

sPlotOpen – An environmentally-balanced, open-access, global dataset of vegetation plots

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Authors

✉ Francesco Maria Sabatini^{1,2,†}, Jonathan Lenoir^{3,†}, Tarek Hattab⁴, Elise Aimee Arnst⁵, Milan Chytrý⁶, Jürgen Dengler^{1,7,8}, Patrice De Ruffray⁹, Stephan M. Hennekens¹⁰, Ute Jandt^{1,2}, Florian Jansen¹¹, Borja Jiménez-Alfaro¹², Jens Kattge¹³, Aurora Levesley¹⁴, Valério D. Pillar¹⁵, Oliver Purschke¹⁶, Brody Sandel¹⁷, Fahmida Sultana¹⁸, Tsipe Aavik¹⁹, Svetlana Ačić²⁰, Alicia T.R. Acosta²¹, Emiliano Agrillo²², Miguel Alvarez²³, Iva Apostolova²⁴, Mohammed A.S. Arfin Khan²⁵, Luzmila Arroyo²⁶, Fabio Attorre²², Isabelle Aubin²⁷, Arindam Banerjee²⁸, Marijn Bauters^{29,30}, Yves Bergeron³¹, Erwin Bergmeier³², Idoia Biurrun³³, Anne D. Bjorkman^{34,35}, Gianmaria Bonari³⁶, Viktoria Bondareva³⁷, Jörg Brunet³⁸, Andraž Čarni^{39,40}, Laura Casella⁴¹, Luis Cayuela⁴², Tomáš Černý⁴³, Victor Chepinoga⁴⁴, János Csiky⁴⁵, Renata Čušterevska⁴⁶, Els De Bie⁴⁷, André Luis de Gasper⁴⁸, Michele De Sanctis²², Panayotis Dimopoulos⁴⁹, Jiri Dolezal⁵⁰, Tetiana Dziuba⁵¹, Mohamed Abd El-Rouf Mousa El-Sheikh^{52,53}, Brian Enquist⁵⁴, Jörg Ewald⁵⁵, Farideh Fazayeli^{56,57}, Richard Field⁵⁸, Manfred Finckh⁵⁹, Sophie Gachet⁶⁰, Antonio Galán-de-Mera^{61,62,63}, Emmanuel Garbolino⁶⁴, Hamid Gholizadeh⁶⁵, Melisa Giorgis⁶⁶, Valentin Golub⁶⁷, Inger Greve Alsos⁶⁸, John-Arvid Grytnes⁶⁹, Gregory Richard Guerin⁷⁰, Alvaro G. Gutiérrez⁷¹, Sylvia Haider^{2,72}, Mohamed Z. Hatim^{73,74}, Bruno Hérault^{75,76,77}, Guillermo Hinojos Mendoza⁷⁸, Norbert Hölzel⁷⁹, Jürgen Homeier⁸⁰, Wannes Hubau^{81,82}, Adrian Indreica⁸³, John A.M. Janssen⁸⁴, Birgit Jedrzejek⁷⁹, Anke Jentsch⁸⁵, Norbert Jürgens⁵⁹, Zygmunt Kački⁸⁶, Jutta Kapfer⁸⁷, Dirk Nikolaus Karger⁸⁸, Ali Kavgaci⁸⁹, Elizabeth Kearsley⁹⁰, Michael Kessler⁹¹, Larisa Khanina⁹², Timothy Killeen⁹³, Andrey Korolyuk⁹⁴, Holger Kreft⁹⁵, Hjalmar S. Kühl^{96,97}, Anna Kuzemko⁹⁸, Flavia Landucci⁶, Attila Lengyel⁹⁹, Frederic Lens¹⁰⁰, Débora Vanessa Lingner¹⁰¹, Hongyan Liu¹⁰², Tatiana Lysenko^{103,104,105}, Miguel D. Mahecha^{97,106}, Corrado Marcenò³³, Vasiliy Martynenko¹⁰⁷, Jesper Erenskjold Moeslund¹⁰⁸, Abel Monteagudo Mendoza¹⁰⁹, Ladislav Mucina¹¹⁰, Jonas V. Müller¹¹¹, Jérôme Munzinger¹¹², Alireza Naqinezhad¹¹³, Jalil Noroozi¹¹⁴, Arkadiusz Nowak^{115,116}, Viktor Onyshchenko¹¹⁷, Gerhard E. Overbeck¹¹⁸, Meelis Pärtel¹¹⁹, Aníbal Pauchard^{120,121}, Robert K. Peet¹²², Josep Peñuelas^{123,124}, Aaron Pérez-Haase^{125,126}, Tomáš Peterka⁶, Petr Petřík¹²⁷, Gwendolyn Peyre¹²⁸, Oliver L. Phillips¹⁴, Vadim Prokhorov¹²⁹, Valerijus Rašomavičius¹³⁰, Rasmus Revermann^{131,132}, Gonzalo Rivas-Torres¹³³, John S. Rodwell¹³⁴, Eszter Ruprecht¹³⁵, Solvita Rūsiņa¹³⁶, Cyrus Samimi¹³⁷, Marco Schmidt¹³⁸, Franziska Schrod⁵⁸, Hanhuai Shan¹³⁹, Pavel Shirokikh¹⁰⁷, Jozef Šibík¹⁴⁰, Urban Šilc¹⁴¹, Petr Sklenář¹⁴², Željko Škvorc¹⁴³, Ben Sparrow¹⁴⁴, Marta Gaia Sperandii^{21,145}, Zvezdana Stančić¹⁴⁶, Jens-Christian Svenning¹⁴⁷, Zhiyao Tang¹⁰², Cindy Q. Tang¹⁴⁸, Ioannis Tsiripidis¹⁴⁹, Kim André Vanselow¹⁵⁰, Rodolfo Vásquez Martínez¹⁰⁹, Kiril Vassilev²⁴, Eduardo Vélez-Martin¹⁵¹, Roberto Venanzoni¹⁵², Alexander Christian Vibrans¹⁰¹, Cyrille Violle¹⁵³, Risto Virtanen^{1,154,155}, Henrik von Wehrden¹⁵⁶, Viktoria Wagner¹⁵⁷, Donald A. Walker¹⁵⁸, Donald Waller¹⁵⁹, Hua-Feng Wang¹⁶⁰, Karsten Wesche^{1,161,162}, Timothy J.S. Whitfeld¹⁶³, Wolfgang Willner¹¹⁴, Susan K. Wiser⁵, Thomas Wohlgemuth¹⁶⁴, Sergey Yamalov¹⁶⁵, Martin Zobel¹⁶⁶, Helge Bruelheide^{1,2}

✉ — To whom correspondence should be addressed: francesco.sabatini@botanik.uni-halle.de

† — These authors contributed equally to this work

2. Martin-Luther University Halle-Wittenberg, Institute of Biology, Am Kirchtor 1, 06108, Halle, Germany
3. Université de Picardie Jules Verne, Unité de Recherche "Ecologie et Dynamique des Systèmes Anthropisés" (EDYSAN), UMR 7058 CNRS, 1 Rue des Louvels, 80000, Amiens, France
4. MARBEC, University of Montpellier, CNRS, IFREMER and IRD, Sète, France
5. Manaaki Whenua - Landcare Research, PO Box 69040, 7640, Lincoln, New Zealand
6. Masaryk University, Department of Botany and Zoology, Kotlářská 2, 611 37, Brno, Czech Republic
7. Zurich University of Applied Sciences (ZHAW), Vegetation Ecology Group, Institute of Natural Resource Sciences (IUNR), Grüentalstr. 14, 8820, Wädenswil, Switzerland
8. University of Bayreuth, Plant Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), Universitätsstr. 30, 95447, Bayreuth, Germany
9. Université de Strasbourg, Institut de biologie moléculaire des plantes-CNRS, 12, rue du Général-Zimmer, F-67084, Strasbourg, France
10. Wageningen Environmental Research, P.O.Box 47, 6700 AA, Wageningen, Netherlands
11. University of Rostock, Faculty of Agricultural and Environmental Sciences, Justus-von-Liebig-Weg 6, 18059, Rostock, Germany
12. University of Oviedo, Research Unit of Biodiversity (CSIC/UO/PA), C. Gonzalo Gutiérrez Quirós s/n, 33600, Mieres, Spain
13. Max Planck Institute for Biogeochemistry, Hans Knöll Str. 10, 07745, Jena, Germany
14. University of Leeds, School of Geography, Woodhouse Lane, LS2 9JT, Leeds, United Kingdom
15. Universidade Federal do Rio Grande do Sul, Department of Ecology, Av. Bento Gonçalves 9500, 91501-970, Porto Alegre, RS, Brazil
16. Medical School of the Martin-Luther University Halle-Wittenberg, Institute for Medical Epidemiology, Biometrics and Informatics (IMEBI), Interdisciplinary Center for Health Sciences, Magdeburger Straße 8, 06112, Halle/Saale, Germany
17. Santa Clara University, Department of Biology, 500 El Camino Real, 95053, Santa Clara CA, United States
18. Shahjalal University of Science & Technology, Forestry & Environmental Science, 3114, Sylhet, Bangladesh
19. University of Tartu, Department of Ecology and Earth Sciences, Department of Botany, Lai 40, Tartu 51005, Estonia
20. University of Belgrade, Faculty of Agriculture, Department of Botany, Nemanjina 6, 11080, Belgrade-Zemun, Serbia
21. Roma Tre University, Department of Sciences, V.le Marconi 446, 00146, Rome, Italy
22. Sapienza University of Rome, Department of Environmental Biology, P.le Aldo Moro 5, 00185, Rome, Italy
23. University of Bonn, Plant Nutrition, INRES, Karlrobert-Kreiten-Str., 53115, Bonn, Germany
24. Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Department of Plant and Fungal Diversity and Resources, Acad. Georgi Bonchev 23, 1113, Sofia, Bulgaria
25. Shahjalal University of Science & Technology, Forestry & Environmental Science, Akhalia, 3114, Sylhet, Bangladesh
26. Universidad Autónoma Gabriel René Moreno, Dirección de la Carrera de Biología, Santa Cruz de la Sierra, Bolivia
27. Canadian Forest Service, Natural Resources Canada, Great Lakes Forestry Centre, 1219 Queen St. East, P6A 2E5, Sault Ste Marie (Ontario), Canada
28. University of Illinois Urbana Champaign, Department of Computer Science, 201 North Goodwin Avenue MC 258, Urbana, IL 61801, 61801.0, Urbana, USA
29. Ghent University, Department Green chemistry and technology, Isotope Bioscience laboratory (UGent-ISOFYS), Coupure Links 653, 9000, Ghent, Belgium
30. Ghent University, Department Environment, Computational and Applied Vegetation Ecology (UGent-CAVELab), Coupure Links 653, 9000, Ghent, Belgium
31. Université du Québec en Abitibi-Témiscamingue, Forest Research Institute, 445 boul. de l'Université, J9X5E4, Rouyn-Noranda, Canada
32. University of Göttingen, Vegetation Ecology and Phytodiversity, Untere Karspüle 2, 37073, Göttingen, Germany
33. University of the Basque Country UPV/EHU, Plant Biology and Ecology, P.O. Box 644, 48080, Bilbao, Spain
34. University of Gothenburg, Department of Biological and Environmental Sciences, Carl Skottsbergs gata 22B, 41319, Gothenburg, Sweden
35. Gothenburg Global Biodiversity Centre, Carl Skottsbergs gata 22B, 41319, Gothenburg, Sweden
36. Free University of Bozen-Bolzano, Piazza Università, 5, 39100, Bolzano, Italy
37. Institute of Ecology of the Volga River Basin, Department of Phytodiversity Problems, Komzina, 10, 445003, Toljatty, Russian Federation
38. Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Sundsvägen 3, 230 53 Alnarp, Sweden
39. Research Center of the Slovenian Academy of Sciences and Arts, Institute of Biology, Novi trg 2, 1000, Ljubljana, Slovenia
40. University of Nova Gorica, School for viticulture and enology, Vipavska 13, 5000, Nova Gorica, Slovenia
41. ISPRA - Italian National Institute for Environmental Protection and Research, Biodiversity Conservation Department, Via Vitaliano Brancati, 60, 00144, Roma, Italy
42. Universidad Rey Juan Carlos, Department of Biology and Geology, Physics and Inorganic Chemistry, c/ Tulipán s/n, 29833, Móstoles, Spain
43. Czech University of Life Sciences Prague, Department of Forest Ecology, Faculty of Forestry and Wood Sciences, Kamýcká 1176, 165 21, Praha 6 - Suchbát, Czech Republic
44. Central Siberian Botanical Garden SB RAS, Zolotodolinskaya Str. 101, 630090, Novosibirsk, Russian Federation
45. University of Pécs, Department of Ecology, Ifjúság u. 6., 7624, Pécs, Hungary

