Research paper

Scale-dependent plant diversity in Palaearctic grasslands: a comparative overview

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Abstract: Here we present an extensive overview of plant diversity values in Palaearctic grasslands for seven standard grain sizes from 0.0001 to 100 m². The data originate from 20 studies, including the Field Workshops of the Eurasian Dry Grassland Group (EDGG), ranging geographically from Spain in the west to Siberia in the east, from Sicily in the south to Estonia in the north and from the sea coast up to 3100 m a.s.l. The majority of data is from dry grasslands (*Festuco-Brometea*, *Koelerio-Corynephoretea*, *Cleistogenetea squarrosae*), but there are also some mesic, wet, saline, acidic, alpine and Mediterranean grasslands included. Among others, we compiled data from 1795 1-m², 1109 10-m² and 338 100-m² plots. In all cases we present mean, minimum and maximum richness for the seven grain sizes, plus, in cases where also terricolous bryophytes and lichens had been recorded, the same values for total "plant" species richness, non-vascular plant species richness and fraction of non-vascular plants. The maximum richness values were 82, 101 and 134 for all "plants", and 79, 98 and 127 vascular plants at grain sizes of 1 m², 10 m² and 100 m², respectively (all in Transylvania, Romania). Our overview comprises new, hitherto unpublished world records of vascular plant species richness at the scales of 0.0001 m² (9) and 0.001 m² (19, both shoot presence), from meso-xeric, basiphilous grasslands in Navarre, Spain, which is much higher than the previously known maxima. The highest values of non-vascular plant richness at 1 m², 10 m² and 100 m², respectively, were 49, 64 and 64, respectively (all in *Sedo-Scleranthenea* communities of Öland, Sweden, and Saaremaa, Estonia). In general, the dry, alpine and Mediterranean grasslands were much richer than the studied mesic, wet or saline grasslands at any spatial scale. The presented set of mean, minimum and maximum values and their metadata is publically available and will be continuously updated. These data can serve as a reference of "normal" richness, both in fundamental and applied research. To facilitate the application, we provide an easy formula based on the power-law species-area relationship that allows the estimation of richness values at intermediate grain sizes not included in our dataset. In conclusion, our data emphasise the role of Palaearctic grasslands as global hotspot of small-scale vascular plant diversity, while at the same time highlighting that in some grassland types also the bryophyte and lichen diversity can be extraordinarily high.

Keywords: alpha diversity; biodiversity; bryophyte; Europe; lichen; Palaearctic biogeographic realm; scale dependence; semi-natural grassland; species-area relationship (SAR); species richness; steppe; world record.

Abbreviations: EDGG = Eurasian Dry Grassland Group; SAR = species-area relationship.

Introduction

Palaearctic semi-natural grasslands are known to host an extraordinarily high plant diversity (Kull & Zobel 1991; Hobohm 1998; Janišová et al. 2011; Michalcová et al. 2014). Some years ago, they were highlighted as world record holders for vascular plant species richness for nearly all grain sizes below 100 m² (Wilson et al. 2012). The call in this paper to beat the given maxima was to our knowledge so far not met by data from any other vegetation type worldwide, while a few slightly higher values have been reported from other Palaearctic semi-natural grasslands meanwhile (Chytrý et al. 2015; Kuzemko et al. 2016).

The reasons for this globally outstanding small-scale diversity are still under debate (Hájková et al. 2011; Merunková et al. 2012; Dengler et al. 2014; Michalcová et al. 2014; Roleček et al. 2014). However, basing the arguments only on single observations of maxima, as largely done in these papers, can provide circumstantial evidence for probable causes of extreme richness, but no statistical support for the assumed reasons. For this purpose, we would need data not only from the richest grassland types in one or a few places, but from many different regions and grassland types. Moreover, maxima alone are problematic because they essentially depend on sampling intensity, i.e. the more plots are analysed the more likely it is that one will find extreme richness values – in any region. Therefore, mean richness values would be more informative for many purposes.

Recent publications about extraordinary richness values largely focussed on semi-natural, semi-dry basiphilous grasslands. This ignores that there is at least some evidence that also natural Palaearctic steppes could be extremely rich at these grain sizes (e.g. Walter & Breckle 1986; Polyakova et al. 2016). Moreover, focussing solely on semi-dry basiphilous grasslands (order *Brometalia erecti* = *Brachypodietalia pinnati* within the class *Festuco-Brometea*), which so far provided most of the records (Wilson et al. 2012), ignores that also in other types of Palaearctic grasslands very high plant species richness can be found (e.g. Hobohm 1998; Chytrý et al. 2015). Last but not least, most recent papers on the diversity of Palaearctic grasslands studied patterns of vascular plant richness, but neglected the ones of bryophytes and lichens, an extremely diverse group in some grassland types (e.g. Dengler 2005; Boch & Dengler 2006; Löbel & Dengler 2008).

We thus conclude that it would be highly beneficial, both for basic research and biodiversity conservation, to have benchmarks of mean and maximum richness values of different grassland types throughout the Palaearctic realm at different spatial grain sizes. The wealth of phytosociological legacy data that is now available in large vegetation-plot databases (Chytrý et al. 2016; Dengler et al. 2016), can serve as a good basis for such an overview and subsequent analyses of underlying drivers. However, such phytosociological data are often biased by incomplete records and by the tendency of some researchers, particularly in the past, to increase plot sizes in

Fig. 1: ***Photos showing multi-scale plant diversity sampling in different Palaearctic grasslands: (a) 1st EDGG Research Expedition 2009 in Transylvania* (Photo: J. Dengler); *(b) 4th EDGG Research Expedition 2012 in Sicily* (Photo: J. Dengler); *(c) 6th EDGG Research Expedition 2013 in Khakassia* (Photo: M. Janišová); *(d) 7th EDGG Field Workshop 2014 in Navarre* (Photo: M. Janišová).**

naturally species-poor subtypes (e.g. Chytrý 2001). Therefore, we base the overview provided here on sampling schemes that were specifically devoted to study diversity patterns, i.e. where we assume that researchers precisely delimited the plots and very thoroughly sampled them in order not to overlook some species that occur only with few tiny non-flowering individuals, which can contribute significantly to a plot's species richness. Since species richness increases with plot size, our aim was to compile data for a wide range of different plot sizes, ranging from 1 cm^2 to 100 m^2. The overview provided here builds on previous compilations of some of the authors (Dengler 2005; Kuzemko et al. 2016). It is the so far most comprehensive reference database of such information, although we certainly missed many relevant datasets. We thus hope that this overview spurs others to contribute their already existing data for future updates or to collect new data with similar protocols in grassland types and regions that are still missing in our overview.

Methods

We aimed at collecting richness data from any type of natural and semi-natural grasslands of the Palaearctic realm. To ensure high-quality data, we only included sampling schemes that were devoted to studying biodiversity patterns, excluding typical phytosociological plots sampled for classification purposes only. To achieve comparability and to be able to report data in a condensed but still informative format, we chose seven standard plot sizes that are used in various standardised sampling schemes: 0.0001 m^2 − 0.001 m^2 − 0.01 m^2 − 0.1 m^2 − 1 m^2 − 10 m^2 − 100 m^2 (Peet et al. 1998; Dupré & Diekmann 2001; Dengler 2009b). These comprise some of the plot sizes most frequently used in vegetation science for different purposes, but through the "geometric scaling" also allow optimal assessment of species-area relationships and interpolation of richness data to other grain sizes (Dengler 2009a).

