

FLORISTIC AND FUNCTIONAL DIVERSITY OF MEADOWS FROM TWO NEIGHBORING BIOGEOGRAPHIC REGIONS

Nataša PIPENBAHER

Department of Biology, Faculty of Natural Sciences and Mathematics, University of Maribor, Koroška 160, SI-2000 Maribor, Slovenia
E-mail: natasa.pipenbaher@uni-mb.si

Norman W. H. MASON

Landcare Research, Private Bag 3127, Hamilton 3240, New Zealand

Sonja ŠKORNIK

Department of Biology, Faculty of Natural Sciences and Mathematics, University of Maribor, Koroška 160, SI-2000 Maribor, Slovenia

ABSTRACT

Physiognomically similar meadows from two different regions, the Dinaric and the Central European, that occur in similar environments and have been subjected to relatively uniform management regimes were compared in order to test for significant differences in floristic diversity, community-weighted mean (CWM) and functional diversity (FD). We found that the Central European meadow community has higher species dominance and lower evenness, but it is less diverse than the Dinaric. Central European meadows contain more annuals, with faster rates of leaf turnover, which suggests that they are more strongly structured by disturbance than the Dinaric meadows. For most traits, diversity was highest in the Central European meadows, probably owing to more severe disturbance impact, which is known as the most potent force creating and sustaining trait divergence. We conclude that the strong evidence for divergence in functional composition between meadows from different regions suggests that functional trait composition is unlikely to be a deterministic function of similarities in environment conditions and land use in geographically disjunct communities. This may have important implications for conservation management of these meadows.

Key words: plant functional traits, semi-dry grasslands, Central European meadows, Dinaric meadows

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SINTESI

Prati fisiognomicamente simili in due regioni diverse, quella dinarica e quella centro-europea, che crescono in ambienti simili e sono stati sottoposti a regimi di gestione relativamente uniformi, sono stati confrontati al fine di verificare differenze significative in diversità floristica, valore medio dei tratti funzionali (CWM) e diversità funzionale (FD). I risultati della ricerca hanno evidenziato che la comunità della regione centro-europea ha una dominanza maggiore di specie, una minore uniformità nell'abbondanza degli esemplari di ogni specie, ed è meno diversificata rispetto alla comunità della regione dinarica. I prati dell'Europa centrale ospitano più specie annuali, con tassi più alti di ricambio di foglie, il che suggerisce che essi siano più fortemente strutturati da vari disturbi che i prati dinarici. Per la maggior parte dei tratti funzionali la diversità è risultata più alta nei prati dell'Europa centrale, probabilmente a causa di un impatto maggiore dei disturbi, riconosciuti come la forza più potente che crea e sostiene le divergenze tra i tratti. Gli autori concludono che la forte evidenza di divergenza nella composizione funzionale tra prati provenienti da diverse regioni suggerisce che la composizione dei tratti funzionali non sia una funzione deterministica di somiglianze in condizioni ambientali e di uso del suolo nelle comunità geograficamente disgiunte. Tale risultato può avere implicazioni importanti per la gestione e la conservazione di queste praterie.

Parole chiave: tratti funzionali delle piante, prati semi-asciutti, prati centro-europei, prati dinarici

INTRODUCTION

There is a long history in plant ecology of grouping communities from geographically disjunct regions that appear physiognomically similar (e.g. Cowling & Campbell, 1980). However, plant communities are increasingly classified by their functional traits as well as by physiognomy (Shipley *et al.*, 2006). The renewed interest in classifying species into groups relating to function rather than to taxonomy (e.g., Keddy, 1992; Lavorel *et al.*, 1997; Westoby, 1998; Weiher *et al.*, 1999) has triggered the search for traits that express meaningful differences in ecological behaviour among plant species.

It is well known that differences in essential constraints, e.g., weather, topography, soil conditions and disturbance regime, lead to different plant communities. The species combination assemblage is based on filtering plants with particular sets of functional traits from the available species pools (Lavorel *et al.*, 1997; Lavorel & Garnier, 2002; de Bello *et al.*, 2005). Morphological-functional traits are recognized as a valuable framework for describing species attributes and determining general patterns of vegetation response to disturbance and environmental gradients (McIntyre *et al.*, 1999). Furthermore, interpreting the functional trait diversity of vegetation (Mason *et al.*, 2005; Grime, 2006; Lepš *et al.*, 2006; Doležal *et al.*, 2011; Ricotta & Moretti, 2011) is emerging as a key indicator of ecosystem function (e.g. Scherer-Lorenzen, 2008) and also of community assembly processes (Mason & Lanoiselee, 2008; Vileger *et al.*, 2008). Functional diversity can have different definitions (Diaz & Cabido, 2001; Tilman *et al.*, 2001; Lepš *et al.*, 2006; Ricotta & Moretti, 2011) and can be quantified using a variety of indices (Ricotta, 2005; Vileger *et al.*, 2008; Doležal *et al.*, 2011). Some authors (e.g., Tilman *et al.*, 2001; Petchey & Gaston, 2002) define functional diversity as the extent of functional trait variation (or differences) among the species in a community (Tilman *et al.*, 2001; Petchey & Gaston, 2002; Lepš *et al.*, 2006), whereas others define it in its broadest sense as the distribution of trait values in a community (Diaz & Cabido, 2001; Diaz *et al.*, 2007). Comparison of the functional trait means and functional diversity between communities, or groups of communities, may reveal differences in the rates of ecosystem functioning (Shipley *et al.*, 2006; Scherer-Lorenzen, 2008). These comparisons may also reveal differences in the relative influence of environmental stress, disturbance and competition on species occurrence in local communities (Grime, 2001).