46. Faculty of Natural Sciences and Mathematics, Institute of Biology, Arhimedova 3, 1000, Skopje, Republic of Macedonia
47. Research Institute for Nature and Forest (INBO), Biotope Diversity, Havenlaan 88, bus 73, 1000, Brussels, Belgium
48. Universidade Regional de Blumenau, Rua Antonio da Veiga, 140, Blumenau, 89030-903, Brazil
49. University of Patras, Laboratory of Botany, Division of Plant Biology, Department of Biology, University Campus, 26504, Patras, Greece
50. Institute of Botany, Czech Academy of Sciences, Department of Functional Ecology, Dukelska 135, 37901, Trebon, Czech Republic
51. M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Geobotany and ecology, Tereshchenkivska, 1004, Kyiv, Ukraine
52. College of Science, King Saud University, Botany and Microbiology Department, P.O. Box 2455, 11451, Riyadh, Saudi Arabia
53. Damanhour University, Botany Department, Faculty of Science, Damanhour, Egypt
54. University of Arizona, Ecology and Evolutionary Biology, 1041 E. Lowell St., AZ 85721, Tucson, United States
55. Hochschule Weihenstephan-Triesdorf, University of Applied Sciences, Hans-Carl-von-Carlowitz-Platz 3, 85354, Freising, Germany
56. Google LLC, 1600 Amphitheatre Pkwy, 94043.0, Mountain View, USA
57. University of Minnesota - Twin Cities, USA
58. University of Nottingham, School of Geography, University Park, NG7 2RD, Nottingham, United Kingdom
59. University of Hamburg, Biodiversity, Ecology and Evolution of Plants, Institute for Plant Science & Microbiology, Ohnhorststr. 18, 22609, Hamburg, Germany
60. Aix Marseille Univ, Avignon Université, CNRS, IRD, IMBE, Campus St-Jérôme Etoile, 13397, Marseille, France
61. Universidad CEU San Pablo, Laboratorio de Botánica, P.O. Box 67, 28660, Boadilla del Monte, Madrid, Spain
62. Universidad Privada Antonio Guillermo Urrelo, Laboratorio de Botánica, Jr. José Sabogal
63. Estudios Fitogeográficos del Perú, Herbario AQP, Sánchez Cerro 219, Manuel Prado, Paucarpata, Arequipa, Peru
64. Climact Data Science (CDS), Nova Sophia - Regus Nova, 291 rue Albert Caquot, CS 40095, 06902, Sophia Antipolis Cedex, France
65. University of Mazandaran, Department of Biology, Babolsar, Iran
66. Instituto Multidisciplinario de Biología Vegetal (IMBIV-CONICET), ECOLOGÍA VEGETAL Y FITOGEOGRAFÍA, Av. Vélez Sársfield 1611, 5000, Córdoba, Argentina
67. Institute of Ecology of the Volga River Basin, Laboratory of Phytocoenology, Komzina, 10, 445003, Toljatty, Russian Federation
68. The Arctic University Museum of Norway, UiT - The Arctic University of Norway, Tromsø, Norway
69. University of Bergen, Department of Biological Sciences, Postbox 7803, Bergen, Norway
70. University of Adelaide, School of Biological Sciences, North Terrace, 5005, Adelaide, Australia
71. Universidad de Chile, Departamento de Ciencias Ambientales y Recursos Naturales Renovables, Facultad de Ciencias Agronomicas, Santa Rosa 11315, La Pintana, 8820808, Santiago, Chile
72. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstraße 4, 04103, Leipzig, Germany
73. Wageningen University, Plant Ecology and Nature Conservation Group - Environmental Sciences Department, P.O. Box Postbus 47, Droevendaalsesteeg 3, 6700 AA, Wageningen, The Netherlands
74. Tanta University, Botany and Microbiology Department - Faculty of Science, El Geish St., 31527, Tanta, Egypt
75. CIRAD, UPR Forêts et Sociétés, Yamoussoukro, Ivory Coast
76. University of Montpellier, Forêts et Sociétés, CIRAD, Montpellier, France
77. INP-HB, Institut National Polytechnique Félix Houphouët-Boigny, Yamoussoukro, Côte d'Ivoire
78. ASES Ecological and Sustainable Services, Pépinière d'Entreprises l'Espéridou, Parc d'Activités du Vinobre, 555 Chemin des Traverses, Lachapelle-sous-Aubenas, 07200, Aubenas, France
79. University of Münster, Institute of Landscape Ecology, Heisenbergstr. 2, 48149, Münster, Germany
80. University of Goettingen, Plant Ecology and Ecosystems Research, Untere Karspuele 2, 37073, Goettingen, Germany
81. Ghent University, Department Environment, Laboratory of Wood Biology (UGent-WoodLab), Coupure Links 653, 9000, Ghent, Belgium
82. Royal Museum for Central Africa, Service of Wood Biology, Leuvensesteenweg 13, 3080, Tervuren, Belgium
83. Transilvania University of Brasov, Department of Silviculture, Sirul Beethoven 1, 500123, Brasov, Romania
84. Wageningen University and Research, Wageningen Environmental Research (Alterra), P.O.Box 47, 6700 AA, Wageningen, Netherlands
85. University of Bayreuth, Disturbance Ecology, Bayreuth Center of Ecology and Environmental Research, Universitaetsstr. 30, 95447, Bayreuth, Germany
86. University of Wrocław, Botanical Garden, Sienkiewicza 23, 50-335, Wrocław, Poland
87. Norwegian Institute of Bioeconomy Research, Holtvegen, 66, Tromsø, 9016, Norway
88. Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Biodiversity and Conservation Biology, Zürcherstrasse 111, 8903, Birmensdorf, Switzerland
89. Karabuk University, Faculty of Forestry, Kilavuzlar Köyü Öte Karsi Üniversite Kampüsü Merkez, 78050, Karabuk, Turkey
90. Ghent University, Department Environment, Computational and Applied Vegetation Ecology (UGent-CAVELab), Coupure Links 653, 9000, Gent, Belgium
91. University of Zurich, Department of Systematic and Evolutionary Botany, Zollikerstrasse 107, 8008, Zurich, Switzerland

92. branch of the M.V. Keldysh Institute of Applied Mathematics of Russian Academy of Sciences, Institute of Mathematical Problems of Biology of RAS, 1 Prof. Vitkevich, 142290.0, Pushchino, Russia
93. Universidad Autonoma Gabriel Rene Moreno, Museo de Historia Natural Noel Kempff Mercado, Santa Cruz de la Sierra, Bolivia
94. Central Siberian Botanical Garden, Siberian Branch, Russian Academy of Sciences, Geosystem Laboratory, Zolotodolinskaya str. 101, 630090, Novosibirsk, Russian Federation
95. University of Göttingen, Department of Biodiversity, Macroecology and Biogeography, Büsgenweg 1, 37077, Göttingen, Germany
96. Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103, Leipzig, Germany
97. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstrasse 4, 04103, Leipzig, Germany
98. M.G. Kholodny Institute of Botany of the National Academy of Sciences of Ukraine, Department of Geobotany and Ecology, 2, Tereshchenkivska str., 01601, Kyiv, Ukraine
99. Centre for Ecological Research, Institute of Ecology and Botany, Alkotmány u. 2-4., 2163, Vácrátót, Hungary
00. Naturalis Biodiversity Center, Research Group Functional Traits, Darwinweg 2, 2333 CR, Leiden, The Netherlands
01. Universidade Regional de Blumenau, Departamento de Engenharia Florestal, Rua São Paulo, 3250, 89030-000, Blumenau, Brazil
02. Peking University, College of Urban and Environmental Sciences, Yiheyuan Rd. 5, 100871, Beijing, China
03. Komarov Botanical Institute RAS, Laboratory of Vegetation Science, Prof. Popov 2, 197376, Saint-Petersburg, Russian Federation
04. Institute of Ecology of the Volga River Basin RAS - Branch of the Samara Scientific Center RAS, Laboratory of Phytodiversity Problems, Komzin str. 10, 445003, Togliatti, Russian Federation
05. Tobolsk complex scientific station of Ural Branch RAS, Group of Ecology of Living Organisms, Academician Yu. Osipov str. 15, 626152, Tobolsk, Russian Federation
06. University of Leipzig, Remote Sensing Centre for Earth System Research, Talstr. 35, 04103, Leipzig, Germany
07. Ufa Federal Scientific Center of the Russian Academy of Sciences, Institute of Biology, prospekt Oktyabrya, 69, 450054, Ufa, Russian Federation
08. Aarhus University, Department of Bioscience, Grenaavej 14, 8410, Roende, Denmark
09. Jardín Botánico de Missouri Oxapampa, Bolognesi Mz-E-6, Oxapampa, Pasco, Peru
10. Murdoch University, Harry Butler Institute, 90 South Street, Building 390, 6150, Murdoch, Australia
11. Royal Botanic Gardens, Kew, Conservation Science, Wakehurst Place, RH17 6TN, Ardingly, West Sussex, United Kingdom
12. AMAP, Université de Montpellier, CIRAD, CNRS, INRAE, IRD, 34000, Montpellier, France
13. University of Mazandaran, Department of Plant Biology, P.O. Box 47416-95447, Mazandaran, Iran
14. University of Vienna, Department of Botany and Biodiversity Research, Rennweg 14, 1030, Vienna, Austria
15. Polish Academy of Sciences, Botanical Garden - Center for Biodiversity Conservation, Prawdziwka 2, 02-950, Warsaw, Poland
16. University of Opole, Institute of Biology, Oleska St. 52, 45-052, Opole, Polska
17. National Academy of Sciences of Ukraine, M.G. Kholodny Institute of Botany, Tereshchenkivska 2, 01601, Kyiv, Ukraine
18. Universidade Federal do Rio Grande do Sul, Department of Botany, Av. Bento Gonçalves 9500, 91501-970, Porto Alegre, Brazil
19. University of Tartu, Institute of Ecology and Earth Sciences, Lai 40, 51005, Tartu, Estonia
20. Universidad de Concepción, Laboratorio de Invasiones Biológicas (LIB). Facultad de Ciencias Forestales., Victoria 631, 4030000, Concepción, Chile
21. Institute of Ecology and Biodiversity (IEB), Chile
22. University of North Carolina, Department of Biology, CB3280, South Road, 27599-3280, Chapel Hill, NC, United States
23. CSIC, Global Ecology Unit CSIC-CREAF-UAB, Edifici C, Campus UAB, 08193, Bellaterra, Spain
24. CREAL, Edifici C, 08193, Cerdanyola del Valles, Espanya
25. University of Vic-Central University of Catalonia, Department of Biosciences, Carrer de la Laura, 13, 08500, Vic, Barcelona, Spain
26. University of Barcelona, Department of Evolutionary Biology, Ecology and Environmental Sciences, Diagonal 643, 08028, Barcelona, Spain
27. Czech Academy of Sciences, Department of vegetation ecology, Institute of Botany, Zámek 1, 25243, Průhonice, Czech Republic
28. University of the Andes, Department of Civil and Environmental Engineering, Carrera 1 Este No. 19A-40, Edificio Mario Laserna, Piso 6, 111711, Bogota, Colombia
29. Kazan Federal University, Institute of Environmental Sciences, Kremlevskaya 18, 420008, Kazan, Russian Federation
30. Nature Research Centre, Institute of Botany, Zaliuju Ezeru 49, 08406, Vilnius, Lithuania
31. University of Hamburg, Biodiversity, Ecology and Evolution of Plants/Institute for Plant Science & Microbiology, Ohnhorststr. 18, 22609, Hamburg, Germany
32. Namibia University of Science and Technology, Faculty of Natural Resources and Spatial Sciences, Windhoek, Namibia
33. Universidad San Francisco de Quito, COCIBA, Diego de Robles, 170177, Quito, Ecuador
34. 7 Derwent Road, LA1 3ES, Lancaster, United Kingdom
35. Babeş-Bolyai University, Hungarian Department of Biology and Ecology, Faculty of Biology and Geology, Republicii street 42., 400015, Cluj-Napoca, Romania

