Scale-dependent species diversity in a semi-dry basiphilous grassland (*Bromion erecti*) of Upper Franconia (Germany)

Dominic Hopp[1] **_& Jürgen Dengler_**[*,2,3]

1) Hoffmann-von-Fallersleben-Str. 38, 95445 Bayreuth, GERMANY; d-hopp@gmx.de

2) Plant Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, GERMANY; juergen.dengler@uni-bayreuth.de

3) Synthesis Centre (sDiv), German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, GERMANY

*) Corresponding author

Abstract: We analysed a semi-dry basiphilous grassland near Bayreuth, Upper Franconia, Germany with nested-plot sampling on areas from 0.0001 to 100 m². The stand clearly belongs to the order *Brachypodietalia pinnati* of the class *Festuco-Brometea*. Within this order, the affinity to the subatlantic alliance *Bromion erecti* was higher than to the subcontinental *Cirsio-Brachypodion pinnati*, while the assignment to any of the current *Bromion erecti* associations remained unclear due to a lack of an up-to-date syntaxonomic revision of the dry grasslands in Germany. The species richness for the different grain sizes was always above those for *Brachypodietalia pinnati* communities in NE Germany, but below the extremely rich stands in the White Carpathians or Transylvania. The species-area relationships also had a very low slope (e.g. z = 0.18 for all species combined), pointing to an unusually high homogeneity of the stand or rather a limited regional species pool. The richness values in Bayreuth at smallest grain sizes reached about ¾ of the known maxima in European grasslands, but only about ½ for the areas from 1 m² upwards. When comparing our richness data with data from the literature, we came across one previously overlooked world record, namely 7 vascular plant species on 1 cm² in two Ukrainian grasslands (the old record was 5 species). In general, our small dataset is a valuable contribution to the envisaged synthesis of scale-dependent diversity patterns in grasslands across the Palaearctic.

Keywords: alpha diversity; Bavaria; beta diversity; biodiversity; *Brachypodietalia pinnati*; *Festuco-Brometea*; species-area relationship (SAR); species pool; species richness; syntaxonomy; world record

Nomenclature: GermanSL (Jansen & Dengler 2008), i.e. Wisskirchen & Haeupler (1998) for vascular plants, Koperski et al. (2000) for bryophytes and Scholz (2000) for lichens.

Introduction

Temperate grasslands hold the world records in vascular plant species richness for grain sizes smaller than 100 m² (Wilson et al. 2012; Chytrý et al. 2015). The majority of these extraordinarily rich grasslands are semi-dry basiphilous meadows in Europe with a long history of low-intensity land use (mostly mowing). While all the named parameters seem to play some role in the establishment and maintenance of extraordinary small-scale species richness, we are far from understanding what the decisive factors are and how they interact (see discussions in Dengler et al. 2014; Michalcová et al. 2014; Roleček et al. 2014). While semi-dry basiphilous grasslands (order *Brachypodietalia pinnati* = *Brometalia erecti* nom. ambig. propos.) are typically among the richest vegetation types in terms of vascular plants in many regions of Europe (Hobohm 1998; Berg et al. 2001; Dengler 2005), their richness varies greatly between regions, and it is poorly understood why. For understanding the scale-dependence of drivers of plant diversity, Dengler (2009b) has proposed a sampling scheme that allows standardised sampling of such data in different vegetation types and biogeographic regions to facilitate broad-scale comparisons. This approach has meanwhile been applied in (dry) grasslands in various regions throughout the Palaearctic, e.g. in Estonia (Dengler & Boch 2008), NE Germany (Dengler et al. 2004), and on the annual EDGG Research Expeditions/Field Workshops since 2009 (see Biurrun et al. 2014). The detailed analysis of the data from the first EDGG Research Expedition to Transylvanian yielded very interesting insights into scale-dependencies of grassland diversity (Turtureanu et al. 2014). As a contribution to a future European synthesis we report here the data from a semi-dry basiphilous grassland in Upper Franconia, Germany.

