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REPORT

Structural, ecological and biogeographical attributes of European vegetation alliances

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Abstract

The first comprehensive phytosociological classification of all vegetation types in Europe (EuroVegChecklist; *Applied Vegetation Science*, 2016, **19**, 3–264) contained brief descriptions of each type. However, these descriptions were not standardized and mentioned only the most distinct features of each vegetation type. The practical application of the vegetation classification system could be enhanced if users had the option to select sets of vegetation types based on various combinations of structural, ecological, and biogeographical attributes. Based on a literature review and expert knowledge, we created a new database that assigns standardized categorical attributes of 12 variables to each of the 1106 alliances dominated by vascular plants defined in EuroVegChecklist. These variables include dominant life form, phenological

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optimum, substrate moisture, substrate reaction, salinity, nutrient status, soil organic matter, vegetation region, elevational vegetation belt, azonality, successional status and naturalness. The new database has the potential to enhance the usefulness of phytosociological classification for researchers and practitioners and to help understand this classification to non-specialists.

KEYWORDS
alliance, attribute, Europe, EuroVegChecklist, parameterization, phytosociology, syntaxon, vegetation survey, vegetation type

1 | INTRODUCTION

Completing the comprehensive hierarchical classification system of European vegetation (Mucina et al., 2016) was a milestone in the history of European vegetation research. The resulting EuroVegChecklist became the primary reference for studies on the diversity of European vegetation and habitat types. The classification system of EuroVegChecklist was cross-linked to the EUNIS Habitat Classification (Chytrý et al., 2020), a European system of habitat classification based on a combination of characteristic vegetation types, environmental features, human impact and biogeographical zones. Moreover, extensive international studies based on the EVA database (Chytrý et al., 2016) were initiated to test individual sections of the EuroVegChecklist classification system (e.g., Peterka et al., 2017, 2023; Willner et al., 2017; Marcenò et al., 2018, 2019; Landucci et al., 2020; Bonari et al., 2021; Kalníková et al., 2021; Jiroušek et al., 2022; Novák et al., 2023).

EuroVegChecklist provides a brief description of each accepted vegetation unit, consisting of one to two lines of text characterizing its ecology and distribution. However, this information is insufficient for a deeper understanding of the structure, composition, ecology and biogeography of individual units. Therefore, a team of experts from the IAVS Working Group European Vegetation Survey prepared distribution maps of all 1106 alliances dominated by vascular plants and accepted in EuroVegChecklist (Preislerová et al., 2022). These maps have significantly helped users understand the biogeographical concept of each alliance, but its ecological delimitation remains poorly characterized. The EuroVegChecklist authors tried to standardize the terms used in the descriptions of vegetation types (Mucina et al., 2016: their appendix S3). However, due to the limited space in that publication and, in many cases, also due to the lack of knowledge, they could only select a few of the most important ecological characteristics of each vegetation type. Therefore, information about many ecological characteristics is missing for individual vegetation types in the EuroVegChecklist.

Here, we aim to improve the characterization of European phytosociological alliances dominated by vascular plants by developing a standardized set of structural, ecological and biogeographical variables, each with standardized attribute values, and assigning relevant attributes to each alliance.

2 | DATABASE COMPILATION

This article deals with 1106 European alliances of vascular plants reported in EuroVegChecklist (Mucina et al., 2016, with recent updates available at https://floraveg.eu). We compiled a database of attributes for each of these alliances using an expert-based approach, searching for a consensus estimate of attributes by an international group of experts familiar with different vegetation types and different European regions. The expert-based approach had to be used because (1) relevant quantitative data have not been collected in European vegetation plots in a standardized manner and are entirely missing for many plots, (2) vegetation plots in the current databases (Chytrý et al., 2016) have often not been assigned to alliances, or the alliance concepts used are inconsistent, and (3) the existing plots provide a geographically or ecologically biased sample for some alliances.

The initial list of variables and variable attributes was prepared by M. Chytrý, and the first data set with attribute values assigned to each alliance was prepared by Z. Preislerová, supported by C. Marcenò, who added values for some Mediterranean alliances. This initial compilation was based on expert knowledge and a review of the literature on European vegetation and habitat types listed in appendix S2 of Mucina et al. (2016) and newer literature listed by Preislerová et al. (2022). Some variables and attributes were adjusted based on the experience from this initial compilation. The result of this compilation was sent for a detailed review to a group of 82 vegetation and habitat experts from the IAVS Working Group European Vegetation Survey. Of these experts, 56 provided comments, which were used by Z. Preislerová, with contributions from M. Chytrý, to prepare a new version. This version also included further adjustments of variables and attributes and changes in attribute values based on the expert recommendations. The resulting database was sent to experts for another round of comments, and the final version was prepared based on these comments.