36. University of Latvia, Faculty of Geography and Earth Sciences, Jelgavas iela 1, LV 1004, Riga, Latvia
37. University of Bayreuth, Climatology, Bayreuth Center of Ecology and Environmental Research (BayCEER), Universitätsstr. 30, 95447, Bayreuth, Germany
38. Stadt Frankfurt am Main - Der Magistrat, Palmengarten, Siesmayerstraße 61, 60323, Frankfurt am Main, Germany
39. Microsoft, One Microsoft Way, 98052.0, Redmond, WA, United States
40. Plant Science and Biodiversity Centre Slovak Academy of Sciences, Institute of Botany, Dubravská cesta 9, 84523, Bratislava, Slovakia
41. Research Centre of Slovenian Academy of Sciences and Arts (ZRC SAZU), Institute of Biology, Novi trg 2, 1000, Ljubljana, Slovenia
42. Department of Botany, Charles University, Benatska 2, 12801 Prague, Czech Republic
43. University of Zagreb, Faculty of Forestry, Svetošimunska 25, 10000, Zagreb, Croatia
44. University of Adelaide, TERN, North Terrace, 5005, Adelaide, Australia
45. CSIC-UV-GV, Centro de Investigaciones sobre Desertificación, Carretera Moncada-Náquera km 4.5, 46113.0, Moncada (Valencia), Spain
46. University of Zagreb, Faculty of Geotechnical Engineering, Hallerova aleja 7, 42000, Varaždin, Croatia
47. Aarhus University, Department of Biology, Ny Munkegade 114, DK-8000, Aarhus C, Denmark
48. Yunnan University, School of Ecology and Environmental Science, Building Shixun, Chenggong Campus, Dongwaihuan South Road, University Town, Chenggong New District, 650504, Kunming, China
49. Aristotle University of Thessaloniki, School of Biology, 54124, Thessaloniki, Greece
50. University of Erlangen-Nuremberg, Department of Geography, Wetterkreuz 15, 91058, Erlangen, Germany
51. ILEX Consultoria Científica, Amelia Telles 184, 9.046007E7, Porto Alegre, Brazil
52. University of Perugia, Department of Chemistry, Biology and Biotechnology, Borgo XX giugno 74, 06124, Perugia, Italy
53. Univ Montpellier, CNRS, EPHE, IRD, Univ Paul Valéry Montpellier 3, CEFE, 1919 route de Mende, 34293, Montpellier, France
54. University of Oulu, Ecology and Genetics Research Unit, Biodiversity Unit, Kaitoväylä 5, 90014, Oulu, Finland
55. Helmholtz Center for Environmental Research - UFZ, Department of Physiological Diversity, Permoserstr. 15, 04318, Leipzig, Germany
56. Leuphana University of Lüneburg, Institute of Ecology, Universitätsallee 1, 21335, Lüneburg, Germany
57. University of Alberta, Department of Biological Sciences, Biological Sciences Building, T6G2E9, Edmonton, Canada
58. University of Alaska, Institute of Arctic Biology, P. O. Box 7570000, 99775, Fairbanks, United States
59. University of Wisconsin-Madison, Botany, 430 Lincoln Drive, 53706, Madison, United States
60. Hainan University, Hainan Key Laboratory for Sustainable Utilization of Tropical Bioresources, College of Tropical Crops, 58 Renmin Avenue, Meilan District, 570228, Haikou, China
61. Senckenberg Museum of Natural History Görlitz, Botany Department, PO Box 300 154, 02806, Görlitz, Germany
62. Technische Universität Dresden, International Institute Zittau, Markt 23, 02763, Zittau, Germany
63. University of Minnesota, Bell Museum, 1445 Gortner Avenue, 55108.0, St. Paul, USA
64. Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Forest Dynamics, Zürcherstrasse 111, CH-8909, Birmensdorf, Switzerland
65. Ufa Scientific Centre, Russian Academy of Sciences, Laboratory of Wild-Growing Flora, South-Ural Botanical Garden-Institute, Mendeleev str., 195/3, 450080, Ufa, Russian Federation
66. University of Tartu, Institute of Ecology and Earth Sciences, Lai st 40, 51005, Tartu, Estonia

Short Running Title

sPlotOpen: a global vegetation plot database

Abstract

Motivation: Assessing biodiversity status and trends in plant communities is critical for understanding, quantifying and predicting the effects of global change on ecosystems, among other applications. Vegetation plots record occurrence or abundance of all plant species present (community composition) in delimited local areas. These data also allow inferring absences, enabling many analyses not possible using the presence-only data provided by existing global plant datasets. Although very many vegetation plots have been recorded, most are not available to the global research community. A recent initiative, sPlot, compiled the first global vegetation plot database, and continues to grow and curate it. However, this large dataset is challenging to work with because it is extremely unbalanced spatially, and because the data are not open-access. Here, we address both these issues by (a) resampling the vegetation plots using a novel algorithm and (b) securing

permission from data holders to openly release data (from 105 local to regional datasets). We thus present sPlotOpen, the largest open-access dataset of vegetation plots ever released. sPlotOpen can be used to explore global patterns of diversity at the plant community level, as ground truthing data in remote sensing applications or as a baseline for biodiversity monitoring.

Main types of variable contained: 95,104 vegetation plots, recording cover or abundance of naturally occurring vascular plant species in delimited areas. Besides geographic location, date, plot size, biome, elevation, slope, aspect, vegetation type, naturalness, coverage of various vegetation layers and source dataset, plot-level data also include community-weighted mean and variance of 18 plant functional traits from the 'TRY' database.

Spatial location and grain: global, 0.01-40,000 m².

Time period and grain: 1888-2015, recording dates.

Major taxa and level of measurement: 42,677 vascular plant taxa, plot-level records.

Software format: three main matrices (.csv), relationally linked.

Keywords

Biodiversity, Big-data, Database, Functional traits, Vascular plants, Vegetation plots

Background & Summary

Biodiversity is facing a global crisis. As many as 1 million species are currently threatened with extinction, the vast majority due to anthropogenic impacts such as land-use and climate change ([1](#), [2](#)). In addition, the rates of biodiversity homogenization and redistribution are accelerating ([3](#), [4](#); [5](#)). Biological assemblages are becoming progressively more similar to each other globally, as local and endemic species go extinct and are replaced by more widespread and competitive native or alien species ([1](#); [5](#)). Many terrestrial and marine species are also shifting their geographical distribution as a response to climate change ([4](#)), including animals hosting pathogens transmissible to humans ([6](#); [7](#)). This has profound potential impacts on ecosystems and human health ([8](#); [9](#)).

Plant communities are no exception to this biodiversity crisis ([10](#); [11](#); [5](#)). This is particularly worrying since terrestrial vegetation accounts for 80% (450 Gt C) of the living biomass on Earth ([12](#)). Given the central role of vegetation in ecosystem productivity, structure, stability and functioning ([11](#)), assessing biodiversity status and trends in plant communities is paramount for other kingdoms of life and human societies alike.

Monitoring trends in plant biodiversity requires adequate data across a range of spatiotemporal scales ([13](#), [14](#)). Large independent collections of plant occurrence data do exist at the global or continental extent via the Botanical Information and Ecology Network (BIEN) ([15](#)), the Global Inventory of Floras and Traits (GIFT) ([16](#)) or the Global Biodiversity Information Facility (GBIF) (<https://www.gbif.org/>). However, these databases are either imbalanced towards tree species only, or neglect how individual plant species co-occur and interact locally to form plant communities, or are collected at spatial resolutions which preclude intersection with high resolution remote sensing data and are too coarse (e.g., one-degree grid cells) to assess biodiversity trends at the plant community scale ([17](#)).

Yet, there is a long tradition among botanists to record the cover or abundance of each plant species that occurs in a vegetation plot location of a given size (i.e. surface area) at a given time (e.g. [18](#)). Compared to presence-only data, vegetation-plot data (termed 'presence-absence' here) present many advantages. As all visible plant species are recorded, plots contain information on which plant species do, and do not, co-occur in the same locality at a given moment in time ([19](#)). This is important for testing hypotheses related to biotic interactions among plant species. Vegetation-plot data also provide crucial information on where and when a species was absent, therefore improving predictions from current species distribution models ([20](#)). Being spatially explicit, vegetation plots can be resurveyed through time to assess potential changes in plant species composition relative to a baseline ([21](#); [22](#), [5](#)). As they normally contain information on the relative cover or abundance of each species, vegetation plots are also more appropriate for detecting biodiversity changes than data representing only the occurrence of individual species ([23](#), [24](#)).

Globally, however, vegetation-plot data are very fragmented, as they typically stem from a myriad of local research and survey projects ([25](#)). Consequently, these data often have high fine-grain spatial resolutions but small spatial extents ([26](#)). Furthermore, with their disparate sampling protocols, standards and taxonomic resolutions, aggregating and harmonizing vegetation plot data proves extremely challenging ([27](#)). It is not surprising, therefore, that these data are rarely used in global-scale research on the biodiversity of plant communities ([28](#); [29](#); [30](#)).

The sPlot initiative tries to close this data gap. It consolidates numerous local to regional vegetation-plot datasets to create a harmonized and comprehensive global database of georeferenced terrestrial plant species assemblages ([25](#)). Established in 2013, sPlot (version 3) currently contains more than 1.9 million vegetation plots, and is fully integrated with the TRY database ([31](#)), from which it derives information on plant functional traits. The sPlot database is increasingly being used to study

continental-to-global scale vegetation patterns, such as the relative contribution of regional vs. local factors on the global patterns of fern richness (32), the mechanisms underlying the spread and abundance of native vs. invasive tree species (33), and worldwide trait–environment relationships in plant communities (27).

Yet, most of these data are not open-access. Here, we secured permission from data holders in the sPlot database to openly release a dataset composed of 95,104 vegetation plots. We selected the plots to release using a replicated environmental stratification, in order to represent the entire environmental space covered by the sPlot database. This maximises the benefits of this large dataset for a wide range of potential uses. The selected vegetation plots stem from 105 databases and span 114 countries (Figure 1). This resampled dataset (sPlotOpen - hereafter) is composed of: (1) plot-level information, including metadata and basic vegetation structure descriptors; (2) the vascular plant species composition of each vegetation plot, including species cover or abundance information when available; and (3) community-level functional information obtained by intersection with the TRY database (31).

