Plant Ecology and Evolution 147 (2): 165–175, 2014
http://dx.doi.org/10.5091/plecevo.2014.885

REGULAR PAPER

Contrasted taxonomic, phylogenetic and functional diversity patterns in semi-natural permanent grasslands along an altitudinal gradient

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Background and aims – Recent methodological and theoretical advances in community ecology have allowed more robust exploration of complementary facets of biodiversity in plant communities. Focusing on semi-natural permanent grasslands of the French Jura Mountains, we assessed how taxonomic, phylogenetic and functional diversity metrics vary among three phytosociological vegetation units.
Methods – We selected a sample of 135 relevés out of a phytosociological database, depicting three phytosociological orders (*Brometalia erecti*, *Arrhenatheretalia elatioris* and *Trifolio repentis-Phleetalia pratensis*) and including 381 vascular plant species. We built a phylogenetic tree based on sequences of two genes encoding chloroplast proteins, from which we computed phylogenetic diversity metrics that we compared to various taxonomic, single-trait and multi-trait functional metrics, including community-weighted means of functional traits (CWMs).
Key results – Most diversity metrics and CWMs significantly differed among vegetation units. Within each facet of biodiversity, the different metrics showed complementary results. Moreover, even when considering diversity metrics comparable in mathematical terms, i.e. based on Rao quadratic entropy, the results were largely non-redundant among the facets of biodiversity. Phylogenetic diversity and multi-trait functional diversity show opposite responses to vegetation units, as well as a low phylogenetic signal. These two results suggest that phylogenetic diversity cannot be used as a simple proxy for functional diversity.
Conclusion – This study highlights the importance of taking into consideration different facets for a better understanding of biodiversity. In particular, phylogenetic and functional facets appear highly informative, and could thus be used in addition to taxonomic diversity metrics as indicators of conservation value.

Key words – Diversity metrics, permanent grasslands, phylogenetic tree, Rao quadratic entropy, Jura Mountains.

INTRODUCTION

Beyond species richness, various diversity metrics have been proposed in community ecology, encompassing the different facets of biodiversity in species assemblages, i.e. taxonomic, functional, and phylogenetic (Devictor et al. 2010, Pavoine & Bonsall 2011). In the meantime, technical facilities in ecology and evolution have progressed rapidly. This is especially the case in phylogenetics, where the availability of numerous genetic sequences, as well as the increase of computing power combined with new computation methods led to reconstruct detailed phylogenies for various families of plants. Recently, some studies have emphasized the interest of studying multiple facets of biodiversity (Devictor et al. 2010), including measures of phylogenetic structure and functional trait variation in communities across environmental gradients (Cianciaruso et al. 2012, Bernard-Verdier et al. 2013).

Despite these promising results arising from this new analytical framework, little is known about the complementarity of taxonomic, phylogenetic and functional facets of biodiversity at regional scale among vegetation units. Indeed, the study of functional and phylogenetic community structures has long aimed at understanding fine-scale community assembly. This is notably based on two main assumptions: (i) the traits are surrogates for individual performance (i.e. growth, reproduction and survival, Violle et al. 2007) and (ii) the phylogenetic structure can be considered as a surrogate of the functional structure of the community, according to

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the niche conservatism assumption (Harvey & Pagel 1991). In contrast, the phytosociological approach is based on the comparison of plot records (i.e. species lists, called floristic relevés) to perform a hierarchical classification of plant community types (syntaxa, i.e. associations, alliances, orders and classes) at regional to continental scale (Braun-Blanquet 1964, Westhoff & van der Maarel 1978). As a consequence, phytosociological classifications are widely used by conservation agencies as a basis to habitat classification and ecosystem health assessment.

Recently, the emergence of large phylogenetic, phytosociological and trait databases, coupled with the standardization of several computation methods, allows community-level studies combining different facets of biodiversity for numerous species, especially in order to compare vegetation units (Benson et al. 2006, Kleyer et al. 2008, de Bello et al. 2010, Dengler et al. 2011). Currently however, little is known about the phylogenetic and functional structures of phytosociological vegetation units, despite the recognized interest of using different aspects of biodiversity in conservation ecology (Stuart-Smith et al. 2013).

In the specific context of permanent semi-natural mountain grasslands, many botanical surveys have been conducted in Europe over the past decades to characterize vegetation units (Schaminée et al. 2009, Dengler et al. 2011). Regional phytosociological classifications of grasslands, although based on taxonomic criteria only, are mainly explained by environmental filtering (e.g. Ferrez et al. 2011). Particularly, agricultural management is assumed to play an important role in community assembly, and therefore phytosociological classifications, by inducing disturbances, such as grazing and mowing, as well as stress gradients (Ferrez 2007). In this context, phylogenetic and functional diversity metrics comparable in mathematical terms could prove useful to better understand anthropogenic impacts on grassland vegetation (e.g. de Bello et al. 2010). In order to develop a more comprehensive approach, they could be supplemented by the community-weighted means (CWMs) of plant functional traits (Ricotta & Moretti 2011). Actually, some response functional traits are known to be related to anthropogenic disturbances in semi-natural grasslands (e.g. Kahmen & Poschlod 2008).