Study area

The sampling took place on the steep SSW-facing slope towards the river Roter Main (former river cliff; 49.9095° N, 11.6179° E; precision: 10 m; 388 m a.s.l.) near Schlehenmühle, Bayreuth, Upper Franconia, Bavaria, Germany, on 13 May 2015. The vegetation of the slope is a semi-dry basiphilous grassland while below the slope there is a wet meadow and the plateau above the slope is used as arable field. The slope itself is mown once a year late in summer and not fertilized. The bedrock is a sandstone of the Keuper, partly with dolomitic arkose. The climate of Bayreuth is temperate -subcontinental with 8.2 °C mean annual temperature and 654 mm mean annual precipitation (Hijmans et al. 2005).

Methods

One square plot of 100 m² was delimited in a homogenous part of the vegetation, following the modified version of Dengler (2009b) by Turtureanu et al. (2014). We recorded complete species composition (vascular plants, bryophytes, lichens) with the any-part system (see Dengler 2008) for two nested-plot series in the NW and SE corner for areas of 0.0001, 0.001, 0.01, 0.1, 1 and 10 m² as well as for the whole 100 m². Species cover (in %) was estimated for the two 10-m² plots, where also environmental parameters were assessed and a mixed soil sample of the uppermost 10 cm drawn for soil analyses (pH in water, C/N).

The species composition was compared with lists of diagnostic species provided from large German overviews (Oberdorfer 1993, Pott 1995, Schubert et al. 2001, Berg et al. 2001, 2004) to allow a placement in the syntaxonomic system. The species richness data for the seven different grain sizes were compared to literature data and used to construct a species-area relationship, as power-law function in the linearized version ($\log_{10} S \sim \log_{10} A$, where S is the species richness and A the area in m²; Dengler 2009a). The vegetation-plot data are stored in and available from the Database Species-Area Relationships in Palaearctic Grasslands (GIVD ID EU-00-003; Dengler et al. 2012b).

Results and discussion

Syntaxonomy

Figure 1 shows the structure of the stand and some typical species. The assignment of the stand to the class *Festuco-Brometea* and the order *Brachypodietalia pinnati* (= *Brometalia erecti* nom. ambig. propos.) is straightforward based on a large number of widely accepted diagnostic species (e.g. Mucina et al. 1993; Berg et al. 2004) (Table 1). At the alliance level the decision between the two

Fig. 1: Stand of the analysed *Bromion erecti* near Schlehenmühle, Bayreuth with some typical species. From left to right: *Ranunculus bulbosus* (Bulbous Buttercup), *Sanguisorba minor* (Salad Burnet), *Plantago media* (Hoary Plantain), *Ajuga genevensis* (Upright Bugle) and *Silene viscaria* (Sticky Catchfly) (Photos: J. Dengler, 2015/05).

Table 1.: Vegetation table of the two 10-m² plots in the NW and SE corner of the 100-m² biodiversity plot. Performance of species is given in percentage cover. Species are grouped into the following functional-taxonomic groups: VW = vascular plant, wood; VG = vascular plant, graminoid, VL = vascular plant, legume, VF = vascular plant, other forb, B = bryophyte, L = lichen. Character and differential species of the class and order are indicated with C and D, respectively; in case of joint differential species with other classes, the other class is indicated (TG = *Trifolio-Geranietea sanguinei*, MA = *Molinio-Arrhenatheretea*, KC = *Koelerio-Corynephoretea*, Sm = *Stellarietea mediae*). In the second column those species are highlighted that are considered as differential for *Bromion erecti* (Be) and *Cirsio-Brachypodion pinnati* (C-B) by Dengler (2003) (1) and Willner et al. (2014) (2).

Subplot	NW	SE
Aspect (°)	**205**	**200**
Slope (°)	**30**	**22**
Microrelief (cm)	**3**	**12**
Soil depth (cm)	**27**	**26**
pH (H2O)	**6.98**	**7.68**
C content (%)	**5.6**	**7.0**
C/N ratio	**11.0**	**12.6**
Cover vegetation (%)	**98**	**96**
Cover herb layer (%)	**90**	**80**
Cover cryptogam layer (%)	**25**	**65**
Cover litter (%)	**25**	**30**
Species richness (total)	**63**	**48**
Species richness (vascular plants)	**55**	**40**
Species richness (non-vascular plants)	**8**	**8**