Generally we gave preference to data sources that studied more than one of the target grain sizes (usually with nested-plot design) and did so not only in one location and one grassland type but for a representative set of plots of a larger variety of grassland types in a region to allow the presentation of meaningful statistics. We appreciated if the sampling also included terricolous non-vascular plants (bryophytes, lichens and macro-"algae"), but accepted also richness data of vascular plants only. The majority of our data originates from the so-called Field Workshops (formerly Research Expeditions) of the Eurasian Dry Grassland Group (EDGG; http://www.edgg.org; see Vrahnakis et al. 2013; Fig. 1). They started in 2009 in Transylvania (Dengler et al. 2012a; Turtureanu et al. 2014), implementing a variant of the nested sampling design proposed by Dengler (2009b). Since then these events have been conducted on a more or less annual basis in various understudied regions of the Palaearctic realm (Vrahnakis et al. 2013; Fig. 2), originally focussing on dry grasslands (classes *Festuco-Brometea* and *Koelerio-*

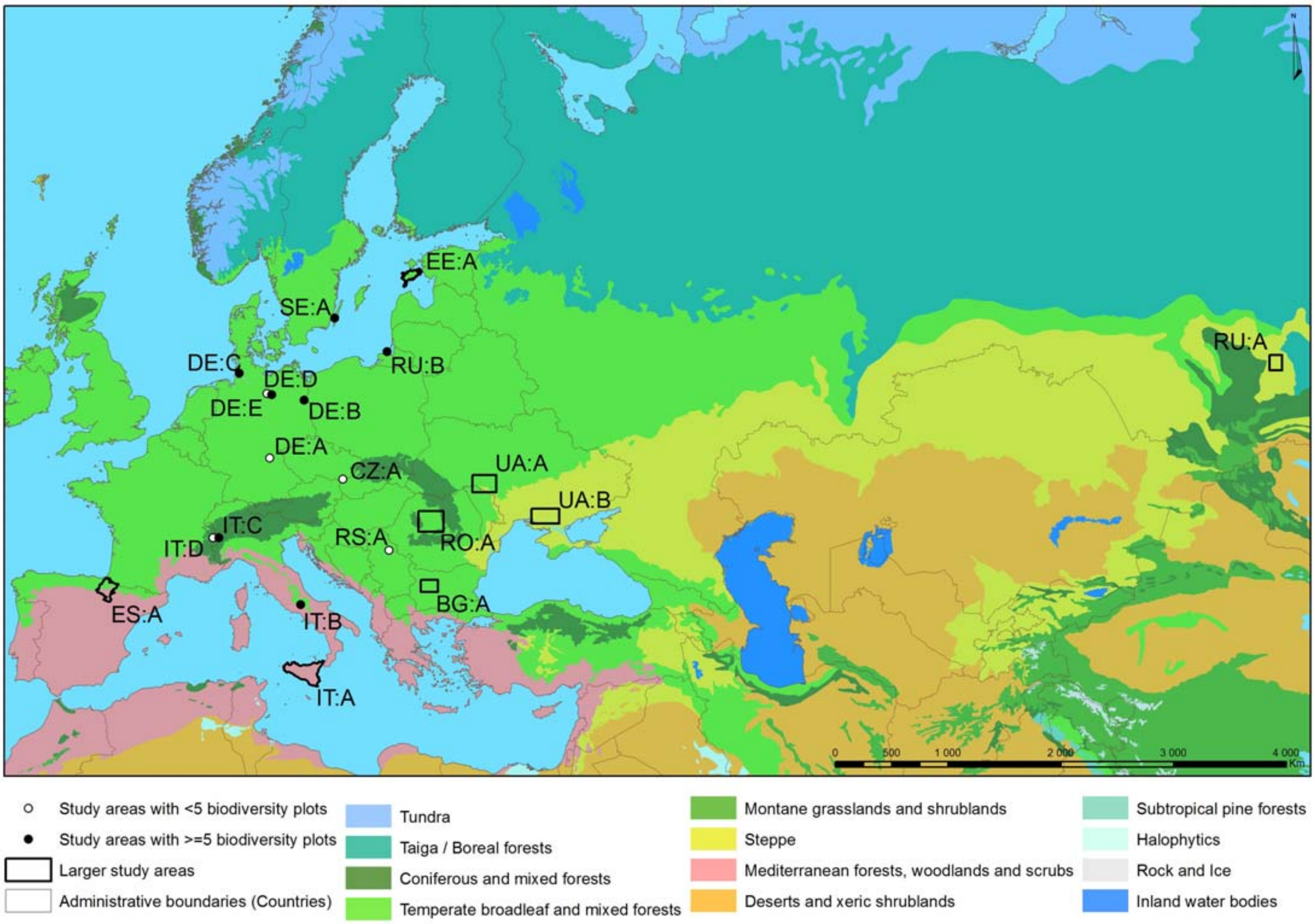

Fig. 2: ***Map showing the location of the 20 study areas of those studies evaluated for this paper. The site labels are those defined in Table 1. Open circles refer to smaller study areas with fewer than five big plots, closed circles to smaller study sites with five and more big plots, while rectangles and irregular polygons delimit larger study areas. The biome map in the background is based on Olson et al. (2001).***

Corynephoretea), but recently including more and more other grassland types, too. In addition, we included data from the co-authors, e.g. in the framework of academic theses or research projects, that were sampled with similar designs. Tables 1−2 and Fig. 2 provide an overview of the sources, qualities and spatial distribution of the compiled data. The majority of the underlying 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).

For all datasets, we extracted and present the information on country, region, vegetation type(s) and number of replicates that were used to derive minimum, maximum and mean values. We further present the statistics of vascular plant species richness for the seven standard grain sizes (0.0001−100 m²), as far as they were available in the individual studies. Data for 9 m² instead of 10 m², 0.09 m² instead of 0.1 m² or 0.0009 m² instead of 0.001 m² were also considered, but marked as such. Depending on the precise slope of the species-area relationship (SAR), plots with 9/10 of the area of a standard grain size are expected to have 1.6−3.1% species less. This range is based on *z*-values of 0.15 and 0.30 respectively, which are already outside the normal values for plot-scale SARs in Palaearctic grasslands (Dengler 2005: 0.193−0.249; Dengler & Boch 2008: 0.173−0.281), i.e. one can simply assume that 9 m² have 2% fewer species than 10 m². Another methodological variation concerns shoot presence vs. rooted presence sampling (Williamson 2003; Dengler 2008; Güler et al. 2016), which is indicated in Table 2. Shoot presence sampling was used in the EDGG expeditions and also most of the other included studies. In these studies, great effort was made to record shoot presence in vegetation that was not affected by the surveyor. Since rooted presence is easier to record, it is preferred in many other small-scale studies, but it has the disadvantage that it does not well reflect the number of interacting species at such small scales and it also poses problems on the analysis of SARs (see Dengler 2008). Rooted species richness is always smaller (or at maximum equal) to shoot presence, and the relative difference between both sampling methods increases towards small grain sizes very strongly (Williamson 2003; Güler et al. 2016).

For studies that included terricolous bryophytes, lichens and macro-"algae", we additionally report total species richness

Table 1: Region, ID, geographic origin, grassland types and sources of the included studies. The studies are grouped into broad geographic regions, and within these according to the ISO country codes. Syntaxa are given according to Mucina et al. (in press), except for the *Koelerio-Corynephoretea* s.l. that follow Dengler (2003). Usually, we provide the class or subclass names, but add order or alliance identity if only a single subunit occurring in the region was included. BR = Biosphere Reserve; NP = National Park; NR = Nature Reserve.

