

sPlot – A new tool for global vegetation analyses

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Abstract

Aims: Vegetation-plot records provide information on the presence and cover or abundance of plants co-occurring in the same community. Vegetation-plot data are spread across research groups, environmental agencies and biodiversity research centers and, thus, are rarely accessible at continental or global scales. Here we present the sPlot database, which collates vegetation plots worldwide to allow for the exploration of global patterns in taxonomic, functional and phylogenetic diversity at the plant community level.

Results: sPlot version 2.1 contains records from 1,121,244 vegetation plots, which comprise 23,586,216 records of plant species and their relative cover or abundance in plots collected worldwide between 1885 and 2015. We complemented the information for each plot by retrieving climate and soil conditions and the biogeographic context (e.g., biomes) from external sources, and by calculating community-weighted means and variances of traits using gap-filled data from the global plant trait database TRY. Moreover, we created a phylogenetic tree for 50,167 out of the 54,519 species identified in the plots. We present the first maps of global patterns of community richness and community-weighted means of key traits.

Conclusions: The availability of vegetation plot data in sPlot offers new avenues for vegetation analysis at the global scale.

KEYWORDS

biodiversity, community ecology, ecoinformatics, functional diversity, global scale, macroecology, phylogenetic diversity, plot database, sPlot, taxonomic diversity, vascular plant, vegetation relevé

1 | INTRODUCTION

Studying global biodiversity patterns is at the core of macroecological research (Costello, Wilson, & Houlding, 2012; Kreft & Jetz, 2007; Wiens, 2011), since their exploration may provide insights into the ecological and evolutionary processes acting at different spatio-temporal scales (Ricklefs, 2004). The opportunities engendered by the compilation of large collections of biodiversity data into widely accessible global (GBIF, www.gbif.org) or continental databases (e.g., BIEN, www.bien.nceas.ucsb.edu/bien) have recently advanced our understanding of global biodiversity patterns, especially for vertebrates, but also for vascular plants (Butler et al., 2017; Engemann et al., 2016; Lamanna et al., 2014; Swenson et al., 2012). Although this development has led to the formulation of several macroecological theories (Currie et al., 2004; Pärtel, Bennett, & Zobel, 2016), a more mechanistic understanding of how assembly processes shape ecological communities, and consequently global biodiversity patterns, is still missing (Lessard, Belmaker, Myers, Chase, & Rahbek, 2012).

Understanding the links between biodiversity patterns and assembly processes requires fine-grain data on the co-occurrence of species in ecological communities, sampled across continental or global spatial extents (Beck et al., 2012; Wisz et al., 2013). For example, such co-occurrence data have been used to compare changes in vegetation composition over time spans of decades (Jandt, von Wehrden, & Bruelheide, 2011; Perring et al., 2018). Unfortunately, up to now information on fine-grain vegetation data has not been readily available, as most of the continental to global biodiversity

datasets have been derived from occurrence data (i.e., presence-only data), and after being aggregated spatially, have a relatively coarse-grain scale (e.g., one-degree grid cells) without information on species co-occurrence at the meaningful scale of local communities (Boakes et al., 2010). In contrast, vegetation-plot data record the cover or abundance of each plant species that occurs in a plot of a given size at the date of the survey, representing the main reservoir of plant community data worldwide (Dengler et al., 2011).

Vegetation-plot data differ in fundamental ways from databases of occurrence records of individual species aggregated at the level of grid cells or regions of hundreds or thousands of square kilometers (Figure 1). First, vegetation plots usually provide information on the relative cover or relative abundance of species, allowing for the testing of central theories of biogeography, such as the abundance-range size relationship (Gaston & Curnutt, 1998) or the relationship between local abundance and niche breadth (Gaston et al., 2000). Second, they contain information on which plant species co-occur in the same locality (Chytrý et al., 2016), which is a necessary precondition for direct biotic interactions among plant individuals. Third, unrecorded species can be considered truly absent from the aboveground vegetation at this scale because the standardized methodology of taking a vegetation record requires a systematic search for all species in a plot, or at least all species of the dominant functional group. Fourth, many plots are spatially explicit and can be resurveyed through time to assess possible consequences of land use and climate change (Perring et al., 2018; Steinbauer et al., 2018). Fifth, vegetation plots represent a snapshot of the primary producers of a terrestrial ecosystem, which can be functionally linked to

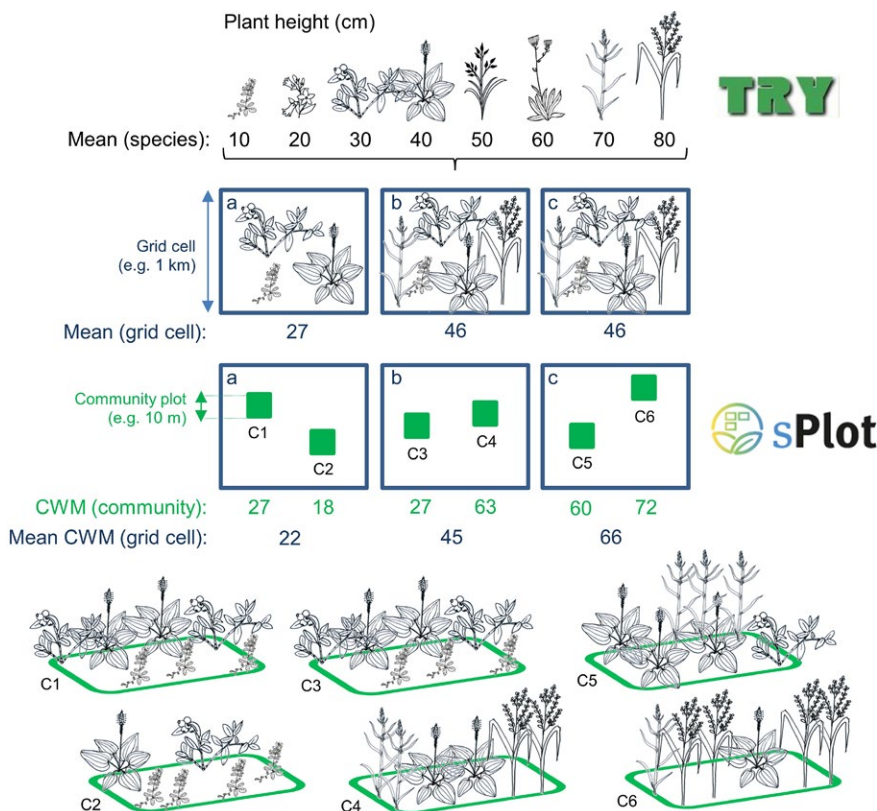


FIGURE 1 Conceptual figure visualizing how functional composition (in this case plant height) differs between calculations based on mean traits for grid cells and community data sampled in vegetation plots. Occurrence data (e.g., from distribution atlases, GBIF, etc.) can be used to calculate mean trait values in grid cells G1–G3. However, community weighted means (CWMs) of traits differ across local plots (P1–P6), while the mean values of CWMs in the grid cells differ from the unweighted values calculated in the grid cells. This example is simplified by showing few species and few plots. In reality, differences are generally more pronounced

organisms from different trophic groups sampled in the same plots (e.g., multiple-taxa surveys) and related processes and services both below (e.g., decomposition, nutrient cycling) and above ground (e.g., herbivory, pollination) (e.g., Schuldt et al., 2018).

Recently several projects at the regional to continental scale have demonstrated the potential of using vegetation-plot databases for exploring biodiversity patterns and the underlying assembly processes. Using vegetation data of French grasslands, Borgy et al. (2017) demonstrated that weighting leaf traits by species abundance in local communities is pivotal to capture leaf trait–environment relationships. Analyzing United States forest assemblages surveyed at the community level, Šímová, Rueda, and Hawkins (2017) were able to relate cold or drought tolerance to leaf traits, dispersal traits and traits related to stem hydraulics. Using plot-based tree inventories of the United States forest service, Zhang, Niinemets, Sheffield, and Lichstein (2018) found that shifts in tree functional composition amplify the response of forest biomass to droughts. Based on >15,000 plots from a wide number of habitat types in Denmark, Moeslund et al. (2017) showed that typical plant species that are part of the site-specific species pool but are absent in a community tend to depend on mycorrhiza, are mostly adapted to low light and low nutrient levels, have poor dispersal abilities and are ruderals and stress-intolerant. By collating >40,000 vegetation plots sampled in European beech forests, Jiménez-Alfaro et al. (2018) found that current local community diversity and species pool sizes calculated at different scales were mainly explained by proximity to glacial refugia and current precipitation.