Besides management-induced disturbances, many other factors such as climatic variations are known to influence the different facets of biodiversity in grassland communities. For instance in Western Europe, altitude is known to be strongly correlated with temperature and precipitation, which subsequently condition the phenological stages of plant species. However, few studies which have investigated the different facets of biodiversity in grasslands have taken into consideration this source of variation.

In this paper, we provide a case study based on phytosociological relevés sampled in semi-natural grasslands of the French Jura Mountains across an altitudinal gradient to address the following questions: (1) What is the influence of the altitudinal gradient on the patterns of diversity metrics and community-aggregated plant functional traits (CWMs)? (2) Is there any difference in taxonomic, functional and phylogenetic alpha diversity metrics among the main phytosociological vegetation units?

MATERIAL AND METHODS

Study area

The study is based on phytosociological data collected in the French Jura Mountains. This region is characterized by an altitudinal gradient divided into three structural units: first plateau (500–800 m a.s.l.), second plateau (800–950 m a.s.l.) and high range (950–1700 m a.s.l.). Climate is nemoral with a strong suboceanic influence. Predominant soils are cambisols developed on limestone with a variable superficial cover of wind silt depositions. Permanent grasslands, either episodically or regularly mown and/or grazed, represent 22% of the area (Mauchamp et al. 2013).

Data selection

From the Taxa database (Ferrez 2007), provided by the CBNFC (Conservatoire Botanique National de Franche-Comté), we extracted 2335 phytosociological relevés recorded in grasslands of the French Jura Mountains. We imported these relevés in Phytobase 8.1, a relational database devoted to vegetation analysis (Gillet 2010). For each floristic relevé, performed on approximately 100 m^2, species abundance-dominance codes (Braun-Blanquet 1964) were converted into relative percentage cover, summing to 100% for each plot (Gillet 2010).

We first selected the subset of relevés related to permanent grasslands of the Jura Mountains at an altitude between 500 and 1300 m a.s.l. We excluded relevés from uplands (subalpine belt) or wetlands. For each selected relevé, we then performed a diagnosis of phytosociological classes, orders and alliances according to Julve's classification (Julve 1993, 2013) and based on species fidelity indices (Gillet 2010). On this basis, we selected all relevés belonging to three phytosociological orders: *Arrhenatheretalia elatioris* (nutrient-rich hay meadows), *Trifolio repentis-Phleetalia pratensis* (nutrient-rich pastures) and *Brometalia erecti* (nutrient-poor limestone grasslands). These three orders include the most frequent semi-natural grasslands in the study area (Ferrez et al. 2011). In the last step, we applied a stratified subsampling to retain approximately fifteen relevés for each combination of altitudinal classes (i.e. first plateau, second plateau and high range) and phytosociological orders, i.e. *Brometalia erecti* (thereafter '*Brometalia*' or 'Be'), *Arrhenatheretalia elatioris* (thereafter '*Arrhenatheretalia*' or 'Ae') and *Trifolio repentis-Phleetalia pratensis* (thereafter '*Trifolio-Phleetalia*' or 'TP'). A minimum geographic distance was chosen between relevés to avoid as much as possible spatial autocorrelation. Finally, our selection resulted in a dataset of 135 relevés encompassing 381 plant species for the subsequent analyses.

Phylogenetic tree

The Angiosperm phylogenetic tree was built from a larger number of species, related to the three previously defined phytosociological orders, but observed on additional surveys in the study area. It is composed of 54 families, 207

genera and 426 species, with significant differences in number of species per genus as well as genera per family (electronic appendix 1). The construction of the phylogenetic tree is based on sequences of two genes encoding chloroplast proteins (*rbcL* and *matK*). Their complementarity allows a good resolution of the tree for the selected species (Hilu et al. 2003). The sequences were obtained using the GenBank database (Benson et al. 2006). For species not yet or partially sequenced for the selected genetic markers, we replaced them by the closest available relative in the light of phylogenetic relationships revealed by the recent literature, including APG III classification (APG 2009). This represented 13% of the *rbcL* dataset and 19% for *matK*. All sequences were first automatically aligned using ClustalX 2.1 software and then manually using Se-Al 1.0al software for both markers (Larkin et al. 2007, Rambaut 1996). A combined analysis of these two datasets was then performed following the Bayesian MCMC (Monte Carlo Markov Chain) approach using BEAST 1.5.3 software (Drummond & Rambaut 2007). The ambiguously aligned regions of the *matK* gene have been excluded (11% of 1010 bp). MrModeltest2 v. 2.0 software was used to choose the model of nucleotide substitution that best fits the data, following Akaike's information criterion (Nylander 2004). The selected model was the general time reversible model (GTR) with among-site substitution rate heterogeneity described by a gamma distribution (Yang 1994). Several family relationships were constrained according to the APG III phylogeny (APG 2009) in BEAST to calibrate the rates of molecular evolution of each lineage for Angiosperms clades (Bell et al. 2005). Finally, for branch length calculation an uncorrelated relaxed molecular clock was used, which takes into account evolution heterogeneity between lineages (Drummond et al. 2006).