				NW	SE
Festuco-Brometea					
C	Be (1)	VG	*Bromus erectus*	40	40
C	Be (2)	VF	*Sanguisorba minor*	3	2
C	C-B (1,2)	VL	*Medicago falcata*	0.5	0.2
C		B	*Thuidium abietinum*	.	20
C		B	*Rhytidium rugosum*	.	0.01
D with TG	C-B (1,2)	VF	*Fragaria viridis*	10	1.5
D with TG		VG	*Poa angustifolia*	3	0.2
D with KC + TG		VF	*Galium verum*	1	1
D mit KC		VF	*Potentilla tabernaemontani*	0.5	0.5
D with TG		VF	*Knautia arvensis*	0.2	0.5
D with KC + TG		VL	*Ononis repens*	.	3
D with TG		B	*Fissidens dubius*	1	.
D mit KC		VF	*Taraxacum sect. Erythrosperma*	0.2	.
D with Sm		B	*Barbula unguiculata*	0.1	.
D with KC + TG		VF	*Silene viscaria*	0.01	.
Brachypodietalia pinnati					
C		B	*Thuidium delicatulum*	2.5	25
C	C-B (1)	VL	*Trifolium montanum*	15	3
C (also C class)		B	*Homalothecium lutescens*	10	7
C (also C class)		VG	*Carex caryophyllea*	6	0.5
C		VF	*Cirsium acaule*	1	5
C		VF	*Leontodon hispidus subsp. hispidus*	1	5
C		VL	*Lotus corniculatus*	1	3
C	Be (2)	VF	*Thymus pulegioides*	2	1
C		VF	*Plantago media*	0.02	2
C	Be (1)	VF	*Ranunculus bulbosus*	0.1	0.5
C (also C class)	Be (2)	VL	*Anthyllis vulneraria subsp. pseudovulneraria*	.	1
C	Be (2)	VF	*Prunella grandiflora*	0.5	.
C		VF	*Leontodon hispidus subsp. danubialis*	0.02	.
C		VF	*Polygala comosa*	0.01	.
D		VG	*Carex flacca*	5	15
D		VF	*Primula veris*	12	3
D		VG	*Brachypodium pinnatum*	10	2
D		VF	*Hieracium pilosella*	0.3	8
D		VG	*Briza media*	5	2
D		VF	*Plantago lanceolata*	2	3
D		B	*Plagiomnium affine*	1	2
D (also C class)		VL	*Medicago lupulina*	0.1	0.5
D		B	*Scleropodium purum*	1	.
D		VG	*Helictotrichon pubescens*	0.5	.
D		VF	*Agrimonia eupatoria*	0.1	.
D		VF	*Linum catharticum*	.	0.1
D		VF	*Leucanthemum ircutianum*	0.01	.
D		VG	*Luzula campestris*	0.01	.

Companion species			NW	SE
	B	*Calliergonella cuspidata*	10	15
	VF	*Viola hirta*	3	0.5
	VF	*Centaurea jacea*	2	0.1
	VG	*Arrhenaterum elatius*	0.5	1
	VF	*Genista tinctoria*	0.5	0.5
	VG	*Dactylis glomerata*	0.5	0.1
	VF	*Taraxacum sect. Ruderalia*	0.3	0.3
C-B (2)	VF	*Veronica chamaedrys*	0.5	0.1
	VF	*Hypericum perforatum*	0.2	0.1
C-B (2)	VL	*Vicia cracca*	0.02	0.2
	VF	*Silene nutans*	0.1	0.1
	B	*Brachythecium rutabulum*	0.1	0.01
	VF	*Convolvulus arvensis*	0.05	0.05
C-B (2)	VF	*Rhinanthus minor*	0.01	0.02
	VG	*Bromus hordeaceus*	0.5	.
	VF	*Galium x pomeranicum*	0.5	.
	VG	*Anthoxanthum odoratum*	0.3	.
	VL	*Vicia angustifolia*	0.3	.
	VG	*Festuca pratensis*	0.2	.
	VF	*Rumex acetosa*	0.2	.
	VW	*Crataegus monogyna (juv.)*	.	0.1
	VF	*Galium album*	0.1	.
	VF	*Achillea millefolium agg.*	0.02	.
	VW	*Pyrus pyraster (juv.)*	.	0.02
	VF	*Tragopogon pratensis subsp. pratensis*	0.02	.
	VG	*Cf. Agrostis sp.*	0.01	.
	L	*Cladonia furcata*	.	0.001
	VF	*Veronica arvensis*	0.001	.

