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SPECIAL FEATURE: MACROECOLOGY OF VEGETATION

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Benchmarking plant diversity of Palaearctic grasslands and other open habitats

Idoia Biurrun[1] | Remigiusz Pielech[2,3] | Iwona Dembicz[4,5] | François Gillet[6] | Łukasz Kozub[4] | Corrado Marcenò[1,7] | Triin Reitalu[8] | Koenraad Van Meerbeek[9] | Riccardo Guarino[10] | Milan Chytrý[7] | Robin J. Pakeman[11] | Zdenka Preislerová[7] | Irena Axmanová[7] | Sabina Burrascano[12] | Sándor Bartha[13] | Steffen Boch[14] | Hans Henrik Bruun[15] | Timo Conradi[16] | Pieter De Frenne[17] | Franz Essl[18] | Goffredo Filibeck[19] | Michal Hájek[7] | Borja Jiménez-Alfaro[20] | Anna Kuzemko[21] | Zsolt Molnár[13] | Meelis Pärtel[22] | Ricarda Pätsch[23] | Honor C. Prentice[24] | Jan Roleček[25] | Laura M. E. Sutcliffe[26] | Massimo Terzi[27] | Manuela Winkler[28,29] | Jianshuang Wu[30] | Svetlana Aćić[31] | Alicia T. R. Acosta[32] | Elias Afif[33] | Munemitsu Akasaka[34] | Juha M. Alatalo[35] | Michele Aleffi[36] | Alla Aleksanyan[37] | Arshad Ali[38] | Iva Apostolova[39] | Parvaneh Ashouri[40] | Zoltán Bátori[41] | Esther Baumann[42] | Thomas Becker[43] | Elena Belonovskaya[44] | José Luis Benito Alonso[45] | Asun Berastegi[46] | Ariel Bergamini[14] | Kuber Prasad Bhatta[47] | Ilaria Bonini[48] | Marc-Olivier Büchler[5] | Vasyl Budzhak[49] | Álvaro Bueno[50] | Fabrizio Buldrini[51] | Juan Antonio Campos[1] | Laura Cancellieri[19] | Marta Carboni[32] | Tobias Ceulemans[52] | Alessandro Chiarucci[51] | Cristina Chocarro[55] | Luisa Conti[32,53,54] | Anna Mária Csergő[56] | Beata Cykowska-Marzencka[5,57] | Marta Czarniecka-Wiera[58,59] | Marta Czarnocka-Cieciura[60] | Patryk Czortek[61] | Jiří Danihelka[7,62] | Francesco de Bello[63] | Balázs Deák[64] | László Demeter[65] | Lei Deng[66] | Martin Diekmann[67] | Jiri Dolezal[62,68] | Christian Dolnik[69] | Pavel Dřevojan[7] | Cecilia Dupré[67] | Klaus Ecker[14] | Hamid Ejtehadi[70] | Brigitta Erschbamer[71] | Javier Etayo[72] | Jonathan Etzold[73] | Tünde Farkas[74] | Mohammad Farzam[75] | George Fayvush[37] | María Rosa Fernández Calzado[76] | Manfred Finckh[77] | Wendy Fjellstad[78] | Georgios Fotiadis[79] | Daniel García-Magro[1] | Itziar García-Mijangos[1] | Rosario G. Gavilán[80] | Markus Germany[81] | Sahar Ghafari[82] |

[†]Deceased 29 November 2019

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[1]Department of Plant Biology and Ecology, University of the Basque Country UPV/EHU, Bilbao, Spain

[2]Department of Forest Biodiversity, Faculty of Forestry, University of Agriculture in Krakow, Krakow, Poland

[3]Foundation for Biodiversity Research, Wrocław, Poland

[4]Department of Ecology and Environmental Conservation, Institute of Environmental Biology, Faculty of Biology, University of Warsaw, Warsaw, Poland

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[5]Vegetation Ecology Group, Institute of Natural Resource Sciences (IUNR), Zurich University of Applied Sciences (ZHAW), Wädenswil, Switzerland
[6]UMR Chrono-environnement, Université Bourgogne Franche-Comté, Besançon, France
[7]Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic
[8]Institute of Geology, Tallinn University of Technology, Tallinn, Estonia
[9]Division of Forest, Nature and Landscape, Department of Earth and Environmental Sciences, KU Leuven, Leuven, Belgium
[10]Department of STEBICEF - Botanical Unit, Università degli studi di Palermo, Palermo, Italy
[11]Ecological Sciences, The James Hutton Institute, Aberdeen, UK
[12]Department of Environmental Biology, Sapienza University of Rome, Rome, Italy
[13]Institute of Ecology and Botany, Centre for Ecological Research, Vácrátót, Hungary
[14]Biodiversity & Conservation Biology, WSL Swiss Federal Research Institute, Birmensdorf, Switzerland
[15]Section for Ecology and Evolution, Department of Biology, University of Copenhagen, Copenhagen, Denmark
[16]Plant Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany
[17]Forest & Nature Lab., Ghent University, Gontrode, Belgium
[18]Division of Conservation Biology, Vegetation and Landscape Ecology, Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria
[19]Department of Agricultural and Forest Sciences (DAFNE), University of Tuscia, Viterbo, Italy
[20]Research Unit of Biodiversity (CSIC, UO, PA), Oviedo University, Mieres, Spain
[21]Geobotany and Ecology Department, M.G. Kholodny Institute of Botany NAS of Ukraine, Kiev, Ukraine
[22]Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia
[23]Wagner Ecology Lab, Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada
[24]Department of Biology, Lund University, Lund, Sweden
[25]Institute of Botany, Department of Paleoecology, Czech Academy of Sciences, Brno, Czech Republic
[26]Plant Ecology and Ecosystem Research, Georg-August University of Göttingen, Göttingen, Germany
[27]Institute of Biosciences and Bioresources (IBBR), Italian National Council of Research (CNR), Bari, Italy
[28]GLORIA co-ordination, Institute for Interdisciplinary Mountain Research, Austrian Academy of Sciences, Vienna, Austria
[29]GLORIA co-ordination, Department of Integrative Biology and Biodiversity Research, University of Natural Resources and Life Sciences Vienna (BOKU), Vienna, Austria
[30]Institute of Environment and Sustainable Development in Agriculture, Chinese Academy of Agricultural Sciences, Beijing, China
[31]Department of Botany, Faculty of Agriculture, University of Belgrade, Belgrade-Zemun, Serbia
[32]Department of Science, Roma Tre University, Rome, Italy
[33]Department of Organisms and Systems Biology, Polytechnic School of Mieres, Oviedo University, Mieres, Spain
[34]Institute of Agriculture, Tokyo University of Agriculture and Technology, Tokyo, Japan
[35]Environmental Science Center, Qatar University, Doha, Qatar
[36]School of Biosciences and Veterinary Medicine, University of Camerino, Camerino, Italy
[37]Department of Geobotany and Plant Eco-Physiology, Institute of Botany aft. A.L. Takhtajyan NAS RA, Yerevan, Armenia
[38]Forest Ecology Research Group, College of Life Sciences, Hebei University, Baoding, Hebei, China
[39]Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria
[40]Agricultural Research, Education and Extension Organization (AREEO), Research Institute of Forests & Rangelands, Tehran, Iran
[41]Department of Ecology, University of Szeged, Szeged, Hungary
[42]Biogeography, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany
[43]Geobotany, Regional and Environmental Sciences, University of Trier, Trier, Germany
[44]Institute of Geography, Russian Academy of Sciences, Moscow, Russia
[45]JOLUBE Consultor Botánico, Jaca, Spain
[46]Department of Biodiversity, Environmental Management of Navarre, Pamplona-Iruña, Spain
[47]Department of Biological Sciences, University of Bergen, Bergen, Norway
[48]Department of Life Sciences, University of Siena, Siena, Italy
[49]Botany, Forestry and Horticulture, Yuriy Fedkovych Chernivtsi National University, Chernivtsy, Ukraine
[50]Instituto de Recursos Naturales y Ordenación del Territorio (INDUROT), Universidad de Oviedo, Mieres, Spain
[51]Department of Biological, Geological and Environmental Sciences (BiGeA), University of Bologna, Bologna, Italy
[52]Plant Conservation and Population Biology, Department of Biology, Leuven University, Leuven, Belgium
[53]Department of Crop and Forest Science, Universitat de Lleida, Lleida, Spain
[54]Institute of Botany, Czech Academy of Sciences, Třeboň, Czech Republic
[55]Faculty of Environmental Sciences, University of Life Sciences Prague, Praha-Suchdol, Czech Republic
[56]Department of Botany, Hungarian University of Agriculture and Life Sciences, Budapest, Hungary

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[57]Department of Mycology, W. Szafer Institute of Botany, Polish Academy of Sciences, Krakow, Poland

[58]Department of Nature Protection and Rural Landscape, Institute of Technology and Life Sciences, Falenty, Poland

[59]Botanical Garden, University of Wrocław, Wrocław, Poland

[60]Laboratory of Statistical Analysis, National Information Processing Institute, Warsaw, Poland

[61]Białowieża Geobotanical Station, Faculty of Biology, University of Warsaw, Białowieża, Poland

[62]Institute of Botany, Czech Academy of Sciences, Průhonice, Czech Republic

[63]Desertification Research Centre (CIDE), Universitat de València & CSIC, Moncada, Spain

[64]Lendület Seed Ecology Research Group, Centre for Ecological Research, Institute of Ecology and Botany, Vácrátót, Hungary

[65]Department of Harghita County, National Agency for Protected Areas, Miercurea-Ciuc, Romania

[66]Institute of Soil and Water Conservation, State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Northwest A&F University, Yangling, China

[67]Vegetation Ecology and Conservation Biology, Institute of Ecology, FB 2, University of Bremen, Bremen, Germany

[68]Department of Botany, Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic

[69]Department of Landscape Ecology, Institute for Natural Resource Conservation, Kiel University, Kiel, Germany

[70]Department of Biology, Ferdowsi University of Mashhad, Mashhad, Iran

[71]Department of Botany, University of Innsbruck, Innsbruck, Austria

[72]Department of Biology and Geology, I.E.S. Zizur Institute, Pamplona, Spain

[73]ESTOK UG, Bernau (bei Berlin), Germany

[74]Aggtelek National Park Directorate, Jósvafő, Hungary

[75]Department of Range and Watershed Management, Ferdowsi University of Mashhad, Mashhad, Iran

[76]Department of Botany, Faculty of Pharmacy, University of Granada, Granada, Spain

[77]Biodiversity, Evolution and Ecology of Plants (BEE), Institute of Plant Science and Microbiology (IPM), University of Hamburg, Hamburg, Germany

[78]Department of Landscape Monitoring, Norwegian Institute of Bioeconomy Research, Ås, Norway

[79]Department of Forestry and Natural Environment Management, Agricultural University of Athens, Karpenisi, Greece

[80]Department of Pharmacology, Pharmacognosy and Botany, Pharmacy, Complutense University, Madrid, Spain