3 | VARIABLES AND ATTRIBUTES

The consensus of the international expert group resulted in a list of the following variables and categorical attributes for each variable. The list includes one variable characterizing vegetation structure (dominant life form), one biogeographical variable (vegetation region) and 10 ecological variables. Names of plants used as examples follow the Euro+Med PlantBase (2023).

3.1 | Dominant life form

Plant species display a range of structural, physiological and morphological adaptations to environmental gradients. Various authors proposed different categories of plant life forms (e.g., Du Rietz, 1931; Raunkiær, 1934; Ellenberg & Mueller-Dombois, 1967). The categories of life forms defined here are based on a combination of traits important for vegetation structure in Europe, including plant height, woodiness, branching type of woody plants (trees vs shrubs), leaf type, life span (annual vs perennial), and habitus (e.g., graminoid, non-graminoid, fern, succulent, aquatic plant). Broad taxa of cryptogams (ferns, bryophytes and lichens) are also considered here as separate life forms based on their specific morphological and ecophysiological features (except for aquatic cryptogams, which are grouped with other aquatic plants).

The dominant life form is the plant life form that usually attains the highest cover in at least one of the four main vegetation layers (tree, shrub, herb or moss layer). More than one dominant life form is given for vegetation types with well-differentiated vegetation layers. For example, conifer trees, dwarf shrubs and bryophytes can be given for a boreal forest alliance, each life form being dominant in a different vegetation layer. However, layers that have, on average, much lower cover than other layers in the given alliance are not considered. We do not report the dominant life form for the layers with a mean cover lower than 20% of the mean cover of the layer with the highest cover. For example, in a grassland vegetation type with a mean herb-layer cover of 80%, shrub layer of 5% and moss layer of 10%, we only include the dominant life form of the herb layer. More than one life form may be reported for the same layer if different life forms dominate this layer at different sites (e.g., perennial graminoids and perennial non-graminoid herbs in a meadow alliance).

Some species may have different life forms depending on the environment or region (e.g., tree in lowlands vs shrub near the timberline). In such cases, the life form prevailing in the given alliance is reported. Tree saplings in the shrub layer are considered trees.

Categories:

- *Coniferous trees* – usually evergreen, single-trunk woody plants with either needle-like or scale-like leaves; examples: *Abies* spp., *Cupressus sempervirens*, *Juniperus thurifera*, *Larix* spp., *Picea* spp., *Pinus nigra*
- *Broad-leaved deciduous trees* – single-trunk woody plants that shed all their leaves at the beginning of the cold season (examples: *Fagus* spp., *Fraxinus* spp., *Ficus carica*, *Ostrya carpinifolia*, *Quercus petraea*, *Sorbus aucuparia*) and marcescent trees that keep their leaves dry on the twigs in winter (example: *Quercus pubescens*)
- *Broad-leaved evergreen trees* – single-trunk woody plants with small (sclerophyllous) or large (laurophyllous) evergreen leaves; examples: *Apollonias barbujana*, *Ceratonia siliqua*, *Laurus nobilis*, *Olea europaea*, *Quercus ilex*, *Q. suber*
- *Palms* – evergreen plants with cylindrical stems that lack secondary growth and with crowns of large feathered or fan-shaped leaves; examples: *Chamaerops humilis*, *Phoenix* spp.
- *Coniferous shrubs* – evergreen woody plants taller than 50 cm with stems branching at the base with either needle-like leaves (examples: *Juniperus communis*, *Pinus mugo* subsp. *mugo*) or scale-like leaves (example: *Juniperus sabina*); tree saplings in the forest shrub layer are not included
- *Broad-leaved deciduous shrubs* – woody plants taller than 50 cm with stems branching at the base that shed all their leaves at the beginning of the cold season; tree saplings in forest shrub layers are not included; examples: *Cornus sanguinea*, *Corylus avellana*, *Prunus spinosa*, *Sambucus nigra*
- *Broad-leaved evergreen shrubs* – evergreen woody plants taller than 50 cm with stems branching at the base with small (sclerophyllous) or large (laurophyllous) evergreen leaves; tree saplings in forest shrub layers are not included; examples: *Arbutus unedo*, *Clethra arborea*, *Maytenus canariensis*, *Nerium oleander*, *Nicotiana glauca*, *Phillyrea angustifolia*, *Pistacia lentiscus*, *Rhamnus alaternus*, *Salvia canariensis*
- *Microphyllous shrubs and small trees* – evergreen or deciduous non-coniferous woody plants taller than 50 cm and shorter than 6 m with tiny, scaly or needle-like leaves; examples: *Erica arborea*, *E. scoparia*, *Myricaria* spp., *Tamarix* spp.
- *Broom shrubs* – woody plants taller than 50 cm with stems branching at the base; they resemble a broom and assimilate primarily through slender green branches; they have sparse, small leaves that drop in summer to reduce water loss; in some species, small branches are transformed into thorns; examples: *Cytisus ruthenicus*, *C. scoparius*, *C. supranubius*, *Genista corsica*, *G. florida*, *G. scorpius*, *Launaea arborescens*, *Retama* spp., *Ulex boivinii*, *U. europaeus*
- *Dwarf shrubs* – small woody or semi-woody plants (chamaephytes) with most of their overwintering buds located up to 50 cm above the soil surface; small suffruticose plants with herbaceous branches and cushion-like shrubs are also included here; examples: *Artemisia hololeuca*, *Astracantha sicula*, *Bupleurum fruticescens* subsp. *spinosum*, *Calluna vulgaris*, *Daphne glomerata*, *Dryas* spp., *Echinospartum horridum*, *Ephedra distachya*, *Erica carnea*, *Euphorbia spinosa*, *Genista hispanica*, *Helichrysum stoechas*, *Loiseleuria procumbens*, *Phyllodoce caerulea*, *Prunus prostrata*, *Salix herbacea*, *Thymus* spp., *Vaccinium myrtillus*, *Vella spinosa*
- *Woody lianas* – creeping or climbing evergreen or deciduous plants with woody bases; examples: *Hedera* spp., *Smilax aspera*, *Vitis* spp.
- *Perennial graminoids* – grass-like herbaceous plants of the order *Poales* (*Cyperaceae*, *Juncaceae*, *Poaceae*, *Typhaceae*) that live for more than one year
- *Perennial non-graminoid herbs* – herbaceous plants not belonging to *Poales* that live for more than one year; leaves are both in rosettes or on long stems; non-woody lianas, clubmosses, horsetails, hemicryptophytes, geophytes and helophytes are included here; some of them can have a cushion-like form; examples: *Androsace*