Although large collections of vegetation-plot data are now available from national to continental levels (e.g., Chytrý et al., 2016; Enquist, Condit, Peet, Schildhauer, & Thiers, 2016; Peet, Lee, Jennings, & Faber-Langendoen, 2012; Schaminée, Hennekens, Chytrý, & Rodwell, 2009; Schmidt et al., 2012), they are rarely used

in global-scale biodiversity research (Franklin, Serra-Diaz, Syphard, & Regan, 2017; Wiser, 2016). This is unfortunate because vegetation-plot data may reveal important patterns that cannot be captured by grid-based datasets (Table 1). Functional composition patterns, for instance, may differ substantially when considering vegetation-plot data rather than single species occurrences aggregated at the level of coarse-grain grid cells. Using plant height as an illustration reveals that the trait means calculated on all the species occurring in a grid cell may differ strongly from the community-weighted means (CWMs) averaged across local communities (Figure 1). Nevertheless, only the grid-based approach has been used to date in studies of the geographic distribution of trait values (e.g., Swenson et al., 2012, 2017; Wright et al., 2017).

Here, we present sPlot, a global database for compiling and integrating plant community data. We describe (a) main steps in integrating vegetation-plot data in a repository that provides taxonomic, functional and phylogenetic information on co-occurring plant species and links it to global environmental drivers; (b) principal sources and properties of the data and the procedure for data usage; and (c) expected impacts of the database in future ecological research. To illustrate the potential of sPlot we also show global diversity patterns that can be readily derived from the current content.

2 | COMPILATION OF THE SPLOT DATABASE

2.1 | Vegetation-plot data

The sPlot consortium currently collates 110 vegetation-plot databases of regional, national or continental extent. Some of the databases have previously been aggregated by and contributed through

TABLE 1 Types of information provided by single vegetation plots, vegetation plots aggregated within grid cells (or other geographic units) and single species occurrence records aggregated within grid cells. The three levels are illustrated in Figure 1

Information from...	Single vegetation plots	Set of vegetation plots aggregated within grid cells	Grid-cell data from floristic inventories
To derive information on the ...	Plot level	Grid cell level	Grid cell level
Type of occurrence	Co-occurrence, occurrence by vegetation type	Occurrence by vegetation type	Occurrence
Community assembly rules	Yes (co-occurrence is a prerequisite for species interactions)	No	No
Absences	Yes (for the target plant group in a study)	No (except for intensive sampling schemes)	Depending on sampling intensity
Floristic composition	... of the local community	... of the species pools of vegetation types	... of the total set of species
Diversity	α	β, γ	γ
Species abundance	Local cover-abundance	Mean cover-abundance and frequency by vegetation type	Occurrence only
Combination with traits	Functional composition of the local community (traits unweighted or weighted by cover: CWM, CWV)	Functional composition of the species pool (unweighted or weighted)	Functional composition of the total set of species (unweighted only)
Environmental filtering	... at the local level	... at the regional level	... at the regional level

two (sub-)continental database initiatives (Table 2 and Appendix S1). All data from Europe and nearby regions were contributed via the European Vegetation Archive (EVA), using the SynBioSys taxon database as a standard taxonomic backbone (Chytrý et al., 2016). Three African databases were contributed via the Tropical African Vegetation Archive (TAVA). In addition, multiple U.S. databases were contributed through the VegBank archive maintained in support of the U.S. National Vegetation Classification (Peet, Lee, Boyle, et al., 2012; Peet, Lee, Jennings, & Faber-Langendoen, 2012). The data from other regions (South America, Asia) were contributed as separate databases.

We stored the vegetation-plot data from the individual databases in the database software TURBOVEG v2 (Hennekens & Schaminée, 2001). Our general procedure was to preserve the original structure and content of the databases as much as possible in order to facilitate regular updates through automated workflows. The individual databases were then integrated into a single SQLite database using TURBOVEG v3 (S.M. Hennekens, ALTErrA, The Netherlands; www.synbiosys.alterra.nl/turboveg3/help/en/index.html). TURBOVEG v3 combines the species lists from the original databases in a single repository and links the plot attributes (so-called header data) to 58 descriptors of vegetation-plots (Table S2.1 in Appendix S2). The metadata of the databases collated in sPlot were managed through the Global Index of Vegetation-Plot Databases (GIVD; Dengler et al., 2011), using the GIVD ID as the identifier. The current sPlot version 2.1 was created in October 2016 and contains 1,121,244 vegetation plots with 23,586,216 plant species × plot observations (i.e., records of a species in a plot). Most records (1,073,737; 95.8%) have information on cover, 29,288 on presence/absence, 5,854 on basal area, 4,883 on number of stems (often in addition to basal area), 148 on importance value (a combination of basal area and number of stems), 3,265 on counts of individuals, 1,895 on percentage frequency, and further 2,174 have a mix of these different types of metrics.

2.2 | Taxonomic standardization

To combine the species lists of the different databases in sPlot, we constructed a taxonomic backbone. To link co-occurrence information in sPlot with plant traits, we expanded this backbone to integrate plant names used in the TRY database (Kattge et al., 2011). The taxon names (without nomenclatural authors) from sPlot 2.1 and TRY 3.0 were first concatenated into one list, resulting in 121,861 names, of which 61,588 (50.5%) were unique to sPlot; 35,429 (29.1%) unique to TRY; and 24,844 (20.4%) shared between TRY and sPlot. Taxon names were parsed and resolved using the Taxonomic Name Resolution Service web application (TNRS version 4.0; Boyle et al., 2013; iPlant Collaborative, 2015), using the five TNRS standard sources ranked by default. We allowed for (a) partial matching to the next higher rank (genus or family) if the full taxon name could not be found and (b) full fuzzy matching, to return names that were matched within a maximum number of four single-character edits (Levenshtein edit distance of 4), which corresponds to the minimum match accuracy of 0.05 in TNRS, with 1 indicating a perfect match.

We accepted all names that were matched, or converted from synonyms, with an overall match score of 1. In cases with no exact match (i.e., the overall match score was <1), names were inspected on an individual basis. All names that matched at taxonomic ranks at or lower than species (e.g., subspecies, varieties) were accepted as correct names. The name matching procedure was repeated for the uncertain names (i.e., with match accuracy scores below the threshold value from the first matching run), with a preference on first using the source 'Tropicos' (Missouri Botanical Garden; <http://www.tropicos.org/>; accessed 19 Dec 2014) because here matching scores were often higher for names of low taxonomic rank. The remaining 9,641 non-matched names were resolved using (a) the additional source 'NCBI' (Federhen, 2010) within TNRS, (b) the matching tools in the Plant List web application (The Plant List 2013), (c) the 'tpl'-function within the R-package 'Taxonstand' (Cayuela, Stein, & Oksanen, 2017) and (d) manual inspection (i.e., to resolve vernacular names). All subspecies were aggregated to the species level. Names that could not be matched were classified as 'No suitable matches found'. Because sPlot and TRY contain taxa of non-vascular plants, we tagged vascular plant names based on their family and phylum affiliation, using the 'rgbif' library in R (Chamberlain, 2017). Of the full list of plant names in sPlot and TRY, 79,171 (94.6%) plant names were matched at the species level, 4,343 (5.2%) at the genus level, 152 (0.2%) at the family level and 13 names at higher taxonomic levels. Overall, this led to 58,066 accepted taxon names in sPlot. Family affiliation was classified according to APG III (APG III, 2009). A detailed description of the workflow, including R-code, is available in Purschke (2017a).

One potential shortcoming of our taxonomic backbone is that for most regions it was necessary to standardize taxa using standard sets of taxonomic synonyms. Thus, if a taxonomic name represents multiple taxonomic concepts, e.g., such as created by the splitting and lumping of taxa, or a name has been misapplied in a region, we must trust that this problem has been addressed in our component databases (Franz, Peet, & Weakley, 2004; Jansen & Dengler, 2010). However, different component databases may have applied different taxonomic concepts for splitting and lumping taxa.