Region	ID	Country	Study area	Latitude (°)	Longitude (°)	Elevation (m a.s.l.)	Diameter of study region (km)	Main grassland type(s)	Main syntaxa	Reference(s)	Year(s) of sampling	No. of EDGG Field Workshop
Asia	RU:A	Russia	Khakassia: northern part	54.2-54-9 N	89.6-90.6 E	391-682	75	dry	*Festuco-Brometea, Cleistogenetea squarrosae*	Janišová et al. (2013), Polyakova et al. (2016)	2013	6
Central Europe	CZ:A	Czech Republic	White Carpathians: Čertoryje	48.8 N	17.4 E	380	0	dry	*Festuco-Brometea*	J. Dengler & K. Fajmon (unpubl.)	2008	-
Central Europe	DE:A	Germany	Upper Franconia: Bayreuth	49.9 N	11.6 E	388	0.02	dry	*Festuco-Brometea: Bromion erecti*	Hopp & Dengler (2015)	2015	-
Central Europe	DE:B	Germany	BR Schorfheide-Chorin: Gabow - Altglietzen	52.8 N	14.1 E	10-50	0.5	dry	*Koelerio-Corynephorenea, Festuco-Brometea*	Dengler et al. (2004)	2004	-
Central Europe	DE:C	Germany	Schleswig-Holstein Wadden Sea NP: southern part	53.9-54.2 N	8.8-9.1 E	0-3	25	saline, wet, mesic	*Juncetea maritimi, Spartinetea maritimae, Molinio-Arrhenatheretea, Phragmito-Magnocaricetea*	K. Jensen & J. Dengler (unpubl. A)	2010	-
Central Europe	DE:D	Germany	Middle Elbe BR: near Lenzen	53.0-53.1 N	11.4-11.6 E	16-20	4.5	mesic, wet	*Molinio-Arrhenatheretea, Phragmito-Magnocaricetea*	K. Jensen & J. Dengler (unpubl. B)	2009	-
Central Europe	DE:E	Germany	Middle Elbe BR: Höhbeck	53.1 N	11.4 E	17-19	1.3	dry	*Koelerio-Corynephorenea*	Schuhmacher & Dengler (2013)	2012	-
Central Europe	IT:C	Italy	Gran Paradiso NP: Valnontey - Col Lauson	45.6 N	7.3 E	1700-3100	3.5	alpine	*Festuco-Brometea, Elyno-Seslerietea, Juncetea trifidi, Molinio-Arrhenatheretea: Poo alpinae-Trisetetalia*	Baumann et al. (2016)	2014	-
Central Europe	IT:D	Italy	Aosta Valley: Cogne	45.6 N	7.4 E	1880	0.04	dry	*Festuco-Brometea*	Wiesner et al. (2015)	2014	-
East Europe	RU:B	Russia	Kaliningrad Oblast: Curonian Spit NP	54.9-55.2 N	20.5-20.9 E	1-35	48	dry, mesic	*Koelerio-Corynephorenea, Molinio-Arrhenatheretea*	Dolnik (2003)	2000	-
East Europe	UA:A	Ukraine	Central Podolia	48.1-49.0 N	27.5-29.4 E	73-251	155	dry	*Festuco-Brometea, Koelerio-Corynephorenea, Sedo-Scleranthenea*	Kuzemko et al. (2014, 2016)	2010	2
East Europe	UA:B	Ukraine	Kherson region	46.4-47.2 N	32.2-34.4 E	17-87	170	dry	*Festuco-Brometea*	Dembicz et al. (2016)	2012-2013	-
North Europe	EE:A	Estonia	Saaremaa	57.8-58.6 N	21.7-23.4 E	1-54	80	dry	*Festuco-Brometea, Koelerio-Corynephorenea, Sedo-Scleranthenea*	Boch (2005), Boch & Dengler (2006), Dengler & Boch (2008)	2004	-
North Europe	SE:A	Sweden	Öland: southern part	56.4-56.7 N	16.3-16.7 E	1-40	30	dry	*Festuco-Brometea, Sedo-Scleranthenea*	Löbel (2002), Löbel & Dengler (2008)	2001	-
South Europe	ES:A	Spain	Navarre	42.7-42.9 N	0.7-2.1 W	581-1795	120	Mediterranean, dry, alpine	*Festuco-Brometea, Lygeo sparti-Stipetea tenacisssimae, Festuco hystricis-Ononidetea striatae, Sedo-Scleranthenea, Elyno-Seslerietea, Juncetea trifidi, Molinio-Arrhenatheretea: Arrhenatheretalia elatioris*	Biurrun et al. (2014)	2014	7
South Europe	IT:A	Italy	Sicily	37.0-38.3 N	12.4-15.2 E	4-1200	240	Mediterranean	*Lygeo sparti-Stipetea tenacissimae, Helianthemetea guttati, Stipo-Trachynietea distachyae, Chenopodietea: Brometalia rubenti-tectorum, Poetea bulbosae, Ammophiletea*	Guarino et al. (2012)	2012	4
South Europe	IT:B	Italy	Abruzzo NP	41.7-41.9 N	13.7-13.9 E	1100-1900	22	dry	*Festuco-Brometea*	L. Cancellieri & G. Filibeck (unpubl.)	2013-2015	-
Southeast Europe	BG:A	Bulgaria	NW Bulgarian mountains	42.5-43.2 N	23.4-24.7 E	633-1460	125	dry	*Festuco-Brometea, Koelerio-Corynephorenea, Sedo-Scleranthenea, Nardetea strictae*	Pedashenko et al. (2013)	2011	3
Southeast Europe	RO:A	Romania	Transylvania	45.9-47.1 N	23.2-25.2 E	321-670	180	dry	*Festuco-Brometea*	Dengler et al. (2012a), Turtureanu et al. (2014)	2009	1
Southeast Europe	RS:A	Serbia	Vojvodina: NR Deliblatska Peščara	44.9 N	21.1 E	142	0.02	dry	*Koelerio-Corynephorenea: Festucion vaginatae*	Krstivojević Ćuk et al. (2015)	2015	-

Table 2: Region, ID, methodological peculiarities and number of replicates per grain size. The studies are grouped into broad geographic regions, and within these according to the ISO country codes.

Region	ID	Country	Study area	Recording method	Terricolous cryptogams included	9 instead of 10	0.0001 m²	0.001 m²	0.01 m²	0.1 m²	1 m²	10 m² (biodiversity)	10 m² (all)	100 m²
Asia	RU:A	Russia	Khakassia: northern part	shoot	yes	no	78	78	78	78	78	78	132	39
Central Europe	CZ:A	Czech Republic	White Carpathians: Čertoryje	rooted	yes	yes	1	1	1	1	1	1	1	1
Central Europe	DE:A	Germany	Upper Franconia: Bayreuth	shoot	yes	no	2	2	2	2	2	2	2	1
Central Europe	DE:B	Germany	BR Schorfheide-Chorin: Gabow - Altglietzen	shoot	yes*	yes	245	245	50	50	50	50	50	10
Central Europe	DE:C	Germany	Schleswig-Holstein Wadden Sea NP: southern part	shoot	no	no	-	118	118	118	118	118	118	55
Central Europe	DE:D	Germany	Middle Elbe BR: near Lenzen	shoot	no	no	-	-	54	54	54	54	54	27
Central Europe	DE:E	Germany	Middle Elbe BR: Höhbeck	shoot	yes	no	-	-	-	-	27	-	-	4
Central Europe	IT:C	Italy	Gran Paradiso NP: Valnontey - Col Lauson	shoot	no	no	26	26	26	26	26	26	26	13
Central Europe	IT:D	Italy	Aosta Valley: Cogne	shoot	no	no	4	4	4	4	4	4	4	2
East Europe	RU:B	Russia	Kaliningrad Oblast: Curonian Spit NP	rooted	yes	yes	17	17	17	17	17	17	17	17
East Europe	UA:A	Ukraine	Central Podolia	shoot	yes	no	42	42	42	42	42	42	226	21
East Europe	UA:B	Ukraine	Kherson region	shoot	no	no	-	-	-	-	1000	-	-	40
North Europe	EE:A	Estonia	Saaremaa	shoot	yes	yes	80	80	80	80	80	80	80	16
North Europe	SE:A	Sweden	Öland: southern part	rooted	yes	yes	31	31	31	31	31	31	31	NA
South Europe	ES:A	Spain	Navarre	shoot	yes**	no	70	70	70	70	70	70	119	35
South Europe	IT:A	Italy	Sicily	shoot	yes	no	42	42	42	42	42	42	67	21
South Europe	IT:B	Italy	Abruzzo NP	shoot	no	no	-	-	324	162	81	-	-	-
Southeast Europe	BG:A	Bulgaria	NW Bulgarian mountains	shoot	yes	no	30	30	30	30	30	30	98	15
Southeast Europe	RO:A	Romania	Transylvania	shoot	yes	no	40	40	40	40	40	40	82	20
Southeast Europe	RS:A	Serbia	Vojvodina: NR Deliblatska Peščara	shoot	yes	no	2	2	2	2	2	2	2	1
Total							**710**	**828**	**1011**	**849**	**1795**	**687**	**1109**	**338**

* also non-terricolous taxa included, but their fraction is negligible
** preliminary data, i.e. number of non-vascular plants, total richness and fraction of non-vascular plants will slightly change in the final version, mostly to the positive

Table 3: Mean, minimum and maximum values of vascular plant species richness on the seven "standard grain sizes" found in different studies throughout the Palaearctic realm. For details on the studies, see Tables 1 and 2. For comparison, we added the maxima given by Wilson et al. (2012) and Chytrý et al. (2015) for Palaearctic grasslands and for any vegetation type world-wide. Studies with fewer than five plots of the biggest size are in italics because they can hardly be representative. Maxima of mean and maximum richness at the different grain sizes are highlighted in red and bold; if such a value is from an "italicised" line, the highest value from a more representative study is set in red.