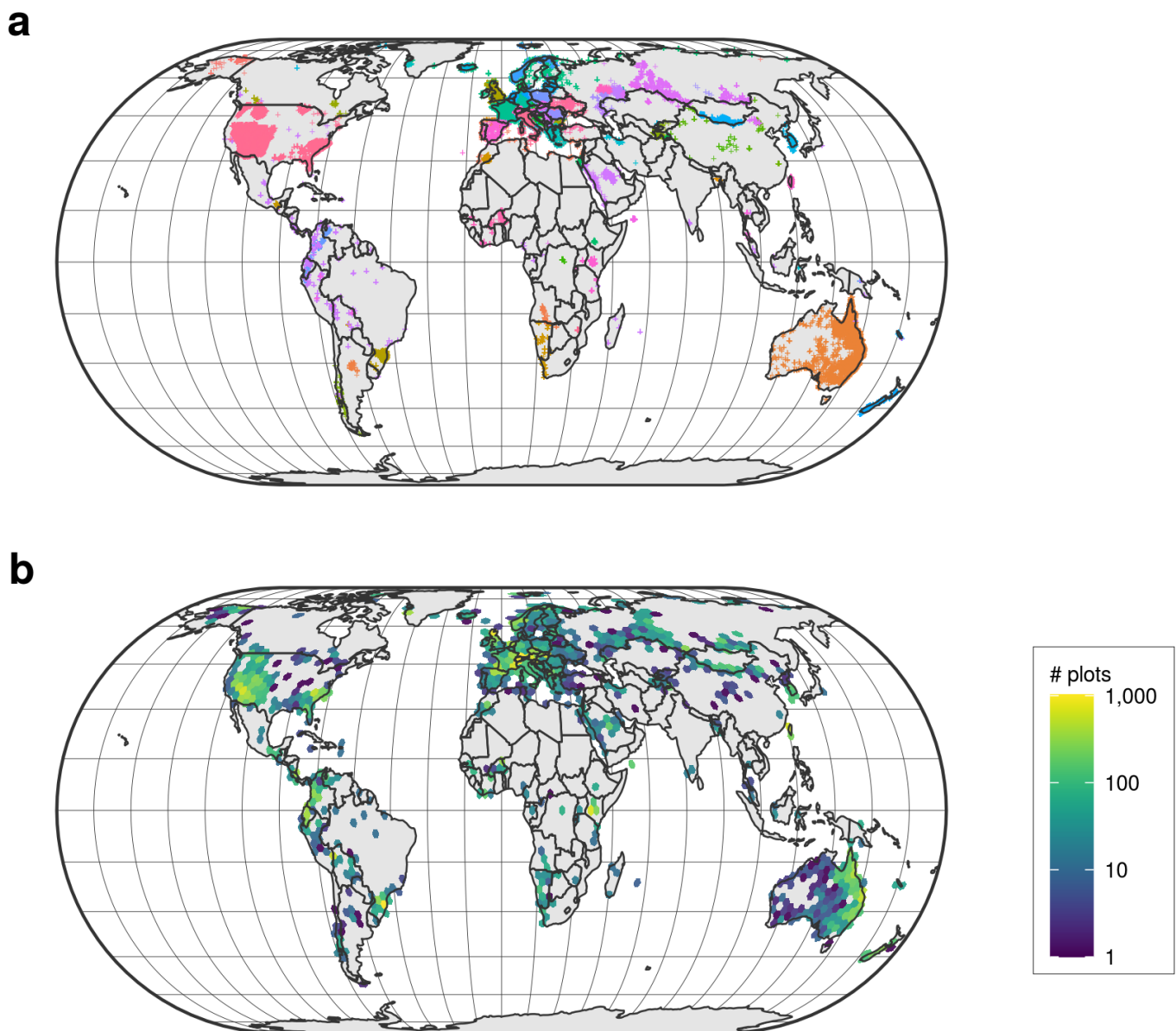


Figure 1: Top: Global distribution of all vegetation plots contained in sPlotOpen ($n = 95,104$). Each color represents a different source dataset ($n = 105$ - different datasets might have the same color). Bottom: Spatial distribution of vegetation plot density in the first resampling iteration ($n = 49,787$). Densities are calculated in hexagonal cells with a spatial resolution of approximately $70,000 \text{ km}^2$. Map projection is Eckert IV.

Methods

Vegetation plot data sources

We started from the sPlot database v2.1 (created in October 2016), which contains 1,121,244 unique vegetation plots (also called 'relevés') and 23,586,216 species records. sPlot focuses on natural vegetation, i.e., plant cover that develops with little or no human interference. Data originate from 110 different vegetation-plot datasets of regional, national or continental extent, some of which stemming from regional or continental initiatives (see [25](#) for more information). For instance: 48 vegetation-plot datasets derive from the European Vegetation Archive (EVA) ([19](#)); three major African datasets derive from the Tropical African Vegetation Archive (TAVA); and multiple vegetation datasets in the USA and Australia derive from the VegBank ([34](#); [35](#)) and TERN's AEKOS ([36](#)) archives, respectively. Data from other continents (South America, Asia) or countries were contributed as separate standalone datasets. The metadata of each individual vegetation-plot dataset stored in sPlot are managed through the Global Index of Vegetation-Plot Databases [GIVD](#) ([37](#)), using the GIVD code as the unique dataset identifier.

Resampling method

Data in the sPlot database are unevenly distributed across vegetation types and geographic regions (see [27](#)). First, we removed vegetation plots without geographical coordinates or with a location uncertainty higher than 3 km. We also removed vegetation plots from wetlands and from anthropogenic vegetation types, since these data were available only for few geographic regions, mostly in Europe. This resulted in a total of 799,400 out of the initial set of 1,121,244 vegetation plots. We then tried to reduce the geographical imbalance. Mid-latitude regions in developed countries (mostly Europe, the USA and Australia) are overrepresented in sPlot, while regions in the tropics and subtropics are underrepresented, which is a typical geographical bias in biodiversity data (e.g., [38](#); [4](#)). To reduce this imbalance as much as possible, we performed a stratified resampling approach, using several environmental variables available at global extent as sampling strata. We considered 30 climatic and soil variables. For climate, we complemented the 19 bioclimatic variables from CHELSA v1.2 ([39](#)), as well as two variables reflecting the growing-season length (growing degree days above 1 °C - GDD1 - and 5 °C - GDD5), which were derived from CHELSA's monthly average temperatures. Specifically we summed the number of days of those months with average temperature greater than 1 °C or 5 °C, respectively. In addition, we considered an index of aridity and a layer for Potential Evapotranspiration from the Consortium of Spatial Information (CGIAR-CSI) [40](#)). For soil, we extracted seven variables from the SOILGRIDS database ([41](#)), namely: soil organic carbon content in the fine earth fraction, cation exchange capacity, pH, as well as the fractions of coarse fragments, sand, silt and clay.

We stratified our sampling effort based on the following procedure. First, we ran a global principal component analysis (PCA) on a matrix of terrestrial grid cells by the 30 above-mentioned environmental variables. We considered the full environmental space of all terrestrial habitats on Earth at a spatial resolution of 2.5 arcmin, totaling 8,384,404 terrestrial grid cells, irrespective of whether a grid cell hosted vegetation plots from the sPlot database v2.1 or not (Figure [S1](#)). We then subdivided the PCA ordination space, represented by the first two principal components (PC1–PC2), which accounted for 47% and 23% of the total environmental variation in terrestrial grid cells, into a regular 100 × 100 grid. This PC1-PC2 two-dimensional space was subsequently used to balance our sampling effort across all PC1-PC2 grid cells for which vegetation plots were available. After projecting the 799,400 vegetation plots onto this PC1-PC2 grid, we calculated how many vegetation plots occurred in each PC1-PC2 grid cell (Figure [2](#)). We then resampled those grid cells ($n = 858$) with more than 50 vegetation plots, which is the median of plots occurring across occupied grid cells. For each of

these cells, we selected up to 50 vegetation plots using the heterogeneity-constrained random resampling algorithm from Lengyel et al. (2011) [42]. This approach optimizes the selection of a random subset of vegetation plots that encompasses the highest variability in species composition while avoiding peculiar and rare communities, which may represent outliers. We quantified the variability in plant species composition among the 50 randomly selected vegetation plots by computing the mean and the variance of the Jaccard's dissimilarity index (43) between all possible pairs of these 50 vegetation plots ($n = 1,225$). More precisely, for a given PC1-PC2 grid cell containing more than 50 vegetation plots, we generated 1,000 random selections of 50 vegetation plots and ranked them according to the mean (ascending order) and variance (descending order) value. Ranks from both sortings were summed for each random selection, and the selection with the lowest summed rank was considered to provide the most balanced/even representation of vegetation types within the focal grid cell. Where a grid cell contained less than 50 plots, we retained all of them. In this way, we reduced the imbalance towards over-sampled climate types while ensuring that the resampled dataset represents the entire environmental gradient covered by the sPlot database. We repeated the resampling procedure three times to get three different possibilities of a heterogeneity-constrained selection of 50 vegetation plots per PC1-PC2 grid cell with, initially, more than 50 vegetation plots. Vegetation plots selected during the first iteration were our first choice, while we considered the vegetation plots additionally selected in the second and third iteration as reserves when asking for permission to release the data as open access to each dataset's contributor(s).