2.3 | Physiognomic information

To achieve a classification into forests versus non-forests that is applicable to all plots irrespective of the structural and habitat data provided by the source database, we defined as forest all plot records that had >25% absolute cover of the tree layer, making use of the attribute data of sPlot. This threshold is similar to the classification of Ellenberg and Müller-Dombois (1967), who defined woodland formations with trees covering more than 30%. There were 16,244 tree species in the sPlot database. As tree layer cover was available for only 25% of all plots, we additionally used the information whether the taxa present in a plot were trees (usually defined as being taller than 5 m), using the plant growth form information from TRY (see below). Thus, plots lacking tree cover information were defined as forests if the sum of relative cover of all tree taxa was

TABLE 2 Plot datasets included in sPlot 2.1

GIVD ID	Database name	# of plots in sPlot 2.1	Custodian	Deputy custodian	Reference
[Aggregator]	European Vegetation Archive (EVA)	950,001	Milan Chytrý	Ilona Knollová	Chytrý et al. (2016)
00-00-004	Vegetation Database of Eurasian Tundra	1,132	Risto Virtanen		
00-RU-001	Vegetation Database Forest of Southern Ural	1,102	Vassiliy Martynenko		
00-RU-003	Database Meadows and Steppes of Southern Ural	2,354	Sergey Yamalov	Mariya Lebedeva	
00-TR-001	Forest Vegetation Database of Turkey - FVDT	919	Ali Kavgacı		
00-TR-002*	Non-forest Vegetation Database of Turkey	3,018	Deniz Işık Gürsoy	Didem Ambarlı	
AS-TR-002	Vegetation Database of Oak Communities in Turkey	1,181	Emin Uğurlu		
EU-00-002	Nordic-Baltic Grassland Vegetation Database (NMGVD)	7,675	Jürgen Dengler	Łukasz Kozub	Dengler and Růsiņa (2012)
EU-00-011	Vegetation-Plot Database of the University of the Basque Country (BIOVEG)	18,441	Idoia Biurrun	Itziar García-Mijangos	Biurrun, García-Mijangos, Campos, Herrera, and Loidi (2012)
EU-00-013	Balkan Dry Grasslands Database	7,683	Kiril Vassilev	Armin Macanović	Vassilev, Dajić, Čušterevska, Bergmeier, and Apostolova (2012)
EU-00-016	Mediterranean Ammophiletea Database	7,359	Corrado Marcenò	Borja Jiménez-Alfaro	Marcenò and Jiménez-Alfaro (2017)
EU-00-017	European Coastal Vegetation Database	4,624	John Janssen		
EU-00-018	The Nordic Vegetation Database	5,477	Jonathan Lenoir	Jens-Christian Svenning	Lenoir et al. (2013)
EU-00-019	Balkan Vegetation Database	9,118	Kiril Vassilev	Hristo Pedashenko	Vassilev et al. (2016)
EU-00-020	WetVegEurope	14,111	Flavia Landucci		Landucci et al. (2015)
EU-00-022	European Mire Vegetation Database	10,147	Tomáš Peterka	Martin Jiroušek	Peterka, Jiroušek, Hájek, and Jiménez-Alfaro (2015)
EU-AL-001	Vegetation Database of Albania	290	Michele De Sanctis	Giuliano Fanelli	De Sanctis, Fanelli, Mullaj, and Attorre (2017)
EU-AT-001	Austrian Vegetation Database	34,458	Wolfgang Willner	Christian Berg	Willner, Berg, and Heiselmayer (2012)
EU-BE-002	INBOVEG	25,665	Els De Bie		
EU-BG-001	Bulgarian Vegetation Database	5,254	Iva Apostolova	Desislava Sopotlieva	Apostolova, Sopotlieva, Pedashenko, Velev, and Vasilev (2012)
EU-CH-005	Swiss Forest Vegetation Database	14,193	Thomas Wohlgemuth		Wohlgemuth (2012)
EU-CZ-001	Czech National Phytosociological Database	104,697	Milan Chytrý	Dana Holubová	Chytrý and Rafajová (2003)

(Continues)

TABLE 2 (Continued)

GIVD ID	Database name	# of plots in sPlot 2.1	Custodian	Deputy custodian	Reference
EU-DE-001	VegMV	53,822	Florian Jansen	Christian Berg	Jansen, Dengler, and Berg (2012)
EU-DE-013	VegetWeb Germany	23,078	Jörg Ewald		Ewald, May, and Kleikamp (2012)
EU-DE-014	German Vegetation Reference Database (GVRD)	30,840	Ute Jandt	Helge Bruelheide	Jandt and Bruelheide (2012)
EU-DK-002	National Vegetation Database of Denmark	24,264	Jesper Erenskjold Moeslund	Rasmus Ejrnæs	
EU-ES-001	Iberian and Macaronesian Vegetation Information System (SIVIM)-Wetlands	6,560	Aaron Pérez-Haase	Xavier Font	
EU-FR-003	SOPHY	209,864	Henry Brisse	Patrice de Ruffray	Brisse, de Ruffray, Grandjouan, and Hoff (1995)
EU-GB-001	UK National Vegetation Classification Database	28,533	John S. Rodwell		
EU-GR-001	KRITI	292	Erwin Bergmeier		
EU-GR-005	Hellenic Natura 2000 Vegetation Database (HelNatVeg)	5,168	Panayotis Dimopoulos	Ioannis Tsiripidis	Dimopoulos and Tsiripidis (2012)
EU-GR-006	Hellenic Woodland Database	3,199	Georgios Fotiadis	Ioannis Tsiripidis	Fotiadis, Tsiripidis, Bergmeier, and Dimopoulos (2012)
EU-HR-001	Phytosociological Database of Non-Forest Vegetation in Croatia	5,057	Zvezdana Stančić		Stančić (2012)
EU-HR-002	Croatian Vegetation Database	8,734	Željko Škvorc	Daniel Krstonošić	
EU-HU-003	CoenoDat Hungarian Phytosociological Database	8,505	János Csiky	Zoltán Botta-Dukát	Lájer et al. (2008)
EU-IT-001	VegItaly	15,332	Roberto Venanzoni	Flavia Landucci	Landucci et al. (2012)
EU-IT-010	Italian National Vegetation Database (BVN/ISPRA)	3,562	Laura Casella	Pierangela Angelini	Casella, Bianco, Angelini, and Morroni (2012)
EU-IT-011	Vegetation-Plot Database Sapienza University of Rome (VPD-Sapienza)	12,780	Emiliano Agrillo	Fabio Attorre	Agrillo et al. (2017)
EU-LT-001	Lithuanian Vegetation Database	7,821	Valerijus Rašomavičius	Domas Uogintas	
EU-LV-001	Semi-natural Grassland Vegetation Database of Latvia	5,594	Solvita Rūsiņa		Rūsiņa (2012)
EU-MK-001	Vegetation Database of the Republic of Macedonia	1,417	Renata Čušterevska		
EU-NL-001	Dutch National Vegetation Database	102,327	Joop H.J. Schaminée	Stephan M. Hennekens	Schaminée et al. (2006)
EU-PL-001	Polish Vegetation Database	22,229	Zygmunt Kaćki	Grzegorz Swacha	Kaćki and Śliwiński (2012)
EU-RO-007	Romanian Forest Database	6,017	Adrian Indreica	Pavel Dan Turtureanu	Indreica, Turtureanu, Szabó, and Irimia (2017)
EU-RO-008	Romanian Grassland Database	1,921	Eszter Ruprecht	Kiril Vassilev	Vassilev et al. (2018)
EU-RS-002	Vegetation Database Grassland Vegetation of Serbia	5,587	Svetlana Aćić	Zora Dajić Stevanović	Aćić, Petrović, Šilc, and Dajić Stevanović (2012)

(Continues)

TABLE 2 (Continued)