Region	ID	Country	Study area	rooted instead of shoot	9 in-stead of 10	Sta-tistics	0.0001 m^2	0.001 m^2	0.01 m^2	0.1 m^2	1 m^2	10 m^2 (biodiversity)	10 m^2 (all)	100 m^2
Asia	RU:A	Russia	Khakassia: northern part			Mean	2.1	4.0	8.2	17.3	29.7	45.1	43.9	65.3
Central Europe	*CZ:A*	*Czech Republic*	*White Carpathians: Čertoryje*	#	#	*Mean*	*2.0*	*4.0*	*11.0*	***31.0***	***58.0***	***79.0***	***79.0***	***105.0***
Central Europe	*DE:A*	*Germany*	*Upper Franconia: Bayreuth*			*Mean*	***4.0***	***6.5***	***14.0***	*25.0*	*37.0*	*47.5*	*47.5*	*65.0*
Central Europe	DE:B	Germany	BR Schorfheide-Chorin: Gabow - Altglietzen		#	Mean	1.6	2.3	4.2	7.5	12.4	19.8	19.8	35.4
Central Europe	DE:C	Germany	Schleswig-Holstein Wadden Sea NP: southern part			Mean	NA	1.7	2.2	3.0	3.9	6.0	6.0	8.3
Central Europe	DE:D	Germany	Middle Elbe BR: near Lenzen			Mean	NA	NA	3.5	5.9	9.6	15.6	15.6	26.2
Central Europe	*DE:E*	*Germany*	*Middle Elbe BR: Höhbeck*			*Mean*	*NA*	*NA*	*NA*	*NA*	*10.0*	*NA*	*NA*	*26.3*
Central Europe	IT:C	Italy	Gran Paradiso NP: Valnontey - Col Lauson			Mean	2.1	3.7	6.2	12.2	18.7	28.0	28.0	43.5
Central Europe	*IT:D*	*Italy*	*Aosta Valley: Cogne*			*Mean*	*2.3*	*3.8*	*5.5*	*7.5*	*16.3*	*27.8*	*27.8*	*45.5*
East Europe	RU:B	Russia	Kaliningrad Oblast: Curonian Spit NP	#	#	Mean	0.8	NA	7.1	NA	19.4	27.1	27.1	35.7
East Europe	UA:A	Ukraine	Central Podolia			Mean	2.5	4.0	7.3	13.8	24.4	39.3	37.2	66.8
East Europe	UA:B	Ukraine	Kherson region			Mean	NA	NA	NA	NA	12.5	NA	NA	45.1
North Europe	EE:A	Estonia	Saaremaa		#	Mean	1.5	2.7	5.0	9.1	15.7	24.0	24.0	38.6
North Europe	SE:A	Sweden	Öland: southern part	#	#	Mean	0.4	1.8	4.6	8.7	15.1	24.2	24.2	NA
South Europe	ES:A	Spain	Navarre			Mean	3.3	5.7	9.7	17.2	28.0	43.0	41.9	64.9
South Europe	IT:A	Italy	Sicily			Mean	1.7	3.2	6.4	12.8	21.0	33.8	35.4	55.4
South Europe	IT:B	Italy	Abruzzo NP			Mean	NA	NA	9.9	18.3	29.0	NA	NA	NA
Southeast Europe	BG:A	Bulgaria	NW Bulgarian mountains			Mean	2.3	3.9	7.6	13.3	22.8	34.7	34.1	56.7
Southeast Europe	RO:A	Romania	Transylvania			Mean	2.3	4.2	9.6	21.1	37.5	57.2	49.7	83.3
Southeast Europe	*RS:A*	*Serbia*	*Vojvodina: NR Deliblatska Peščara*			*Mean*	*0.5*	*1.0*	*4.0*	*12.0*	*18.5*	*25.0*	*25.0*	*35.0*
Asia	RU:A	Russia	Khakassia: northern part			Min	0	0	2	7	15	22	22	35
Central Europe	*CZ:A*	*Czech Republic*	*White Carpathians: Čertoryje*	#	#	*Min*	*2*	*4*	*11*	*31*	*58*	*79*	*79*	*105*
Central Europe	*DE:A*	*Germany*	*Upper Franconia: Bayreuth*			*Min*	*4*	*4*	*9*	*19*	*31*	*40*	*40*	*65*
Central Europe	DE:B	Germany	BR Schorfheide-Chorin: Gabow - Altglietzen		#	Min	0	0	1	2	2	4	4	9
Central Europe	DE:C	Germany	Schleswig-Holstein Wadden Sea NP: southern part			Min	NA	0	0	0	0	1	1	1
Central Europe	DE:D	Germany	Middle Elbe BR: near Lenzen			Min	NA	NA	1	1	2	4	4	9
Central Europe	*DE:E*	*Germany*	*Middle Elbe BR: Höhbeck*			*Min*	*NA*	*NA*	*NA*	*NA*	*3*	*NA*	*NA*	*22*
Central Europe	IT:C	Italy	Gran Paradiso NP: Valnontey - Col Lauson			Min	0	0	1	1	4	9	9	17
Central Europe	*IT:D*	*Italy*	*Aosta Valley: Cogne*			*Min*	*1*	*2*	*4*	*6*	*9*	*19*	*19*	*39*
East Europe	RU:B	Russia	Kaliningrad Oblast: Curonian Spit NP	#	#	Min	0	NA	1	NA	4	7	7	9
East Europe	UA:A	Ukraine	Central Podolia			Min	0	0	3	6	13	26	14	42
East Europe	UA:B	Ukraine	Kherson region			Min	NA	NA	NA	NA	2	NA	NA	21
North Europe	EE:A	Estonia	Saaremaa		#	Min	0	0	0	0	1	3	3	9
North Europe	SE:A	Sweden	Öland: southern part	#	#	Min	0	0	1	3	7	11	11	NA
South Europe	ES:A	Spain	Navarre			Min	0	0	0	2	10	18	18	37
South Europe	IT:A	Italy	Sicily			Min	0	0	0	1	5	9	9	13
South Europe	IT:B	Italy	Abruzzo NP			Min	NA	NA	0	8	17	NA	NA	NA
Southeast Europe	BG:A	Bulgaria	NW Bulgarian mountains			Min	1	1	1	3	7	15	8	38
Southeast Europe	RO:A	Romania	Transylvania			Min	0	0	3	7	16	33	9	52
Southeast Europe	*RS:A*	*Serbia*	*Vojvodina: NR Deliblatska Peščara*			*Min*	*0*	*0*	*2*	*12*	*17*	*24*	*24*	*35*
Asia	RU:A	Russia	Khakassia: northern part			Max	5	9	17	28	52	72	72	94
Central Europe	*CZ:A*	*Czech Republic*	*White Carpathians: Čertoryje*	#	#	*Max*	*2*	*4*	*11*	*31*	*58*	*79*	*79*	*105*
Central Europe	*DE:A*	*Germany*	*Upper Franconia: Bayreuth*			*Max*	*4*	*9*	*19*	*31*	*43*	*55*	*55*	*65*
Central Europe	DE:B	Germany	BR Schorfheide-Chorin: Gabow - Altglietzen		#	Max	5	6	9	15	22	36	36	55
Central Europe	DE:C	Germany	Schleswig-Holstein Wadden Sea NP: southern part			Max	NA	5	8	11	13	17	17	20
Central Europe	DE:D	Germany	Middle Elbe BR: near Lenzen			Max	NA	NA	8	15	19	34	34	48
Central Europe	*DE:E*	*Germany*	*Middle Elbe BR: Höhbeck*			*Max*	*NA*	*NA*	*NA*	*NA*	*17*	*NA*	*NA*	*34*
Central Europe	IT:C	Italy	Gran Paradiso NP: Valnontey - Col Lauson			Max	5	6	12	23	29	42	42	65
Central Europe	*IT:D*	*Italy*	*Aosta Valley: Cogne*			*Max*	*4*	*6*	*7*	*9*	*23*	*35*	*35*	*52*
East Europe	RU:B	Russia	Kaliningrad Oblast: Curonian Spit NP	#	#	Max	4	NA	15	NA	40	61	61	71
East Europe	UA:A	Ukraine	Central Podolia			Max	7	11	13	21	42	56	64	86
East Europe	UA:B	Ukraine	Kherson region			Max	NA	NA	NA	NA	28	NA	NA	73
North Europe	EE:A	Estonia	Saaremaa		#	Max	5	7	14	25	35	49	49	70
North Europe	SE:A	Sweden	Öland: southern part	#	#	Max	2	5	11	20	28	42	42	NA
South Europe	ES:A	Spain	Navarre			Max	**9**	**19**	23	34	50	82	82	104
South Europe	IT:A	Italy	Sicily			Max	4	9	14	27	39	68	68	98
South Europe	IT:B	Italy	Abruzzo NP			Max	NA	NA	20	31	47	NA	NA	NA
Southeast Europe	BG:A	Bulgaria	NW Bulgarian mountains			Max	6	9	14	25	36	58	60	87
Southeast Europe	RO:A	Romania	Transylvania			Max	5	8	18	**43**	79	**98**	**98**	127
Southeast Europe	*RS:A*	*Serbia*	*Vojvodina: NR Deliblatska Peščara*			*Max*	*1*	*2*	*6*	*12*	*20*	*26*	*26*	*35*
Old Palaearctic grassland record			Multiple			Max	5	12	**25**	43	**82**	98	98	**133**
Old world record			Multiple			Max	5	12	25	43	89	98	98	233

Table 4: Mean, minimum and maximum values of total plant species richness on the seven "standard grain sizes" found in different studies throughout the Palaearctic realm. For details on the studies, see Tables 1 and 2. Studies with fewer than five plots of the biggest size are in italics because they can hardly be representative. Maxima of mean and maximum richness at the different grain sizes are highlighted in red and bold; if such a value is from an "italicised" line, the highest value from a more representative study is set in red.