Functional traits

The functional approach is based on a set of response traits known to be related to management-induced disturbances in grasslands. These traits involve leaf morphology, plant morphology and reproductive characteristics (table 1). The selected traits are known to be specifically related to mowing, grazing and fertilization impacts, these management regimes leading to major compositional and structural changes in grassland communities (Jacquemyn et al. 2003, Bernhardt-Römermann et al. 2011, Gaujour et al. 2012).

Diversity metrics

Among taxonomic alpha diversity metrics, species richness N_0 and inverse Simpson species diversity N_2 were computed, based on the Rényi general entropy and expressed as species number equivalent (Hill 1973).

For the phylogenetic and functional facets of biodiversity, the Rao quadratic entropy (thereafter 'Rao') with Jost's correction (2007) was used, thereby obtaining a synthetic diversity index directly comparable to N_2 (de Bello et al. 2010). To compute Rao phylogenetic diversity, the ultrametric distance from the phylogenetic tree was considered. To compute Rao functional diversity, Euclidean distance for quantitative traits (i.e. FlD, Height, SLA, LMDC and square-root transformed SM, to meet normality), Sokal-Michener binary dis-

Table 1 – Plant traits, their attributes, their related functions and some practical information on the dataset.

trait	code	data type	values (min, max)	related function	missing data	percent of relative cover	data source
Flowering duration	FlD	semi-quantitative	2–12 months	reproductive strategy	0%	100%	Landolt et al. (2010)
Maximum canopy height	Height	quantitative	0.03–1.8 m	light capture competition	0.4%	100% (90–100%)	Jäger (2000)
Leaf dry matter content	LDMC	quantitative	79–424 mg g^{-1}	leaf physical tolerance	30.9%	86.1% (54.1–100%)	Kleyer et al. (2008)
Seed mass (only germinules)	SM	quantitative	0.001–39.44 mg	seedling competition, dispersal ability	10.7%	91.7% (47.8–100%)	Kleyer et al. (2008)
Specific leaf area	SLA	quantitative	8.5–59.19 mg mm^{-2}	photosynthetic rate	13.6%	94.2% (72.2–100%)	Kleyer et al. (2008)
Leafdistribution along the stem	LD	categorical	1–6	space competition	3.6%	99.1% (89.1–100%)	Klotz et al. (2002)
Clonal growth organs	CGO	multichoice binary	1–17 or no CGO	reproductive strategy, storage capacity	3.4%	99% (87.1–100%)	Klimešová & de Bello (2009)

Table 2 – Phylogenetic signal for five functional traits based on Blomberg's K index.
The phylogenetic signal was first computed on the whole data set, then separately for monocot and dicot species. The number of species indicates the size of the species pool used to compute the phylogenetic signal for each trait. Bold font indicates significant phylogenetic signals ($P < 0.05$).

trait	number of species (monocots / dicots)	Blomberg's K		
		all species	monocots	dicots
Leaf dry matter content	244 (60 / 183)	0.0077	**0.0288**	0.0046
Seed mass (only germinules)	321 (61 / 259)	0.0007	**0.0299**	0.0008
Maximum canopy height	360 (77 / 282)	0.0037	0.0065	0.0037
Specific leaf area	310 (72 / 237)	0.0029	0.0092	0.0026
Flowering duration	362 (77 / 284)	0.0014	0.0006	0.0025

tance for nominal and multichoice nominal traits coded as dummy variables (i.e. LD and CGO, respectively), or Gower distance for the computation of multi-trait diversity metrics (see table 1 for details) were applied, respectively. In order to compare the mean trait values among plant communities, the CWMs (Garnier et al. 2004) were also computed.

For the single-trait functional facet of biodiversity, species with missing information were removed, so metrics were sometimes computed on less than 90% of the relative percentage cover (especially for LDMC and SM, see table 1 for details). Moreover, the abundance-weighted version of the metrics was always applied, because presence-absence data may miss ecologically interesting patterns. Finally, woody plants were ignored in functional analysis, considering their low relative cover (i.e. 0.2% on average) and because trait data at the seedling stage were generally unavailable.

Phylogenetic signal testing

Phylogenetic signal is primarily defined as the tendency of phylogenetically related species to resemble from each other, e.g. functionally, more than species drawn at random from the phylogenetic tree (Blomberg et al. 2003). Blomberg's K was used as a ranking index for trait phylogenetic signals (i.e. the higher the K values, the stronger the signal). The index expresses the strength of phylogenetic signal as the ratio of the mean squared error of the tip data measured from the phylogenetic corrected mean, and the mean squared error based on the variance-covariance matrix derived from the given phylogeny, assuming Brownian motion. In this way, $K = 1$ corresponds to trait evolution according to a Brownian motion evolution model. Following Bernard-Verdier et al. (2013), K values were compared to null distributions by shuffling species labels at the tip of the phylogeny 10000 times. The observed values in the upper fifth quantile of the null distribution were assumed significant. The number of species included in the phylogeny for testing phylogenetic signal varied depending on traits, ranging from 244 for leaf dry matter content to 362 for the flowering duration (table 2). The phylogenetic signal and functional trait conservation are not always uniform along the phylogenetic tree (Davies et al. 2013). Grasses are important components of grassland plant communities that structure habitats. Consequently, we proceeded to separate computations for monocot and dicot species as proxies for grasses and forbs, respectively, to test their own information and potential hidden signal.