GIVD ID	Database name	# of plots in sPlot 2.1	Custodian	Deputy custodian	Reference
EU-RU-002	Lower Volga Valley Phytosociological Database	14,853	Valentin Golub	Viktoria Bondareva	Golub et al. (2012)
EU-RU-003	Vegetation Database of the Volga and the Ural Rivers Basins	1,516	Tatiana Lysenko		Lysenko, Mitroshenkova, and Kalmykova (2012)
EU-RU-011	Vegetation Database of Tatarstan	7,471	Vadim Prokhorov	Maria Kozhevnikova	Prokhorov, Rogova, and Kozhevnikova (2017)
EU-SI-001	Vegetation Database of Slovenia	10,986	Urban Šilc	Filip Kuzmič	Šilc (2012)
EU-SK-001	Slovak Vegetation Database	36,405	Milan Valachovič	Jozef Šibík	Šibík (2012)
EU-UA-001	Ukrainian Grasslands Database	4,043	Anna Kuzemko	Yulia Vashenyak	Kuzemko (2012)
EU-UA-006	Vegetation Database of Ukraine and Adjacent Parts of Russia	3,326	Viktor Onyshchenko	Vitaliy Kolomyichuk	
[Aggregator]	Tropical African Vegetation Archive (TAVA)	6,677	Marco Schmidt	Stefan Dressler	Janßen et al. (2011)
AF-00-001	West African Vegetation Database	3,129	Marco Schmidt	Georg Zizka	Schmidt et al. (2012)
AF-00-008	PANAF Vegetation Database	2,469	Hjalmar Kühl	TeneKwetché Sop	
AF-BF-001	Sahel Vegetation Database	1,079	Jonas V. Müller	Marco Schmidt	Müller (2003)
	Other databases	164,566			
00-00-001	RAINFOR data managed by ForestPlots.net	1,827	Oliver L. Phillips	Aurora Levesley	Lopez-Gonzalez, Lewis, Burkitt, and Phillips (2011)
00-00-003	SALVIAS	4,883	Brian Enquist	Brad Boyle	
00-00-005	Tundra Vegetation Plots (TundraPlot)	577	Anne D. Bjorkman	Sarah Elmendorf	Elmendorf et al. (2012)
00-RU-002	Database of Masaryk University's Vegetation Research in Siberia	1,547	Milan Chytrý		Chytrý (2012)
AF-00-003	BIOTA Southern Africa Biodiversity Observatories Vegetation Database	1,666	Norbert Jürgens	Gerhard Mucbe	Mucbe, Schmiedel, and Jürgens (2012)
AF-00-006	SWEA-Dataveg	2,704	Miguel Alvarez	Michael Curran	
AF-00-009	Vegetation Database of the Okavango Basin	590	Rasmus Revermann	Manfred Finckh	Revermann et al. (2016)
AF-CD-001	Forest Database of Central Congo Basin	292	Elizabeth Kearsley	Hans Verbeeck	Kearsley et al. (2013)
AF-ET-001	Vegetation Database of Ethiopia	74	Desalegn Wana	Anke Jentsch	Wana and Beierkuhnlein (2011)
AF-MA-001	Vegetation Database of Southern Morocco	1,337	Manfred Finckh		Finckh (2012)
AF-ZA-003*	SynBioSys Fynbos Vegetation Database	3,810	John Janssen		
AF-ZW-001*	Vegetation Database of Zimbabwe	36	Cyrus Samimi		Samimi (2003)
AS-00-001	Korean Forest Database	4,885	Tomáš Černý	Petr Petřík	Černý et al. (2015)
AS-00-003	Vegetation of Middle Asia	1,381	Arkadiusz Nowak	Marcin Nobis	Nowak et al. (2017)
AS-00-004	Rice Field Vegetation Database	179	Arkadiusz Nowak		

(Continues)

TABLE 2 (Continued)

GIVD ID	Database name	# of plots in sPlot 2.1	Custodian	Deputy custodian	Reference
AS-BD-001	Tropical Forest Dataset of Bangladesh	211	Mohammed A.S. Arfin Khan	Fahmida Sultana	
AS-CN-001	China Forest-Steppe Ecotone Database	148	Hongyan Liu	Fengjun Zhao	Liu, Cui, Pott, and Speier (2000)
AS-CN-002	Tibet-PaDeMoS Grazing Transect	146	Karsten Wesche		Wang et al. (2017)
AS-CN-003*	Vegetation Database of the BEF China Project	27	Helge Bruelheide		Bruelheide et al. (2011)
AS-CN-004*	Vegetation Database of the Northern Mountains in China	485	Zhiyao Tang		
AS-CN-005*	Database Steppe Vegetation of Xinjiang	129	Kohei Suzuki		
AS-EG-001	Vegetation Database of Sinai in Egypt	926	Mohamed Z. Hatim		Hatim (2012)
AS-ID-001	Sulawesi Vegetation Database	24	Michael Kessler		
AS-IR-001	Vegetation Database of Iran	2,335	Jalil Noroozi	Parastoo Mahdavi	
AS-KG-001	Vegetation Database of South-Western Kyrgyzstan	452	Peter Borchardt	Udo Schickhoff	Borchardt and Schickhoff (2012)
AS-KZ-001	Database of Meadow Vegetation in the NW Tian Shan Mountains	94	Viktoria Wagner		Wagner (2009)
AS-MN-001	Southern Gobi Protected Areas Database	1,516	Henrik von Wehrden	Karsten Wesche	von Wehrden, Wesche, and Miehe (2009)
AS-RU-001	Wetland Vegetation Database of Baikal Siberia (WETBS)	2,381	Victor Chepinoga		Chepinoga (2012)
AS-RU-002	Database of Siberian Vegetation (DSV)	9,116	Andrey Korolyuk	Andrei Zverev	
AS-RU-004	Database of the University of Münster - Biodiversity and Ecosystem Research Group's Vegetation Research in Western Siberia and Kazakhstan	445	Norbert Hölzel	Wanja Mathar	
AS-SA-001*	Vegetation Database of Saudi Arabia	919	Mohamed Abd El-Rouf Mousa El-Sheikh		
AS-TJ-001	Eastern Pamirs	282	Kim André Vanselow		Vanselow (2016)
AS-TW-001	National Vegetation Database of Taiwan	930	Ching-Feng Li	Chang-Fu Hsieh	
AS-YE-001	Socotra Vegetation Database	396	Michele De Sanctis	Fabio Attorre	De Sanctis and Attorre (2012)
AU-AU-002	TERN AEKOS	21,261	Anita Smyth	Ben Sparrow	Turner, Smyth, Walker, and Lowe (2017)
AU-NC-001	New Caledonian Plant Inventory and Permanent Plot Network (NC-PIPPN)	201	Jérôme Munzinger	Philippe Birnbaum	Ibanez et al. (2014)
AU-NZ-001	New Zealand National Vegetation Databank	1,895	Susan Wisser		Wisser, Bellingham, and Burrows (2001)
AU-PG-001	Forest Plots from Papua New Guinea	63	Timothy Whitfield	George Weiblen	Whitfield et al. (2014)

(Continues)

TABLE 2 (Continued)

GIVD ID	Database name	# of plots in sPlot 2.1	Custodian	Deputy custodian	Reference
NA-00-002	Tree Biodiversity Network (BIOTREE-NET)	1,757	Luis Cayuela		Cayuela et al. (2012)
NA-CA-003	Database of Timberline Vegetation in NW North America	110	Viktoria Wagner	Toby Spribille	Wagner, Spribille, Abrahamczyk, and Bergmeier (2014)
NA-CA-004	Understory of Sugar Maple Dominated Stands in Quebec and Ontario (Canada)	156	Isabelle Aubin		Aubin, Gachet, Messier, and Bouchard (2007)
NA-CA-005*	Boreal Forest of Canada	89	Yves Bergeron	Louis De Grandpré	
NA-GL-001	Vegetation Database of Greenland	664	Birgit Jedrzejek	Fred J.A. Daniëls	Sieg, Drees, and Daniëls (2006)
NA-US-002	VegBank	67,352	Robert K. Peet	Michael T. Lee	Peet et al. (2012)
NA-US-006	Carolina Vegetation Survey Database	17,221	Robert K. Peet	Michael T. Lee	Peet et al. (2012)
NA-US-014	Alaska-Arctic Vegetation Archive	1,363	Donald A. Walker	Amy Breen	Walker et al. (2016)
SA-00-002	VegPáramo	2,643	Gwendolyn Peyre	Xavier Font	Peyre et al. (2015)
SA-AR-002	Vegetation Database of Central Argentina	218	Marcelo R. Cabido	Alicia Acosta	
SA-BO-003	Bolivia Forest Plots	75	Michael Kessler	Sebastian Herzog	
SA-BR-002	Forest Inventory, State of Santa Catarina, Brazil (IFFSC Project)	1,669	Alexander Christian Vibrans	André Luis de Gasper	Vibrans, Sevegnani, Lingner, de Gasper, and Sabbagh (2010)
SA-BR-003	Grasslands of Rio Grande do Sul, Brazil	320	Eduardo Vélez-Martin	Valério De Patta Pillar	
SA-BR-004	Grassland Database of Campos Sulinos	161	Gerhard E. Overbeck	Valério De Patta Pillar	
SA-CL-002	SSAForests_Plots_db	261	Alvaro G. Gutierrez		
SA-CL-003*	Chilean Park Transects - Fondecyt 1040528	165	Anibal Pauchard	Alicia Marticorena	Pauchard, Fuentes, Jiménez, Bustamante, and Marticorena (2013)
SA-EC-001	Ecuador Forest Plot Database	172	Jürgen Homeier		

Note. GIVD ID refers to the ID in the Global Index of Vegetation-Plot Databases (<http://www.givd.info>), which manages the metadata for sPlot and provides updated online descriptions of these databases; * after the GIVD ID indicates that the respective database description is currently not visible on the GIVD website. Datasets contributed in harmonized format from a continental data aggregator ("collective database" according to the sPlot Rules) are listed under its name. Further references, attributions and disclaimers for particular datasets are found Appendix S1.