Region	ID	Country	Study area	rooted instead of shoot	9 instead of 10	Statistics	0.0001 m^2	0.001 m^2	0.01 m^2	0.1 m^2	1 m^2	10 m^2 (biodiversity)	10 m^2 (all)	100 m^2
Asia	RU:A	Russia	Khakassia: northern part			Mean	2.3	4.7	9.6	19.7	33.3	50.0	50.7	73.4
Central Europe	*CZ:A*	*Czech Republic*	*White Carpathians: Čertoryje*	#	#	*Mean*	*4.0*	*6.0*	*14.0*	***34.0***	***65.0***	***88.0***	***88.0***	***117.0***
Central Europe	*DE:A*	*Germany*	*Upper Franconia: Bayreuth*			*Mean*	***7.0***	***10.0***	***20.0***	*31.5*	*45.0*	*55.5*	*55.5*	*77.0*
Central Europe	DE:B	Germany	BR Schorfheide-Chorin: Gabow - Altglietzen		#	Mean	2.3	3.4	6.5	11.1	17.9	27.5	27.5	50.2
Central Europe	*DE:E*	*Germany*	*Middle Elbe BR: Höhbeck*			*Mean*	*NA*	*NA*	*NA*	*NA*	*13.9*	*NA*	*NA*	*33.5*
East Europe	RU:B	Russia	Kaliningrad Oblast: Curonian Spit NP	#	#	Mean	2.2	NA	11.2	NA	29.1	40.9	40.9	56.0
East Europe	UA:A	Ukraine	Central Podolia			Mean	2.9	4.7	8.5	15.9	27.2	43.7	41.1	73.6
North Europe	EE:A	Estonia	Saaremaa		#	Mean	3.2	5.9	10.5	17.2	28.0	42.2	42.2	69.2
North Europe	SE:A	Sweden	Öland: southern part	#	#	Mean	1.1	4.4	12.6	24.5	40.4	56.4	56.4	NA
South Europe	ES:A	Spain	Navarre			Mean	4.0	6.8	11.5	20.5	32.6	47.9	49.8	79.9
South Europe	IT:A	Italy	Sicily			Mean	2.1	3.9	7.6	15.4	25.1	40.5	42.4	67.2
Southeast Europe	BG:A	Bulgaria	NW Bulgarian mountains			Mean	2.7	3.9	8.5	14.8	25.5	39.5	38.5	65.3
Southeast Europe	RO:A	Romania	Transylvania			Mean	2.6	4.6	10.2	22.8	40.0	60.5	52.8	88.2
Southeast Europe	*RS:A*	*Serbia*	*Vojvodina: NR Deliblatska Peščara*			*Mean*	*2.5*	*3.0*	*6.0*	*14.0*	*21.0*	*27.5*	*27.5*	*38.0*
Asia	RU:A	Russia	Khakassia: northern part			Min	0	1	2	7	17	30	28	46
Central Europe	*CZ:A*	*Czech Republic*	*White Carpathians: Čertoryje*	#	#	*Min*	*4*	*6*	*14*	*34*	*65*	*88*	*88*	*117*
Central Europe	*DE:A*	*Germany*	*Upper Franconia: Bayreuth*			*Min*	*7*	*8*	*14*	*25*	*39*	*48*	*48*	*77*
Central Europe	DE:B	Germany	BR Schorfheide-Chorin: Gabow - Altglietzen		#	Min	0	0	1	5	7	10	10	19
Central Europe	*DE:E*	*Germany*	*Middle Elbe BR: Höhbeck*			*Min*	*NA*	*NA*	*NA*	*NA*	*7*	*NA*	*NA*	*29*
East Europe	RU:B	Russia	Kaliningrad Oblast: Curonian Spit NP	#	#	Min	0	NA	2	NA	6	13	13	33
East Europe	UA:A	Ukraine	Central Podolia			Min	0	2	3	6	13	27	15	47
North Europe	EE:A	Estonia	Saaremaa		#	Min	0	1	3	6	9	17	17	34
North Europe	SE:A	Sweden	Öland: southern part	#	#	Min	0	0	3	6	10	26	26	NA
South Europe	ES:A	Spain	Navarre			Min	0	0	0	4	12	19	19	48
South Europe	IT:A	Italy	Sicily			Min	0	0	0	1	5	9	9	13
Southeast Europe	BG:A	Bulgaria	NW Bulgarian mountains			Min	1	1	1	3	7	15	10	47
Southeast Europe	RO:A	Romania	Transylvania			Min	0	0	3	7	18	37	9	58
Southeast Europe	*RS:A*	*Serbia*	*Vojvodina: NR Deliblatska Peščara*			*Min*	*2*	*2*	*4*	*14*	*19*	*26*	*26*	*38*
Asia	RU:A	Russia	Khakassia: northern part			Max	5	11	18	34	54	80	80	106
Central Europe	*CZ:A*	*Czech Republic*	*White Carpathians: Čertoryje*	#	#	*Max*	*4*	*6*	*14*	*34*	*65*	*88*	*88*	*117*
Central Europe	*DE:A*	*Germany*	*Upper Franconia: Bayreuth*			*Max*	*7*	*12*	***26***	*38*	*51*	*63*	*63*	*77*
Central Europe	DE:B	Germany	BR Schorfheide-Chorin: Gabow - Altglietzen		#	Max	6	8	11	18	25	41	41	69
Central Europe	*DE:E*	*Germany*	*Middle Elbe BR: Höhbeck*			*Max*	*NA*	*NA*	*NA*	*NA*	*21*	*NA*	*NA*	*41*
East Europe	RU:B	Russia	Kaliningrad Oblast: Curonian Spit NP	#	#	Max	4	NA	22	NA	50	70	70	75
East Europe	UA:A	Ukraine	Central Podolia			Max	7	11	14	26	48	62	67	108
North Europe	EE:A	Estonia	Saaremaa		#	Max	8	13	22	32	49	72	72	100
North Europe	SE:A	Sweden	Öland: southern part	#	#	Max	4	11	25	43	63	81	81	NA
South Europe	ES:A	Spain	Navarre			Max	**9**	**19**	**26**	43	64	98	98	132
South Europe	IT:A	Italy	Sicily			Max	8	15	22	35	50	72	72	124
Southeast Europe	BG:A	Bulgaria	NW Bulgarian mountains			Max	6	9	17	28	41	61	62	89
Southeast Europe	RO:A	Romania	Transylvania			Max	5	9	20	**45**	**82**	**101**	**101**	**134**
Southeast Europe	*RS:A*	*Serbia*	*Vojvodina: NR Deliblatska Peščara*			*Max*	*3*	*4*	*8*	*14*	*23*	*29*	*29*	*38*

Table 5: Mean, minimum and maximum values of non-vascular plant species richness (i.e. terricolous bryophytes, lichens and macro-“algae”) on the seven “standard grain sizes” found in different studies throughout the Palaearctic realm. For details on the studies, see Tables 1 and 2. Studies with fewer than five plots of the biggest size are in italics because they can hardly be representative. Maxima of mean and maximum richness at the different grain sizes are highlighted in red and bold; if such a value is from an “italicised” line, the highest value from a more representative study is set in red.