Data analysis

Statistical analyses were performed using R 3.0.2 (R Development Core Team 2013), its packages 'ade4' (Chessel et al. 2013), 'FD' (Laliberté & Shipley 2013), 'picante' (Kembel et al. 2013), 'phytools' (Revell 2013), 'phylotools' (Zhang et al. 2012) and 'vegan' (Oksanen et al. 2013), as well as specific R functions implemented by various authors including de Bello et al. (2010) and Borcard et al. (2011).

We tested Spearman rank correlation between each pair of quantitative traits. The spatial autocorrelation was tested among sites for each diversity metric using Moran's I statistic.

Variation in taxonomic composition among vegetation units was explored with a Principal Component Analysis (PCA) performed on Hellinger-transformed species data. Moreover, to express the main potential gradients of disturbances and fertilization in species composition, we projected on the PCA plot some relevant community-weighted mean ecological indicator values, using 'rda' and 'envfit' functions available in 'vegan' package. These indicator values are grazing tolerance, trampling tolerance, mowing tolerance from Biolflor database (Klotz et al. 2002), and the nutrient value, indicating the nitrogen and phosphorus content in the soil as a proxy of soil fertility and grassland productivity, from Flora Indicativa (Landolt et al. 2010).

To assess the relative importance of altitude and vegetation units on the metric values, we performed a partial redundancy analysis (pRDA) with diversity metrics as response variables, vegetation units as explanatory variable, and altitude as covariable (Borcard et al. 2011).

In addition, we tested Spearman rank correlation between altitude and metric values for each phytosociological order independently. The three vegetation units were compared, for each metric and indicator, with a non-parametric Kruskal-Wallis test associated with a post-hoc test for multiple comparisons. Given the number of pairwise comparisons,

a sequential Bonferroni-Holm correction was applied to all multiple comparison tests (Holm 1979).

RESULTS

We found significant Spearman rank correlations between LMDC and SLA (rho = -0.440), SM and Height (rho = 0.334), and LDMC and Height (rho = -0.216).

The spatial autocorrelation of the different diversity metrics was mostly non-significant. However, some metrics (6/16), especially including taxonomic (2/2) and phylogenetic (1/1) metrics, were clustered across the region (electronic appendix 2A). This could partly be explained by the existence of the three altitudinal structural units on which the selection of relevés was made.

The PCA of Hellinger-transformed species cover data shows a clear segregation of relevés according to vegetation units (fig. 1). The first axis (18.6% of the total variance) expresses a gradient of disturbance and soil fertility, opposing *Arrhenatheretalia* and *Trifolio-Phleetalia* to *Brometalia*, the latter showing low nutrient and mowing tolerance indicator values. The second axis (7.9%) is more correlated with grazing and trampling tolerance, and thus allows distinguishing *Arrhenatheretalia* and *Trifolio-Phleetalia*.

Relative influence of vegetation units and altitudinal gradient on metrics

The partial RDA of diversity metrics constrained by vegetation unit and conditioned by altitude reveals that only 0.79% of the variance is explained by the altitude covariable, while the vegetation unit alone explains 23.20%. In addition, when split by vegetation unit and after applying Bonferroni-Holm correction, Spearman tests only detect few significant correlations between diversity metrics and altitude (electronic appendix 2B). Thus, in our dataset, the altitudinal effect on diversity metrics is negligible compared to the differences among vegetation units.

Comparison of diversity metrics among vegetation units

Numerous metrics differed significantly among vegetation units, as evidenced by Kruskal-Wallis tests. Therefore, we used post-hoc tests to specify the response of taxonomic, functional and phylogenetic metrics (figs 2 & 3).

The two components of taxonomic diversity (i.e. species richness and evenness) seem to be partly complementary, and may differentiate phytosociological orders. The *Brometalia* have greater species richness N_0, but show no difference in species diversity N_2, compared to the *Arrhenatheretalia* and *Trifolio-Phleetalia* (fig. 2), due to a lower species evenness (data not shown).