>25%. Similarly, we defined non-forests by calculating the cover of all taxa that were not defined as trees or shrubs (also taken from the TRY plant growth form information) and that were not taller than 2 m, using the TRY data on mean plant height. In total, 21,888 taxa belonged to this category. We defined all plots as non-forests if the sum of relative cover of these low-stature, non-tree and non-shrub taxa was >90%. As we did not have the growth form and height information for all taxa, a fraction of about 25% of the plots remained unassigned (i.e., neither forest, nor non-forest). In addition, more detailed classifications of plots into physiognomic formations (Table S3.2 in Appendix S3) and naturalness (Table S3.3 in Appendix S3) were derived from various types of plot-level or database-level information provided by the sources and stored in five separate fields (see Table S2.1 in Appendix S2).

2.4 | Phylogenetic information

We developed a workflow to generate a phylogeny of the vascular plant species in sPlot, using the phylogeny of Zanne et al. (2014), updated by Qian and Jin (2016). Species present in sPlot but missing from this phylogeny were added next to a randomly selected congener (see also Maitner et al., 2018). This approach has been demonstrated to introduce less bias into subsequent analyses than adding missing species as polytomies to the respective genera (Davies, Kraft, Salamin, & Wolkovich, 2012). We only added species based on taxonomic information on the genus level, thus not making use of family affiliation. Because of the absence of congeners in the reference phylogeny, 7,147 species could not be added (11.7% of all resolved taxa in sPlot and TRY). This resulted in a phylogeny

with 54,067 resolved taxon names from 61,214 standardized taxa in the combined list of sPlot and TRY. The tree was finally pruned to the vascular plant taxa of the current sPlot version 2.1, resulting in a phylogenetic tree for 53,489 out of the 58,066 taxa in sPlot. Of these 53,489 names, 16,026 are also found among the 31,389 taxa in the phylogenetic tree of Qian and Jin (2016), i.e., 51.1%. The full procedure and the R code are available in Purschke (2017b).

2.5 | Associated environmental plot information

To complement the plot data, we harmonized geographical coordinates (in decimal degrees), elevation (m above sea level), aspect (degrees) and slope (degrees) as provided by the contributing databases. All other variables were too sparsely and too inconsistently sampled across databases to be combined in the global set, but were retained in the original data sources and can be retrieved for particular purposes.

We used the geographic coordinates to create a geodatabase in ArcGIS 14.1 (ESRI, Redlands, CA) to link sPlot 2.1 to these climate and soil data. We retrieved data for all the 19 bioclimatic variables provided by CHELSA v1.1 (Karger et al., 2017) by averaging climatic data from the period 1979–2013 at 30 arc seconds (about 1 km in grid cells near to the equator). These variables are the same as the ones used in WorldClim (www.worldclim.org; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), but calculated with a downscaling approach based on estimates of the ERA-Interim climatic reanalysis (Dee et al., 2011). While the CHELSA climatological data have a similar accuracy as other products for temperature, they are more precise for precipitation patterns (Karger et al., 2017). We also

calculated growing degree days for 1°C (GDD1) and 5°C (GDD5), according to Synes and Osborne (2011) and based on CHELSA data, and included the index of aridity and potential evapotranspiration extracted from the CGIAR-CSI website (www.cgiar-csi.org). In addition, we extracted seven soil variables from the SOILGRIDS project (https://soilgrids.org/; licensed by ISRIC – World Soil Information), downloaded at 250-m resolution and then converted to the same 30-arc second grid format of CHELSA. To explore the distribution of sPlot data in the global environmental space, we subjected all 30 climate and soil variables of the global terrestrial surface rasterized on a 2.5 arc-minute grid resolution to a principal component analysis (PCA) on standardized and centered data. We subsequently created a grid of 100 cells × 100 cells within the bi-dimensional environmental space defined by the first two PCA axes (PC1 and PC2) and counted the number of terrestrial cells per environmental grid cell of the PC1–PC2 space. Then, we counted the number of plots in sPlot in the same PCA grid (Figure 2).

We linked all vegetation plots to two global biome classifications. We used the World Wildlife Fund (WWF) spatial information on terrestrial ecoregions (Olson et al., 2001) to assign plots to one of the 867 ecoregions, 14 biomes and eight biogeographic realms. The WWF approach is based on a bottom-up expert system using various regional biodiversity sources to define ecoregions, which in turn are grouped into realms and biomes (Olson et al., 2001). In addition, we created a shapefile for the ecozones defined by Schultz (2005) to represent major biomes in response to global climatic variation. Since these zones are climatically heterogeneous in mountain regions, we differentiated an additional “alpine” biome for mountain areas above the lower mountain thermal

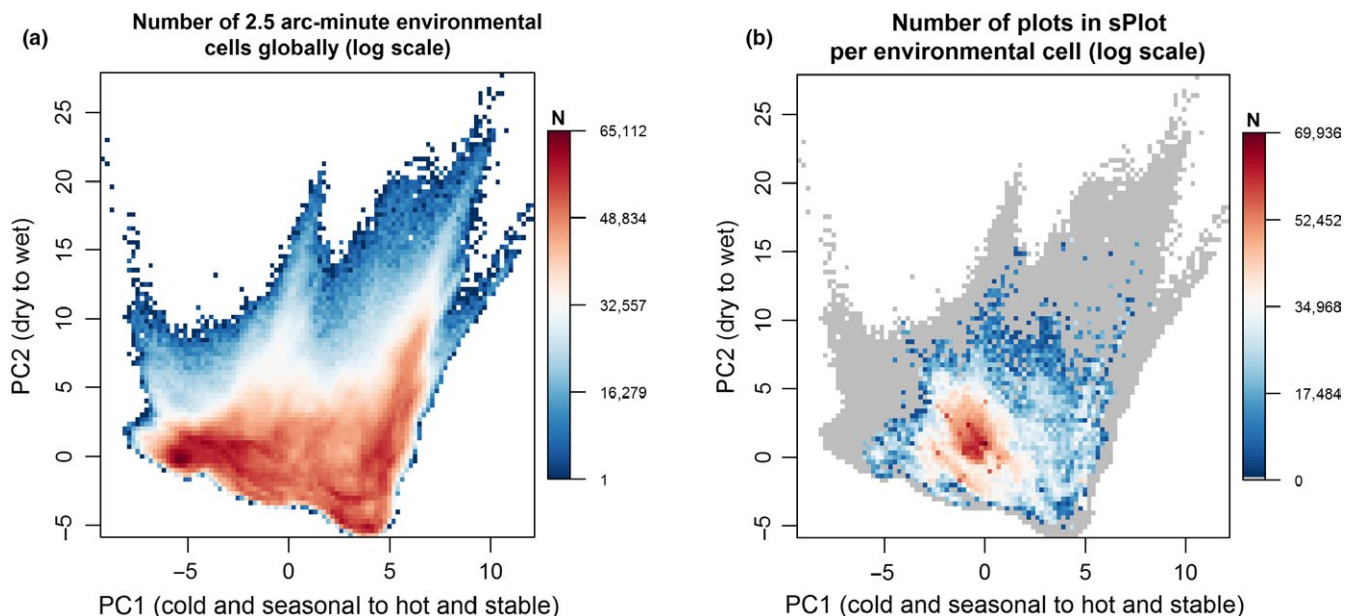


FIGURE 2 Distribution of vegetation plots from sPlot 2.1 in the global environmental space. Comparison of the distribution of all terrestrial 2.5 arc-minute cells (a) and plots in sPlot 2.1 (b) in the principal component analysis (PCA) space defined on 30 environmental (climate and soil) variables. The PCA space was divided into a 100 × 100 regular grid. For each element of this grid, the graphs show the number of 2.5 arc-minute cells (a) and plots (b), respectively. Colors refer to the logarithm of number of plots, with the legend showing untransformed number of plots. The first and second PCA axis explained 48.6% and 27.3% of the total variance

belt, as defined in the classification of world mountain regions by Körner et al. (2017). This resulted in a distinction of 10 major biomes (Figure S4.5 in Appendix S4), whose shapefile is freely available (Appendix S5).