[81]Institute for Ecosystem Research, Kiel University, Kiel, Germany

[82]Department of Range and Watershed Management, University of Mohaghegh Ardabili, Ardabil, Iran

[83]Department of Biological, Geological and Environmental Sciences, University of Catania, Catania, Italy

[84]Biology Education, Dokuz Eylul University, Buca, İzmir, Turkey

[85]Department of Biodiversity, Ecology and Evolution, Complutense University, Madrid, Spain

[86]Disturbance Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany

[87]Department of Environmental and Bioscience, Rydberg Laboratory of Applied Science, Halmstad University, Halmstad, Sweden

[88]Geobotany and Botanical Garden, Institute of Biology, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany

[89]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[90]Institute of Botany, Plant Science and Biodiversity Center, Slovak Academy of Sciences, Banská Bystrica, Slovakia

[91]Agroscope, Research Division Agroecology and Environment, Zurich, Switzerland

[92]Plant Ecology and Nature Conservation, University of Potsdam, Potsdam, Germany

[93]Applied Plant Ecology, Biocentre Klein Flottbek, University of Hamburg, Hamburg, Germany

[94]Asian Demographic Research Institute, Shanghai University, Shanghai, China

[95]Natural Resources and Watershed Management Administration of Alborz Province, Karaj, Iran

[96]Vegetation Ecology and Botany, Faculty of Agricultural Sciences and Landscape Architecture, Osnabrück University of Applied Sciences, Osnabrück, Germany

[97]Center for Biodiversity, Forestry and Forest Products Research Institute, Tsukuba, Japan

[98]Stiftung Naturschutzfonds Brandenburg, Potsdam, Germany

[99]Laboratory of Plant Systematics and Phytogeography, Department of Biology, University of Florence, Florence, Italy

[100]School of Forestry and Resource Conservation, National Taiwan University, Taipei, Taiwan

[101]Ministry of Education Key Laboratory of Ecology and Resource Use of the Monoglian Plateau & School of Ecology and Environment, Inner Mongolia University, Hohhot, China

[102]Department of Physical Geography, Stockholm University, Stockholm, Sweden

[103]Landscape Ecology and Environmental Systems Analysis, Institute of Geoecology, TU Braunschweig, Braunschweig, Germany

[104]Research Centre in Biodiversity and Genetic Resources (CIBIO) - Research Network in Biodiversity and Evolutionary Biology (InBIO), University of Porto, Vairão, Vila do Conde, Portugal

[105]Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos, Móstoles, Spain

[106]Institute of Biology, Department of Plant Sciences, University of Graz, Graz, Austria

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[107]Department of Botany, University of Wrocław, Wrocław, Poland
[108]Botanical Garden of Medicinal Plants, Wrocław Medical University, Wrocław, Poland
[109]Institute of Botany and Landscape Ecology, Greifswald University, Greifswald, Germany
[110]Anastasie Fatu Botanical Garden, Alexandru Ioan Cuza University of Iași, Iași, Romania
[111]Theoretical Ecology, Institute of Biology, Freie Universität Berlin, Berlin, Germany
[112]Department of Botany, Research Center for Plant Sciences, Ferdowsi University of Mashhad, Mashhad, Iran
[113]Department of Industrial Economics and Technology Management, Norwegian University of Science and Technology, Trondheim, Norway
[114]Department of Plant Science, School of Biology, College of Science, University of Tehran, Tehran, Iran
[115]Department of Botany, Kherson State University, Kherson, Ukraine
[116]Department of Plant Biology, Faculty of Basic Sciences, University of Mazandaran, Babolsar, Iran
[117]Department of Evolutionary Biology, Ecology and Environmental Sciences, Faculty of Biology, University of Barcelona, Barcelona, Spain
[118]Institute of Botany, Jagiellonian University, Krakow, Poland
[119]Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria
[120]Botanical Garden Center for Biological Diversity Conservation in Powsin, Polish Academy of Sciences, Warsaw, Poland
[121]Institute of Biology, University of Opole, Opole, Poland
[122]Ecology and Plant Geography, Lomonosov Moscow State University, Moscow, Russia
[123]National Museum of Natural History, Bulgarian Academy of Sciences, Sofia, Bulgaria
[124]Department of Biology, University of North Carolina, Chapel Hill, North Carolina, USA
[125]Department of Biosciences, Faculty of Sciences and Technology, University of Vic - Central University of Catalonia, Vic, Barcelona, Spain
[126]Michael-Succow-Foundation, Greifswald, Germany
[127]Biology Department, Faculty of Natural Sciences and Mathematics, University of Maribor, Maribor, Slovenia
[128]Department of Botany, School of Biology, Aristotle University of Thessaloniki, Thessaloniki, Greece
[129]School of Agricultural, Forest, Food and Environmental Sciences, University of Basilicata, Potenza, Italy
[130]Institute of Environmental Sciences, University of Castilla-La Mancha, Toledo, Spain
[131]Department of Zoology and Animal Ecology, V.N. Karazin Kharkiv National University, Kharkiv, Ukraine
[132]Hungarian Department of Biology and Ecology, Babeș-Bolyai University, Cluj-Napoca, Romania
[133]Faculty of Geography and Earth Sciences, University of Latvia, Riga, Latvia
[134]Institute for Botany and Botanical Garden "Jevremovac", Faculty of Biology, University of Belgrade, Belgrade, Serbia
[135]CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, China
[136]Group GAMES and Department of Horticulture, Botany and Landscaping, University of Lleida, Lleida, Spain
[137]Centre for Applied Ecology “Professor Baeta Neves”, CEABN/InBIO, School of Agriculture, University of Lisbon, Lisbon, Portugal
[138]Department of Ecology, University of Debrecen, Debrecen, Hungary
[139]MTA-DE Lendület Functional and Restoration Ecology Research Group, Debrecen, Hungary
[140]Department of Ecology, Centro de Investigaciones Sobre Desertificación (CSIC-UV-GV), Moncada, Valencia, Spain
[141]Department of Geobotany and Plant Ecology, University of Łódź, Łódź, Poland
[142]Lancaster Environment Centre, Lancaster University, Lancaster, United Kingdom
[143]Institute for Alpine Environment, Eurac Research, Bolzano, Italy
[144]The Franciszek Górski Institute of Plant Physiology, Polish Academy of Sciences, Krakow, Poland
[145]Faculty of Natural Sciences, Matej Bel University in Banská Bystrica, Banská Bystrica, Slovakia
[146]Graduate School of Human Development and Environment, Kobe University, Kobe, Japan
[147]PXL Bio-Research, PXL University of Applied Sciences and Arts, Diepenbeek, Belgium
[148]Department of Chemistry, Biology and Biotechnologies, Vasul’ Stus Donetsk National University, Vinnytsia, Ukraine
[149]Instituto Pirenaico de Ecología IPE-CSIC, Consejo Superior de Investigaciones Científicas, Jaca, Huesca, Spain
[150]Ecology & Genetics, University of Oulu, Oulu, Finland
[151]Department of Agricultural Botany, Faculty of Agriculture, University of Zagreb, Zagreb, Croatia
[152]Department of Botany, Eszterházy Károly University of Applied Sciences, Eger, Hungary
[153]Department of Botany, Senckenberg Museum of Natural History Görlitz, Görlitz, Germany
[154]Technische Universität Dresden, International Institute Zittau, Zittau, Germany
[155]School of Natural Sciences, Trinity College Dublin, The University of Dublin, Dublin, Ireland
[156]Life Science Center Weihenstephan, Technical University of Munich, Freising, Germany
[157]Institute for Organic Farming, Soil and Resource Management, Bavarian State Research Center for Agriculture, Freising, Germany
[158]Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, Taiwan

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Correspondence
Idoia Biurrun, Department of Plant Biology and Ecology, University of the Basque Country UPV/EHU, Bilbao, Spain.
Email: idoia.biurrun@ehu.es

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Abstract

Aims: Understanding fine-grain diversity patterns across large spatial extents is fundamental for macroecological research and biodiversity conservation. Using the GrassPlot database, we provide benchmarks of fine-grain richness values of Palaearctic open habitats for vascular plants, bryophytes, lichens and complete vegetation (i.e., the sum of the former three groups).

Location: Palaearctic biogeographic realm.

Methods: We used 126,524 plots of eight standard grain sizes from the GrassPlot database: 0.0001, 0.001, 0.01, 0.1, 1, 10, 100 and 1,000 m^2 and calculated the mean richness and standard deviations, as well as maximum, minimum, median, and first and third quartiles for each combination of grain size, taxonomic group, biome, region, vegetation type and phytosociological class.

Results: Patterns of plant diversity in vegetation types and biomes differ across grain sizes and taxonomic groups. Overall, secondary (mostly semi-natural) grasslands and natural grasslands are the richest vegetation type. The open-access file "GrassPlot Diversity Benchmarks" and the web tool "GrassPlot Diversity Explorer" are now available online (https://edgg.org/databases/GrasslandDiversityExplorer) and provide more insights into species richness patterns in the Palaearctic open habitats.

Conclusions: The GrassPlot Diversity Benchmarks provide high-quality data on species richness in open habitat types across the Palaearctic. These benchmark data can be used in vegetation ecology, macroecology, biodiversity conservation and data quality checking. While the amount of data in the underlying GrassPlot database and their spatial coverage are smaller than in other extensive vegetation-plot databases, species recordings in GrassPlot are on average more complete, making it a valuable complementary data source in macroecology.

KEYWORDS
benchmark, bryophyte, fine-grain biodiversity, grassland, GrassPlot Diversity Explorer, lichen, open habitat, Palaearctic, scale dependence, species–area relationship, vascular plant, vegetation plot

1 | INTRODUCTION

Documenting and understanding patterns of biodiversity is a central issue in biogeography and macroecology (Gaston, 2000; Barthlott et al., 2007; Pärtel et al., 2016) and is also fundamental for sustainable land use and biodiversity conservation (Whittaker et al., 2015), as ecosystem function and stability are dependent on biodiversity (Tilman & Downing, 1994; Hooper et al., 2005). The increasing awareness of the current environmental crisis makes biodiversity studies even more valuable and necessary, especially for ecosystems such as grasslands, which are massively threatened by land-use change (Fischer et al., 2018). Plant species richness has been mapped globally using coarse-grain data (Barthlott et al., 2005; Kier et al., 2005; Brummit et al., 2020). However, fine-grain data on the local co-occurrence of species in plant communities across continental or global spatial extents are required for macroecological studies that link diversity patterns and assembly processes (Bruelheide et al., 2019). Nevertheless, information on broad-scale, fine-grain plant distribution is still scattered, inconsistent, and often of uncertain quality, especially for bryophytes and lichens (Beck et al., 2012).