Tests of whether communities that occur in similar environments and are subject to similar disturbance regimes are also similar in functional trait structure have been rare, and where such tests have been performed, they have studied a relatively small number of communities and mainly considered only the widely used community-weighted mean of a trait (CWM hereafter) (Smith *et al.*, 1994; Smith & Wilson, 2002; Watkins & Wilson, 2003).

It has already been established (Pipenbahr *et al.*, 2013a) that the semi-natural dry meadows of Slovenia provide a great opportunity for studying the ecological basis of floristic richness and community functional structure in two distinct biogeographical regions (i.e. the Central European and the Dinaric; biogeographical regions are used as defined in Pipenbahr *et al.* (2013a)), where these plant communities occur on similar parent rock types (calcareous loamy soils), and all have historically been subjected to a relatively uniform management regime of mowing for hay at least annually (Kaližarič, 1997; Škornik, 2000; Pipenbahr *et al.*, 2013a). The floristic distinctiveness of the Central European and Dinaric dry-meadows has already been described as substantial (Pipenbahr *et al.*, 2013a), and comparison of these communities considering only a CWM for a few plant traits revealed that the species composition of dry meadow communities in different regions may be influenced to varying degrees by stress and disturbance (Pipenbahr *et al.*, 2013a). However, the comparison of functional trait diversity between these meadows, considered as the overall difference among species in a community in terms of their traits, remains to be tested. This manuscript thus aims to interpret the functional diversity of the Central European and Dinaric dry-meadows. By calculating the functional diversity, we may reveal differences in the relative importance of complementarity or convergence in ecological strategy in community assembly. Higher functional diversity than expected by chance indicates that co-occurring species tend to differ more in ecological strategy than expected, which would provide evidence for limiting similarity.

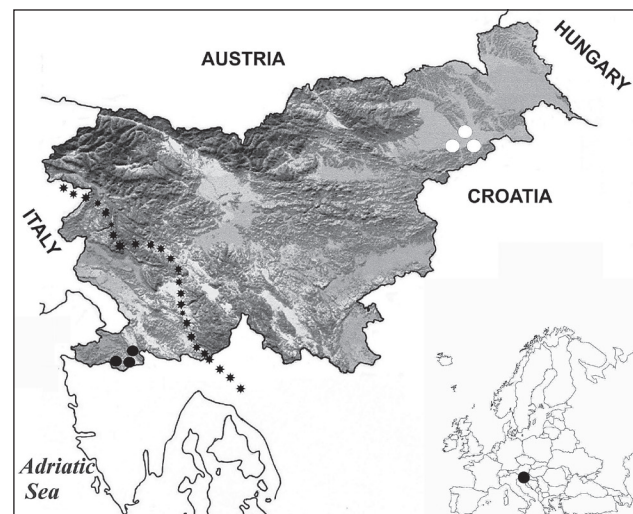


Fig. 1: Map of study areas - Central European (○) and Dinaric (●) meadows. The stars line shows border between the biogeographic zones/ regions.

Sl. 1: Prikaz območij raziskave – srednjeevropski (○) in dinarski travniki (●). Linija ponazarja mejo med biogeografskima območjema.

Lower functional diversity than expected indicates that co-occurring species tend to be more similar in ecological strategy, and provides evidence that environmental filtering is the dominant process. We used a previously published dataset with species and trait data (Pipenbaher *et al.*, 2013a) to answer the following questions: (1) Do the Slovenian Central European and Dinaric calcareous semi-dry meadows differ in their species richness and species diversity? (2) Is there any evidence that functional trait variations (*i.e.*, functional diversity) among the species differ between regions?

MATERIAL AND METHODS

Study area and field methods

We studied semi-dry grassland communities (class Festuco-Brometea) in two biogeographic regions in Slovenia: the Dinaric (NW Balkan, sub-Mediterranean-Ilyrian) and the Central European, which meet in the pre-Alps, Dinaric and pre-Dinaric Mountains that are stretching along the eastern Adriatic to the Alps. On the basis of the typology of grasslands, we summarized the names on a biogeographic basis (Central European vs. Dinaric (NW Balkan grasslands)), based on in the distributional ranges of both types (Pipenbaher *et al.*, 2013a).

The Dinaric study area lies in Slovenia's Northern Adriatic karst zone (45° 28.38' N, 13° 58.34' E) and represents the most north-western part of the Balkan Peninsula (Fig. 1). The climate is transitional between Mediterranean and continental pre-Alpine, with cool, rainy winters and long, dry summers (Poldini, 1989). The mean annual temperature in the study area is 10.5 °C, the coldest in January (-2 °C) and the warmest in July (19.8 °C). The average annual precipitation is around 1400 mm (ARSO, 2009). The semi-natural, extensively managed dry grasslands in the area are still distributed over large unfragmented surfaces. There is a floristic distinction between the *Scorzonion villosae* alliance, used as unfertilized hay meadows, and the *Satureion subspicatae* alliance, used as semi-natural pastures (Pipenbaher *et al.*, 2011).