2.6 | Trait information

To broaden the potential applications of the global vegetation database in functional contexts, we linked sPlot to TRY. We accessed plant trait data from TRY version 3.0 on August 10, 2016, and included 18 traits that describe the leaf, wood and seed economics spectra (Westoby, 1998; Reich, 2014; Table S6.4 in Appendix S6), and are known to affect different key ecosystem processes and to respond to macroclimatic drivers. These traits were represented across all species in the TRY database by at least 1,000 trait records. We excluded trait records from manipulative experiments and outliers (Kattge et al., 2011), which resulted in a matrix with 632,938 individual plant records on 52,032 taxa in TRY, having data records for an average of 3.08 of the 18 selected traits. On average, each trait has been measured at least once in 17.1% of all taxa. In order to attain data for these 18 traits for all species with at least one trait value in TRY, we employed hierarchical Bayesian modeling, using the R package 'BHPMF' (Fazayeli, Banerjee, Kattge, Schrodtt, & Reich, 2017; Schrodtt et al., 2015), to fill a gap in the matrix of individual plant records in TRY. Gap filling allows obtaining trait values for a species on which this trait has not been measured, but for which other traits are available. To assess gap-filling quality, we used the probability density distributions provided by BHPMF for each imputation and removed highly uncertain imputations with a coefficient of variation >1. We then \log_e -transformed all gap-filled trait values and averaged each trait by taxon. For taxa recorded at genus level only, we calculated genus means, resulting in a full trait matrix for 26,632 out of the 54,519 taxa in sPlot (45.9%), with 6, 1,510 and 25,116 taxa at the family, genus and species level, respectively. These species covered 88.7% of all species-by-plot combinations.

For every trait j and plot k , we calculated the community-weighted mean (CWM) and the community-weighted variance (CWV) for each of the 18 traits in a plot (Enquist et al., 2015):

$$CWM_{j,k} = \sum_i^{n_k} p_{i,k} t_{i,j}$$

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

where n_k is the number of species with trait information in plot k , $p_{i,k}$ is the relative abundance of species i in 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 . CWMs and CWVs were calculated for 18 traits in 1,117,369 and 1,099,463 plots, respectively, the second being a smaller number as at least two taxa were needed for CWV calculation.

3 | CONTENT OF S PLOT 2.1

3.1 | Plot community data

sPlot 2.1 contains 1,121,244 vegetation plots from 160 countries and from all continents (Figure 3). The global coverage is biased towards Europe, North America and Australia, reflecting unequal sampling effort across the globe (Table 1). At the ecoregion level, major gaps occur in the wet tropics of South America and Asia, as well as in subtropical deserts worldwide and in the North American taiga. Although the plots are highly clustered geographically, their coverage in the environmental space is much more representative: the highest concentration of plots is found in environments that are most abundant globally (Figure 2), while they are lacking in the very moist parts of the environmental space, which are also spatially rare, and in the very cold parts, which are sparsely vegetated.

In most cases (98.4%), plot records in sPlot include full species lists of vascular plants, while 1.6% had only wood species above a certain diameter or only the most dominant species recorded. Terricolous bryophytes and lichens were additionally identified in 14% and 7% of plots, respectively (Table S2.1 in Appendix S2). Forest and non-forest plots comprise 330,873 (29.7%) and 513,035 (46.0%) of all plots in sPlot, respectively. In most cases, species abundance was estimated using different variants of the Braun-Blanquet cover-abundance scale (66%), followed by percentage cover (15%) and 55 other numeric or ordinal scales. The temporal extent of the data spans from 1885 to 2015, but >94% of vegetation plots were recorded later than 1960 (Figure S2.1 in Appendix S2). Almost all plots are georeferenced (1,120,686) and the majority of plots have location uncertainty of 10 m or less (Figure S2.2 in Appendix S2).

Vascular plant richness per plot ranges from 1 to 723 species (median = 17 species). The most frequent richness class is between 20 and 25 species (Figure S2.3 in Appendix S2). Plot size is reported in 65.4% of plots, ranging from <1 m² to 25 ha, with a median of 36 m². While forest plots have plot sizes ≥ 100 m², and in most cases $\leq 1,000$ m², non-forest plots range between 5 and 100 m² (Figure S2.4 in Appendix S2). When using these size ranges, forest plots tend to be richer in species (Figure 4a). The fact that the gradient in richness found in our plots was at least one order of magnitude stronger than differences that could be expected by the differences in plot size prompted us to produce the first global maps of plot-scale species richness, separately for forests and non-forests (Figure 4a). While plots with complete vascular species composition are largely lacking from the wet tropics, for the remaining biomes the plot-scale richness data do not show the typical latitudinal richness gradient in either formation. Particularly species-rich forests are found in the wet subtropics (such as SE United States, Taiwan and the East coast of Australia) as well as in some mountainous regions of the nemoral and steppic biomes of Eurasia. Likewise, non-forest communities have a particularly high mean vascular plant species in mountainous regions of the nemoral and steppic biomes of Eurasia.