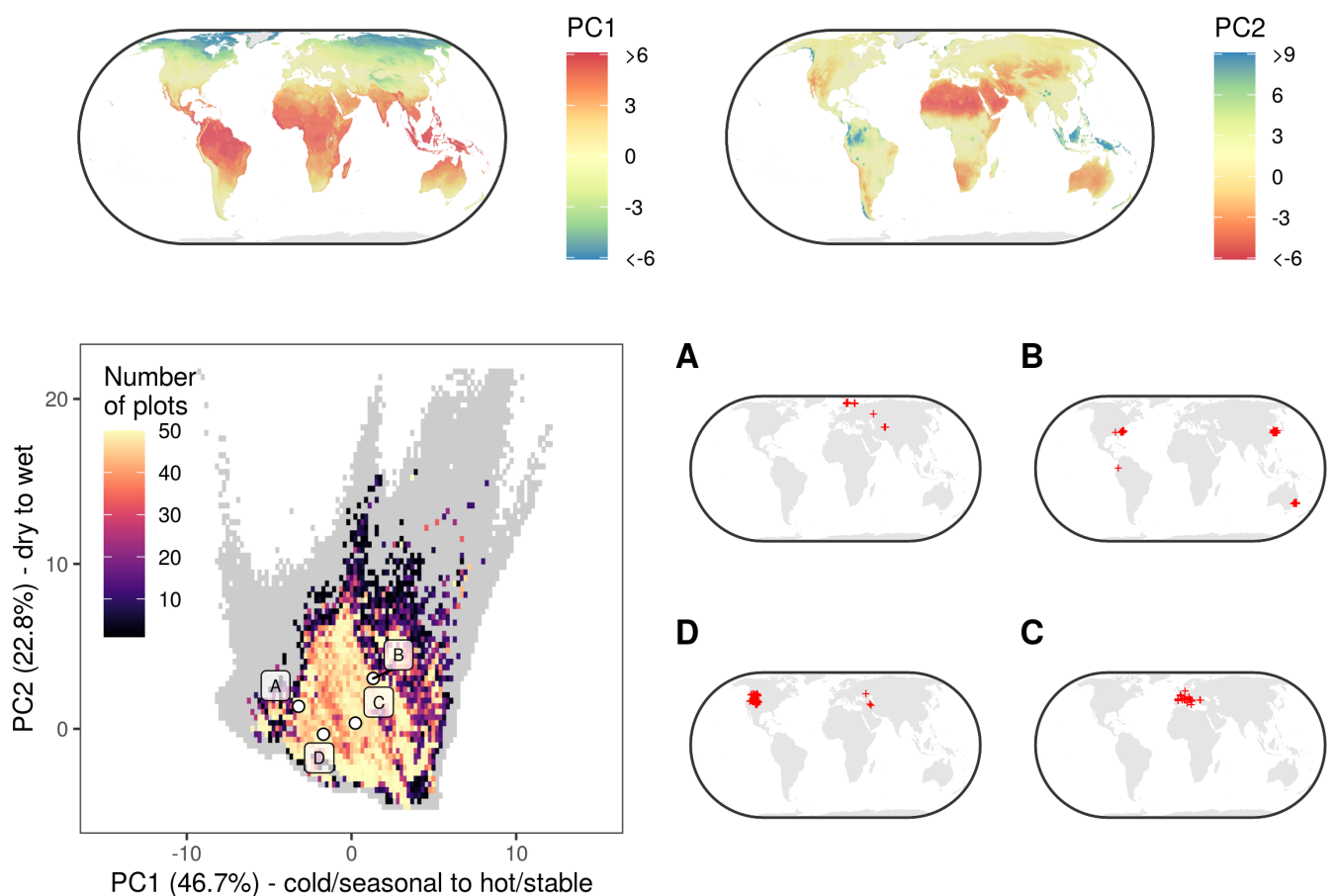


Figure 2: Distribution of vegetation plots from sPlotOpen in the global environmental space based on a principal component analysis (PCA) using 30 climate and soil variables. Top: Spatial distribution of PCA values across all terrestrial grid cells ($n = 8,384,404$, spatial grain = 2.5 arcmin). Bottom Left: Distribution of plots compared to the distribution of all terrestrial 2.5 arc-minute cells (gray background) in the PCA space. The PCA space was divided into a 100×100 regular grid. The first and second PCA axis explained 47% and 23% of the total variance. Bottom right: Geographic distribution of the vegetation plots contained in four randomly selected grid cells.

Permission to release the data as open access

The resampling procedure resulted in a preliminary selection of 107,238 vegetation plots across the three resamplings. Since the sPlot database is a consortium of independent datasets whose copyright belongs to the data contributor, we used this preliminary potential selection to ask each dataset's custodian (i.e., either the owner of a dataset or its authorized representative in case of a collective dataset) for permission to release the data of each selected vegetation plot as open access. For 12,035 vegetation plots, permission could not be granted because, for instance, the data are unpublished, confidential or sensitive. Of these 6,625 were first choice plots, and were distributed across 770 PC1-PC2 grid cells (44.1% of occupied cells). For these vegetation plots, we used the reserve pool to randomly select replacements, for which such permission could be granted. We imposed the constraint that each candidate vegetation plot in the reserve pool should belong to the same environmental stratum, i.e., the same PC1-PC2 grid cell, of the confidential vegetation plot, even if we acknowledge that this procedure does not maximize the variability in plant species composition of the replacement plots. There were 3,150 plots that could not be replaced from the reserve pool. These were distributed across 279 PC1-PC2 grid cells (16.2% of occupied cells), each cell having on average 11 irreplaceable plots (min = 1, median = 5, max = 50).

Trait information

For each vegetation plot for which open access could be granted, we computed the community weighted mean and variance for eighteen plant functional traits derived from the TRY database v3.0 (31). These traits were selected among those that describe the leaf, wood and seed economics spectra (44; 45), and are known to either affect different key ecosystem processes or respond to macroclimatic drivers, or both (25). The eighteen plant functional traits (all concentrations based on dry weight) were: (1) leaf area [mm²]; (2) stem specific density [g cm⁻³]; (3) specific leaf area [m²kg⁻¹]; (4) leaf carbon concentration [mg g⁻¹]; (5) leaf nitrogen concentration [mg g⁻¹]; (6) leaf phosphorus concentration [mg g⁻¹]; (7) plant height [m]; (8) seed mass [mg]; (9) seed length [mm]; (10) leaf dry matter content [g g⁻¹]; (11) leaf nitrogen per area [g m⁻²]; (12) leaf N:P ratio [g g⁻¹]; (13) leaf $\delta^{15}\text{N}$ [per million]; (14) seed number per reproductive unit; (15) leaf fresh mass [g]; (16) stem conduit density [mm⁻²]; (17) dispersal unit length [mm]; and (18) conduit element length [μm].

Because missing values were particularly widespread in the species-trait matrix, we calculated community weighted means using the gap-filled version of these traits we received from TRY (31). Gap-filling was performed at the level of individual observations and relies on a hierarchical Bayesian modeling (R package 'BHPMF', 46; 47). This is a Bayesian machine learning approach, with no a priori assumptions, except for assuming that the data are missing completely at random. The algorithm "learns" from the data, i.e. if there was a phylogenetic signal in the data, this was used to fill the gaps but where no such signal was apparent, none was introduced. After gap-filling, we transformed to the natural logarithm all gap-filled trait values and averaged each trait by taxon (i.e., at species, or genus level). The gap-filling approach was run only for species having at least one trait observation (n = 21,863). Additional information on the gap-filling procedure is available in [25].

Community-weighted means (CWM) and variances (CWV) were calculated for every plant functional trait j and every vegetation plot k as follows (48):

$$CWM_{j,k} = \sum_i^{n_k} p_{i,k} t_{i,j} \quad (1)$$

$$CWV_{j,k} = \sum_i^{n_k} p_{i,k} (t_{i,j} - CWM_{j,k})^2 \quad (2)$$

where n_k is the number of species with trait information in vegetation plot k , $p_{i,k}$ is the relative abundance of species i in vegetation plot k calculated as the species' fraction in cover or abundance of total cover or abundance, and $t_{i,j}$ is the mean value of species i for trait j .

Data Records

sPlotOpen contains 95,104 vegetation plots from 114 countries and all continents except Antarctica (Figure 1). This randomized selection comes from 105 constitutive datasets (Table 1). The number of plots selected in each of the three resampling iterations is 49,787, 49,811 and 49,789. After replacing confidential plots with reserves from the same PC grid cell, the first resampling iteration contains 53,262 plots. The number of plots shared across all the three iterations is 19,672, while 14,939 plots are shared between two iterations. sPlotOpen only contains the species composition of vascular plants; information on the composition of bryophytes and lichens was discarded since it was only available for a minority of plots ($n = 11,001$ and $n = 6,801$, respectively). Information on the size (surface area) of the vegetation survey is available for 65,461 vegetation plots, and ranges between 0.03 and 40,000 m² (mean = 377 m²; median = 100 m²). Specifically, sPlotOpen contains 12,894 plots with size smaller than 10 m², 25,742 with size 10-100 m², 24,750 plots with size 100-1,000 m² and 2,075 plots with size greater or equal to 10,000 m². Similarly, only for a minority of plots ($n = 24,167$) information on the exact group of plants sampled in the field is available (e.g., complete vegetation, only trees, only trees > 1 m height, and so on). However, as most data were collected using the phytosociological method, we deem safe to assume that, unless otherwise specified, plots contain information on all vascular plants. We retained plots with incomplete vegetation, because they were mostly located in the tropics, i.e., in areas where vegetation plots are particularly scarce otherwise. The average number of vascular plant species per vegetation plot ranges between 1 (i.e. monospecific stands) and 271 species (mean = 20; median = 16).

By capping the number of vegetation plots in overrepresented environmental conditions, the resampling procedure described above strongly reduced the bias in the distribution of vegetation plots within the environmental niche space. Yet, due to the lack or scarcity of data from some geographical regions, like the tropics, the spatial distribution of vegetation plots remains unbalanced across geographical regions (Figure 1). This is evident when comparing the number of plots across continents or biomes. When considering the first resampling iteration only, Europe is by far the best represented continent, with 15,920 vegetation plots. In contrast, in Africa and South America the remaining plots after data edition and selection were 3,709, and 5,498 vegetation plots, respectively. Compared to continents, the representation of biomes is better balanced. With the exception of the 'Temperate mid-latitudes' biome, which includes 14,100 vegetation plots, all other biomes have a number of plots comprised between 1,558 ('Polar and subpolar zone') and 6,245 ('Subtropics with year-round rain') vegetation plots (Figure 3, left). Despite these imbalances, all the Whittaker biomes are covered by sPlotOpen (Figure 3, right), and our resampling algorithm has resulted in a much more balanced dataset than many other large global datasets that are available, such as GBIF.

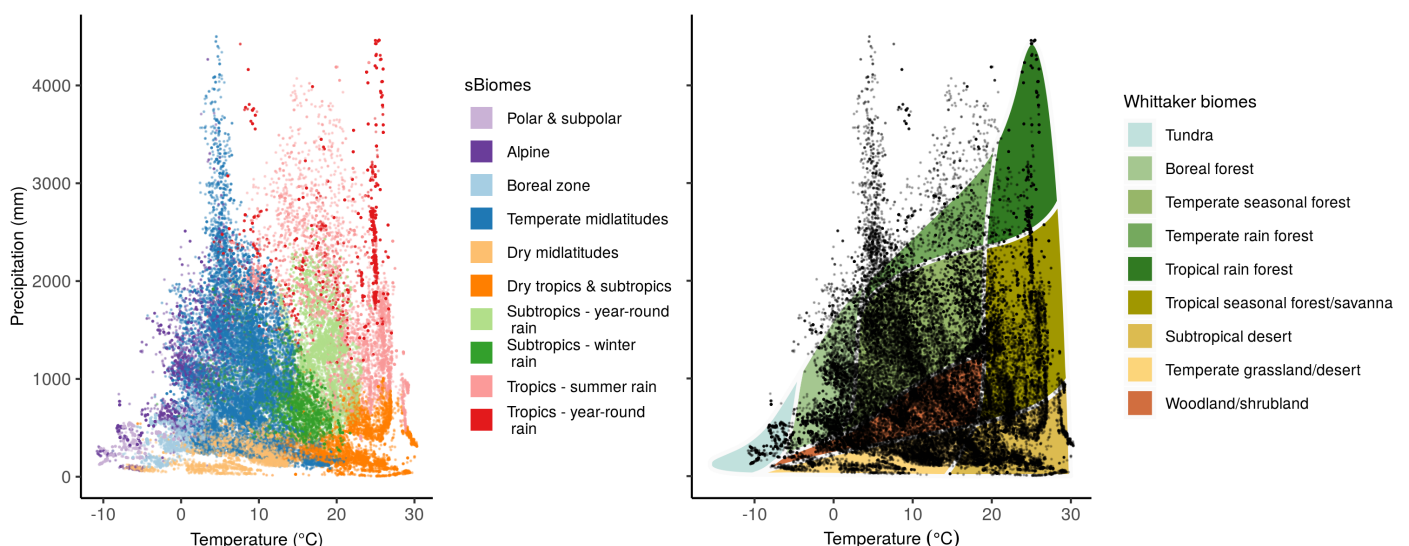


Figure 3: Distribution of vegetation plots in the first resampling iteration of sPlotOpen (n = 49,787) in the two-dimensional climatic space represented by mean annual temperature and mean annual precipitation. Left: plots are color coded based on sBiomes, i.e., sPlot's definition of biomes ([25](#)), which derives from Schultz 2005 ([49](#)) ecozones, modified to include also the alpine biome from Körner et al. 2017 ([50](#)). Right: the same plots superimposed onto Whittaker (1975) biomes ([51](#)), as adapted by Rickleff 2008 ([52](#)) and plotted using the R package *plotbiomes*.