Region	ID	Country	Study area	rooted instead of shoot	9 instead of 10	Statistics	0.0001 m²	0.001 m²	0.01 m²	0.1 m²	1 m²	10 m² (biodiversity)	10 m² (all)	100 m²
Asia	RU:A	Russia	Khakassia: northern part			Mean	0.2	0.6	1.5	2.4	3.5	4.8	4.6	8.2
Central Europe	*CZ:A*	*Czech Republic*	*White Carpathians: Čertoryje*	#	#	*Mean*	*2.0*	*2.0*	*3.0*	*3.0*	*7.0*	*9.0*	*9.0*	*12.0*
Central Europe	*DE:A*	*Germany*	*Upper Franconia: Bayreuth*			*Mean*	***3.0***	***3.5***	*6.0*	*6.5*	*8.0*	*8.0*	*8.0*	*12.0*
Central Europe	DE:B	Germany	BR Schorfheide-Chorin: Gabow - Altglietzen		#	Mean	0.7	1.1	2.2	3.6	5.5	7.7	7.7	14.8
Central Europe	*DE:E*	*Germany*	*Middle Elbe BR: Höhbeck*			*Mean*	*NA*	*NA*	*NA*	*NA*	*3.9*	*NA*	*NA*	*7.3*
East Europe	RU:B	Russia	Kaliningrad Oblast: Curonian Spit NP	#	#	Mean	1.4	NA	4.2	NA	9.8	13.8	13.8	20.3
East Europe	UA:A	Ukraine	Central Podolia			Mean	0.4	0.6	1.2	2.1	2.8	4.4	3.9	6.8
North Europe	EE:A	Estonia	Saaremaa		#	Mean	1.7	3.1	5.5	8.1	12.3	18.2	18.2	30.6
North Europe	SE:A	Sweden	Öland: southern part	#	#	Mean	0.7	2.6	**7.9**	**15.6**	**25.0**	**32.0**	**32.0**	**NA**
South Europe	ES:A	Spain	Navarre			Mean	0.7	1.1	1.8	3.1	4.6	5.8	6.5	13.3
South Europe	IT:A	Italy	Sicily			Mean	0.4	0.7	1.2	2.6	4.0	6.7	7.0	11.8
Southeast Europe	BG:A	Bulgaria	NW Bulgarian mountains			Mean	0.4	0.5	0.9	1.4	2.7	4.8	4.4	8.5
Southeast Europe	RO:A	Romania	Transylvania			Mean	0.2	0.4	0.6	1.7	2.6	3.3	3.1	4.9
Southeast Europe	*RS:A*	*Serbia*	*Vojvodina: NR Deliblatska Peščara*			*Mean*	*2.0*	*2.0*	*2.0*	*2.0*	*2.5*	*2.5*	*2.5*	*3.0*
Asia	RU:A	Russia	Khakassia: northern part			Min	0	0	0	0	0	0	0	0
Central Europe	*CZ:A*	*Czech Republic*	*White Carpathians: Čertoryje*	#	#	*Min*	*2*	*2*	*3*	*3*	*7*	*9*	*9*	*12*
Central Europe	*DE:A*	*Germany*	*Upper Franconia: Bayreuth*			*Min*	*3*	*3*	*5*	*6*	*8*	*8*	*8*	*12*
Central Europe	DE:B	Germany	BR Schorfheide-Chorin: Gabow - Altglietzen		#	Min	0	0	0	0	1	3	3	10
Central Europe	*DE:E*	*Germany*	*Middle Elbe BR: Höhbeck*			*Min*	*NA*	*NA*	*NA*	*NA*	*1*	*NA*	*NA*	*5*
East Europe	RU:B	Russia	Kaliningrad Oblast: Curonian Spit NP	#	#	Min	0	NA	0	NA	0	3	3	3
East Europe	UA:A	Ukraine	Central Podolia			Min	0	0	0	0	0	0	0	1
North Europe	EE:A	Estonia	Saaremaa		#	Min	0	0	1	2	4	5	5	13
North Europe	SE:A	Sweden	Öland: southern part	#	#	Min	0	0	0	0	1	10	10	NA
South Europe	ES:A	Spain	Navarre			Min	0	0	0	0	0	0	0	1
South Europe	IT:A	Italy	Sicily			Min	0	0	0	0	0	0	0	0
Southeast Europe	BG:A	Bulgaria	NW Bulgarian mountains			Min	0	0	0	0	0	0	0	2
Southeast Europe	RO:A	Romania	Transylvania			Min	0	0	0	0	0	1	0	2
Southeast Europe	*RS:A*	*Serbia*	*Vojvodina: NR Deliblatska Peščara*			*Min*	*2*	*2*	*2*	*2*	*2*	*2*	*2*	*3*
Asia	RU:A	Russia	Khakassia: northern part			Max	3	6	8	14	14	22	22	26
Central Europe	*CZ:A*	*Czech Republic*	*White Carpathians: Čertoryje*	#	#	*Max*	*2*	*2*	*3*	*3*	*7*	*9*	*9*	*12*
Central Europe	*DE:A*	*Germany*	*Upper Franconia: Bayreuth*			*Max*	*3*	*4*	*7*	*7*	*8*	*8*	*8*	*12*
Central Europe	DE:B	Germany	BR Schorfheide-Chorin: Gabow - Altglietzen		#	Max	3	4	9	12	14	17	17	26
Central Europe	*DE:E*	*Germany*	*Middle Elbe BR: Höhbeck*			*Max*	*NA*	*NA*	*NA*	*NA*	*8*	*NA*	*NA*	*10*
East Europe	RU:B	Russia	Kaliningrad Oblast: Curonian Spit NP	#	#	Max	4	NA	9	NA	19	26	26	35
East Europe	UA:A	Ukraine	Central Podolia			Max	3	3	5	6	9	16	20	28
North Europe	EE:A	Estonia	Saaremaa		#	Max	**8**	10	17	24	29	45	45	**64**
North Europe	SE:A	Sweden	Öland: southern part	#	#	Max	3	**11**	**22**	**30**	**49**	**64**	**64**	**NA**
South Europe	ES:A	Spain	Navarre			Max	4	7	7	13	14	21	21	27
South Europe	IT:A	Italy	Sicily			Max	5	8	9	10	13	21	21	33
Southeast Europe	BG:A	Bulgaria	NW Bulgarian mountains			Max	3	4	5	6	7	19	19	19
Southeast Europe	RO:A	Romania	Transylvania			Max	1	2	2	6	7	10	13	18
Southeast Europe	*RS:A*	*Serbia*	*Vojvodina: NR Deliblatska Peščara*			*Max*	*2*	*2*	*2*	*2*	*3*	*3*	*3*	*3*

Table 6: Mean, minimum and maximum values of fraction of non-vascular plant species (i.e. terricolous bryophytes, lichens and macro-“algae”) on the seven “standard grain sizes” found in different studies throughout the Palaearctic realm. For details on the studies, see Tables 1 and 2. Studies with fewer than five plots of the biggest size are in italics because they can hardly be representative. Extreme values of means are highlighted in blue (minima) and red (maxima).