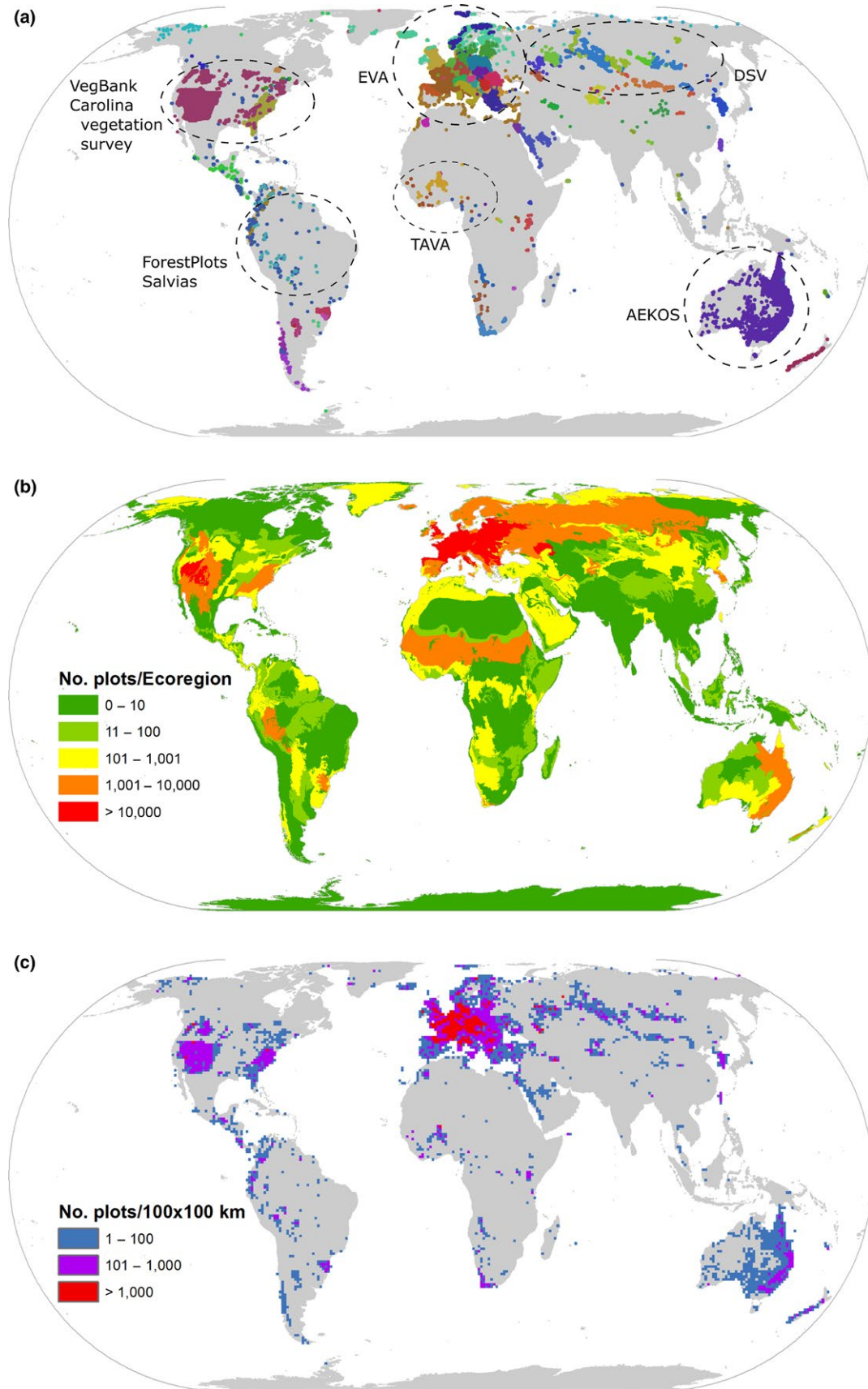


FIGURE 3 Global coverage of sPlot 2.1. (a) Contributing databases identified by different colours with indication of the two data aggregators (EVA, TAVA) and a few particularly large individual databases; (b) available plot numbers per WWF Ecoregion; and (c) available plot density in grid cells of 100 km × 100 km

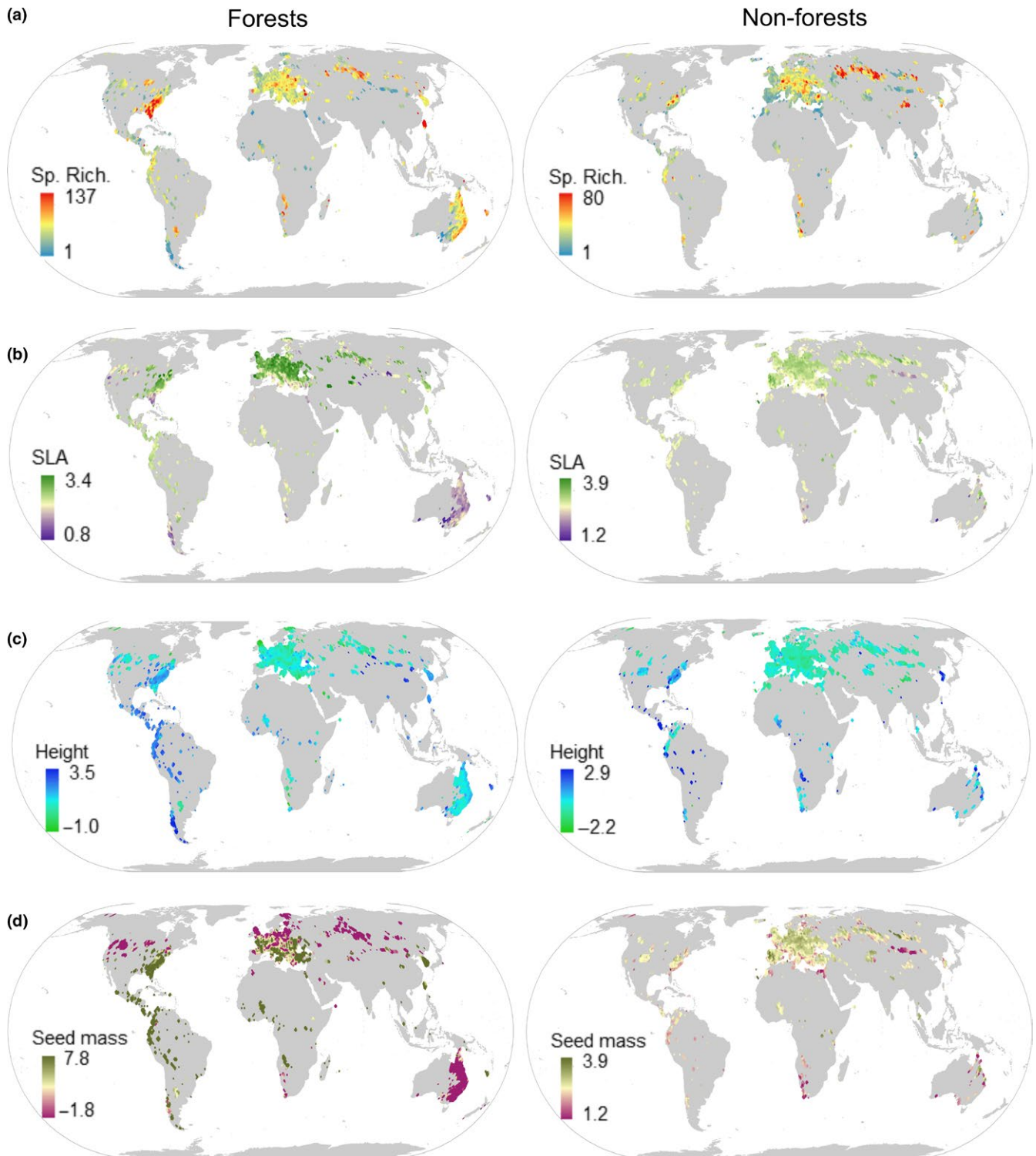


FIGURE 4 Examples of global community-level patterns that can be derived from (a) sPlot alone and (b–d) sPlot combined with TRY, here shown as raw data averaged by 1-degree grid cells. There are only a very few cells (142 out of 2633) comprising only a single plot. For the maps, only plots with full vascular species composition and spatial accuracy <5 km were used. They are based on 148,474 and 218,051 plots for forests and non-forests, respectively. Note that these maps are not corrected for biases caused by the facts that not all community types were recorded in all grid cells and that plot sizes as well as the fraction of species with available trait data varied spatially. Maps show patterns of (a) fine-grain alpha diversity, expressed as vascular plant species richness (only plots with plot sizes of 100–1000 m² for forests and 5–100 m² for non-forests); (b) community-weighted means (CWMs) for log_e-transformed trait values of specific leaf area (SLA, m²/kg); (c) plant height (m); and (d) seed mass (mg)

3.2 | Phylogenetic information

The phylogenetic tree for sPlot was produced from 53,489 vascular plant names contained in the database, comprising 5518 genera (Appendix S7). Moderately to highly frequent species in sPlot 2.1 are equally distributed across the phylogeny (corresponding to yellowish to reddish colors for low and high peaks, respectively, in Figure S7.6 in Appendix S7). Coverage of species included in the phylogeny ranges from 89% of species that occur only once in all plots to 100% of species with a frequency >10,000 plots (Figure S7.7 in Appendix S7).

3.3 | Functional information

The proportion of species with trait information increases with the species' frequency in plots. Gap-filled trait information is available for 77.2% and 96.2% for taxa that occurred in more than 100 and 1,000 plots, respectively. Trait coverage is similar across biomes (Figure S8.8 in Appendix S8). Across all biomes, the proportion of species for which gap-filled trait data are available increases with the species' frequency across plots. Compared to gap-filled data, trait coverage for the original trait data is considerably lower, being highest for height, seed mass, leaf area and specific leaf area (SLA, Figure S8.9 in Appendix S8).

The high representation of the 18 traits in the gap-filled trait data and the high degree of trait coverage for frequent species across all biomes (>75%) made us confident to produce the first maps of global patterns of community-weighted means (CWMs) (Figure 4b–d). The maps show the main trait dimensions of SLA, height and seed mass, separately for forests and non-forests, for those regions of the world that are already sufficiently covered by sPlot data. Accordingly, CWMs of SLA are quite similar for forest and non-forest plots, being highest in western North America and Europe and lowest in eastern North America, East and South Australia (Figure 4b). Non-forest vegetation shows lowest CWMs of SLA in the desert regions of the Namib and Sinai. Forests with highest CWMs of canopy height are found along the western and eastern coast of North America, some regions in Europe, East Asia and southern Australia (Figure 4c). These areas only partly coincide with those of highest seed masses for forests, while seed mass in non-forests is highest in the eastern Mediterranean Basin and in Central Asia (Figure 4d). The corresponding patterns for CWV are shown in Figure S9.10 in Appendix S9.

4 | DATA USAGE

The sPlot database (the vegetation-plot data, including the environmental information for each plot and the species phylogeny) is released in fixed versions to allow reproducibility of results, but also due to the enormous effort needed for data integration and harmonization and for updating the phylogeny. By delivering few fixed versions while keeping older versions available, the sPlot consortium

ensures that the same data can be used in parallel projects and that the data underlying a specific study remain accessible in the future, thus allowing re-analysis. Each new version will be matched to the current TRY database.