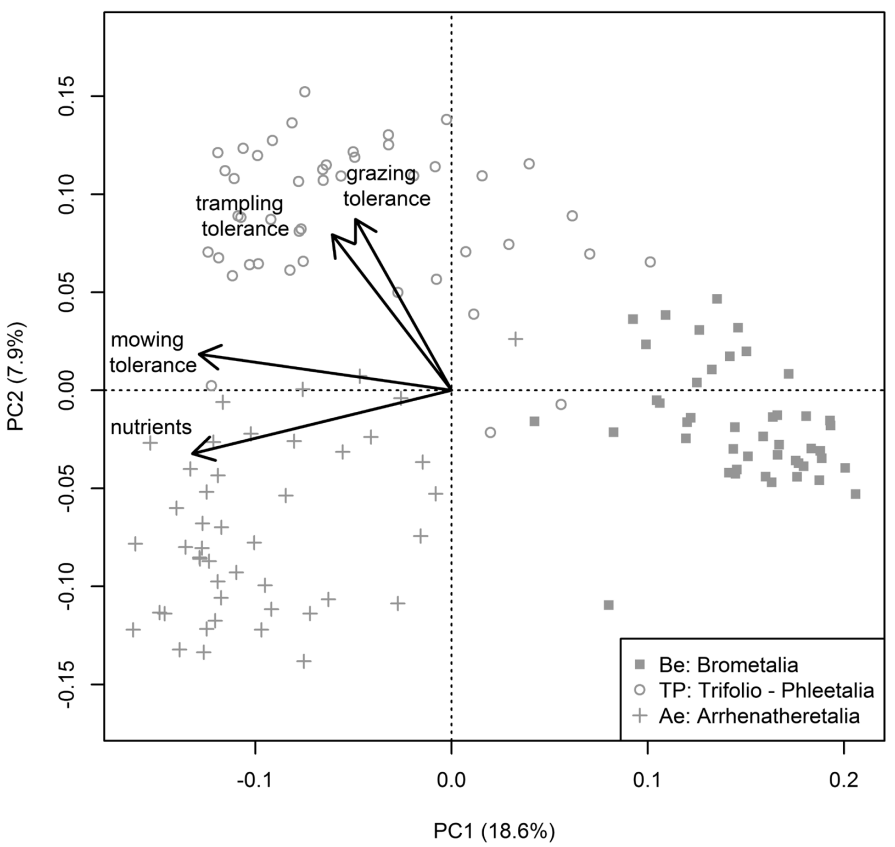


Figure 1 – PCA of the Hellinger-transformed species cover data of 135 grasslands of the Jura Mountains, and a posteriori projection of four ecological indicator values.

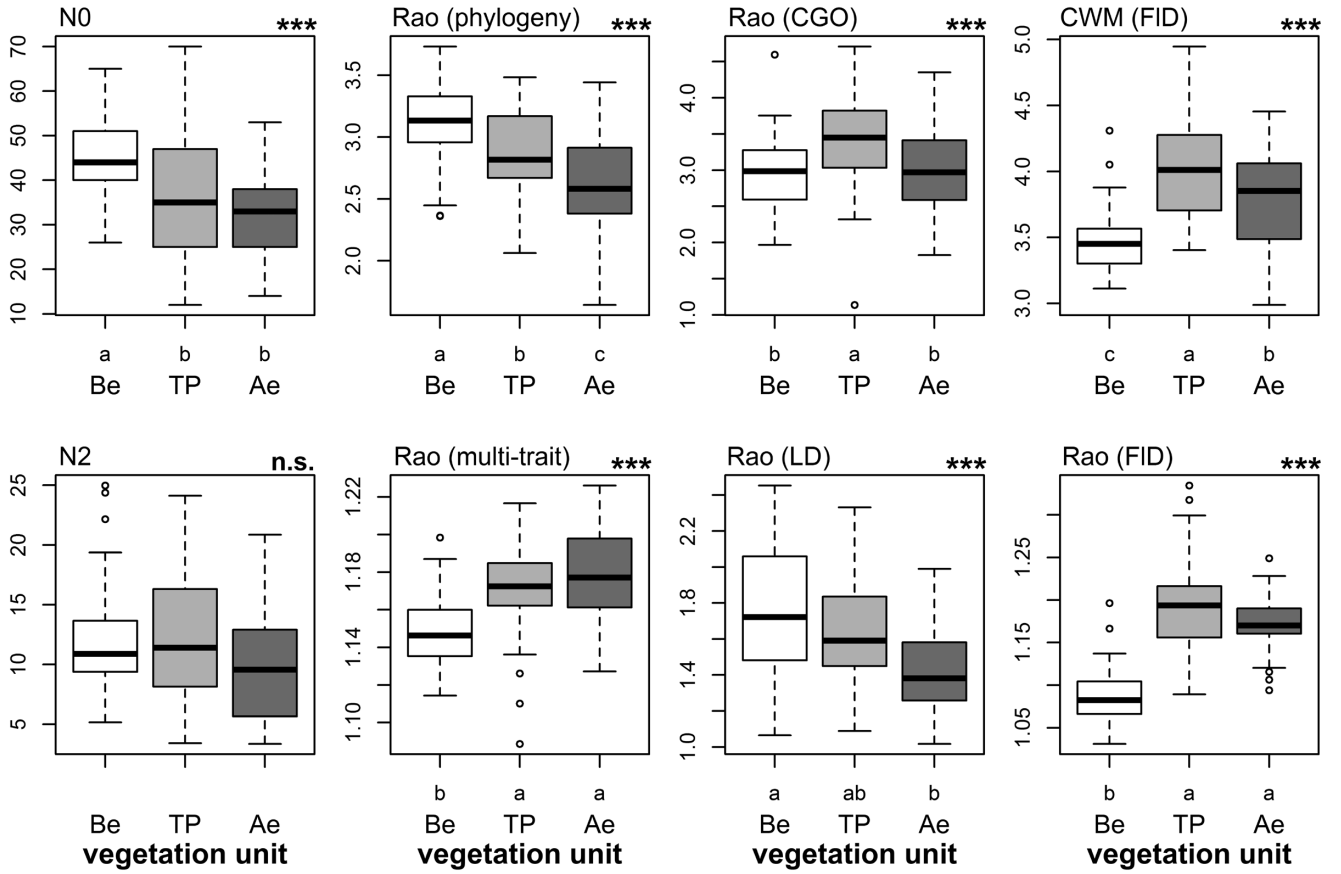


Figure 2 – Taxonomic, phylogenetic and functional metrics split by vegetation unit (n = 135), with results of Kruskal-Wallis tests. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. non significant. Letters indicate significant different values according to non-parametric post-hoc tests.