The Central European study area (Fig. 1) is located in the tertiary hilly region of the NE region of Slovenia, (46° 18.74' N, 15° 49.03' E), at ca. 300400 m above sea level. The mean annual temperature is 9.7 °C. The coldest month is January (-2.4 °C) and the warmest July (19.4 °C). The average annual rainfall is about 1050 mm (ARSO, 2009). The landscape is characterized by a mosaic of deciduous forest, arable fields and semi-natural grasslands. Large proportions of this type of vegetation have been lost during recent decades, owing to the forest encroachment that has followed the abandonment of traditional management, which consisted of extensive mowing (12 times a year), extensive grazing and no fertilizer addition. The semi-dry *extensively used meadows* in this study occur in the area on sites with middle-deep

eutric cambisols on steep slopes with dry, sunny conditions (Kaligarič & Škornik, 2002).

In this study we used a previously published dataset (Kaligarič, 1997; Škornik, 2000; Pipenbaher *et al.*, 2013a), comprising 205 species in 118 vegetation samples (relevés collected by authors of this study) that met the following criteria in both regions: (1) the sampled meadows occur on mesic eutric cambisols developed on carbonate flysch; (2) the traditional extensive management regime consists of mowing once a year. From 118 vegetation samples it is 67 relevés from Dinaric region (association *Danthonio-Scorzoneretum villosae*, alliance *Scorzonion villosae*) and 51 relevés from Central European region (association *Onobrychido-Brometum*, alliance *Mesobromion erecti*) (Kaligarič, 1997; Škornik, 2000). In each 25 m² quadrat, vascular plants were sampled using a seven-point cover-abundance scale according to Braun-Blanquet (1964). All plant species occurring only in one relevé were removed, to exclude casual occurrences from the analysis. These species were thus not included in dataset. Taxonomic nomenclature follows by Martinčič *et al.* (2007); syntaxonomic nomenclature follows by Kaligarič & Škornik (2002) and Kaligarič (1997).

Species richness and diversity

For species by relevé matrix we calculated two indices: Species richness and Simpson diversity index. Species richness was noted as the number of species recorded on each plot. For calculation Simpson diversity index we followed de Bello *et al.* (2006). For species richness we used present/absence data.

Selected plant functional traits

In choosing key traits, we followed different literature sources (Hodgson *et al.*, 1999; Kahmen *et al.*, 2002; Cornelissen *et al.*, 2003). We selected 14 traits for each species. Traits were chosen from our own database (protocol standardized by Cornelissen *et al.* (2003). Information on species traits was also taken from two existing trait databases BioFlor (Klotz *et al.*, 2002) and LEDA (Kleyer *et al.*, 2008). Species were characterized by basic traits as well as composite traits (such as C-S-R strategy). Owing to the variety of species sets, we focused on traits that were easy to measure. The traits selected were as follows: "life cycle", "growth form", "vegetation propagation", "storage organs", "spinescence", "hairiness", "height", "specific leaf area (SLA)", leaf dry matter content (LDMC)", "flowering start", "flowering length", "leaf persistence", "leaf anatomy" and "type of reproduction".

The list of traits with the description of classes in the matrix and the sources of information are presented in Table 1. Categorical traits were all transformed into binary variables, with one for each possible level of the factor (dummy variables). In this way the number of traits in the matrix increased from 14 to 40.

Tab. 1: Plant traits, recorded on 205 vascular plant species of Central European and Dinaric meadows. Scales of measurement were originally categorical (cat), continuous (cont) or binary (bin).

Tab. 1: Morfološko-funkcionalne poteze za 205 rastlinskih vrst srednjeevropskih in dinarskih travnikov. Podatki so bili v osnovi kategorični (cat), zvezni (cont) ali binarni (bin).

Traits	Abbreviation and description	Data source
Life cycle	LC_Annu = annual; LC_Bien = biennial; LC_Pere = perennial	Hegi, 1958, 1963, 1964, 1965, 1966, 1974, 1987; Martinčič <i>et al.</i> , 2007
Growth form	GF_Tuss = tussocks; GF_Rose = rosette; GF_le_st = leafy stem; GF_ro_le = rosette and leafy stem; GF_clim = climb	Hegi, 1958, 1963, 1964, 1965, 1966, 1974, 1987; Rothmaler, 1995; Martinčič <i>et al.</i> , 2007
Vegetation propagation	Veg_0 = absent; Stolon = stolons; Rhizom = rhizomes; Bulb_il = Bulb and Bulbil; Root_sho = root shoot; Tuber = bud with root and shoot tuber; Fragment = Fragmentation	BiolFlor (Klotz <i>et al.</i> , 2002); own measurements;
Storage organs	Sto_org = present; Sto_org0 = absent	own measurements
Spinescence	Spi_pres = present; Spine_0 = absent	Hegi, 1958, 1963, 1964, 1965, 1966, 1974, 1987; Martinčič <i>et al.</i> , 2007
Hairiness	Hair_low = low; Hair_hig = high; Hair_0 = absent	Hegi, 1958, 1963, 1964, 1965, 1966, 1974, 1987; Poldini, 1991; Martinčič <i>et al.</i> , 2007
Height	Plan_hig = cm	own measurements
Specific leaf area	SLA = mm ² /mg	LEDA database (Kleyer <i>et al.</i> , 2008); own measurements
Leaf dry matter content	LDMC = mg/g	LEDA database (Kleyer <i>et al.</i> , 2008); own measurements
Flowering start	Flo_star = months	Hegi, 1958, 1963, 1964, 1965, 1966, 1974, 1987; Poldini, 1991; Martinčič <i>et al.</i> , 2007
Flowering length	Flo_peri = months	Hegi, 1958, 1963, 1964, 1965; 1966, 1974, 1987; Poldini, 1991; Martinčič <i>et al.</i> , 2007
Leaf persistence	LP_1 = spring green; LP_2 = summer green; LP_3 = overwintering green; LP_4 = persistent green	BiolFlor (Klotz <i>et al.</i> , 2002); own measurements
Leaf anatomy	LA_1 = succulent; LA_2 = scleromorphic; LA_3 = mesomorphic; LA_4 = hygromorphic	BiolFlor (Klotz <i>et al.</i> , 2002); own measurements
Type of reproduction	Repr_1 = by seed/by spore; Repr_2 mostly by seed, rarely vegetatively; Repr_3 = by seed and vegetatively; Repr_4 = mostly vegetatively, rarely by seed; Repr_5 = vegetatively	BiolFlor (Klotz <i>et al.</i> , 2002)