Vegetation plots stored in large databases (e.g., European Vegetation Archive, EVA, Chytrý et al., 2016; sPlot, Bruelheide et al., 2019) are increasingly used to explore fine-grain plant diversity patterns and underlying assembly processes at continental to global extents (Bruelheide et al., 2018; Večeřa et al., 2019; Axmanová et al., 2021). The use of vegetation plots also allows the identification of regions with high fine-grain α-diversity for particular habitats, called richness hotspots (Divíšek & Chytrý, 2018; Večeřa et al., 2019). However, it should be considered that vegetation plots derived from phytosociological sampling may vary in plot size by several orders of magnitude, even within the same vegetation type (Chytrý, 2001). Sometimes information on plot size may be lacking or only

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approximate. Therefore, diversity inference from phytosociological data has to consider plot sizes and should be interpreted with caution (Chytrý, 2001; Chytrý & Otýpková, 2003).

Ecologists and conservationists need reliable species richness benchmarks (i.e., maximum, minimum, mean and other basic statistics) to assess plant communities as being above or below average in richness for a specific region or vegetation type (Yen et al., 2019). To produce reliable benchmarks, plot size should be integrated into any analysis, and large amounts of high-quality vegetation-plot data are needed. Previous studies providing global richness data at several plot sizes focused on maximum values and left out information on the distribution of richness values (Wilson et al., 2012; Chytrý et al., 2015). This information is needed for both fundamental research and biodiversity conservation (Dengler et al., 2016a; Yen et al., 2019), e.g., when establishing thresholds between average and species-rich grasslands or identifying species-poor degraded grasslands for restoration.

Palaearctic grasslands host a considerable part of the realm's diversity (Dengler et al., 2020a). At fine spatial grains (<100 m^2), they can even hold higher plant diversity than tropical forests (Wilson et al., 2012). After an early and rudimentary attempt of benchmarking grassland diversity globally (Faber-Langendoen & Josse, 2010), Dengler et al. (2016a) provided a first overview of benchmarking plant diversity of Palaearctic grasslands based on a relatively small data set.

Here, we use GrassPlot, the database of multi-scale plant diversity in Palaearctic grasslands (https://edgg.org/databases/GrassPlot; Dengler et al., 2018) to provide comprehensive benchmarks of fine-grain plant richness values of Palaearctic open habitats across biomes at eight plot sizes, each separated by an order of magnitude: 0.0001, 0.001, 0.01, 0.1, 1, 10, 100 and 1,000 m^2. We aim to display hotspots and coldspots of fine-grain α-diversity (species richness) across biomes and vegetation types. Besides total plant richness (complete vegetation), we separately assess vascular plant, bryophyte and lichen richness, as it has been already demonstrated that the richness of these taxonomic groups should be assessed separately (Dengler et al., 2016a). In summary, we: (a) present major diversity patterns in Palaearctic open habitats that can be derived from GrassPlot; (b) introduce the GrassPlot Diversity Benchmarks (a data set made public together with this article) and the GrassPlot Diversity Explorer (an online tool released together with this article); and (c) outline some potential applications and impacts of both.

2 | METHODS

2.1 | Data compilation

We used plot-based data from the collaborative vegetation database GrassPlot (Dengler et al., 2018; https://edgg.org/databases/GrassPlot), affiliated to the Eurasian Dry Grassland Group (EDGG), and registered in the Global Index of Vegetation-Plot Databases (EU-00-003; GIVD; Dengler et al., 2011). GrassPlot incorporates standardized vegetation-plot data sampled in precisely delimited plots together with methodological, environmental and structural information from open habitats, e.g., grasslands and other plant communities dominated by herbs, dwarf-shrubs or cryptogams from the Palaearctic biogeographic realm (i.e., Europe, North Africa, and West, Central, North and East Asia). Besides individual plots, GrassPlot specifically contains multi-scale data sets from nested-plot sampling schemes (e.g., Dengler et al., 2016b) with plot sizes ranging from 0.0001 m^2 to 1,024 m^2. The last published version of the database (GrassPlot v.2.00; Biurrun et al., 2019) contained more than 190,000 plots of different grain sizes across 22,422 individual plots and 5,749 nested-plot series with at least two grain sizes.

For this benchmarking study, we retrieved all plots with grain sizes 0.0001, 0.001, 0.01, 0.1, 1, 10, 100 and 1,000 m^2 contained in GrassPlot v.2.10 (version of 1 Oct 2020), belonging to 225 data sets (Appendix S1). According to the typical species–area relationships (SARs) in Palaearctic grasslands (Dengler et al., 2020b), 10% difference in the area means only about 2% difference in richness or less, which is negligible compared to any other source of richness variation. Thus, 2,372 plots deviating less than 10% from standard grain sizes (0.0009, 0.09, 9, 10.89, 900 and 1,024 m^2) were also selected and used for the benchmarks of the respective grain size. The final data set contained 126,524 plots (Table 1) distributed across 49 countries (Appendix S2), eight biomes throughout the Palaearctic realm and a wide range of open habitats, such as grasslands, dwarf shrublands, wetlands, and deserts (Figure 1, Appendix S2).

Biomes were assigned using the biome classification provided in Bruelheide et al. (2019), which is based on the nine ecozones of Schultz (2005) plus an additional alpine biome based on Körner et al. (2017). Plots were also assigned to ten geographic regions following Dengler et al. (2020a). We created a two-level vegetation typology with 22 vegetation types grouped into six coarse categories: natural grasslands, secondary grasslands, azonal communities, dwarf shrublands, tall-forb and ruderal communities and deserts and semi-deserts (more details in Appendix S2). Plots were assigned to vegetation types based on expert knowledge either individually by data owners or using general assignment rules of phytosociological syntaxa to vegetation types (see Appendix S2). Among the plots in the data set, 75% have a phytosociological assignment at least at the class level.

GrassPlot includes plot data sampled following two alternative methods for recording the presence of vascular plant species: "rooted presence", which only records individuals as present in the plot if they root inside, and "shoot presence", which records individuals as present if any part of stems or leaves are inside the plot (Dengler, 2008). The majority of plots in the data set were recorded using the "shoot presence" method, and 13.4% of plots used "rooted presence", while only a small fraction (0.1%) used a combined method, where shrubs were recorded using "rooted presence" and grasses and forbs using the "shoot presence", or the recording method was not known (0.2%).

For linguistic convenience, we include lichens under the generic term "plants". Thus, we considered four taxonomic groups: vascular

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plants, bryophytes, lichens and complete vegetation (i.e., the sum of the former three groups).

2.2 | Establishing and providing benchmark values

We calculated mean species richness values and standard deviations, as well as maximum, minimum, median, and first and third quartiles for each combination of grain size, taxonomic group, biome, region, country, vegetation type (at coarse and fine classification level), phytosociological class and method (shoot vs rooted, nested series with seven standard grain sizes vs any plots). The data are organized as a spreadsheet, in which each of the 728,396 lines represents one combination of these factors, and the columns provide the statistics, i.e., number of plots, number of independent observations, minimum, maximum, mean, standard deviation, median, and first and third quartiles. We call these data the GrassPlot Diversity Benchmarks and provide them in Appendix S3 in the Supporting Information as a spreadsheet file (70 MB). This file is open access and is also provided on the website of the GrassPlot Diversity Explorer (https://edgg.org/databases/GrasslandDiversityExplorer) for free download. We intend to update it at regular intervals while keeping former versions available to make any studies based on these data reproducible.

Many nested series contain several subplots of the same size. Sometimes these are multiple contiguous subplots covering the entire surface of the largest plot. Because of a high degree of spatial pseudoreplication, using these richness values separately for calculating mean richness might bias the results. Thus, for all benchmarks, except for the maximum and minimum richness, we used the averaged values of each grain size in each nested series, i.e., only the independent observations. The number of independent observations decreased from 126,524 to 48,449 plots (Table 1), 6,509 of them belonging to nested series with at least seven of our standard grain sizes, 16,499 belonging to nested series with less than seven standard sizes, and 25,441 individual plots. In the data set containing only independent observations, the percentage of plots using "rooted presence" rose from 13.4 to 23.4%.

We also added two filtering options as they can have significant effects on resulting richness patterns. (a) We allow filtering for data that were sampled with "rooted presence" or "shoot presence". As has been shown theoretically (Williamson, 2003) and empirically (Güler et al., 2016; Cancellieri et al., 2017; Zhang et al., 2021), species richness recorded with the rooted method deviates increasingly negatively from values recorded with the shoot-presence method as grain size decreases. (b) Subsetting to only those plots belonging to nested series with at least the seven "EDGG standard grain sizes" (0.0001 m^2 to 100 m^2; see Dengler et al., 2016b) is also possible. This function can be important when analyzing SARs, which otherwise might be distorted by uneven representation of different grain sizes in specific regions.

2.3 | Richness hotspots

In this study we aim at identifying fine-grain α-diversity hotspots (hereafter, richness hotspots). These richness hotspots are different from the biodiversity hotspots of Myers et al. (2000), who emphasized a concentration of endemic species in larger regions combined with severe habitat loss. Other criteria such as the number of rare or threatened species and total species richness are also currently used to identify these hotspots; moreover, this term is now most commonly used with reference to regions of high species richness (Reid, 1998). Another difference with the most widely used concept of the biodiversity hotspot is that we are using fine-grain resolution (plot level, e.g., lower than 1 km^2), while most studies identify hotspots using coarse-grain resolution maps, generally at 10,000 km^2 (Küper et al., 2005) or even coarser (Myers et al., 2000).

2.4 | Development of the GrassPlot Diversity Explorer

The GrassPlot Diversity Explorer (https://edgg.org/databases/GrasslandDiversityExplorer) was developed to provide a dynamic version

TABLE 1 The number of available plots per taxonomic group and grain sizes. Standard sizes are indicated; 0.001 m^2 also includes 0.0009 m^2; 0.1 m^2 includes 0.09 m^2; 10 m^2 includes 9 and 10.89 m^2; and 1,000 m^2 includes 900 and 1,024 m^2. N_{all} = total number of plots. $N_{ind.}$ = number of independent observations, i.e., after averaging several subplots of the same grain size in the same nested series

	All groups		Vascular plants		Bryophytes		Lichens	
Grain size [m^2]	N_{all}	$N_{ind.}$	N_{all}	$N_{ind.}$	N_{all}	$N_{ind.}$	N_{all}	$N_{ind.}$
0.0001	1,959	774	2,904	1,440	1,973	781	1,959	774
0.001	1,900	707	4,341	1,727	1,914	714	1,900	707
0.01	2,653	877	70,548	4,875	2,688	905	6,820	1,876
0.1	1,925	717	5,756	3,788	1,939	724	1,925	717
1	2,821	1,583	25,432	20,500	3,044	1,799	3,002	1,764
10	2,924	2,171	11,035	9,658	4,599	3,839	2,925	2,172
100	1,336	1,316	6,321	6,274	1,363	1,343	1,436	1,416
1,000	45	45	187	187	45	45	45	45
All sizes	15,563	8,190	126,524	48,449	17,565	10,150	20,012	9,471