chorologically possible options, the subatlantic *Bromion erecti* and the subcontinental *Cirsio-Brachypodion pinnati*, is less clear. Taking the differential species elaborated by the two studies that analysed *Brachypodietalia pinnati* communities from a larger geographic area (Dengler 2003; Willner et al. 2013), it appears that in our stands there is a similar number of differential species of the *Bromion erecti* (e.g. *Bromus erectus*, *Thymus pulegiodes*, *Prunella grandiflora*; seven in total) as those of the *Cirsio-Brachypodion pinnati* (e.g. *Trifolium montanum*, *Fragaria viridis*, *Medicago falcata*, six in total), but the cover values of the first group is clearly higher (Table 1). Therefore, we tentatively assign our stands to the subatlantic *Bromion erecti*.

Within this alliance, however, a clear placement into an accepted association is currently not possible. Syntaxonomic overviews for Germany tend to recognise three associations within this alliance, ignoring those with high cover of *Sesleria albicans* and other dealpine species (e.g. Oberdorfer 1993; Pott 1995; Schubert et al. 2001 – names not checked nomenclaturally): *Onobrychido-Brometum* T. Müller 1966 (mown), *Gentiano-Koelerietum pyramidatae* Knapp ex Bornkamm 1960 (grazed), and *Viscario-Avenetum* Oberd. 1949 (loamy, slightly acidic soils, dominated by *Helictotrichon pratense*). The dominance of *Bromus erectus* and the fact that the site is mown would support the placement into the *Onobrychido-Brometum*, but we did not find any of the more specific taxa, such as *Onobrychis viciifolia*, *Orchis militaris* or *Gymnadenia conopsea*. *Potentilla tabernaemontani*, *Carex caryophyllea* and *Cirsium acaule* would support the assignment to the *Gentiano-Koelerietum*, but *Koeleria pyramidata* itself occurred only rarely on the 100-m² plot. Finally, *Silene viscaria* is a differential species for the *Viscario-Avenetum*. This points to the long recognised need for a modern syntaxonomic revision of the dry grasslands in Germany based on a comprehensive vegetation-plot database of the whole country and followed by statistical elaboration of diagnostic species (Jandt et al. 2013).

Species richness

Both 1-cm² plots already comprised seven species (four vascular plants, three non-vascular plants). For the larger plot sizes, the plot series in the NW corner was systematically richer than that in the SE corner (+ 30-86%), reaching 51 species on 1 m² and 63 species on 10 m². The total richness on 100 m² was 77 species (Table 2). The contribution of non-vascular plants to total richness continuously decreased from 43% at 1 cm² to 16% at 100 m².

Compared to the documented maxima of vascular plant species richness in European grasslands, the values in our NW corner reach about ¾ for the scales from 10-1000 cm², but only around ½ for the smallest (1 cm²) and the three biggest grain sizes (Table 2). This might be a matter of chance for the 1 cm² because richness values become increasingly valuable towards smaller scales (Dengler 2006), and two replicates are certainly not enough to find the local maximum of the slope at the Schlehenmühle. However, for the grain sizes from 1 m² upwards, there should be much less variability, thus we should have a rather representative value, which is not too far below the maximum of Upper Franconia. While our 55 species on 10 m² are much less than found in Transylvania (98 maximum, but also an average of 70 species in the *Brachypodietalia pinnati* stands: Dengler et al. 2012a) or the White Carpathians (maximum of 88 species already on 4 m²: Chytrý et al. 2015), but on the other hand they clearly exceed the values found in similar communities in NE Germany, where the maximum in nearly 200 plots of that order was 51 vascular plant species on 10 m², with an average of only 29 (unpublished data underlying Dengler 2005). For grain sizes from 1 m² upwards the plot-scale richness values seem to parallel the regional species pools (Transylvania/White Carpathians > Bavaria > NE Germany). By contrast, richness values at the smallest grain sizes seem to be largely independent from the size of regional species pools.