Functional trait indices

To assess the functional trait composition we are using two approaches, which are increasingly used in functional composition (Diaz *et al.*, 2007). For that we combined the species by relevé matrix with the corresponding species by trait matrix.

First was calculated the community-weighted mean trait values (CWM) for each relevé as the average of trait values weighted by the relative abundance of each species (Garnier *et al.*, 2004; Lepš *et al.*, 2006; Lavorel *et al.*, 2008; Moretti *et al.*, 2009; Ricotta & Moretti, 2010, 2011). The metric is computed simply as:

$$CWM_{jk} = \sum_{i=1}^S p_{ik} \times x_{ij}$$

Where CWM_{jk} is the community-weighted mean value of trait j at site k , p_{ik} is the relative abundance of species i ($i = 1, 2 \dots S$) at site k ; and x_{ij} is the value of trait j for species i (Ricotta & Moretti, 2010). This operation results in a matrix of 40 new traits by 118 relevés (matrix CWM).

Secondly, the functional diversity index (FD hereafter) was proposed by Lepš *et al.* (2006) to measure the functional diversity index of single traits with the Rao

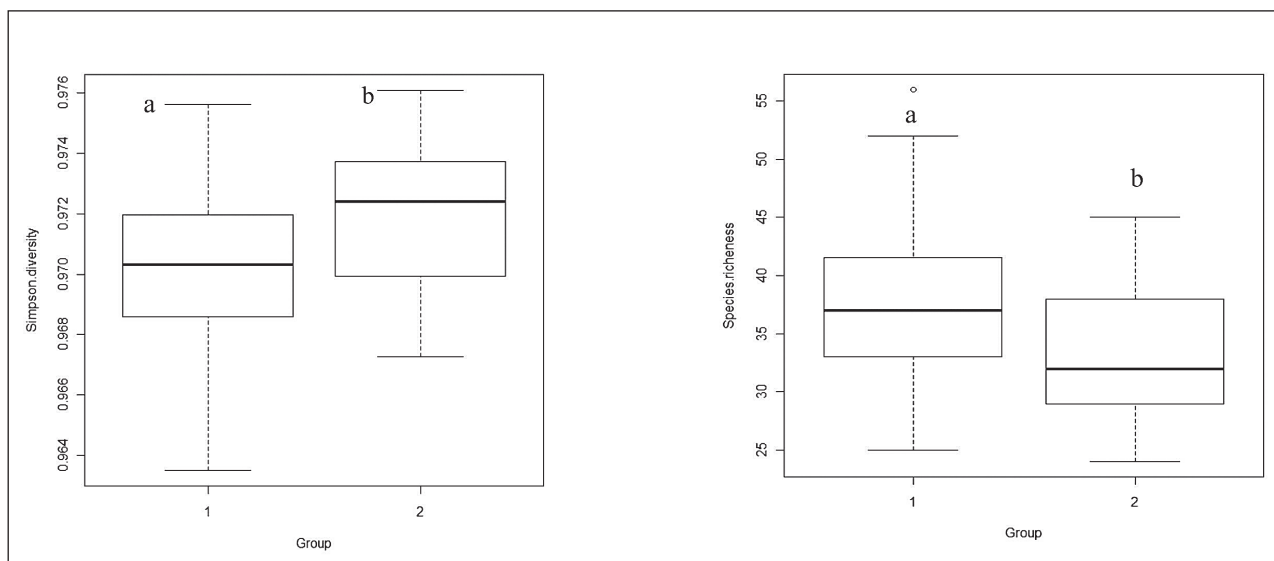


Fig 2: Simpson diversity (left) and species richness (right) from two neighbouring biogeographic regions. Group 1 is from Central European meadows and Group 2 is from Dinaric meadows. Different letters indicate significant differences among locations (Student's *t*-test, $p < 0.05$).

Sl. 2: Simpson diverzitetni indeks (levo) in vrstna pestrost (desno) iz dveh sosednjih biogeografskih območij. Skupina 1 so srednjeevropski travniki, Skupina 2 pa dinarski travniki. Črke prikazujejo statistično značilne razlike med območjema (Studentov *t*-test, $p < 0,05$).