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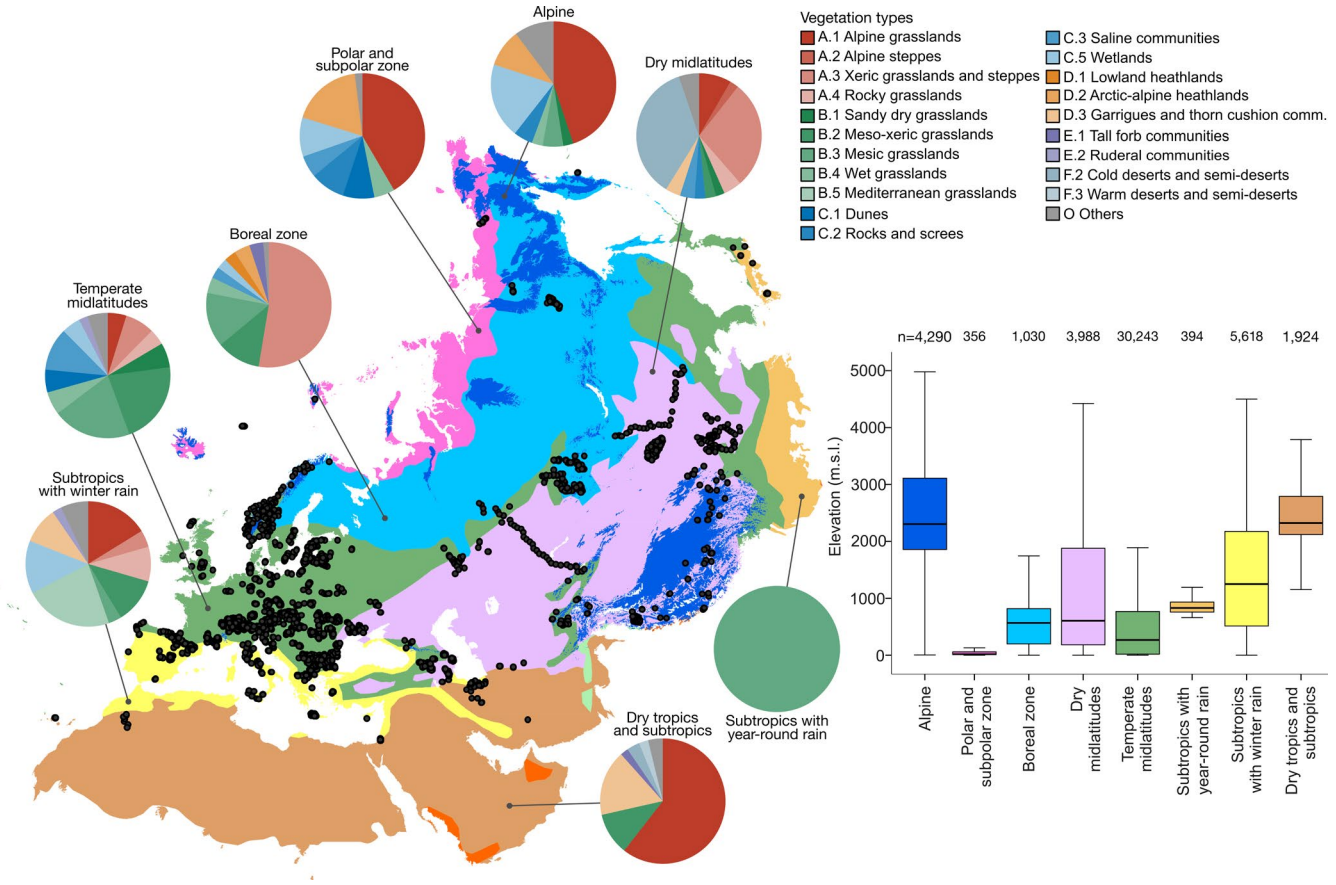

FIGURE 1 Distribution of plots in the Palaearctic realm. Biomes are shown in different colours, pie-charts show the fraction of vegetation types represented by the plots (black dots) included in each biome. The category "Others" includes vegetation types represented by <2% plots in each particular biome. C.4 Saline steppes and semi-deserts and F.1 Alpine deserts do not reach this threshold in any biome. The box plots show the elevation distribution of plots across biomes, with the number of plots (*n*) above each bar. To fill in the Arabian Peninsula, the biome Tropics with summer rain is indicated in orange colour although GrassPlot does not contain any data from this biome

of the GrassPlot Diversity Benchmarks. We did this in R version 4.0.2 (R Core Team, 2020), using the *shiny* package (Chang et al., 2020). We also used other R packages, including *tidyr* and *dplyr* for data preparation (Wickham & Henry, 2020; Wickham et al., 2020), *ggplot2*, *ggpubr* and *sunburstR* for visualization of the outcomes (Wickham, 2016; Bostock et al., 2020; Kassambara, 2020), *summarytools* for generating summary statistics (Comtois, 2020), *leaflet* for producing an interactive map (Cheng et al., 2019), and *shinyWidgets* and *shinycssloaders* to increase the functionality of the shiny package (Perrier et al., 2020; Sali & Attali, 2020). The GrassPlot Diversity Explorer was then deployed on a dedicated server using the *rsconnect* package (Allaire, 2019).

3 | RESULTS

3.1 | GrassPlot Diversity Benchmarks

Richness hotspots of vascular plants in grasslands and other open habitats are scattered across the Palaearctic. However, they may vary across grain sizes, both regarding mean richness (Figure 2) and maximum richness (Appendix S4). Richness hotspots also change according to vegetation type and taxonomic group (Appendix S4). Maximum richness hotspots of bryophytes, lichens and complete vegetation also vary with grain size (Appendix S4).

Patterns of plant diversity in vegetation types differ across grain sizes (Figure 3) and taxonomic groups (Figure 4). Secondary grasslands show the highest mean richness of vascular plants across the smallest sizes, but natural grasslands are equally diverse in the largest ones (Figure 3); this pattern is found in both the plots recorded using "rooted presence" and "shoot presence" if they are analyzed separately (Appendix S5). Plant diversity patterns in biomes are even more dependent on grain size, with the highest means in the boreal biome at 0.01 m^2 and 10 m^2 (Figure 3). More detailed results on richness patterns across grain sizes for the combination of biomes and coarse-level vegetation types are shown in Appendix S5. This inconsistency of diversity patterns across grain sizes and taxonomic groups is even more evident if we use a fine-level vegetation typology (Appendix S5), although some patterns emerge, such as meso-xeric grasslands showing the highest mean richness for vascular plants across most grain sizes. The mean richness of bryophytes, lichens and complete vegetation strongly vary with

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grain size. In addition to arctic-alpine heathlands, sandy dry grasslands, rocky grasslands and mesic grasslands show the highest values, as well as several azonal communities such as saline, rocks and screes, and wetlands (Appendix S5). Maximum richness corresponds to secondary grasslands across most grain sizes, but once again, the pattern changes for bryophytes and lichens, with maxima often in natural grasslands (Table 2). As regards biomes, the maximum richness slightly changes across grain sizes and taxonomic groups, although the temperate mid-latitudes hold most of the maxima for all taxonomic groups (Appendix S5).

Species–area relationships of the six best-represented grassland types show similar patterns for vascular plants and complete vegetation, both with a continuous upward curvature in the semi-log space (Figure 5). Meso-xeric grasslands show the highest means across grain sizes, both for vascular plants and for complete vegetation, while sandy dry grasslands are the poorest type. Alpine grasslands outperform meso-xeric grasslands for complete vegetation at smallest sizes due to the strong richness increase related to the inclusion of non-vascular plants. The relative importance of this fraction in the total richness is even stronger for sandy dry grasslands and Mediterranean grasslands, the latter reaching the second position in the richness ranking for the largest sizes. Appendix S5 combines SARs generated with all GrassPlot data with SARs corresponding to the subset of plots belonging to nested series with seven standard grain sizes for all fine-level vegetation types and the four taxonomic groups. In most cases, lines of SARs using all plots are below lines of SARs of the subset of nested series.

3.2 | GrassPlot Diversity Explorer

The GrassPlot Diversity Explorer is an easy-to-use online interactive tool that provides users flexibility in exploring and visualizing richness data collected in the GrassPlot database. The GrassPlot Diversity Explorer can be accessed via the EDGG website (https://edgg.org/databases/GrasslandDiversityExplorer). The tool is organized into eight panels (Figure 6). The first panel shows species richness in different vegetation types. Two vegetation typologies are used, including the two-level vegetation typology used in the GrassPlot database and phytosociological classes (for details, see Appendix S2). Users can explore species richness by generating boxplots for eight standard size grains and selected taxonomic groups. The second panel presents species richness in geographical regions and biomes and the third one SARs for selected vegetation units. Details on the two-level vegetation typology can be found in the fourth panel, and the fifth panel presents descriptive statistics for the selected data set. Users can generate these statistics for filtered data sets based on taxonomic group, vegetation types and region of interest. Besides graphs and descriptive statistics, users can also explore the distribution of plots based on selected criteria. Filtered plots are displayed on background maps in the "Map" panel. The seventh panel contains links to the main file of the GrassPlot Diversity Benchmarks. Finally, the last panel, "Information", explains the concepts of biomes, geographical regions and vegetation typologies used in the GrassPlot Diversity Explorer.

4 | DISCUSSION

4.1 | General diversity patterns

Fine-grain α-diversity patterns of Palaearctic open habitats are not consistent across grain sizes, as shown in Figure 2. While grain size as a determinant of species richness patterns has previously been reported in many coarse-grain studies (see Rahbek, 2005, for a review), here we demonstrate that it is also influential at the scale of ecological communities. Consequently, plant richness hotspots in Palaearctic open habitats are not necessarily consistent across scales, as already demonstrated for vertebrates (McKerrow et al.,

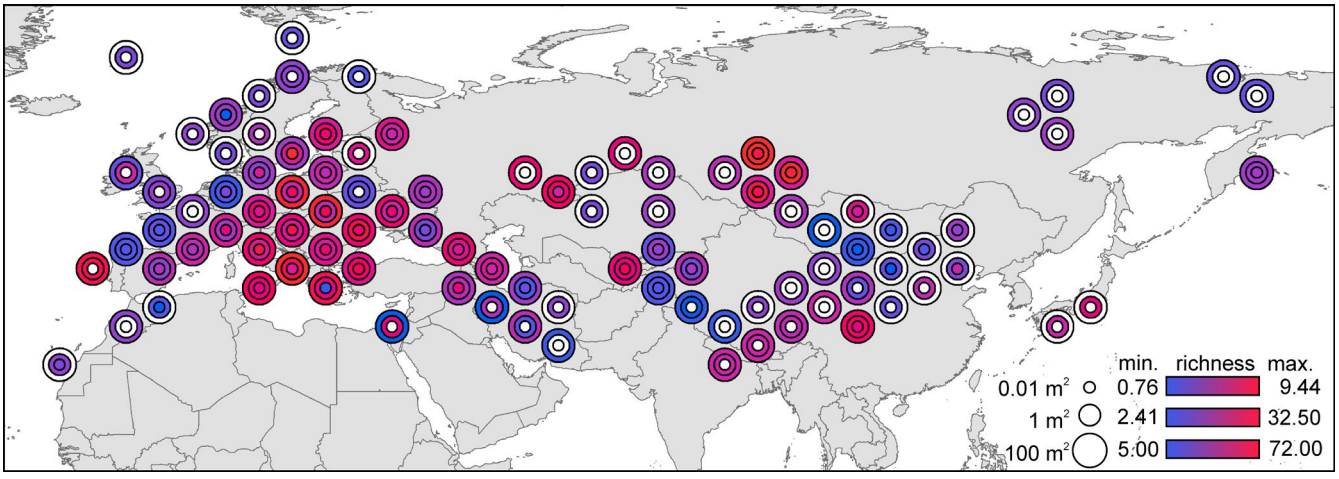

FIGURE 2 Richness hotspots and coldspots of vascular plants across spatial grains in grasslands and other open habitats across the Palaearctic realm. Concentric circles represent mean species richness at grain sizes 0.01, 1 and 100 m^2 within hexagons of ca. 5° x 5°, from the lowest (blue) to the highest (red), while white indicates the absence of data of that grain size