Table 2: Maximum richness values found in this study compared to the documented maximum richness values in European grasslands. BT = Bayreuth; EU = Europe; * = this value is currently the highest value recorded in any vegetation type worldwide; ** = this is a new global maximum that was not documented in the "world record papers" by Wilson et al. (2012) and Chytrý et al. (2015) and not highlighted in the original source (7 species instead of 5 species); the same value was found in two plots of different localities and associations. All mentioned alliances belong to the order *Brachypodietalia pinnati* (semi-dry basiphilous grasslands) except the *Stipion lessingianae* (*Festucetalia valesiacae*).

Plot size [m²]	BT all species	BT vascular plants	EU vascular plants	Ratio BT / EU	Country	Alliance	Reference
0.0001	7	4	7	57%	Ukraine**	*Agrostio-Avenulion schelliana* & *Stipion lessingianae*	Kuzemko et al. (2014)
0.001	12	9	12	75%	Sweden*	*Filipendulo-Helictotrichion*	van der Maarel & Sykes (1993)
0.01	26	19	25	76%	Estonia*	*Filipendulo-Helictotrichion*	Kull & Zobel (1991)
0.1	38	31	43	72%	Romania*	*Cirsio-Brachypodion*	Dengler et al. (2012a)
1	51	43	82	52%	Czechia	*Cirsio-Brachypodion*	Chytrý et al. (2015)
10	63	55	98	56%	Romania*	*Cirsio-Brachypodion*	Dengler et al. (2012a)
100	77	65	133	49%	Czechia	*Cirsio-Brachypodion*	Chytrý et al. (2015)

Species-area relationships

The species-area relationships could be well described by power laws as can be seen from the relatively good fit and lack of systematic deviations for the three linear regressions in the log-log space (Fig. 1). The slopes (*z*-

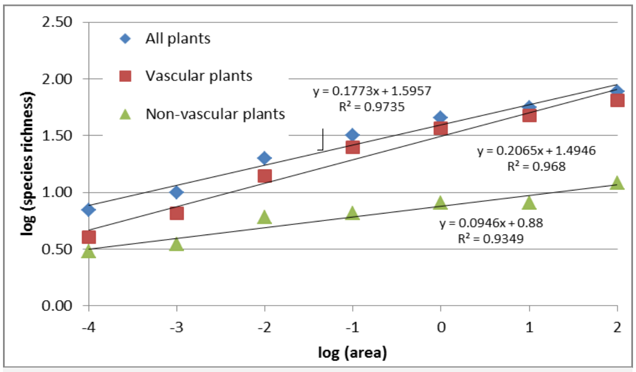

Fig. 1: Species-area relationships in double-log representation for the averaged richness values of both corners together with linear regression functions (equivalent to power laws).

Low *z*-values indicate, from the vegetation perspective, a homogeneous stand and low patchiness. From the species point-of-view they stand for low species turnover, which in abiotically heterogeneous patches would indicate wide niche breadths and in homogenous environments good dispersal capabilities – compared to species groups with higher *z*-values in the same situation. We assume that the second reason is decisive as bryophytes with their very light spores can reach potential sites much more easily than vascular plants with their diaspores being several orders of magnitude heavier. Lower *z*-values for bryophytes vs. vascular plants have been consistently reported both at plot scale (e.g. Dengler & Allers 2006) and at biogeographic scales (Patiño et al. 2014).

Typically, z-values in dry grasslands for total species composition are in the range of 0.17–0.34 (0.18–0.25 for community means: Dengler 2005; Dengler & Boch 2008; Pedashenko et al. 2013) and only exceptionally reach higher values (0.20–0.40 or 0.26–0.29 for community means in Transylvania: Dengler et al. 2012a). However, our observed value of only z = 0.18 is at the lowest end of what was observed elsewhere and can be seen as an expression of particular low beta-diversity (for possible explanations, see under Species richness).

Acknowledgements

We thank Pedro Gerstberger for pointing us to this nice dry grassland and to Marga Wartinger for carrying out the soil analyses.

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Cirsium acaule . Photo: J. Dengler

Campanula patula. Photo: J. Dengler

Scabiosa columbaria. Photo: J. Dengler

Pulsatilla vulgaris. Photo: J. Dengler