(1982) quadratic diversity. If the proportion of *i*-th species in a community is p_i and the dissimilarity of species *i* and *j* is d_{ij} , the Rao coefficient takes the form:

$$FD = \sum_{ij} d_{ij} \times p_i \times p_j$$

S is the number of species in the community. Calculations were performed using an Excel macro (Lepš *et al.*, 2006). This operation results in a matrix of 14 FD indices for each trait by 118 relevés (matrix FD).

Data analysis

Changes in species composition (Species richness and Simpson diversity) between Central European and Dinaric meadows was analysed with a Student's *t*-test for independent samples (R Development Core Team, 2008) (Fig. 2).

To test differences in the CWM and FD indices between Central European and Dinaric meadows, we analysed data with a Student's *t*-test for independent samples (R Development Core Team, 2009) (Tab. 2). Type error I was controlled by Bonferonni correction of significance values (Rice, 1989).

The CWM and FD indices was further analysed by means of Principal Component Analysis (PCA) (Goodall, 1954). Only traits with significant differences in

their CWM and FD values between Central European and Dinaric meadows (Student's *t*-test) were used for PCA. Gradient length for the first PCA axis of ordination was in both cases lower than three, indicating that linear ordination methods are suitable for the analysis. The ordination method (PCA) and visualization of the result was carried out using the Canoco and CanoDraw programs (ter Braak & Šmilauer, 2002).

RESULTS

Across 118 plots (relevés) we recorded and included in dataset 205 vascular plant species with 68 species common to both regions, 83 species exclusive to the Dinaric and 54 exclusive to the Central European meadows. Student's *t*-test revealed strongly significant differences in both Species richness ($p < 0.001$) and Simpson diversity ($p < 0.001$) of meadows between regions. There was evidently higher species richness in Central European region (37 ± 6) in comparison to Dinaric region (33 ± 5). By contrast, Simpson species diversity was higher for Dinaric region (0.97 ± 0.003) than for the Central European region (0.96 ± 0.002). This indicates that Dinaric semi-dry meadows have lower species dominance and higher evenness than the Central European meadows.

In order to identify the predominant plant traits for studied vegetation, the (CWM) were analyzed with PCA. The ordination graph is presented in Figure 3, where only traits with significant differences in their CWM values ($n = 25$) between both type of meadows are shown.

Tab. 2: Results of Student's *t*-test for aggregated traits (CWM community-weighted means) values and functional trait diversity (FD) between Central European (*n* = 67) and Dinaric (NW Balkan) meadows (*n* = 51). CWM values for binary and categorical plant traits are in percentages.

Tab. 2: Rezultati Studentovega *t*-testa za CWM (srednje vrednosti morfološko-funkcionalne poteze) vrednosti in funkcionalne pestrosti (FD) med srednjeevropskimi (*n* = 67) in dinarskimi (S Balkan) travniki (*n* = 51). CWM vrednosti za binarne in kategorične morfološko-funkcionalne poteze so v procentih.

Plant functional traits	Abbreviation of specific plant	Abbreviation of specific plant	CWM			FD		
			Central European	Dinaric	<i>p</i>	Central European	Dinaric	<i>p</i>
Life cycle	LC	LC_Annu	5.09	3.83	/	0.181	0.102	***
		LC_Bien	4.81	1.51	***			
		LC_Pere	90.10	94.67	***			
Growth form	GF	GF_Tuss	30.74	26.10	***	0.665	0.626	***
		GF_Rose	8.56	12.43	***			
		GF_le_st	44.65	51.24	***			
		GF_ro_le	15.41	10.23	***			
		GF_clim	0.64	0	/			
Vegetation propagation	Veg	Veg_0	8.34	11.04	***	0.710	0.625	***
		Stolo	23.50	10.90	***			
		Rhizom	41.30	54.94	***			
		Bulb_il	0.33	0.19	/			
		Root_sho	5.34	5.46	/			
		Tuber	4.27	1.24	***			
Storage organs	Sto_Org	Sto_org	91.97	92.70	/	0.143	0.128	/
		Sto_org0	7.84	7.11	/			
Spinescence	Spine	Spi_pres	1.91	4.50	***	0.036	0.085	***
		Spine_0	98.09	95.50	***			
Hairiness	Hairness	Hair_low	33.62	42.18	***	0.658	0.635	***
		Hair_hig	35.06	23.42	***			
		Hair_0	31.33	34.40	/			
Plant height	Plant_he	Plan_hig = cm	38.01	36.84	/	0.182	0.176	/
Specific leaf area	SLA	SLA = mm ² /mg	17.38	14.54	***	0.153	0.118	***
Leaf dry matter content	LDMC	LDMC = mg/g	283.95	304.82	***	0.177	0,179	/
Phenology	Phenolog					0.445	0.474	***
		Flo_star = months	5.35	5.45	/			
		Flo_peri = months	3.66	3.44	***			
Leaf persistence	LP	LP_1	1.54	1.47	/	0.504	0.451	***
		LP_2	57.96	66.93	***			
		LP_3	1.41	1.04	/			
		LP_4	39.09	30.56	***			
Leaf anatomy	LA	LA_1	0	0.05	/	0.424	0.486	***
		LA_2	30.89	47.78	***			
		LA_3	68.73	52.33	***			
		LA_4	0.71	0.19	***			
Type of reproduction	Repr	Repr_1	34.00	35.40	/	0.674	0.628	***
		Repr_2	20.88	16.61	***			
		Repr_3	39.56	44.69	/			
		Repr_4	5.05	2.78	/			
		Repr_5	0.51	0.52	/			