The Rao phylogenetic analysis mainly suggests that the *Arrhenatheretalia* communities are dominated by phylogenetically closer species than communities belonging to the other orders (fig. 2). In contrast, *Brometalia* show a more even distribution of dominant species along the phylogenetic tree.

The analysis of functional diversity using a set of response traits also shows numerous significant and complementary results. The *Brometalia* relevés are significantly more diverse than the *Arrhenatheretalia* (fig. 2) due to a substantial proportion of species with leaves distributed regularly along the stem, while rosette and semi-rosette species strongly dominate in the latter (electronic appendix 3A). Regarding clonal growth organs, the *Trifolio-Phleetalia* show more diverse communities with a more regular representation of the four main CGO forms (fig. 2 & electronic appendix 3B). Some quantitative traits show highly distinct responses according to the computed metric while others exhibit common trends, regardless of the metric (e.g. respectively SLA and LDMC, fig. 3). Besides, several traits show similar trends, despite the non-significance of correlation among trait values.

The mean and diversity aspects of the panel of quantitative functional traits clearly differentiate the three vegetation units. The *Brometalia* relevés show on average heavier seeds and higher but more diverse LDMC than the *Arrhenathereta-lia* and *Trifolio-Phleetalia* relevés (fig. 3). The *Arrhenatheretalia* communities are characterized by taller species with higher SLA values, whereas the *Trifolio-Phleetalia* communities show a longer duration of flowering (figs 2 & 3). The functional diversity also presents distinct trends. Thus, the *Brometalia* appear less diverse than the *Arrhenatheretalia* regarding the flowering duration, while it does not show more diversity regarding SLA (fig. 2). Due to these differences among traits, the multi-trait Rao quadratic entropy index does not differentiate between *Arrhenatheretalia* and *Trifolio-Phleetalia*, both more variable than the *Brometalia*.

Comparisons of diversity facets

The significance of phylogenetic signal is quite low in all chosen traits, and the K values lower than expected under a Brownian motion model when considering all the species (table 2). Indeed, in general and for dicots, we observe a high trait variance within lineages ($K < 1$). When considering monocots only, both the LDMC and the seed mass show a signal, albeit weakly significant (table 2), meaning that evolution of traits follows a Brownian motion.

Besides, there are several correlations among taxonomic, functional and phylogenetic abundance-weighted diversity metrics, both positive and negative (electronic appendix 4). For instance, the diversity of flowering duration is negatively

correlated to the diversity of seed mass and LMDC, while positively to the canopy height (electronic appendix 4)

Finally, some metrics show opposite trends for different diversity facets among vegetation units (figs 2 & 3). As an example, the Rao quadratic entropy based on phylogeny shows clear opposite trends to the Height. In addition, the Rao quadratic entropy computed on multiple traits presents a distinct pattern compared to the phylogenetic metric, showing no significant correlation (fig. 2 & electronic appendix 4).

DISCUSSION

Negligible influence of the altitude on diversity metrics

The altitude effect on diversity metrics seems negligible in this study, although we could not exclude the influence of a climatic gradient on the functional facets of biodiversity (Pellissier et al. 2010). However, in order to test this potential effect, it may need to perform field measurements, especially to capture the intraspecific variability. This variability seems otherwise more influenced by local conditions, such as management, than by climate (Pakeman 2013).

Differences in taxonomic, functional and phylogenetic metrics among vegetation units

The diversity metrics show many differences among phytosociological orders, both within and among facets of biodiversity.

Taxonomic metrics appear of some utility to underscore the differences between vegetation units. Whereas species richness is significantly lower in *Arrhenatheretalia* and *Trifolio-Phleetalia*, Simpson's diversity index N_2 does not show any difference. In contrast, the lowest local species evenness (i.e. N_2/N_0, Gillet et al. 1999) is found in *Brometalia* relevés. This set of taxonomic differences could potentially be explained by a higher number of rare species per community in oligotrophilous semi-natural grasslands, otherwise known to be remarkably species-rich at fine spatial scale (Wilson et al. 2012, Mauchamp et al. 2013).

Using phylogenetic data, the Rao metric highlights highly distinct responses among vegetation units. The dominance of closely related species in the *Arrhenatheretalia* order may be explained by 54.7% of relative cover of Poaceae compared to 39.1% and 35.8% in *Trifolio-Phleetalia* and *Brometalia*, respectively. Besides, in the *Trifolio-Phleetalia*, the phylogenetic diversity is higher than in *Arrhenatheretalia*, despite comparable species richness and dominance, meaning that species are more evenly distributed along the phylogenetic tree, thus representing more lineages.