Almost one third of vegetation plots in sPlotOpen belong to forest (n = 38,264), one half to non-forest vegetation (n = 45,753) vegetation, with 11.6 % of plots remaining unassigned (n = 11,087). When not directly done by data providers, the assignment of plots to forests and non-forests was based on multiple lines of evidence, including the plot-level information on the cover of the tree layer, as well as traits of species composing a plot, such as growth form and height. In short, a plot record was considered as forest if the cover of the tree layer, or alternatively, the sum of the (relative) cover of all tree taxa (normalized to 100%), was greater than 25%. It was considered a non-forest record if the sum of relative cover of low-stature, non-tree and non-shrub taxa was greater than 90%. For an extensive explanation of this classification scheme, we refer the reader to Bruelheide et al. (2019) [[25](#)]. Even if the proportion of forest vs. non-forest vegetation plots is relatively well-balanced, the geographical distribution of vegetation plots belonging to different vegetation types is likely not balanced in the geographical space, as it depends on the idiosyncrasies of the constitutive datasets composing the sPlot database. For instance, the data from New Zealand only include plots collected in non-forest ecosystems, while data from Chile only refer to forests. We urge potential users to carefully read the description of each individual dataset in [GIVD](#), or to contact the custodians of each dataset before using sPlotOpen.

Database Organization

sPlotOpen is organized into three main matrices, relationally linked through the key column *'PlotObservationID'*.

The **'header'** matrix contains plot-level information for the 95,104 vegetation plots provided in sPlotOpen, including: metadata (e.g., plot ID, ownership, sampling date, geographical location, positional accuracy); sampling design information (e.g., the total surface area used during the vegetation survey); and a plot-level description of vegetation structure (e.g., vegetation type, percentage cover of each vegetation layer), vegetation type, and naturalness level (i.e., whether a plot belongs to the same formation that would occupy the site without human interference). Plots in Europe are also classified according to the EUNIS habitat classification (column *'ESY'*), based on the habitat classification expert system described in Chytrý et al. (2020) ([53](#)). For each vegetation plot, we further provide information on the dataset it originates from, based on the IDs used in [GIVD](#). We also report four binary fields describing whether a plot belongs to the three resampling iterations (columns *'Resample_1'*, *'Resample_2'*, *'Resample_3'*), or to the first resampling iteration after the inclusion of replacement plots (column *'Resample_1_consensus'*). A brief summary of all the 47 variables in the header matrix is provided in Table [2](#).

The **'DT'** matrix contains data on the species composition of each plot. It is structured in a long format and contains 1,938,401 records from 42,677 vascular plant taxa, mostly resolved at the species level. For each record, we report both the taxon name as originally contributed by the data custodian (column *'Original_species'*), and the taxon name after taxonomic standardization (column *'Species'*), together with its cover/abundance values. These follow different standards across the datasets constituting the sPlot database. We, therefore, provide both the cover/abundance value as reported in the original data (column *'Original_abundance'*), together with the abundance scale that was originally used (column *'Abundance_scale'*). This can take seven values: *'CoverPerc'* = percentage cover, *'pa'* = presence-absence, *'x_BA'* = basal area (m²/ha, only for woody species), *'x_IC'* = individual count, i.e., number of individuals in plot, *'x_SC'* = stem count, i.e., number of stems in plot, *'x_IV'* = importance value index, *'x_PF'* = presence frequency. The great majority of entries, however, use the percentage cover scale (n = 1,709,000). Finally, for each entry, we calculated a *'Relative_cover'*, i.e., the cover/abundance of a given taxon divided by the total cover/abundance of all taxa in that vegetation plot.

The **'CWM_CWV'** matrix contains the community-weighted means and variances calculated for each of the 18 functional traits mentioned above. It also contains three additional columns. The column *'Species_richness'* returns the number of species recorded in each plot. The columns *'Trait_coverage_cover'* and *'Trait_coverage_pa'* return, respectively, the proportion of total cover and species in a plot for which functional trait information was available. Functional trait information was available for 21,863 species. The average proportion of species in each plot for which we have functional trait information is 0.85 (median = 0.95). For 42,025 plots, the coverage is complete, while for only 482 plots do we have no functional trait information for any of the species occurring in it. When considering relative cover, the average trait coverage is 0.87. As many as 68,137 and 74,374 plots have functional trait information for 80% or more of the species or relative cover, respectively.

sPlotOpen contains two additional objects. The **'metadata'** matrix contains plot-level metadata, which provide information on the origin of each individual vegetation plot. This object contains 15 columns, with information on the dataset of origin (column *'GIVD_ID'* - [37](#)), author or surveyor names (columns *'Releve_author'* and *'Releve_coauthor'*), bibliographic references both at the dataset (column *'DB_BIBTEXKEY'*) and plot level (*'Plot_Biblioreference'* and *'BIBTEXKEY'*), when available. Similarly, the column *'Project_name'* provides information on the project in which a vegetation plot was collected. When available, we also provide information on the numbering of the plots in the publication where

they originally appeared (columns *'Nr_table_in_publ'*, *'Nr_releve_in_table'*), or in the dataset where they were initially stored (*'Original_nr_in_database'*). In the case of nested plots (n = 300), we also provide the original plot and subplot IDs (columns: *'Original_plotID'*, *'Original_subplotID'*). The last two columns report plot-level *'Remarks'*, and the unique identifier produced by Turboveg when the vegetation plot was first stored (*'GUID'*).

Finally, the object **'references'**, contains all the bibliographic references formatted according to a BibTex standard. Each reference is tagged with a key corresponding to the fields *'DB_BIBTEXKEY'* and *'BIBTEXKEY'* in the metadata. We further provide an R function (*'sPlotOpen_citation'*) to create reference lists, based on a selection of plots and/or datasets.

Except for the 'reference' file (format .bib), all objects/matrices are provided in tab-delimited .txt files. All objects, including the *'sPlotOpen_citation'* function, are also compiled inside an .RData object.

Technical Validation

The original sPlot database has a nested structure and consists of several individual datasets, each validated and maintained by its respective dataset custodian. In many cases, individual datasets are also collections whose vegetation plots were provided by their respective owners (the person who performed the actual vegetation survey) or by someone who digitized the original data from the scientific published or grey literature. We obviously have no direct control over the individual vegetation plots that we provide here in sPlotOpen. Yet, all these vegetation plots stem from trained professional botanists, or published scientific work, and are accompanied by detailed information on the sampling protocols used, thus ensuring data quality and reliability.

Before integration into the sPlot database, each dataset was further checked for consistency and, if it was in a different format, we converted it to a Turboveg 2 dataset ([54](#)). During this conversion, we checked that all datasets contained the required metadata information, and cross-checked that each plot was located within the geographic scopes of its respective dataset. All individual Turboveg 2 datasets were then integrated into a Turboveg 3 database, and exported to comma-separated files. Finally, we harmonized all the taxonomic names from all datasets, based on the sPlot's taxonomic backbone ([55](#)). This backbone matched all the taxonomic names (without nomenclatural authors) from all datasets in sPlot 2.1 and TRY v3.0 ([31](#)) to their resolved version based on the Taxonomic Name Resolution Service web application (TNRS version 4.0; [56](#); iPlant Collaborative, 2015). This allowed us to (1) harmonize all datasets to a common nomenclature, and (2) link the sPlot database to the TRY database ([31](#)). The final backbone only retained matched taxonomic names at the rank of species or higher. Additional detail on the taxonomic resolution is reported in Bruehlheide et al. (2019) [[25](#)], while a description of the workflow, including R-code, is available in Purschke (2017) [[55](#)].

Usage Notes

The sPlotOpen database can be downloaded from <https://www.idiv.de> (link to PlantHub). Users are urged to cite the original sources when using sPlotOpen in addition to the present paper, particularly when using data contained in BioTIME ([57](#)). For two datasets (AF-00-009, AF-CD-001), the identification of taxa at species level is still in progress. Data on lichens and mosses, where available (e.g., dataset NA-GL-001), can be obtained on request from the respective dataset custodian or sPlot coordinator. As most of the constitutive datasets remain under continuous development, sPlotOpen users are encouraged to get in touch with the custodian(s) of the data they are planning to use (custodian names are reported in <https://www.idiv.de/sPlot>).

The data included in the present paper represent the subset of sPlot for which we were able to secure permission for making these data open. The additional data in sPlot are available under sPlot's Governance and Data Property Rules (www.idiv.de/sPlot). Using the full sPlot dataset is also recommended if a stratification is desired that is different from the environmental factors used here, for example by geographical region or plot size.

Code Availability

The R code used to produce sPlotOpen from the sPlot 2.1 database is contained in the *sPlotOpen_code* GitHub repository: (https://github.com/fmsabatini/sPlotOpen_Code/). This manuscript was produced using the Manubot workflow ([58](#)). The code for reproducing this manuscript is stored in the *sPlotOpen_manuscript* GitHub repository: (https://github.com/fmsabatini/sPlotOpen_Manuscript).

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Author contributions

FMS wrote the first draft of the manuscript, with considerable input from JL and HB. JL and TH wrote the resampling algorithm. FMS set up the GitHub projects, curated the database, and produced the graphs. He also coordinated the sPlot consortium. SMH wrote the Turboveg software, which holds the sPlot database. JK provided the trait data from TRY and FS performed the trait data gap filling. HB secured the funding for sPlot as a strategic project of iDiv. All other authors contributed data and/or helped set up the database and/or helped develop the resampling algorithm. All authors contributed to revising the manuscript.

Competing interests

The authors declare no competing interests.

Biosketch

sPlot is a collaborative initiative to integrate existing local and national vegetation-plot dataset into a global harmonized database. It was initiated in 2013, within the sDiv working group “Plant trait-environment relationships across the world’s biomes”. Since then, it became established as the largest vegetation-plot databases worldwide and coordinates a consortium of 251 individual active members, representing 167 local and national datasets. sPlot’s overarching scientific goal is the exploration of all aspects of global plant community diversity, including taxonomic, functional and phylogenetic diversity, across biomes, vegetation types, taxonomic or functional guilds and scales. Central to sPlot’s mission are the exploration of the relationships between environmental drivers, trait variation, and assembly processes in local plant communities worldwide.

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124. How resilient are northern hardwood forests to human disturbance? An evaluation using a plant functional group approach

I. Aubin, S. Gachet, C. Messier, A. Bouchard
Ecoscience (2007)

125. Vegetation and altitudinal zonation in continental West Greenland

B. Sieg, B. Drees, F. J. A. Daniëls
Meddelelser om Grønland Bioscience (2006)

126. VegBank – a permanent, open-access archive for vegetation-plot data

Robert Peet, Michael Lee, Michael Jennings, Don Faber-Langendoen
Biodiversity & Ecology (2012-09-10) <https://doi.org/ghgvcm>
DOI: [10.7809/b-e.00080](https://doi.org/10.7809/b-e.00080)

127. Vegetation-plot database of the Carolina Vegetation Survey

Robert Peet, Michael Lee, Forbes Boyle, Thomas Wentworth, Michael Schafale, Alan Weakley
Biodiversity & Ecology (2012-09-10) <https://doi.org/ghgvcn>
DOI: [10.7809/b-e.00081](https://doi.org/10.7809/b-e.00081)

128. The Alaska Arctic Vegetation Archive (AVA-AK)

Donald A. Walker, Amy L. Breen, Lisa A. Druckenmiller, Lisa W. Wirth, Will Fisher, Martha K. Reynolds, Jozef Šibík, Marilyn D. Walker, Stephan Hennekens, Keith Boggs, ... Donatella Zona
Phytocoenologia (2016-09-01) <https://doi.org/f877ht>
DOI: [10.1127/phyto/2016/0128](https://doi.org/10.1127/phyto/2016/0128)

129. VegPáramo, a flora and vegetation database for the Andean páramo

Gwendolyn Peyre, Henrik Balslev, David Martí, Petr Sklenář, Paul Ramsay, Pablo Lozano, Nidia Cuello, Rainer Bussmann, Omar Cabrera, Xavier Font
Phytocoenologia (2015-07-01) <https://doi.org/f7m9cj>
DOI: [10.1127/phyto/2015/0045](https://doi.org/10.1127/phyto/2015/0045)

130. The Floristic and Forest Inventory of Santa Catarina State (IFFSC): methodological and operational aspects

A. C. Vibrans, L. Sevegnani, D. V. Lingner, A. L. Gasper, S. Sabbagh
Pesquisa Florestal Brasileira (2010)

131. Plant Invasions in Protected Areas

Springer Science and Business Media LLC
(2013) <https://doi.org/ghgt8v>
DOI: [10.1007/978-94-007-7750-7](https://doi.org/10.1007/978-94-007-7750-7)

Supplementary Material

Table 1: List of databases contributing sPlotOpen, the open access dataset extracted from the sPlot database. Databases are ordered based on their ID in the Global Index of Vegetation Databases (GVID ID).