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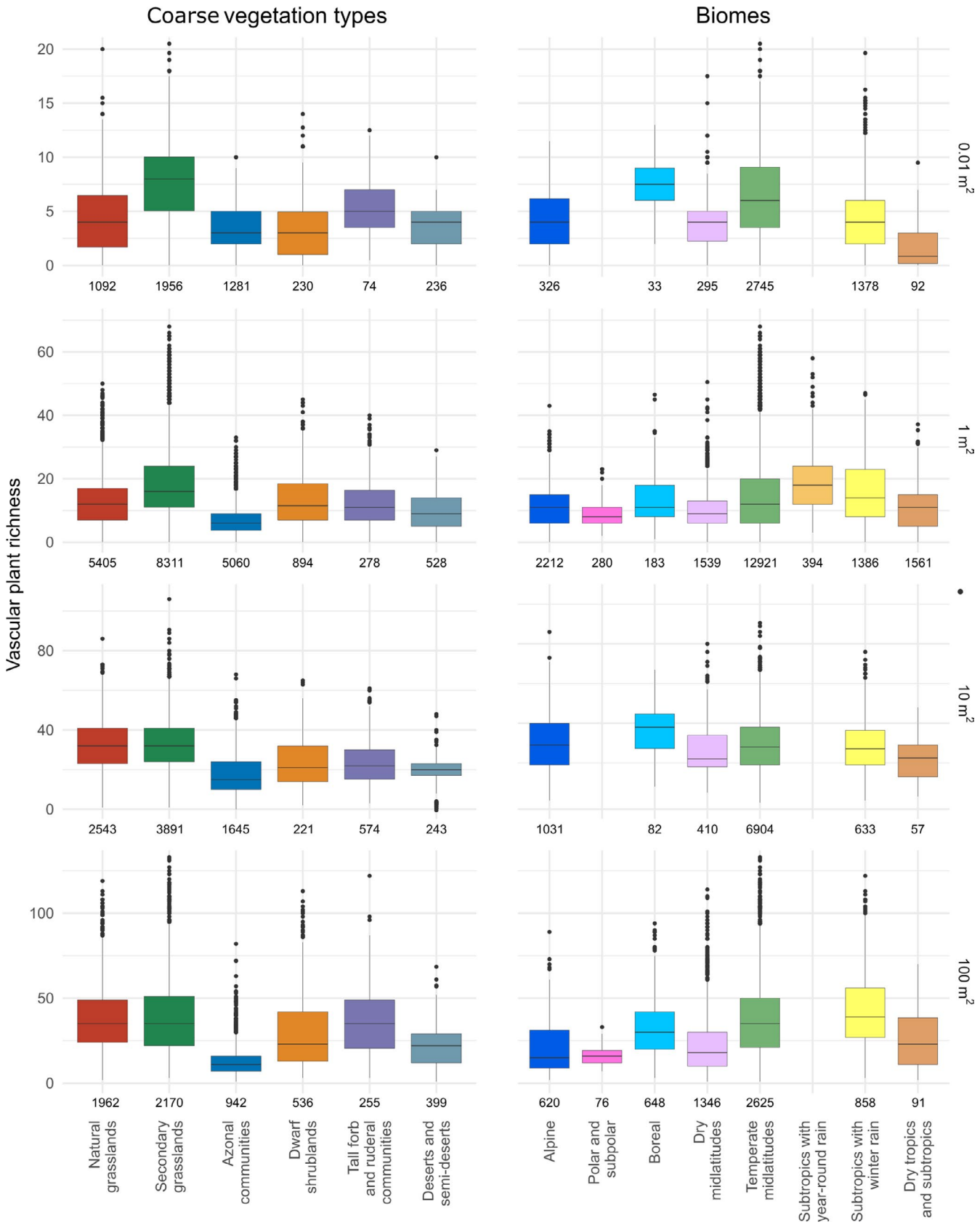

FIGURE 3 Richness of vascular plants across coarse-level vegetation types and biomes for the four most represented grain sizes (0.1, 1, 10, 100 m^2). Under each bar, the number of plots is given. No filtering by sampling method (rooted vs shoot) was applied

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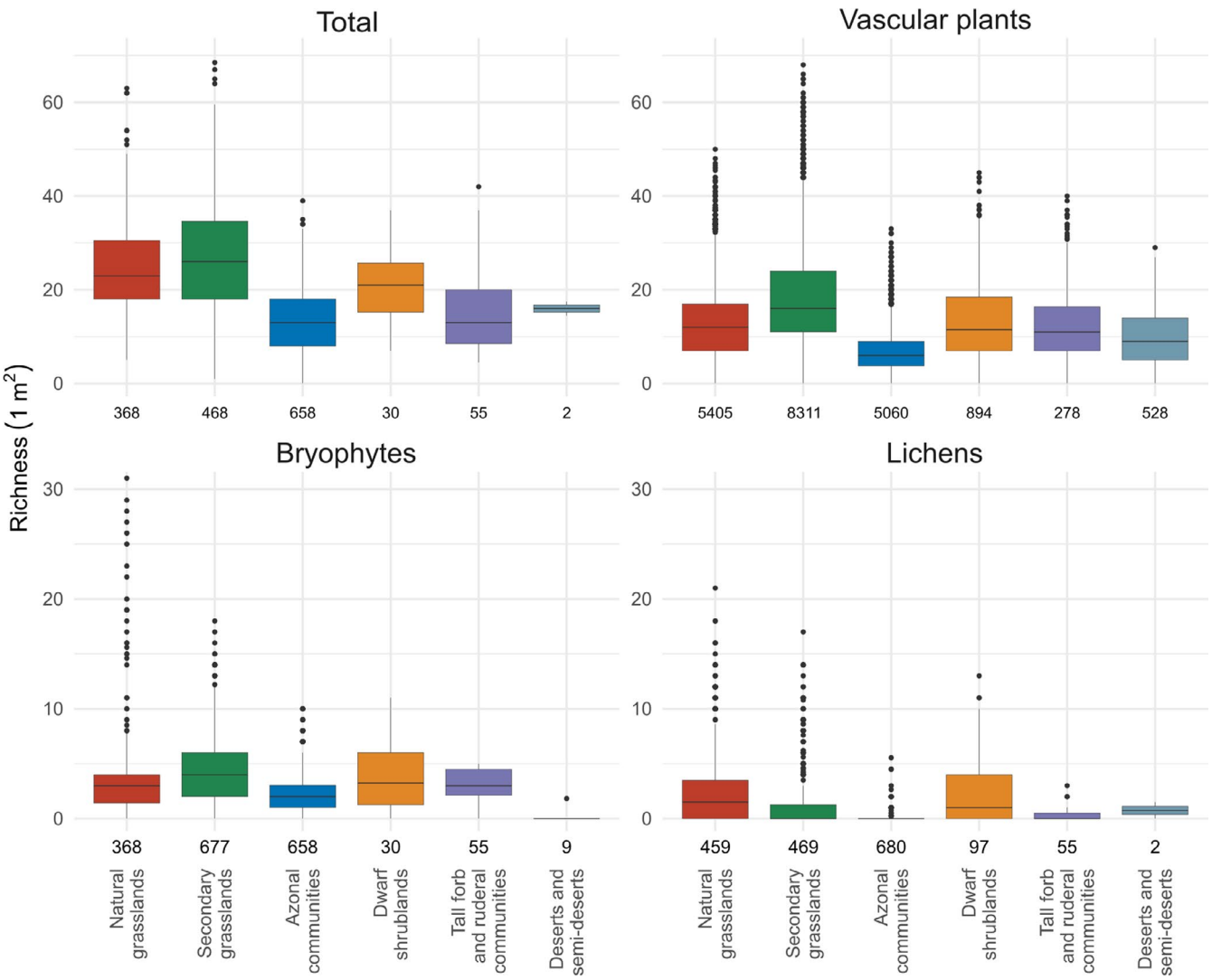

FIGURE 4 Richness at 1 m^2 of the four taxonomic groups across coarse-level vegetation types. Under each bar, the number of plots is given. No filtering by sampling method (rooted vs shoot) was applied

2018; Shriner et al., 2006). Given that GrassPlot data still have large geographic gaps, we refrain from comparing our emerging richness hotspots with those obtained from coarse-grain data (e.g., Barthlott et al., 2005, for vascular plants; Geffert et al., 2013, for bryophytes) and with other community-level patterns in grasslands emerging from fine-grain data (e.g., Wilson et al., 2012; Chytrý et al., 2015; Bruelheide et al., 2019).