*** *p* < 0.001

/ not significant

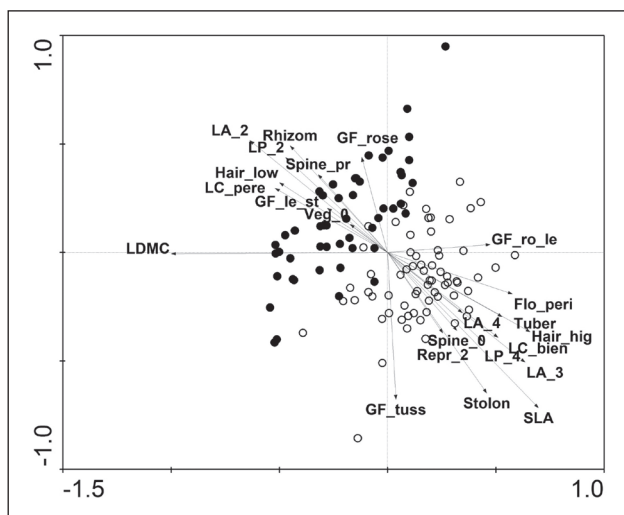


Fig. 3: PCA ordination diagram of matrix CWM with 118 relevés and 23 plant functional traits. Only traits ($n = 23$) with significant differences in their CWM values between Central European and Dinaric meadows (Student's t -test) are shown. Eigenvalues: axis 1 = 0.993, axis 2 = 0.006. Relevés divided in two groups according to region: ● – Dinaric, ○ – Central-European. Abbreviations of plant traits are explained in Table 1.

Sl. 3: PCA-ordinacija matrike CWM s 118 popisi in 23 morfološko-funkcionalnimi potezami. Prikazane so samo tiste morfološko-funkcionalne poteze ($n = 23$), pri katerih so statistično značilne razlike (Studentov t -test) med srednjeevropskimi in dinarskim travniki. Lastne vrednosti: os 1 = 0,993, os 2 = 0,006. Popisi so ločeni v dve skupini glede na območje: ● – dinarski travniki, ○ – srednjeevropski travniki. Razlage okrajšav za morfološko-funkcionalne poteze so v tabeli 1.

Relevés of both vegetation types are again clearly divided, which indicates that the Central European and Dinaric meadows differ in community trait composition. Analysis of plant life form and cycle showed that the Dinaric meadows had significantly higher CWM for perennials (LC_pere), whereas that of annuals (LC_annu) was significantly higher in the Central European meadows. The Dinaric meadows also had significantly higher CWM for spinescens present (Spin_pres), rosette and leafy stem growth form (GF_rose, GF_le_st), while the Central European meadows had more tussock (e.g. grasses) (GF_tuss) and hairy plants (Hair_low, Hair_hig). There were no significant differences in CWM for plant height (Plan_hei).

The two meadow communities differed in most foliar traits. Compared to Central European meadows, Dinaric meadows had significantly greater CWM values for LDMC and summer green and scleromorphic leaves (LP_2, LA_2) and consequently lower CWM values for SLA, persistent green (LP_4) and mesomorphic (LA_3) leaves. Analysis of flower phenology showed that the

onset of flowering was significantly earlier and the flowering period longer in the Central European meadows. Analysis of clonality revealed that non-clonal plants (Veg_0) and clonal plants with rhizomes (Rhizom) were proportionally higher in Dinaric meadows, while plants with stolons (Stolon) and tubers (Tuber) were more common in the Central European region (Tab. 2).

The Central European and Dinaric meadows differed significantly in FD (Fig. 4) of most analysed traits or trait groups (Tab. 2). FD for the flower phenology, spinescence and leaf anatomy was significantly greater in the Dinaric semi-dry meadows, when compared to the central European semi-dry meadows, while the diversity in SLA, life cycle, growth form, vegetation propagation, hairiness, leaf persistence and type of reproduction was significantly higher in the Central European sites. There were no significant differences in FD for storage organs, plant height and LDMC between the floristic regions ($p < 0.001$) (Tab. 2).

DISCUSSION

Semi-natural dry grasslands are the main remnants of the traditional agricultural landscape in Europe, and they are among the most species-rich habitats in terms of the number of plant species they support per unit area (Zobel *et al.*, 1996; Wallis DeVries *et al.*, 2002; Kaligarič *et al.*, 2006; Purschke *et al.*, 2012). Therefore, many studies on plant biodiversity have been concerned with these plant communities (Pärtel & Zobel, 1999; Eriksson *et al.*, 2002; Johansson *et al.*, 2011; Vitasović-Kosić *et al.*, 2011; Habel *et al.*, 2013; Pipenbaher *et al.*, 2013a, 2013b).

The high species richness of the Slovenian Central European and Dinaric semi-dry meadows has already been confirmed by previous studies (Kaligarič *et al.*, 2006; Škornik *et al.*, 2010; Pipenbaher *et al.*, 2013a). This study supports these findings. Additionally, we found greater species richness per plot for the Central European meadow community. Focusing on species richness, could, however mask important differences among species in abundance (or evenness), and since the Central European meadow community has higher species dominance and lower evenness (*Briza media*, *Bromus erectus*, *Salvia pratensis*, etc.) it is less diverse than the Dinaric, in which several different species have a similar abundance.