GVID ID	Dataset name	Custodian	Deputy custodian	Nr. open-access plots	Ref
00-00-001	ForestPlots.net	Oliver L. Phillips	Aurora Levesley	169	59
00-00-003	SALVIAS	Brian Enquist	Brad Boyle	3403	
00-00-004	Vegetation Database of Eurasian Tundra	Risto Virtanen		519	
00-00-005	Tundra Vegetation Plots (TundraPlot)	Anne D. Bjorkman	Sarah Elmendorf	309	60
00-RU-001	Vegetation Database Forest of Southern Ural	Vasiliy Martynenko	Pavel Shirokikh	68	
00-RU-002	Database of Masaryk University`s Vegetation Research in Siberia	Milan Chytrý		158	61
00-RU-003	Database Meadows and Steppes of Southern Ural	Sergey Yamalov	Mariya Lebedeva	238	
00-TR-001	Forest Vegetation Database of Turkey - FVDT	Ali Kavgacı		45	
AF-00-001	West African Vegetation Database	Marco Schmidt	Georg Zizka	258	62
AF-00-003	BIOTA Southern Africa Biodiversity Observatories Vegetation Database	Norbert Jürgens	Ute Schmiedel	1015	63
AF-00-006	SWEA-Dataveg	Miguel Alvarez	Michael Curran	1675	
AF-00-008	PANAF Vegetation Database	Hjalmar Kühl	TeneKwetché Sop	884	
AF-00-009	Vegetation Database of the Okavango Basin	Rasmus Revermann	Manfred Finckh	378	64
AF-BF-001	Sahel Vegetation Database	Jonas V. Müller	Marco Schmidt	556	65
AF-CD-001	Forest Database of Central Congo Basin	Kim Sarah Jacobsen	Hans Verbeeck	140	66
AF-ET-001	Vegetation Database of Ethiopia	Desalegn Wana	Anke Jentsch	67	67
AF-MA-001	Vegetation Database of Southern Morocco	Manfred Finckh		621	68
AF-ZW-001	Vegetation Database of Zimbabwe	Cyrus Samimi		31	69
AS-00-001	Korean Forest Database	Tomáš Černý	Jiri Dolezal	1039	70
AS-00-003	Vegetation of Middle Asia	Arkadiusz Nowak	Marcin Nobis	314	71
AS-00-004	Rice Field Vegetation Database	Arkadiusz Nowak		32	
AS-BD-001	Tropical Forest Dataset of Bangladesh	Mohammed A.S. Arfin Khan	Fahmida Sultana	87	
AS-CN-001	China Forest-Steppe Ecotone Database	Hongyan Liu	Fengjun Zhao	117	72
AS-CN-002	Tibet-PaDeMoS Grazing Transect	Karsten Wesche		58	73
AS-CN-003	Vegetation Database of the BEF China Project	Helge Bruehlheide		24	74

GIVD ID	Dataset name	Custodian	Deputy custodian	Nr. open-access plots	Ref
AS-CN-004	Vegetation Database of the Northern Mountains in China	Zhiyao Tang		124	
AS-EG-001	Vegetation Database of Sinai in Egypt	Mohamed Z. Hatim		143	75
AS-ID-001	Sulawesi Vegetation Database	Michael Kessler		24	
AS-IR-001	Vegetation Database of Iran	Jalil Noroozi	Parastoo Mahdavi	277	
AS-KZ-001	Database of Meadow Vegetation in the NW Tien Shan Mountains	Viktoria Wagner		13	76
AS-MN-001	Southern Gobi Protected Areas Database	Henrik von Wehrden	Karsten Wesche	1032	77
AS-RU-001	Wetland Vegetation Database of Baikal Siberia (WETBS)	Victor Chepinoga		9	78
AS-RU-002	Database of Siberian Vegetation (DSV)	Andrey Korolyuk	Andrei Zverev	3634	79
AS-RU-004	Database of the University of Münster - Biodiversity and Ecosystem Research Group's Vegetation Research in Western Siberia and Kazakhstan	Norbert Hölzel	Wanja Mathar	207	
AS-SA-001	Vegetation Database of Saudi Arabia	Mohamed Abd El-Rouf Mousa El-Sheikh		711	80
AS-TJ-001	Eastern Pamirs	Kim André Vanselow		221	81
AS-TW-001	National Vegetation Database of Taiwan	Ching-Feng Li	Chang-Fu Hsieh	912	
AS-YE-001	Socotra Vegetation Database	Michele De Sanctis	Fabio Attorre	236	82
AU-AU-002	AEKOS	Ben Sparrow		10976	36
AU-NC-001	New Caledonian Plant Inventory and Permanent Plot Network (NC-PIPPN)	Jérôme Munzinger	Philippe Birnbaum	98	83
AU-NZ-001	New Zealand National Vegetation Databank	Susan K. Wiser		1127	84
AU-PG-001	Forest Plots from Papua New Guinea	Timothy J.S. Whitfeld	George D. Weiblen	60	85
EU-00-002	Nordic-Baltic Grassland Vegetation Database (NBGVD)	Jürgen Dengler	Łukasz Kozub	54	86
EU-00-011	Vegetation-Plot Database of the University of the Basque Country (BIOVEG)	Idoia Biurrun	Itziar García-Mijangos	2142	87
EU-00-013	Balkan Dry Grasslands Database	Kiril Vassilev	Armin Macanović	269	88
EU-00-016	Mediterranean Ammophiletea Database	Corrado Marcenò	Borja Jiménez-Alfaro	783	89
EU-00-017	European Coastal Vegetation Database	John A.M. Janssen		356	
EU-00-018	The Nordic Vegetation Database	Jonathan Lenoir	Jens-Christian Svenning	1735	90

GIVD ID	Dataset name	Custodian	Deputy custodian	Nr. open-access plots	Ref
EU-00-019	Balkan Vegetation Database	Kiril Vassilev	Hristo Pedashenko	484	91
EU-00-020	WetVegEurope	Flavia Landucci		127	92
EU-00-022	European Mire Vegetation Database	Tomáš Peterka	Martin Jiroušek	2560	93
EU-AL-001	Vegetation Database of Albania	Michele De Sanctis	Giuliano Fanelli	31	94
EU-AT-001	Austrian Vegetation Database	Wolfgang Willner	Christian Berg	2310	95
EU-BE-002	INBOVEG	Els De Bie		119	
EU-BG-001	Bulgarian Vegetation Database	Iva Apostolova	Desislava Sopotlieva	160	96
EU-CH-005	Swiss Forest Vegetation Database	Thomas Wohlgemuth		2134	97
EU-CZ-001	Czech National Phytosociological Database	Milan Chytrý	Ilona Knollová	1287	98
EU-DE-001	VegMV	Florian Jansen	Christian Berg	15	99
EU-DE-013	VegetWeb Germany	Florian Jansen	Jörg Ewald	587	100
EU-DE-014	German Vegetation Reference Database (GVRD)	Ute Jandt	Helge Bruelheide	762	101
EU-DK-002	National Vegetation Database of Denmark	Jesper Erenskjold Moeslund	Rasmus Ejrnæs	332	
EU-ES-001	Iberian and Macaronesian Vegetation Information System (SIVIM) - Wetlands	Aaron Pérez-Haase	Xavier Font	580	
EU-FR-003	SOPHY	Emmanuel Garbolino	Patrice De Ruffray	7986	102
EU-GB-001	UK National Vegetation Classification Database	John S. Rodwell		3182	
EU-GR-001	KRITI	Erwin Bergmeier		22	
EU-GR-005	Hellenic Natura 2000 Vegetation Database (HelNatVeg)	Panayotis Dimopoulos	Ioannis Tsiripidis	620	103
EU-GR-006	Hellenic Woodland Database	Ioannis Tsiripidis	Georgios Fotiadis	17	104
EU-HR-001	Phytosociological Database of Non-Forest Vegetation in Croatia	Zvezdana Stančić		193	105
EU-HR-002	Croatian Vegetation Database	Željko Škvorc	Daniel Krstonošić	585	
EU-HU-003	CoenoDat Hungarian Phytosociological Database	János Csiky	Zoltán Botta-Dukát	46	106
EU-IT-001	VegItaly	Roberto Venanzoni	Flavia Landucci	754	107
EU-IT-010	Vegetation database of Habitats in the Italian Alps – HabItAlp	Laura Casella	Pierangela Angelini	247	108
EU-IT-011	Vegetation-Plot Database Sapienza University of Rome (VPD-Sapienza)	Emiliano Agrillo	Fabio Attorre	967	109
EU-LT-001	Lithuanian Vegetation Database	Valerijus Rašomavičius	Domas Uogintas	81	

GIVD ID	Dataset name	Custodian	Deputy custodian	Nr. open-access plots	Ref
EU-LV-001	Semi-natural Grassland Vegetation Database of Latvia	Solvita Rūsiņa		369	110
EU-MK-001	Vegetation Database of the Republic of Macedonia	Renata Čušterevska		28	
EU-NL-001	Dutch National Vegetation Database	Stephan M. Hennekens	Joop H.J. Schaminée	1098	111
EU-PL-001	Polish Vegetation Database	Zygmunt Kącki	Grzegorz Swacha	692	112
EU-RO-007	Romanian Forest Database	Adrian Indreica	Pavel Dan Turtureanu	166	113
EU-RO-008	Romanian Grassland Database	Eszter Ruprecht	Kiril Vassilev	82	114
EU-RS-002	Vegetation Database Grassland Vegetation of Serbia	Svetlana Ačić	Zora Dajić Stevanović	217	115
EU-RU-002	Lower Volga Valley Phytosociological Database	Valentin Golub	Andrey Chuvashov	383	116
EU-RU-003	Vegetation Database of the Volga and the Ural Rivers Basins	Tatiana Lysenko		174	117
EU-RU-011	Vegetation Database of Tatarstan	Vadim Prokhorov	Maria Kozhevnikova	206	118
EU-SI-001	Vegetation Database of Slovenia	Urban Šilc	Filip Kuzmič	1029	119
EU-SK-001	Slovak Vegetation Database	Milan Valachovič	Jozef Šibík	2394	120
EU-UA-001	Ukrainian Grasslands Database	Anna Kuzemko	Yulia Vashenyak	301	121
EU-UA-006	Vegetation Database of Ukraine and Adjacent Parts of Russia	Viktor Onyshchenko	Vitaliy Kolomiychuk	96	
NA-00-002	Tree Biodiversity Network (BIOTREE-NET)	Luis Cayuela		241	122
NA-CA-003	Database of Timberline Vegetation in NW North America	Viktoria Wagner	Toby Spribille	63	123
NA-CA-004	Understory of Sugar Maple Dominated Stands in Quebec and Ontario (Canada)	Isabelle Aubin		13	124
NA-CA-005	Boreal Forest of Canada	Yves Bergeron	Louis De Grandpré	57	
NA-GL-001	Vegetation Database of Greenland	Birgit Jedrzejek	Fred J.A. Daniëls	441	125
NA-US-002	VegBank	Robert K. Peet	Michael T. Lee	14965	126
NA-US-006	Carolina Vegetation Survey Database	Robert K. Peet	Michael T. Lee	3263	127
NA-US-014	Alaska-Arctic Vegetation Archive	Donald A. Walker	Amy Breen	771	128
SA-00-002	VegPáramo	Gwendolyn Peyre	Xavier Font	2010	129
SA-AR-002	Vegetation Database of Central Argentina	Melisa Giorgis	Alicia T.R. Acosta	86	
SA-BO-003	Bolivia Forest Plots	Michael Kessler	Sebastian Herzog	44	
SA-BR-002	Forest Inventory, State of Santa Catarina, Brazil (IFFSC Project)	Alexander Christian Vibrans	André Luís de Gasper	1561	130