Region	ID	Country	Study area	rooted instead of shoot	9 instead of 10	Statistics	0.0001 m²	0.001 m²	0.01 m²	0.1 m²	1 m²	10 m² (biodiversity)	10 m² (all)	100 m²
Asia	RU:A	Russia	Khakassia: northern part			Mean	**6.0%**	11.2%	12.9%	10.9%	10.2%	9.6%	8.9%	11.0%
Central Europe	*CZ:A*	*Czech Republic*	*White Carpathians: Čertoryje*	#	#	*Mean*	*50.0%*	*33.3%*	*21.4%*	*8.8%*	*10.8%*	*10.2%*	*10.2%*	*10.3%*
Central Europe	*DE:A*	*Germany*	*Upper Franconia: Bayreuth*			*Mean*	*42.9%*	*37.5%*	*31.3%*	*21.2%*	*18.1%*	*14.7%*	*14.7%*	*15.6%*
Central Europe	DE:B	Germany	BR Schorfheide-Chorin: Gabow - Altglietzen		#	Mean	29.3%	33.9%	34.3%	33.9%	33.2%	30.7%	30.7%	32.1%
Central Europe	*DE:E*	*Germany*	*Middle Elbe BR: Höhbeck*			*Mean*	*NA*	*NA*	*NA*	*NA*	*28.9%*	*NA*	*NA*	*21.8%*
East Europe	RU:B	Russia	Kaliningrad Oblast: Curonian Spit NP	#	#	Mean	35.0%	NA	37.0%	NA	34.0%	34.0%	34.0%	36.0%
East Europe	UA:A	Ukraine	Central Podolia			Mean	15.3%	14.8%	14.1%	12.3%	10.0%	9.7%	9.3%	8.8%
North Europe	EE:A	Estonia	Saaremaa		#	Mean	56.8%	54.9%	53.4%	49.1%	46.7%	45.9%	45.9%	**46.9%**
North Europe	SE:A	Sweden	Öland: southern part	#	#	Mean	68.2%	55.0%	**56.4%**	**59.5%**	**58.3%**	**54.9%**	**54.9%**	NA
South Europe	ES:A	Spain	Navarre			Mean	18.0%	16.8%	15.9%	15.3%	14.6%	12.0%	13.0%	16.5%
South Europe	IT:A	Italy	Sicily			Mean	10.5%	10.0%	8.9%	12.3%	13.9%	15.2%	15.3%	15.8%
Southeast Europe	BG:A	Bulgaria	NW Bulgarian mountains			Mean	12.5%	12.4%	10.4%	9.5%	10.5%	12.5%	12.2%	13.7%
Southeast Europe	RO:A	Romania	Transylvania			Mean	10.0%	**6.2%**	**5.3%**	**7.6%**	**6.9%**	**5.8%**	**5.6%**	**5.9%**
Southeast Europe	*RS:A*	*Serbia*	*Vojvodina: NR Deliblatska Peščara*			*Mean*	*83.3%*	*75.0%*	*37.5%*	*14.3%*	*11.8%*	*9.0%*	*9.0%*	*7.9%*
Asia	RU:A	Russia	Khakassia: northern part			Min	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Central Europe	*CZ:A*	*Czech Republic*	*White Carpathians: Čertoryje*	#	#	*Min*	*50.0%*	*33.3%*	*21.4%*	*8.8%*	*10.8%*	*10.2%*	*10.2%*	*10.3%*
Central Europe	*DE:A*	*Germany*	*Upper Franconia: Bayreuth*			*Min*	*42.9%*	*25.0%*	*26.9%*	*18.4%*	*15.7%*	*12.7%*	*12.7%*	*15.6%*
Central Europe	DE:B	Germany	BR Schorfheide-Chorin: Gabow - Altglietzen		#	Min	0.0%	0.0%	0.0%	0.0%	6.7%	7.9%	7.9%	17.5%
Central Europe	*DE:E*	*Germany*	*Middle Elbe BR: Höhbeck*			*Min*	*NA*	*NA*	*NA*	*NA*	*1.1%*	*NA*	*NA*	*17.1%*
East Europe	RU:B	Russia	Kaliningrad Oblast: Curonian Spit NP	#	#	Min	0.0%	NA	0.0%	NA	0.0%	6.0%	6.0%	5.1%
East Europe	UA:A	Ukraine	Central Podolia			Min	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	1.3%
North Europe	EE:A	Estonia	Saaremaa		#	Min	0.0%	0.0%	10.0%	9.5%	11.1%	10.2%	10.2%	15.7%
North Europe	SE:A	Sweden	Öland: southern part	#	#	Min	0.0%	0.0%	0.0%	0.0%	10.0%	22.2%	22.2%	NA
South Europe	ES:A	Spain	Navarre			Min	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	2.1%
South Europe	IT:A	Italy	Sicily			Min	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Southeast Europe	BG:A	Bulgaria	NW Bulgarian mountains			Min	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	2.2%
Southeast Europe	RO:A	Romania	Transylvania			Min	0.0%	0.0%	0.0%	0.0%	0.0%	1.6%	0.0%	1.6%
Southeast Europe	*RS:A*	*Serbia*	*Vojvodina: NR Deliblatska Peščara*			*Min*	*66.7%*	*50.0%*	*25.0%*	*14.3%*	*10.5%*	*7.7%*	*7.7%*	*7.9%*
Asia	RU:A	Russia	Khakassia: northern part			Max	100.0%	100.0%	60.0%	48.3%	42.4%	38.6%	38.6%	38.6%
Central Europe	*CZ:A*	*Czech Republic*	*White Carpathians: Čertoryje*	#	#	*Max*	*50.0%*	*33.3%*	*21.4%*	*8.8%*	*10.8%*	*10.2%*	*10.2%*	*10.3%*
Central Europe	*DE:A*	*Germany*	*Upper Franconia: Bayreuth*			*Max*	*42.9%*	*50.0%*	*35.7%*	*24.0%*	*20.5%*	*16.7%*	*16.7%*	*15.6%*
Central Europe	DE:B	Germany	BR Schorfheide-Chorin: Gabow - Altglietzen		#	Max	100.0%	100.0%	90.0%	75.0%	75.0%	69.2%	69.2%	52.6%
Central Europe	*DE:E*	*Germany*	*Middle Elbe BR: Höhbeck*			*Max*	*NA*	*NA*	*NA*	*NA*	*60.0%*	*NA*	*NA*	*28.6%*
East Europe	RU:B	Russia	Kaliningrad Oblast: Curonian Spit NP	#	#	Max	100.0%	NA	88.9%	NA	80.6%	70.4%	70.4%	75.0%
East Europe	UA:A	Ukraine	Central Podolia			Max	100.0%	100.0%	45.5%	37.5%	31.0%	33.3%	52.8%	25.9%
North Europe	EE:A	Estonia	Saaremaa		#	Max	100.0%	100.0%	100.0%	100.0%	91.7%	88.0%	88.0%	73.5%
North Europe	SE:A	Sweden	Öland: southern part	#	#	Max	100.0%	100.0%	88.0%	87.9%	79.0%	81.0%	81.0%	NA
South Europe	ES:A	Spain	Navarre			Max	100.0%	100.0%	50.0%	59.1%	45.5%	40.0%	40.0%	37.9%
South Europe	IT:A	Italy	Sicily			Max	66.7%	66.7%	60.0%	45.5%	34.5%	38.2%	38.2%	35.9%
Southeast Europe	BG:A	Bulgaria	NW Bulgarian mountains			Max	75.0%	80.0%	50.0%	45.5%	31.8%	31.8%	41.4%	28.4%
Southeast Europe	RO:A	Romania	Transylvania			Max	100.0%	40.0%	25.0%	31.6%	22.6%	20.0%	30.2%	23.4%
Southeast Europe	*RS:A*	*Serbia*	*Vojvodina: NR Deliblatska Peščara*			*Max*	*100.0%*	*100.0%*	*50.0%*	*14.3%*	*13.0%*	*10.3%*	*10.3%*	*7.9%*

Fig. 3: ***Photos showing Palaearctic grasslands that are extreme for certain aspects of plant diversity. (a) World record stand for 0.1-m² and 10-m² vascular plant species richness (43 and 98 species, respectively) (Transylvania, Romania: Cirsio-Brachypodion pinnati, Festuco-Brometea); (b) new world record stand for 0.001-m² vascular plant richness (19 species, Belagua at 939 m a.s.l., Navarre, Spain: intensively grazed, Potentillo-Brachypodion pinnati, Festuco-Brometea); (c) stand of the Tortello tortuosae-Sedion albi, Sedo-Scleranthenea, the Palaearctic grassland type richest in non-vascular plants at all considered spatial scales with e.g. up to 64 species on 9 m² (the photo is from Saaremaa, Estonia, while stands in Öland, Sweden, are known to be slightly richer); (d) dune grassland (Sicily, Italy: Alkanno-Malcolmion parviflorae, Tuberarietea guttatae), which is among the poorest types in our overview in terms of vascular plant species richness, with e.g. only 13 species on 100 m²*** **(Photos: J. Dengler).**

(i.e. terricolous vascular plants, bryophytes, lichens and macro -"algae"), non-vascular plant species richness, and percentage of non-vascular plants (non-vascular plant species richness / total species richness). For the sake of linguistic convenience, we include lichens in the following under the generic term "plants", acknowledging that they actually are symbioses between fungi and photo-autotrophic partners. The data published here as tables, can be requested from the corresponding author in spread sheet format.

Results

The highest mean richness values for vascular plant species richness were reported for all grain sizes between 0.1 and 100 m² in Transylvania, Romania, for 0.01 m² in Central Italy and for the two smallest grain sizes in Navarre, Spain (Table 3). The absolutely highest values, were similarly distributed: 0.1 m² (43 species) and 10 m² (98) are the still valid world records from Transylvania (Wilson et al. 2012), while for 0.0001 m² (9) and for 0.001 m² (19) we report new world records from Navarre, Spain. The three other maxima in Palaearctic grasslands (25 on 0.01 m², 82 on 1 m² and 133 on 100 m²) are from other studies not included here. However, all the maxima belong to the meso-xeric, basiphilous grasslands of the order *Brachypodietalia pinnati* (= *Brometalia erecti*; *Festuco-Brometea*; Fig. 3). When considering total plant species richness (i.e. including bryophytes, lichens and other macroscopic photoautotrophic organisms), the picture remains essentially the same (Table 4).