We found a strong scale dependence of plant diversity not only across regions but also across vegetation types and biomes, as shown in Figure 3. Diversity patterns also strongly differ between the three taxonomic groups, both across biomes and across vegetation types. For vascular plants, secondary grasslands, and particularly meso-xeric grasslands, are overall the richest vegetation type, with the highest maxima in the temperate midlatitudes, where exceptionally rich meso-xeric grasslands have already been reported (Chytrý et al., 2015; Roleček et al., 2019; Hájek et al., 2020). The richest vegetation types for bryophytes and lichens strongly vary with grain size. However, it is worth reporting that communities found at high latitudes or high elevations often host the highest richness values, such as arctic-alpine heathlands, alpine grasslands and rocks and screes, following the well-documented pattern of increasing diversity of non-vascular plants towards high latitudes or elevations (Grau et al., 2007; Mateo et al., 2016; Chytrý et al., 2017). The relative importance of non-vascular plants in the total vegetation is highest in alpine grasslands and arctic-alpine heathlands and also high in sandy dry grasslands and Mediterranean grasslands. In summary, our results show that non-vascular plants can constitute a major part of the plant diversity in various habitats and thus should be more frequently considered in biodiversity studies. Moreover, we demonstrate that the richness of vascular plants is not a good proxy for fine-grain bryophyte and lichen richness, as they may behave differently, depending on vegetation type. This finding questions the use of vascular plant species richness as a surrogate for the overall diversity in open vegetation, which is suggested in several studies based on simpler assessments in forests (Pharo et al., 1999; Sætersdal et al., 2003). Likewise, Chiarucci et al. (2006) and Santi

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TABLE 2 Maximum richness values for each taxonomic group and grain size across coarse-level vegetation types. The highest values for each taxonomic group are shown in bold. A: natural grasslands; B: secondary grasslands; C: azonal communities; D: dwarf shrublands; E: tall-forb and ruderal communities; F: deserts and semi-deserts. + or − before the maximum values indicates that they are derived from slightly smaller (+) or bigger (−) grain sizes than the standard ones, i.e., 0.0009, 0.09, 9, 10.89, 900 or 1,024 m^2, respectively. Maximum richness for the exact grain size, if available, is indicated in brackets in upper case. No filtering by sampling method (rooted vs shoot) was applied

	Complete vegetation						Vascular plants					
Area [m^2]	A	B	C	D	E	F	A	B	C	D	E	F
0.0001	**10**	**10**	4	6	7	1	8	**11**	4	5	7	4
0.001	14	**19**	8	7	10	3	12	**19**	7	7	9	5
0.01	25	**29**	11	10	18	7	21	**24**	10	18	16	10
0.1	43	**46**	20	35	30	12	34	**43**	16	34	28	18
1	63	**82**	39	39	49	20	59	**79**	33	49	44	29
10	90	**101**	64	69	71	51	86	**−106$^{(98)}$**	68	65	68	+48$^{(47)}$
100	128	**159**	65	93	123	48	119	**144**	82	113	122	71
1,000	–	**+123$^{(58)}$**	+89	–	–	–	**134**	+97$^{(83)}$	+82$^{(30)}$	96	126	95
	Bryophytes						**Lichens**					
Area [m2]	A	B	C	D	E	F	A	B	C	D	E	F
0.0001	**5**	5	3	2	2	1	2	**4**	1	0	0	1
0.001	**+9$^{(6)}$**	8	3	2	3	+1$^{(0)}$	**+6$^{(2)}$**	+5$^{(3)}$	1	1	0	+1$^{(0)}$
0.01	**18**	10	3	3	4	1	**8**	7	2	3	0	1
0.1	**+24$^{(9)}$**	+14$^{(10)}$	4	4	8	+1$^{(0)}$	**+15$^{(8)}$**	+10$^{(5)}$	4	2	2	+1$^{(0)}$
1	**31**	18	10	11	8	2	**21**	17	6	13	3	2
10	**+40$^{(18)}$**	+22$^{(19)}$	27	10	16	+11$^{(1)}$	**+24$^{(23)}$**	+20$^{(12)}$	7	2	3	+10$^{(1)}$
100	**38**	32	19	16	21	1	25	31	15	13	4	0
1,000	–	**+22$^{(2)}$**	+11	–	–	–	–	**+35$^{(5)}$**	+10	–	–	–

et al. (2010) found that vascular plant diversity was not a good surrogate for cryptogam diversity in any habitat type.

While the SARs were not the focus of this paper, our data illustrate some general patterns. The SARs plotted in "semi-log" space (i.e., with area logarithmized, but not species richness; Figure 5 and Appendix S5) invariably show an upward curvature, at least those that are based on the nested-plot data. This shape corresponds to a power function (see Dengler, 2008), which has recently been shown as the overall best model across the non-forest habitat types of the Palaearctic (Dengler et al., 2020b), with little variation of its exponent (z value) across grain sizes (Zhang et al., 2021). Moreover, as the example in Figure 5 illustrates, the curves only rarely cross each other, meaning that vegetation types mainly differ in their *c*-values (corresponding to α-diversity), while there are few systematic differences concerning *z*-values (corresponding to β-diversity). As shown by Dembicz et al. (2021), *z*-values are much more affected by disturbance regimes and heterogeneity — which are largely independent of vegetation type.

4.2 | Data quality and methodological settings

GrassPlot only includes phytodiversity data that were carefully sampled with the aim of recording complete species lists within precisely delimited plots. Large vegetation-plot databases at regional and national (see Dengler et al., 2011 for an overview), continental (Chytrý et al., 2016) or global (Bruelheide et al., 2019) scales are naturally less selective as their main aim is to get as many vegetation-plot records as possible. They include, to a large extent, traditional phytosociological relevés, in which the plot borders were often not precisely delimited in the field. Since the analysis of Chytrý (2001) of the plot data contained at that time in the Czech National Phytosociological Database, it is well known that there are also other biases in the data. This study found, in several phytosociological classes, that the mean richness decreased above a certain threshold area, a pattern explained by the tendency of phytosociologists to select larger-than-average plots in vegetation types that are inherently poorer in species. When comparing the mean richness data from Chytrý (2001) for the three classes that are also contained in GrassPlot (*Festuco-Brometea*, *Molinio-Arrhenatheretea*, *Phragmito-Magnocaricetea*) we found substantially lower mean richness in the phytosociological database than in GrassPlot (not shown). Similarly, comparing the mean richness data of *Festuco-Brometea* grasslands from the Nordic-Baltic Grassland Vegetation Database (Dengler et al., 2006) with GrassPlot data from the same geographic region, we found a good match at 1 m^2, but increasing relative difference toward larger grain sizes (not shown). The consistently higher richness values in GrassPlot were unexpected as it is often assumed that phytosociologists preferentially

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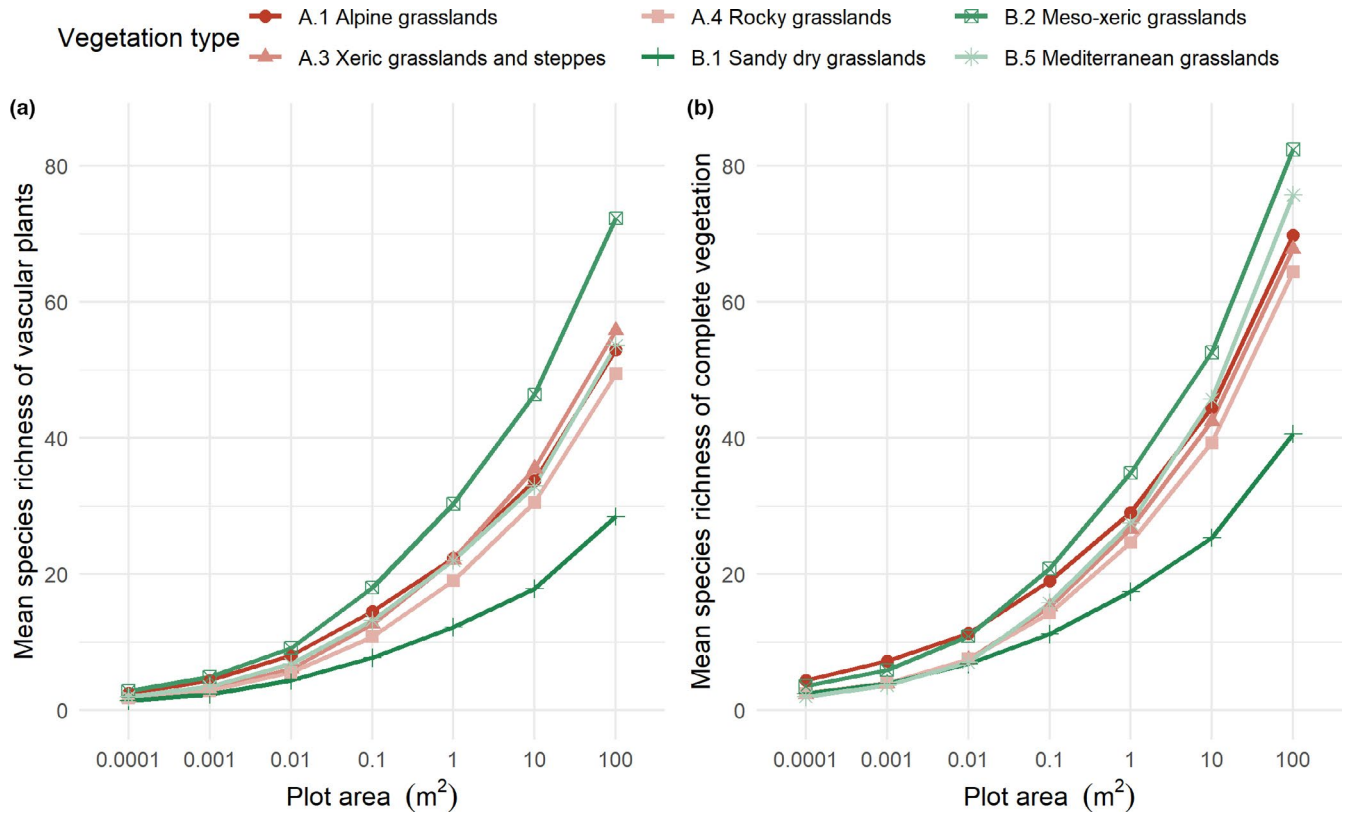

FIGURE 5 Species–area relationships for vascular plants (a) and complete vegetation (b) for six selected grassland types. Only plots belonging to nested series with at least seven standard grain sizes were included. No filtering by sampling method (rooted vs shoot) was applied

sample plots with a species richness above average (Holeksa & Woźniak, 2005; Diekmann et al., 2007). By contrast, most GrassPlot data are based on systematic or random sampling or the approach of the EDGG Field Workshops (Dengler et al., 2016b), which aims to maximize between-plot heterogeneity, i.e., both presumably species-rich and species-poor stands are selected for making plots (which should not bias means, but possibly increase variance). A plausible explanation for the pattern found is that the average completeness of plots in phytosociological databases is lower than most researchers, including ourselves, would have guessed. This indicates that it might be risky to take the richness data from large phytosociological databases at face value. A more comprehensive study comparing the GrassPlot benchmarks with the mean richness values derived from EVA or sPlot should explore how prevalent such a pattern is and whether its strength varies systematically between regions, vegetation types and grain sizes.

While these findings underline the good suitability of typical data contained in GrassPlot for biodiversity analyses, we do not claim that the richness records are 100% complete. It has been shown repeatedly that this is nearly impossible, even when plots are sampled by more than one experienced author (see Lepš & Hadincová, 1992; Klimeš et al., 2001; Archaux et al., 2006). However, the results support the view that the fraction of overlooked species must be minor compared to average phytosociological data and possibly even compensated by an equally minor fraction of erroneously recorded species. When the complete GrassPlot data are used, in very few cases, we also found that richness above a certain threshold appeared to stagnate or even slightly decline (Appendix S5). However, this can be easily explained by biases caused by large numbers of plots that were sampled in local clusters and only for one grain size but not for the others. The effect disappeared when considering only nested-plot series that contain all seven standard grain sizes (Appendix S5). When comparing the continuous and dashed lines in these figures, it turns out that the dashed line (the values for any plots) are largely below the continuous lines (nested plots with all the seven grain sizes). This indicates that apart from biases due to adding local clusters (which equally often should be above and below the average), even within GrassPlot data, there is a "quality gradient": on average, the richness records in nested plots are more complete, but the differences are much smaller than between GrassPlot and conventional phytosociological databases. Finally, also the way of recording plants as present in a plot, shoot presence vs rooted presence (Dengler, 2008), can influence richness records as highlighted by Williamson (2003). In the habitats studied here, a visible effect occurs at grain sizes below 1 m^2 (Appendix S5) which is consistent with findings of Güler et al. (2016), Cancellieri et al. (2017) and Zhang et al. (2021).