GIVD ID	Dataset name	Custodian	Deputy custodian	Nr. open-access plots	Ref
SA-BR-003	Grasslands of Rio Grande do Sul, Brazil	Eduardo Vélez-Martin	Valério D. Pillar	306	
SA-BR-004	Grassland Database of Campos Sulinos	Gerhard E. Overbeck	Valério D. Pillar	147	
SA-CL-002	SSAForests_Plots_db	Alvaro G. Gutiérrez		155	
SA-CL-003	Chilean Park Transects - Fondecyt 1040528	Aníbal Pauchard	Alicia Marticorena	44	131
SA-EC-001	Ecuador Forest Plot Database	Jürgen Homeier		166	

Table 2: Description of the variables contained in the ‘header’ matrix, together with their range (if numeric) or possible levels (if nominal or binary), and the number of non-empty (i.e., non NA) records. Variable types can be n - nominal (i.e., qualitative variable), o - ordinal, q - quantitative, or b - binary (i.e., boolean), or d - date. . Additional details on the variables is in Bruelheide et al. (2019) [[25](#)]. GIVD codes derive from Dengler et al. (2011) [[37](#)]. Biomes refer to Schultz 2005 [[49](#)], modified to include also the world mountain regions by Körner et al. (2017)[[50](#)]. The column ESY refers to the EUNIS Habitat Classification Expert system described in Chytrý et al. (2020) [[53](#)].

Variable	Range/Levels	Unit of Measurement	Nr. of plots with information	Type
GIVD_ID			95104	n
Dataset			95104	n
Continent	Africa, Asia, Europe, North America, Oceania, South America		95104	n
Country			95104	n
Biome	Alpine, Boreal zone, Dry midlatitudes, Dry tropics and subtropics, Polar and subpolar zone, Subtropics with year-round rain, Subtropics with winter rain, Temperate midlatitudes, Tropics with summer rain, Tropics with year-round rain		95104	n
Date_of_recording	1888-07-05 - 2015-02-03	dd-mm-yyyy	80085	d
Latitude	-54.82303 - 80.149116	° (WGS84)	95104	q
Longitude	-162.741433 - 176.4221	° (WGS84)	95104	q
Location_uncertainty	1 - 2750	m	95075	q
Releve_area	0.03 - 40000	m ²	65461	q
Plant_recorded	All vascular plants, All trees & dominant understory, Dominant trees, Only dominant species, Dominant woody plants >= 2.5 cm dbh, All woody plants, Woody plants >= 1 cm dbh, Woody plants >= 2.5 cm dbh, Woody plants >= 5 cm dbh, Woody plants >= 10 cm dbh, Woody plants >= 20 cm dbh, Woody plants >= 1 m height, Not specified		95104	n
Elevation	-30 - 5960	m a.s.l.	62968	q
Aspect	1 - 360	°	42178	q

Variable	Range/Levels	Unit of Measurement	Nr. of plots with information	Type
Slope	0 - 90	°	51246	q
is_forest	FALSE = 45753; TRUE = 38264		84017	b
ESY			39632	n
Naturalness	1 = Natural, 2 = Semi-natural		60192	o
Forest	FALSE = 36282; TRUE = 33170		69452	b
Shrubland	FALSE = 58245; TRUE = 11207		69452	b
Grassland	FALSE = 33800; TRUE = 35652		69452	b
Wetland	FALSE = 59196; TRUE = 10256		69452	b
Sparse_vegetation	FALSE = 66177; TRUE = 3275		69452	b
Cover_total	1 - 990	%	19407	q
Cover_tree_layer	0.5 - 150	%	12094	q
Cover_shrub_layer	0.5 - 170	%	16804	q
Cover_herb_layer	0.2 - 199	%	29668	q
Cover_moss_layer	1 - 100	%	9681	q
Cover_lichen_layer	1 - 90	%	708	q
Cover_algae_layer	1 - 100	%	41	q
Cover_litter_layer	1 - 107	%	3161	q
Cover_bare_rocks	1 - 100	%	2747	q
Cover_cryptogams	1 - 90	%	772	q
Cover_bare_soil	-1 - 99	%	2746	q
Height_trees_highest	1 - 99	m	8220	q
Height_trees_lowest	1 - 90	m	447	q
Height_shrubs_highest	0.1 - 9.9	m	3389	q
Height_shrubs_lowest	0.1 - 9	m	263	q
Height_herbs_average	0.1 - 600	cm	5901	q
Height_herbs_lowest	1 - 150	cm	490	q
Height_herbs_highest	1 - 600	cm	1083	q
SoilClim_PC1	-6.233 - 8.172		95104	q
SoilClim_PC2	-4.824 - 15.466		95104	q
Resample_1	FALSE = 45317; TRUE = 49787		95104	b
Resample_2	FALSE = 45293; TRUE = 49811		95104	b
Resample_3	FALSE = 45315; TRUE = 49789		95104	b
Resample_1_consensus	FALSE = 41842; TRUE = 53262		95104	b

Supplementary Material

Figure S1

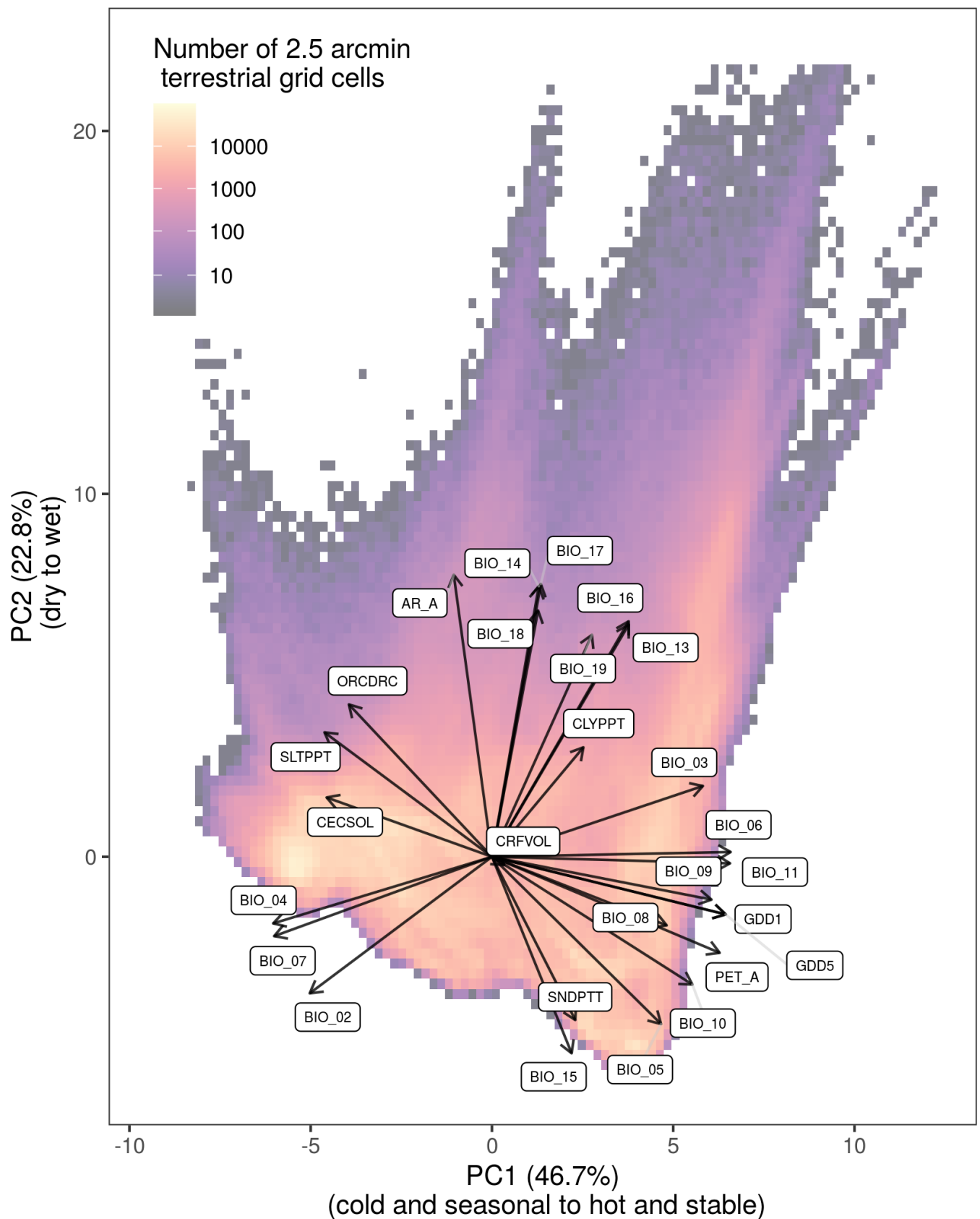


Figure S1: Global principal component analysis (PCA) of the world environmental conditions. The PCA is based on the matrix of all terrestrial grid cells ($n = 8,384,404$, spatial grain = 2.5 arcmin) by 30 environmental variables. The PCA space

represents the full environmental space of all terrestrial habitats on Earth, irrespective of whether a grid cell hosted vegetation plots from the sPlotOpen or not. The PCA space is divided into a 10,000 regular tiles (100 x 100), and the number of 2.5 arcmin terrestrial grid cells counted for each tile. Abbreviations - Climate - Bio1 = Annual Mean Temperature, Bio2 = Mean Diurnal Range, Bio3 = Isothermality, Bio4 = Temperature Seasonality, Bio5 = Max Temperature of Warmest Month, Bio6 = Min Temperature of Coldest Month, Bio7 = Temperature Annual Range, Bio8 = Mean Temperature of Wettest Quarter, Bio9 = Mean Temperature of Driest Quarter, Bio10 = Mean Temperature of Warmest Quarter, Bio11 = Mean Temperature of Coldest Quarter, Bio12 = Annual Precipitation, Bio13 = Precipitation of Wettest Month, Bio14 = Precipitation of Driest Month, Bio15 = Precipitation Seasonality, Bio16 = Precipitation of Wettest Quarter, Bio17 = Precipitation of Driest Quarter, Bio18 = Precipitation of Warmest Quarter, Bio19 = Precipitation of Coldest Quarter. Soil - CEC SOL = Cation Exchange capacity of soil, ORCDRC = Soil Organic Carbon Content, PHIHOX = Soil pH, BLDFIE = Bulk Density, CLYPPT = Clay mass fraction, SLTPPT = Silt mass fraction, SNDPPT = Sand mass fraction, CRFVOL = Coarse fragments.