In most studies linking biodiversity to ecosystem functioning, species richness has been used as the main index (Lepš, 2004; Schmidt & Hector, 2004). However, since it is generally understood that species make a difference in the functioning of ecosystems because of their differences in traits, measures of community trait composition and functional diversity tend to correlate more strongly than those of traditional species-diversity with ecosystem functions (Petchey & Gaston, 2006; Ricotta & Moretti, 2010, 2011). According to our results, meadow

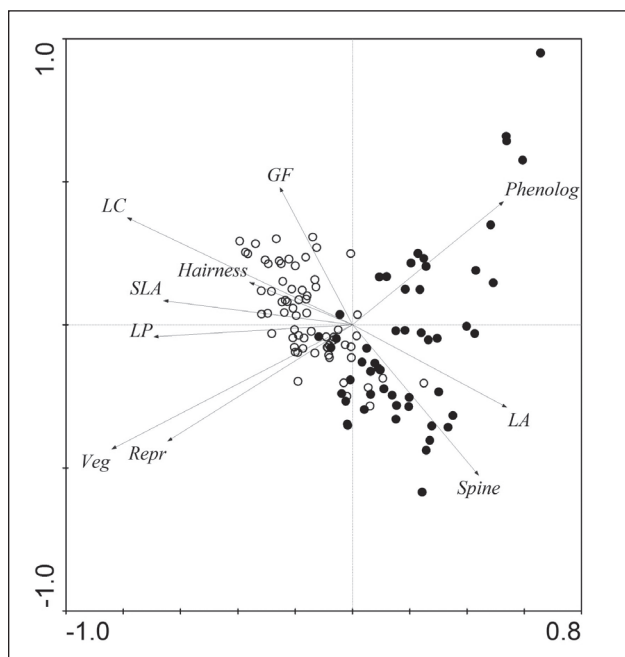


Fig. 4: PCA ordination diagram of Functional diversity matrix with 118 relevés and 10 indices of functional diversity. Only traits ($n = 10$) with significant differences in their FD values between Central European and Dinaric meadows (Student's t -test) are shown. Eigenvalues: axis 1 = 0.412, axis 2 = 0.144. Relevés divided in two groups according to region: ● – Dinaric; ○ – Central-European. Abbreviations of plant traits are explained in Table 1.

Sl. 4: PCA-ordinacija matrice funkcionalne pestrosti s 118 popisi in 10 indeksi funkcionalne pestrosti. Prikazane so samo tiste morfološko-funkcionalne poteze ($n = 23$), pri katerih so statistično značilne razlike v funkcionalni pestrosti (Studentov t -test) med srednjeevropskimi in dinarskim travniki. Lastne vrednosti: os 1 = 0,412, os 2 = 0,144. Popisi so ločeni v dve skupini glede na območje: ● – dinarski travniki; ○ – srednjeevropski travniki. Razlage okrajšav za morfološko-funkcionalne poteze so v tabeli 1.

communities from separate regions differed markedly in community trait composition at least for the set of traits studied. This is remarkable, given that meadows in both regions occur on similar substrate types and experience similar management practices.

While some authors (Lavorel *et al.*, 2008) consider CWM to be one of the indices for "functional diversity", most authors do not (e.g., Mouchet *et al.*, 2010; Schleuter *et al.*, 2010). Whereas the term "diversity" is related to the concept of variety, variability, etc., CWM is rather a measure of central tendency, like the mean or the median (Ricotta & Moretti, 2011). In our study, differences in CWM between communities are mainly associated with dominant and subdominant species

with particular traits. In the Central European meadows where we found lower species diversity tussock species are dominant, whereas in the Dinaric region these meadows are dominated by species with rosettes and leafy stems. In addition, our results confirm the suggestion of Pipenbahr *et al.* (2013a) about the stronger effect of eutrophication and local disturbance on the Central European semi-dry meadows. These plant communities are distinguished not only by higher SLA and LDMC (Pipenbahr *et al.*, 2013a) but also by higher numbers of species with mesomorphic leaves and annuals. It has been shown in other studies that annuals (therophytes) are promoted by intensification of land use (Bullock *et al.*, 1994; Škornik *et al.*, 2010), as they are more tolerant of disturbance, owing to their fast growth rates and early, prolific seed set (Grime, 1974). A similar interpretation could also apply to reproductive strategies. In our study, early flowering also appears to be promoted in Central European meadows, since annuals (*Rhinanthus aristatus*, *Veronica arvensis*,) tend to flower early in the vegetation season.

While differences in CWM between communities are mainly associated with dominant and subdominant species with particular traits, differences in functional diversity are related to differences in the number of niches available along the ecological gradients (Ricotta & Moretti, 2011). Therefore, along gradients, environmental filters may operate with different intensities and assemble different plant communities from the available species pool (Grime, 2006; Pausas & Verdú, 2010). According to our results, the strong floristic distinctiveness of the Central European and Dinaric regions (Pipenbahr *et al.*, 2013a) is also accompanied by strong functional diversification. For most traits, the diversity was greater in the Central European meadows. In these meadows functional variation in growth form, vegetation propagation, SLA and leaf persistence, provide evidence for limiting similarity probably owing to stronger disturbance impact in this community than in the Dinaric meadows, which is consistent also with our explanation of the observed differences among regions comparing the CWM. Disturbance is known as the most potent force creating and sustaining trait divergence (Grime, 2006), although this declines at high disturbance frequencies (Grime, 1974).