While we trust that our richness data for individual plots are more reliable than most other sources, the aggregated richness patterns reported in this paper in some cases might still be biased or misleading. First, data coverage in GrassPlot is sparser than in other big vegetation-plot databases. Consequently there might

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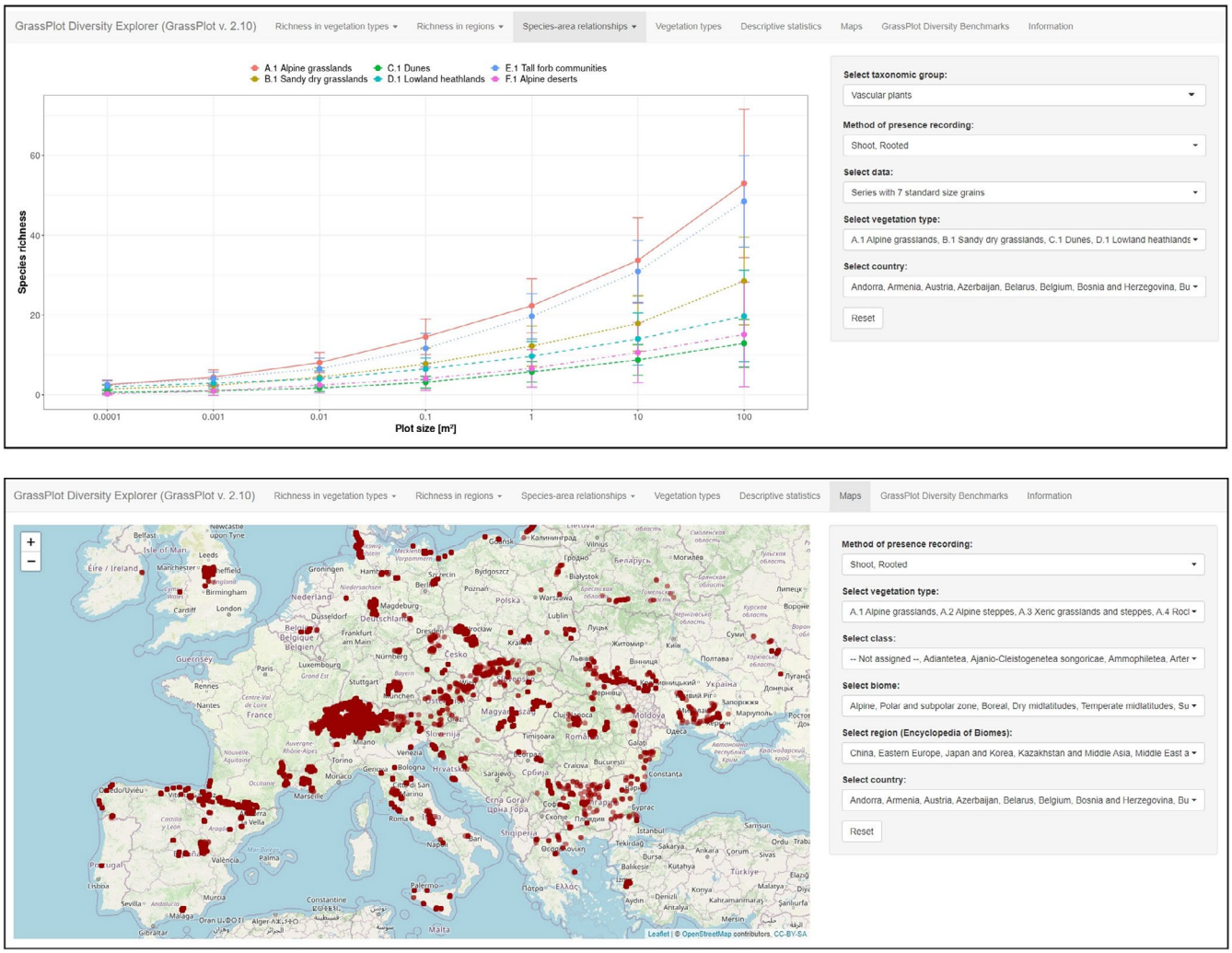

FIGURE 6 Screenshots presenting selected functionalities of the GrassPlot Diversity Explorer. Top: SARs for six selected vegetation types in the panel Species–area relationships; bottom: map showing the overall plot distribution in western, Central and southern Europe in the panel Maps

be stronger biases concerning geography and vegetation types. Second, there are a few data sets in GrassPlot that have specifically been collected with the aim of studying sites of exceptional richness (e.g. Merunková et al., 2012; Roleček et al., 2014; Hájek et al., 2020). However, GrassPlot also contains data that have been sampled in regions where a certain vegetation class is known to be poorer in species than in other parts of the respective country. In addition, a prevalence of vegetation plots from one subtype of a certain category might make this entire category appear relatively richer or poorer in species than it is in reality. Similarly, not all biomes contain the same subtypes of a vegetation type. However, the magnitude of such potential biases can be assessed using the GrassPlot Diversity Explorer/Benchmarks via filtering at different levels. Third, our results are necessarily affected by the classification systems used for biomes and vegetation types. While the categories *per se* are widely used, their border might differ between different sources. For example, the relatively high mean richness values of boreal grasslands in our results are partly related to the biome classification of Schultz (2005), which includes significant areas of the forest–steppe zone in the boreal biome, while other typologies consider it a continental variant of the temperate biome (Erdős et al., 2018). Some bias may also be caused by disputed borders between vegetation types. Since the assignments to the fine-level vegetation types were largely based on syntaxonomy, and the fine-level types were fully nested in coarse categories, there are some "gray zones", e.g., some rocky, alpine and xeric grasslands might be secondary, and, vice versa, some meso-xeric grasslands might be natural, particularly those in the transition to the steppic natural grasslands (e.g., forest-steppes, Erdős et al., 2020), often maintained through grazing by wild herbivores and fire (Pärtel et al., 2005).

4.3 | Potential uses and impact

4.3.1 | Vegetation ecology

In studies on certain vegetation types, it is useful for authors to compare not only the richness values within their sample, but also

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to know where these are positioned in relation to the average of this vegetation type in the country or biome. Modeling studies could also benefit if they had reliable benchmarks. For example, Bruelheide et al. (2020) used a sophisticated approach to create richness maps of *Festuco-Brometea* communities in Germany at 1, 10, 100 and 1,000 m^2 with three different approaches based on a traditional phytosociological database, but in the end, they could only "guess" which of their approaches performed best because they lacked benchmarks from more reliable data from exhaustively sampled plots.

4.3.2 | Macroecology

An increasing number of studies use the enormous amount of vegetation-plot data from national and regional (see Dengler et al., 2011), continental (EVA; Chytrý et al., 2016) and global (sPlot; Bruelheide et al., 2019) vegetation-plot databases. This approach has great potential for macroecology as it combines fine-grain sizes with large spatial extents, a combination that could contribute to a more mechanistic understanding of patterns, but for a long time was underrepresented in macroecology (Beck et al., 2012). Moreover, vegetation-plot data allow for a much wider range of macroecological analyses than species occurrence databases do (Dengler et al., 2011; Bruelheide et al., 2019). Most of such plot-based macroecological papers take the information in the underlying databases as unquestioned facts. While such studies often address the unequal distribution of plots in space and time (Lengyel et al., 2011) and the preferential sampling of more species-rich communities (Divíšek & Chytrý, 2018), and sometimes also their different plot sizes (Večeřa et al., 2019), to our knowledge, the issue that the recorded species lists might be incomplete was hitherto not addressed in macroecological studies. Moreover, given the different traditions of phytosociology in different countries (Guarino et al., 2018), one can assume that the average degree of incompleteness might vary regionally, leading not only to biased absolute numbers but also unreliable patterns. Incomplete species lists are particularly problematic for macroecological studies on α-diversity and some studies on β-diversity, while studies on community-weighted means of traits or assembly rules are probably less affected, at least not when assuming that the overlooked species mostly were the rare ones with low cover. Depending on the sensitivity of the study topic toward biased species richness values, macroecological users of vegetation-plot databases have several options: (a) use a subset of regions, vegetation types and/or grain sizes that, according to the comparison with the GrassPlot Diversity Benchmarks, are least affected; (b) apply context-dependent "correction factors"; or (c) conduct the study instead with the GrassPlot database. Depending on the question at hand, researchers should also take into account the spatial coverage and representativeness of the respective vegetation-plot databases. For example, EVA is much less spatially clustered than either GrassPlot or sPlot. In some cases, a combination of EVA and GrassPlot or sPlot and GrassPlot might be the best solution. Plots duplicated in EVA or sPlot are already documented in GrassPlot, so there is no major problem when using both sources together.

4.3.3 | Biodiversity conservation

In conservation, a typical challenge is to prioritize areas that deserve protection. Here our benchmarks could become a useful and applicable tool. As species richness is generally seen as one of the leading criteria for such prioritizations (Brooks et al., 2006; Brum et al., 2017), one could set an objective criterion for prioritization such as plots above the third quartile or 50% above the mean value. Since the GrassPlot Diversity Benchmarks provide such values for any grain size up to 100 m^2 and specifically for each vegetation type, one can even compare across these categories, e.g., the threshold for alpine grasslands will be different from that for wetlands. In any case, we would like to emphasize that species richness cannot be used as a single criterion, as several naturally species-poor habitats are more species-rich after degradation, such as lower levels of salinity in saline communities. Another typical question in this context is whether a particular management or restoration measure was successful or what is the restoration potential of a specific habitat type. Did the measure achieve the typical diversity of that habitat type? Referring to richness data from the literature is troublesome in such cases as they were often recorded on different grain sizes and usually only at a single grain size, making the "translation" to another grain size challenging. All this is much easier with the GrassPlot Diversity Benchmarks, acknowledging that they largely reflect the situation during the past two decades as there is only a small fraction of 20th-century plots included. We also acknowledge that species number should not always be used as a unique criterion for such assessments, as restoration projects often monitor richness of habitat-specific target species to avoid bias caused by sites with high richness of ruderal or alien species. Finally, we would like to advise again to carefully check plot number and spatial representativeness using the Explorer tool when using these benchmarks.

