amount of species with grazing may not reflect a high conservation value in species composition. This evidences that species

diversity might not always be a synonym of ecological quality (Canals and Sebastià 2000), for example in terms of conservation priorities, because species identity is not taken into account into biodiversity indices (Magurran 2004).

Finally, the use of different biodiversity indices could lead to the definition of different criteria by which areas/management should be promoted. However, at the same time, the independence of different biodiversity components might offer the advantage of a better insight into mechanisms that regulate species coexistence and their links with ecosystem properties. Biodiversity studies can thus attain a more complete understanding of diversity, and its functioning, by the compared analyses of various components of diversity.

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