By contrast, maximum small-scale richness of non-vascular plants at nearly any spatial scale is know so far from the Baltic island of Öland (Table 5). Only at the two smallest grain sizes the similar grasslands of the Baltic island of Saaremaa had higher values. In both cases, the maximum richness values were in communities of the alliance *Tortello tortuosae-Sedion albi* (*Alysso-Sedetalia*; *Sedo-Scleranthenea*, *Koelerio-Corynephoretea*; see Dengler & Löbel 2006, Dengler et al. 2006; Fig. 3). If considering how much vascular and non-vascular plants contribute to overall phytodiversity, it appears that the non-vascular fraction is by far highest in the dry grasslands of the two Baltic islands Öland and Saaremaa in the hemiboreal zone (Table 6). The smallest fraction of non-vascular plants on average was found in the Transylvanian dry grasslands at nearly all grain sizes except the smallest, where Khakassia was the cold spot of this fractional diversity (Table 6).

Discussion

This paper provides the so far most comprehensive overview of plot-scale plant diversity in Palaearctic grasslands from 0.0001 to 100 m² and thus is a valuable reference source for assessing the diversity of a particular grassland stand. While the majority of our datasets are still from dry grasslands (*Festuco-Brometea*, *Koelerio-Corynephoretea*, *Cleistogenetea squarrosae*), we also included several datasets from mesic, wet, acidic, saline, alpine and Mediterranean grasslands. Most importantly, compared to previous overviews such as Wilson et al. (2012) and Chytrý et al. (2015), we provide mean and minimum values, in addition to maxima. While maxima are "exciting", they depend to a significant part on sampling intensity (i.e. the more plots are recorded, the higher the likelihood to find an extremely rich plot) – this is why we also report the number of replicates on which our maxima are based. By contrast, means (unless based on very few and unrepresative plots) are informative irrespective of sample size. While it would be valuable to have such means, they were hardly available before, one exception being the stratified random grassland plots of the Swiss biodiversity monitoring (Koordinationsstelle Biodiversitäts-Monitoring Schweiz 2009): they reported 95% confidence intervals of 25−31, 31−35 and 41−47 vascular plant species on 10 m², for colline, montane and subalpine grasslands, respectively, while the numbers for bryophytes were 2−4, 4−6 and 9−13. This is well within the ranges found in our studies (Tables 3 and 5).

We could only present values for certain plot sizes and did so for a well-established series of grain sizes that are always separated by one order of magnitude as suggested by Peet et al. (1998) and Dengler (2009b). However, the fact that mean species richness (e.g. Dengler & Boch 2008) and maximum species richness (Wilson et al. 2012) follow power-law species-area relationships rather closely at these scale allows an easy and rather precise interpolation to intermediate grain sizes, such as some that are widely used in grassland research, e.g. 4 m², 16 m² or 25 m² (Chytrý & Otýpková 2003). If the target area is A_t, the expected richness S_t can be estimated from the richness values S_1 and S_2 of the next lower and next bigger area A_1 and A_2 as follows:

For example, mean total plant species richness of 50.0 on 10 m² and 73.4 on 100 m² as in Khakassia (Polyakova et al. 2016) would correspond to the following mean richness at 25 m²:

$$S_t = S_1 \left(\frac{A_t}{A_1}\right)^z = S_1 \left(\frac{A_t}{A_1}\right)^{(\log S_2 - \log S_1)}$$

Our paper comprises new world records for vascular plant species richness at 0.0001 m² (9) and at 0.001 m² (19, both shoot presence) from the EDGG Field Workshop in Navarre, Spain (Biurrun et al. 2014) (Table 3). Both are much higher

$$S_{25\,\mathrm{m}^2} = S_{10\,\mathrm{m}^2} \left(\frac{25\ \mathrm{m}^2}{10\ \mathrm{m}^2}\right)^{(\log S_{100\,\mathrm{m}^2} - \log S_{10\,\mathrm{m}^2})} = 50.0 \left(\frac{25\ \mathrm{m}^2}{10\ \mathrm{m}^2}\right)^{(\log(73.4) - \log(50.0))} = 58.3$$

than the old published records (Wilson et al. 2012; Chytrý et al. 2015) of 5 species on 0.0001 m² (+80%) and 12 species on 0.001 m² (+58%). However, at 0.0001 m² the values of Wilson et al. (2012) had already been beaten by the EDGG Research Expeditions in Bulgaria (6 species: Pedashenko et al. 2013) and Ukraine (7 species: Kuzemko et al. 2014), but these records had not been noticed at that time due to the absence of such an overview as the one presented here. With 23 species on 0.01 m² and 34 on 0.1 m², Navarran grasslands are also close to the world records at these scales (25 and 43).

For the first time, we are able to provide mean and maximum richness values for the non-vascular component of grasslands, too. While the partly extraordinarily high small-scale richness of some dry grassland types in bryophytes and lichens was known before (e.g. Dengler 2005), we present now an assessment across various grassland types and regions. The highest richness values at any spatial scale, with maxima about twice as high than in the next-ranked region are found in the dry grasslands of the hemiboreal zone (Öland, Sweden and Saaremaa, Estonia) with extreme values such as 64 species on 10 m² (Table 5). These numbers do not even represent the full bryophyte and lichen richness of these stands because they can contain a significant additional number of saxicolous and epiphytic taxa, which we excluded here to achieve comparability (but see Dengler & Boch 2008). However, the next-richest region in terms of non-vascular plants after the hemiboreal zone turned out to be the Mediterranean and sub-Mediterranean dry grasslands, where we found on 100 m² up to 33 species in Sicily and up to 27 (preliminary count) in Navarre (Table 5). This highlights the great importance of bryophytes and lichens in dry grassland communities, also of southern Europe, where they are usually not considered in phytosociological or biodiversity studies. For considering the relevance of non-vascular plants for total plant species richness of grasslands, the fraction of non-vascular plants is a good parameter. Again the values are highest in the hemiboreal grasslands with a mean of 46% in Saaremaa and 55% in Öland at the 10-m² scale.

Outlook

We hope that the reference data provided here will find wide use and at the same time spur the sampling of similar standardised phytodiversity data from Palaearctic grasslands, but also from other vegetation types and other biogeographic realms. If you have collected similar diversity data in Palaearctic grasslands, matching the methodological standards defined above, and wish to make them freely available to the scientific public (or at least their summary statistics), please submit them in the given format to the first author of this paper. We plan to update the accompanying open access data spread sheet continuously and to publish follow-up articles in peer-reviewed journals once a sufficient number of new datasets have accumulated.

The next EDGG Field Workshops are planned for Central Italy in 2017 (see page 3 in this issue), and preliminarily envisaged for the Eastern valleys of the Alps in 2018 as well as for Armenia in 2019. People interested in joining the EDGG or participating in an EDGG Field Workshop are invited to contact the two first authors of this paper. The ultimate goal of the EDGG Field Workshops is, of course, not only data collection and provision (as here), but also data analysis. There is already a series of papers analysing biodiversity patterns and their drivers within single study areas (Turtureanu et al. 2014; Kuzemko et al. 2016; Polyakova et al. 2016). For the future, however, we also plan to use the combined wealth of data from the EDGG Field Workshops and related sampling approaches to conduct multiple-site analyses of species, phylogenetic and functional diversity as well as community assembly patterns and their drivers, which will strongly benefit from the fact that in each 10-m² plot we also recorded a set of standardised soil and other environmental parameters. Suggestions for such paper projects to the team of data originators are welcome.

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Author contributions

J.D. "invented" the EDGG Field Workshops in 2009 and since then is responsible for them in his function as EDGG Field Workshop Coordinator, supported by I.B. as his Deputy. J.D. also conceived the idea of this paper, planned it and wrote the first draft, which was then revised by the co-authors. H.P. prepared the map. All co-authors contributed significantly to the data underlying this paper, be it as organiser or regular participant of EDGG Field Workshops, as originator of other included studies or as bryophyte and lichen specialist who helped to determine collected material.

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