Data access to sPlot is regulated by the Governance and Data Property Rules (www.idiv.de/sPlot) to ensure a fair balance between the interests of data contributors and data analysts. In brief, the sPlot Rules state that: (a) all contributing vegetation-plot databases become members of the sPlot consortium, represented by their custodian and deputy custodian; (b) vegetation-plot data contributed to sPlot remain the property of the data contributors and can be withdrawn at any time except for approved projects; (c) other scientists (e.g., data managers or participants of the sPlot workshops) with particular responsibilities may also be appointed as personal members to the sPlot consortium; (d) sPlot data can be requested for projects that involve at least one member of the sPlot consortium; (e) whenever a project has been proposed, all sPlot consortium members will be informed and can declare their interest in becoming co-authors of manuscripts resulting from this project and then becoming actively involved in data evaluation and writing; and (f) if also the matched gap-filled or original trait data from TRY are requested for a project, likewise members from the TRY consortium can opt-in as co-authors. The sPlot database is, therefore, available according to a 'give-and-receive' system. Moreover, the data are available to any researcher by establishing a collaboration that includes and is supported by at least one sPlot consortium member.

The sPlot consortium is governed by a Steering Committee elected by all consortium members for two-year, renewable terms. Project proposals can be submitted to the Steering Committee, which ensures that the sPlot Rules are followed and redundant work between overlapping projects is avoided. The lists of databases, sPlot consortium members and the Steering Committee members are updated regularly on the sPlot website, as are the sPlot Rules and the list of approved projects.

5 | EXPECTED IMPACT AND LIMITATIONS

The main aim of the sPlot database is to catalyze a collaborative network for understanding global diversity patterns of plant communities in space and time. sPlot provides a unique, integrated global repository of data that would otherwise be fragmented in unconnected and structurally inconsistent databases at regional, national or continental levels. Together with the provision of harmonized phylogenetic, functional and environmental information, sPlot allows, for the first time, global analyses of plant community data. Compared to approaches using data aggregated from species occurrences in grid cells, sPlot will significantly advance ecological analyses and future interdisciplinary research in at least four different ways.

1. Using sPlot, one can predict the species that can co-exist in a community and also the frequencies of their co-occurrence

(Breitschwerdt, Jandt, & Bruelheide, 2015) or niche overlap (Broennimann et al., 2012). In addition, emerging tools such as Markov networks can be used to infer strengths of interspecific interactions (Harris, 2016). When investigating community assembly rules, the same information can be used to derive species pools for specific vegetation types (de Bello et al., 2016; Karger et al., 2016; Lewis, Szava-Kovats, & Pärtel, 2016). Moreover, the co-occurrence data from sPlot can be used to address fundamental patterns and drivers of plant invasions better than information on large geographic entities (e.g., van Kleunen et al., 2015) alone could.

2. sPlot data can be aggregated across all types of plots, by grid cells, ecoregions, environment, or even vegetation type or formation. Furthermore, replicated plots within grid cells, ecoregions, or any other subdivision of environmental conditions or vegetation types allow users to derive measures of compositional differences between plant communities within grid cells (= beta diversity; Table 1). Thus, the community data are an important complement to regional-scale species occurrence data (e.g., Enquist et al., 2016; Kreft & Jetz, 2007).
3. sPlot data provide information on the proportion of species in a community (in terms of cover, basal area, frequency). When combined with functional trait information, relative abundance of species allows calculation of community abundance-weighted mean trait values (Bruelheide et al., 2018). Information on the relative contribution of species to a community-aggregated trait value is particularly necessary when traits are used as proxies for vegetation functions and processes, allowing to test, among other things, the mass ratio hypothesis (Garnier et al., 2004; Grime, 1998) and to assess the roles of divergent traits (Díaz et al., 2007; Kröber et al., 2015).
4. Plant species within plots can be linked to traits that predict interactions with organisms from other trophic groups, both below-ground (mycorrhizae, soil decomposers) and above-ground (herbivores and pollinators). This will allow linking vegetation plot information to ecosystem processes and services such as pest control, pollination and nutrient cycling (e.g., de Bello et al., 2010).

Despite the large amount of available data and its potential suitability for global research, a number of limitations must be considered by future users of sPlot, such as (a) biases towards certain regions and communities, (b) near-complete lack of plots with complete vascular plant species composition for certain regions (e.g., the wet tropics), (c) identification or sampling errors by the surveyors and incomplete records because the detection of some species may be precluded in certain seasons by their phenology, (d) taxonomic uncertainty, particularly in the tropics, (e) strongly varying plot sizes employed in different studies and regions, (f) lack of trait measures at the plot level. For example, patterns of diversity components are typically affected by grain size. This means that using sPlot data for such studies either requires filtering for plots with identical or at least similar size or accounting for the plot-size effects in the statistical model. In addition, analyses of functional diversity with sPlot data are limited by the absence of

trait data for a (small) portion of the species and by the lack of plot-specific trait measures. Furthermore, the non-random and geographically and ecologically very unequal distribution of the plots contained in sPlot call for stratified resampling to balance records of different environments (e.g., stratified by climate, Figure 2) or physiognomic formations (Figure 4). Users of sPlot need to be aware of these and other limitations and to correct potential biases for their specific research question.

6 | CONCLUSION

sPlot is a unique global database of plant community records sampled with relatively similar methods widely used in vegetation ecology. The integration of co-occurrence data into a unified database that can be directly linked to environmental, functional and phylogenetic information, makes sPlot an unprecedented and essential tool for analyzing global plant diversity, the structure of plant communities and the co-occurrence of plant species. The compatibility of this consolidated database with other global databases, e.g., via a joint taxonomic backbone with TRY and the Global Naturalized Alien Flora (GloNAF; van Kleunen et al., 2015) (via taxon names), or via standardized geo-reference with databases of environmental information such as CHELSA, WorldClim or SoilGrids (Bruelheide et al., 2018), facilitates data integration and creates new research opportunities. The adaptive management of the database employed by the sPlot consortium allows regular incorporation of new data, resulting in a dynamic platform for storing and analyzing the most comprehensive compilation of plant community data worldwide.

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AUTHOR CONTRIBUTIONS

H.Bru. had the original idea and led the consortium from the start, while O.Pu. and J.D. coordinated the sPlot workshops. J.D., S.M.H. and U.J. compiled the databases to be included in sPlot. J.D. and later B.J.-A. and F.M.S. coordinated the network and the database. O.P. prepared the taxonomic and phylogenetic data. S.M.H. programmed the Turboveg software. B.Sa., F.J., H.Bru., J.D., J.K., M.Ch., and V.D.P.

organized the network in the Steering Committee. B.J.-A. and H.Bru. led the writing together with J.D. and input from S.M.H., O.Pu., M.Ch., F.J., J.K., V.D.P., B.Sa., I.Au., I.B., R.K.P., R.F., S.H., U.J., J.L., G.P., F.M.S., M.S., F.S. and M.W. The rest of authors (ordered alphabetically) contributed the plot and trait data. All authors agreed with the final manuscript.

DATA ACCESSIBILITY

The data contained in sPlot (the vegetation-plot data complemented by species phylogeny and environmental information) are available on request, through contacting any of the consortium members for submitting a paper proposal. The proposals should follow the Governance and Data Property Rules of the sPlot Working Group, which are available on the sPlot website (www.idiv.de/sPlot). After acceptance, the respective data will be provided. In addition to the plot data, CWMs and CWVs of 18 plant traits are available for every plot.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1 Additional references, attributions and disclaimers for datasets included in sPlot 2.1

Appendix S2 Data associated to the vegetation plot records stored in sPlot 2.1

Appendix S3 Details on the workflow for setting up plot definitions in sPlot 2.1

Appendix S4 Biome classification created for sPlot 2.1

Appendix S5 Zip file of the biome classification of Appendix S4 containing the shapefile (Geospatial vector data for geographic

information system (GIS) software) and accompanying accessory files (database, projection etc.)

Appendix S6 Trait information in sPlot 2.1

Appendix S7 Phylogenetic information in sPlot 2.1

Appendix S8 Gap-filled trait information

Appendix S9 Global patterns of community-weighted variances

Appendix S10 Detailed acknowledgements

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