4.3.4 | Quality check of data

In all the above-mentioned applications, the GrassPlot Diversity Explorer can be helpful for researchers and students alike to get feedback on how complete their field records likely are. The GrassPlot Diversity Benchmarks provide vegetation-plot databases with the option of checking the reliability of data sets before including them. For example, data sets with mean richness below the first quartile of the respective vegetation type × region × grain size should be considered carefully. They do not necessarily need to be excluded but could be labeled as doubtful unless the originators provide convincing reasons that the studied stands are actually so species-poor. This quality check may also be used when data from large vegetation-plot databases are selected for specific projects.

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Although we only provide benchmarks for eight specific grain sizes, interpolation of richness data to any other grain sizes can be easily done, as explained in Appendix S6.

5 | CONCLUSIONS AND OUTLOOK

The GrassPlot Diversity Benchmarks provide high-quality richness data from a wide range of open habitat types across the Palaearctic realm. The restriction to eight standard grain sizes, each separated by a factor of 10, is similar to some standardized sampling schemes on other continents, such as the Carolina Vegetation Survey in North America (Peet et al., 1998) and the BIOTA Observatories in Africa (Jürgens et al., 2012). Seven of the eight grain sizes are already well populated with data, only high-quality observations for 1,000 m^2 are still sparse (which is understandable, given the enormous time effort for a complete sampling of such an area; see Dolnik, 2003). The amount of data in the underlying GrassPlot database and their spatial coverage are much lower than in the EVA (Chytrý et al., 2016) and sPlot (Bruelheide et al., 2019) databases, which is an important constraint that may affect the aggregated patterns reflected in the diversity benchmarks. However, we have shown that species recordings are, on average, apparently much more complete in GrassPlot. Thus, depending on the research question, either EVA/sPlot, GrassPlot or a combination of both might be the best data source. Our study further emphasizes the advantages of standardized methodologies and a set of uniform standard grain sizes.

We release this information open access in an easy-to-use format as the GrassPlot Diversity Benchmarks and in the conveniently queried online tool, the GrassPlot Diversity Explorer. Given the uneven representation of vegetation types across biomes, regions and countries, we advise users to check the number of plots available for the selected combination of region and vegetation type in order to obtain reliable benchmarks. While the GrassPlot Diversity Explorer is already quite powerful, we are considering further extensions in the future, such as an online interface to interpolate richness data between two of our standard grain sizes based on the function presented in Appendix S6, provision of the slope parameter *z* of SARS as a β-diversity measure (see Dengler et al., 2020b), a selection option for different sampling designs and for phytosociological units below the class level, or maps of mean and maximum richness. While the provided open-access data will suffice for many purposes, it is also possible to approach the GrassPlot Consortium with a project proposal (according to the GrassPlot Bylaws; available at https://edgg.org/databases/GrassPlot) for individual plot-based richness records together with environmental data. Last but not least, GrassPlot is a "living database", which is constantly enriched and improved. Those who would like to join the GrassPlot Consortium with suitable data can approach the first author (IB), who is serving as database manager. The GrassPlot Diversity Explorer will be dynamically updated with the newest versions of GrassPlot, while a new fixed version of the GrassPlot Diversity Benchmarks is planned to be released regularly.

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AUTHOR CONTRIBUTIONS

JD and IB conceived of the research idea; IB compiled the data and managed the database; IB and JD wrote the paper; RPi developed the GrassPlot Diversity Explorer and ID the GrassPlot Diversity Benchmarks; ID, FG, LK, CorM, TR and KVM created the figures; RG managed the author list; IAx, SBu, SBa, SBo, HHB, MCh, TCo, PDF, FE, MHá, BJA, AKu, ZM, RJP, MP, RPä, RPi, ZP, HCP, JR, LS, MTe, KVM and JWu discussed the results and commented on the manuscript; all authors contributed data and approved the manuscript.

DATA AVAILABILITY STATEMENT

The aggregated data (as used in this paper) for any combination of the taxonomic group, grain size, vegetation type, region, biome, and methodological settings (rooted vs shoot; subsetting to only those plots belonging to nested series with at least seven standard grain sizes) are provided in Appendix S3. Future updates will be made available as GrassPlot Diversity Benchmarks (fixed versions) and dynamically in the GrassPlot Diversity Explorer (both at https://edgg.org/databases/GrasslandDiversityExplorer). The underlying plot-level data are available upon request from the GrassPlot database, following its Bylaws (https://edgg.org/databases/GrassPlot).

ORCID

Idoia Biurrun https://orcid.org/0000-0002-1454-0433
Remigiusz Pielech https://orcid.org/0000-0001-8879-3305
Iwona Dembicz https://orcid.org/0000-0002-6162-1519
François Gillet https://orcid.org/0000-0002-3334-1069
Łukasz Kozub https://orcid.org/0000-0002-6591-8045
Corrado Marcenò https://orcid.org/0000-0003-4361-5200
Triin Reitalu https://orcid.org/0000-0002-6555-3066
Koenraad Van Meerbeek https://orcid.org/0000-0002-9260-3815
Riccardo Guarino https://orcid.org/0000-0003-0106-9416
Milan Chytrý https://orcid.org/0000-0002-8122-3075
Robin J. Pakeman https://orcid.org/0000-0001-6248-4133
Irena Axmanová https://orcid.org/0000-0001-9440-7976
Sabina Burrascano https://orcid.org/0000-0002-6537-3313
Sándor Bartha https://orcid.org/0000-0001-6331-7521
Steffen Boch https://orcid.org/0000-0003-2814-5343
Hans Henrik Bruun https://orcid.org/0000-0003-0674-2577
Timo Conradi https://orcid.org/0000-0003-2360-9284
Pieter De Frenne https://orcid.org/0000-0002-8613-0943
Franz Essl https://orcid.org/0000-0001-8253-2112
Goffredo Filibeck https://orcid.org/0000-0002-4187-9467
Michal Hájek https://orcid.org/0000-0002-5201-2682
Borja Jiménez-Alfaro https://orcid.org/0000-0001-6601-9597
Anna Kuzemko https://orcid.org/0000-0002-9425-2756

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Zsolt Molnár https://orcid.org/0000-0001-5454-4714
Meelis Pärtel https://orcid.org/0000-0002-5874-0138
Ricarda Pätsch https://orcid.org/0000-0002-3349-0910
Honor C. Prentice https://orcid.org/0000-0003-2548-0525
Jan Roleček https://orcid.org/0000-0002-0023-1111
Massimo Terzi https://orcid.org/0000-0001-8801-6733
Manuela Winkler https://orcid.org/0000-0002-8655-9555
Jianshuang Wu https://orcid.org/0000-0002-6768-8255
Juha M. Alatalo https://orcid.org/0000-0001-5084-850X
Kuber Prasad Bhatta https://orcid.org/0000-0001-7837-1395
Alessandro Chiarucci https://orcid.org/0000-0003-1160-235X
Cristina Chocarro https://orcid.org/0000-0003-0405-0737
Marta Czarnocka-Cieciura https://orcid.org/0000-0002-0168-0410
Patryk Czortek https://orcid.org/0000-0002-4909-8032
Jiří Danihelka https://orcid.org/0000-0002-2640-7867
Francesco de Bello https://orcid.org/0000-0001-9202-8198
Balázs Deák https://orcid.org/0000-0001-6938-1997
Martin Diekmann https://orcid.org/0000-0001-8482-0679
Jiri Dolezal https://orcid.org/0000-0002-5829-4051
Pavel Dřevojan https://orcid.org/0000-0003-0802-3509
Hamid Ejtehadi https://orcid.org/0000-0003-0681-5377
Manfred Finckh https://orcid.org/0000-0003-2186-0854
Itziar García-Mijangos https://orcid.org/0000-0002-6642-7782
Rosario G. Gavilán https://orcid.org/0000-0002-1022-445X
Monika Janišová https://orcid.org/0000-0002-6445-0823
Zygmunt Kącki https://orcid.org/0000-0002-2241-1631
Jutta Kapfer https://orcid.org/0000-0002-8077-8917
András Kelemen https://orcid.org/0000-0002-2480-5669
Lorenzo Lazzaro https://orcid.org/0000-0003-0514-0793
Jan Lepš https://orcid.org/0000-0002-4822-7429
Ching-Feng Li https://orcid.org/0000-0003-0744-490X
Diego Liendo https://orcid.org/0000-0002-4816-4093
Zdeňka Lososová https://orcid.org/0000-0001-9152-7462
Pavel Lustyk https://orcid.org/0000-0002-2514-9691
Arantzazu L. Luzuriaga https://orcid.org/0000-0001-5023-7813
Simona Maccherini https://orcid.org/0000-0002-2025-7546
Eliane Seraina Meier https://orcid.org/0000-0002-9545-1167
Michele Mugnai https://orcid.org/0000-0003-4315-2920
Alireza Naqinezhad https://orcid.org/0000-0002-4602-6279
Arkadiusz Nowak https://orcid.org/0000-0001-8638-0208
Salza Palpurina https://orcid.org/0000-0003-0416-5622
Robert K. Peet https://orcid.org/0000-0003-2823-6587
Eulàlia Pladevall-Izard https://orcid.org/0000-0002-6693-5314
Zuzana Plesková https://orcid.org/0000-0003-0153-1623
Maria Pilar Rodríguez-Rojo https://orcid.org/0000-0001-5449-9386
Solvita Rusina https://orcid.org/0000-0002-9580-4110
Anvar Sanaei https://orcid.org/0000-0001-8334-6944
Dariia Shyriaieva https://orcid.org/0000-0001-7140-7201
Vasco Silva https://orcid.org/0000-0003-2729-1824
Eva Šmerdová https://orcid.org/0000-0003-4589-6317
Judit Sonkoly https://orcid.org/0000-0002-4301-5240
Marta Gaia Sperandii https://orcid.org/0000-0002-2507-5928
Sebastian Świerszcz https://orcid.org/0000-0003-2035-0035
Amir Talebi https://orcid.org/0000-0002-5065-1368
Lubomír Tichý https://orcid.org/0000-0001-8400-7741
Csaba Tölgyesi https://orcid.org/0000-0002-0770-2107
Péter Török https://orcid.org/0000-0002-4428-3327
Orsolya Valkó https://orcid.org/0000-0001-7919-6293
Thomas Vanneste https://orcid.org/0000-0001-5296-917X
Risto Virtanen https://orcid.org/0000-0002-8295-8217
Denys Vynokurov https://orcid.org/0000-0001-7003-6680
Yun Wang https://orcid.org/0000-0002-8238-5367
David Zelený https://orcid.org/0000-0001-5157-044X
Liqing Zhao https://orcid.org/0000-0002-8478-5786
Jürgen Dengler https://orcid.org/0000-0003-3221-660X

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Overview of the 225 datasets included in GrassPlot v2.10 and their references.
Appendix S2. Complementary information on the data.
Appendix S3. The GrassPlot Diversity Benchmarks, version 2.10.
Appendix S4. Additional richness maps.
Appendix S5. Additional detailed results.
Appendix S6. Interpolation of richness data to other grain sizes.
Appendix S7. Funding information.

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