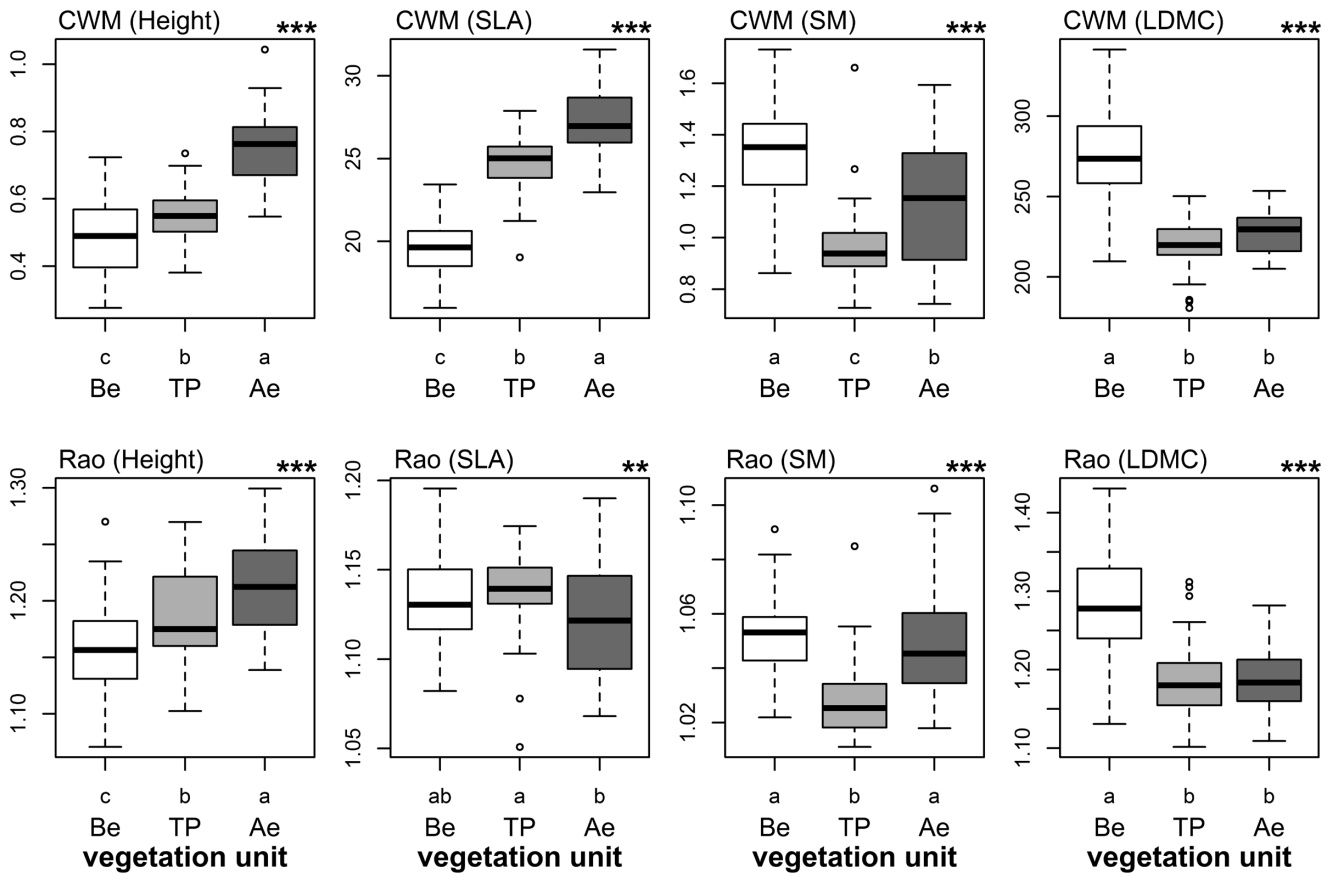


Figure 3 – Four quantitative functional metrics split by vegetation unit (n = 135), with results of Kruskal-Wallis tests. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. non significant. Letters indicate significant different values according to non-parametric post-hoc tests.

Functional metrics may capture the complex structure of a community, thus providing potential interpretations of the underlying processes acting on disturbed plant communities (Mouillot et al. 2013). The chosen traits, although showing sometimes correlations, seem to adequately differentiate the three phytosociological units, revealing their complementarity. The *Brometalia* are characterized by communities with shorter flowering period, dominated by species with a lower canopy height, but producing heavier seeds and characterized by a higher LDMC. In contrast, the communities of the *Arrhenatheretalia* and *Trifolio-Phleetalia* orders are characterized by taller species with a higher SLA and a broader, though more variable flowering period. Finally, within the same phytosociological class, i.e. the *Agrostio stoloniferae-Arrhenatheretea elatioris*, the *Trifolio-Phleetalia* differ from the *Arrhenatheretalia* by smaller species with lighter seeds and lower SLA.