The differences in functional diversity between regions suggest that communities which appear physiognomically similar (analysis of plant height confirmed a similar community vertical structure in the two meadow types) may be markedly different in the number of available niches. The strong evidence for divergence in functional composition between meadows from different regions suggests that functional trait composition is unlikely to be a deterministic function of similar environmental conditions (e.g., substrate type) and land use in geographically disjunct communities. Meadows from the Central European region had a functional trait

composition typical of more ruderal communities, which may reflect the higher density of ruderal seed resources in this region, arising from increased anthropogenic disturbance. This may have important implications for conservation management of these meadows. For example, given that traits characteristic of ruderal strategists were more common in the Central European region, maintenance of species diversity in these meadows is likely to be much more dependent on the application of a regular disturbance regime, such as mowing, than for the Dinaric region. Moreover, functional composition is

very likely a key factor determining the susceptibility of a grassland community to a community changes, very often in the direction of lower conservation value for the grasslands. Traditional management practices and land abandonment in general have occurred almost everywhere in the montane belt of Central and South-Eastern Europe, but within the Balkan range, meadows are still common and currently not yet endangered, as the Central European ones certainly are (Kaligarič & Škornik, 2002; Molnár *et al.*, 2008; Vitasović-Kosić *et al.*, 2011; Pipenbahr *et al.*, 2013a).

PRIMERJAVA FLORISTIČNE IN FUNKCIONALNE PESTROSTI MED TRAVNIKI IZ DVEH SOSEDNIH BIOGEOGRAFSKIH OBMOČIJ

Nataša PIPENBAHER

Oddelek za biologijo, Fakulteta za naravoslovje in matematiko, Univerza v Mariboru, SI-2000 Maribor, Koroška cesta 160
E-mail: natasa.pipenbahr@uni-mb.si

Norman W.H. MASON

Landcare Research, Private Bag 3127, Hamilton 3240, Nova Zelandija

Sonja ŠKORNIK

Oddelek za biologijo, Fakulteta za naravoslovje in matematiko, Univerza v Mariboru, SI-2000 Maribor, Koroška cesta 160

POVZETEK

V pričujočem članku smo proučevali floristično in funkcionalno pestrost sekundarnih travnišč, in sicer na stičnem območju dveh biogeografskih regij – srednjeevropske in dinarske (S Balkanske). Primerjali smo dva tipa fiziognomsko podobnih travnišč iz asociacij *Danthonio-Scorzoneretum* (dinarski travniki) in *Onobrychido vicifoliae-Brometum* (srednjeevropski travniki). Travniki so se v obeh regijah razvila v podobnih okoljskih razmerah (tip tal, nadmorska višina in količina padavin) in imajo podobno rabo. To so polsuhi travniki, ki so se razvili na naravno rodovitnih rjavih pokarbonatnih tleh. Primerjali smo ju glede na vrstno pestrost, srednjo vrednost funkcionalnih potez (angl. community-weighted mean, CWM) in funkcionalno pestrost (angl. functional diversity, FD). Medtem ko je CWM merjena, kot povprečna vrednost posamezne morfološko-funkcionalne poteze (MFP), predstavlja indeks funkcionalne pestrosti povezavo z raznolikostjo posamezne MFP. Baza podatkov je obsegala 118 fitocenoloških popisov omenjenih asociacij. V popisnih ploskvah smo zabeležili skupaj 205 različnih rastlinskih vrst. Ugotovili smo, da imajo srednjeevropski travniki v povprečju večje število vrst na popisno ploskev kot dinarski. Ker pa imajo srednjeevropski travniki več dominantnih vrst in manjšo enakomernost številčnosti osebkov posamezne vrste, je njihova vrstna pestrost nižja v primerjavi z dinarskimi travniki. Srednjeevropski polsuhi travniki vsebujejo več enoletnic, večje število rastlin z višjimi vrednostmi za specifično listno površino (SLA) in nižjimi vsebnostmi suhe snovi lista (LDMC). Na podlagi teh rezultatov lahko sklepamo, da so ti travniki bolj podvrženi motnjam kot dinarski travniki. Našli smo tudi velike razlike v funkcionalni pestrosti med obema tipoma travnikov. Za večino MFP je raznolikost večja na srednjeevropskih travnikih. Ti rezultati potrjujejo, da so ti travniki močnejše izpostavljeni motnjam. Kot ugotavljajo avtorji različnih študij, je motnja med najpomembnejšimi dejavniki, ki ustvarjajo funkcionalno raznolikost v rastlinskih skupnostih. Naše ugotovitve so pomembne in uporabne tudi pri načrtovanju naravovarstvenih strategij za ohranjanje teh travnišč. Glede na to, da motnja tako odločilno vpliva na vrstno sestavo srednjeevropskih travnikov, lahko sklepamo, da je vzdrževanje redne košnje le-teh pomembnejše kot v primeru dinarskih polsuhih travnikov. Zaključimo lahko, da je funkcionalna sestava med ključnimi dejavniki, ki odražajo občutljivost vegetacije na spremembe v okolju, posledica katerih je pogosto razvoj vegetacije nižje naravovarstvene vrednosti.

Ključne besede: morfološko-funkcionalne poteze, polsuhi travniki, srednjeevropski travniki, dinarski travniki

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