Complementary responses of biodiversity facets

Our study shows the relative limitations of taxonomic diversity metrics used alone, and underlines the importance of taking into account the different facets of biodiversity.

The results of taxonomic metrics are consistent with Wilsey & Polley (2003) that demonstrated an opposite pattern of species richness and evenness, emphasizing the limitations of an approach in which species richness is the only surrogate of biodiversity.

The functional diversity highlights several complementary responses among vegetation units, which mainly depend on the chosen trait. These single-trait responses could partly explain the absence of significant differences between *Arrhenatheretalia* and *Trifolio-Phleetalia* when considering the multi-trait approach. This suggests the need to use a set of trait × metric combinations before any interpretation of community structure of semi-natural grasslands, given that several mechanisms can operate simultaneously on community assembly (Bernard-Verdier et al. 2012, Price et al. 2013). In this context, the phylogenetic diversity could reinforce and complement the functional approach, especially when a lack of phylogenetic signal is observed in grasslands (Silvertown et al. 2006). In some cases, the phylogeny cannot constitute a good surrogate of functional structure within communities due to the weak relationship between species relatedness and the strength of competition (Cahill et al. 2008, Bernard-Verdier et al. 2013). As an example, in this study, the *Brometalia* seems more phylogenetically dispersed, while a multi-trait approach reveals a more under-dispersed pattern. Thus, in agreement with other recent studies (Kluge & Kessler 2011, Cianciaruso et al. 2012), our analysis suggests that the phylogeny might not be the better surrogate of the functional space. However, this conclusion may depend on the chosen traits, and needs to consider the relative importance of biotic and abiotic filters shaping a community. For instance, competition may sometimes eliminate phylogenetically distant species despite the traits are phylogenetically conserved (Mayfield & Levine 2010).

Potential management-induced effects

Given the theoretical relations between functional traits and disturbances (Mouillot et al. 2013), we assumed that the functional metrics may indicate potential management-induced disturbance differences among phytosociological vegetation units. Besides, these management regimes were considered in the ecological characterization of syntaxa (Ferrez 2007).

In this context, the observation of shrubs and tree saplings in relevés of the *Brometalia* suggests an extensive grazing with no mowing, while a potential trampling disturbance could explain the larger proportion of rosette and semi-rosette species and lower LDMC (Bakker 1998).

In contrast, in the other orders, taller communities with higher SLA values rather suggest nutrient inputs promoting the development of fast-growing annual species, especially competitive for light resource. Thus, a high canopy height allows the overtopping of the surrounding vegetation, a process associated with shade avoidance strategy. On the contrary, a high SLA is frequently considered as a complementary strategy of shade tolerance, even though both may be observed in the same community (Gubsch et al. 2011). The higher values of these two traits, combined with the existence of heavier seeds, thus potentially suggests a mowing management of the *Arrhenatheretalia* order, as considered in the syntaxa description (Ferrez 2007). On the contrary, the *Trifolio-Phleetalia* may be mainly grazed (Ferrez 2007). Indeed, the well-known fine-scale spatial heterogeneity due to cattle behavior leads gaps in canopy, making the competition for light lower in grazed than mowed grasslands, and thus promoting seedling recruitment from lighter seeds, including several annual species (Eriksson & Eriksson 1997, Jacquemyn et al. 2003, Kahmen & Poschlod 2008).

Limitations and prospects

We are cognizant that several limitations require further studies to confirm the results. As an example, the use of mean-trait values retrieved from databases, although often close to the field data values (Kazakou et al. 2013), seems less reliable than field measurements when studying fine-scale processes (Cordlandwehr et al. 2013). Moreover, the knowledge of direct information on land-use history, landscape characteristics as well as a detailed characterization of farming practices, especially when mixed management was applied (i.e. mowing and grazing during the same season) seems crucial to better understand the community assembly.

Further analyses using data about management practices applied to grasslands in the study area will be carried out, especially to address the question of the impact of such mixed management regime on biodiversity.

SUPPLEMENTARY DATA

Supplementary data are available in pdf at *Plant Ecology and Evolution*, Supplementary Data Site (http://www.ingentaconnect.com/content/botbel/plecevo.supp-data), and consists of the following: (1) taxonomic composition of the Angiosperm phylogenetic tree composed of 54 families, 207

genera and 426 species; (2) Moran's I statistic for each of sixteen diversity metrics and Spearman rank correlation coefficients among each diversity metric and the altitude per site split by phytosociological orders; (3) percentage of the different categories of leaves distribution along the stem, and percentage of the different categories of the most represented CGO weighted by the relative abundance of species in each phytosociological order; and (4) Spearman rank correlations among diversity metrics.

ACKNOWLEDGEMENTS

We thank Yorick Ferrez and the CBNFC (Conservatoire Botanique National de Franche-Comté) for the provision of phytosociological relevés. This research was supported by the Conseil Régional of Franche-Comté and the Comité Interprofessionnel du Gruyère de Comté. We are grateful to the two anonymous reviewers who helped us improving the manuscript.

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Manuscript received 10 May 2013; accepted in revised version 14 Apr. 2014.

Communicating Editor: Elmar Robbrecht.