villosa, *Butomus umbellatus*, *Calystegia sepium*, *Cerastium arcticum*, *Dactylorhiza* spp., *Equisetum* spp., *Galanthus* spp., *Mentha* spp., *Onopordum* spp., *Plantago media*, *Verbascum* spp.

- *Ferns* – terrestrial or epiphytic herbaceous plants with feathery or tongue-like fronds that reproduce by spores; examples: *Asplenium* spp., *Blechnum* spp., *Dryopteris* spp., *Ophioglossum* spp., *Woodsia* spp.; aquatic ferns are classified as aquatic macrophytes; horsetails (Equisetopsida) are classified as perennial non-graminoid herbs
- *Succulents* – annual or perennial plants (both hemicryptophytes and chamaephytes) with thick fleshy leaves or stems; examples: *Aeonium* spp., *Anabasis aphylla*, *Astydamia* spp., *Climacoptera* spp., *Crithmum maritimum*, *Euphorbia canariensis*, *E. lamarckii*, *E. regis-jubae*, *Kalidium* spp., *Salicornia* spp., *Salsola* spp., *Sedum* spp., *Sempervivum* spp., *Suaeda* spp.
- *Annual graminoids* – grass-like herbaceous plants (*Cyperaceae*, *Juncaceae*, *Poaceae*) that complete their life cycle during one growing season or start to germinate in the autumn and reproduce in the following year (winter therophytes or biennial therophytes); they survive harsh conditions during unfavorable seasons as seeds; examples: *Aegilops* spp., *Aira* spp., *Anisantha tectorum*, *Brachypodium distachyon*, *Isolepis setacea*, *Juncus bufonius*, *Vulpia* spp.
- *Annual non-graminoid herbs* – herbaceous plants other than *Cyperaceae*, *Juncaceae* and *Poaceae* that complete their life cycle during one growing season or start to germinate in the autumn and reproduce the following year (biennial therophytes); they survive harsh conditions during unfavorable seasons as seeds; examples: *Bidens cernua*, *Bupleurum rotundifolium*, *Gypsophila elegans*, *Myosurus minimus*, *Plantago lagopus*, *Ranunculus sardous*, *Sisymbrium loeselii*, *Thlaspi arvense*
- *Floating aquatic plants* – vascular plants or bryophytes floating on or below the water surface (pleustophytes); examples: *Lemna* spp., *Riccia fluitans*, *Salvinia natans*
- *Rooted aquatic plants* – vascular plants, bryophytes or macroalgae living in water and rooted in the bottom, some of them submerged and others with natant leaves; examples: *Chara* spp., *Cinclidotus* spp., *Fontinalis* spp., *Isoetes* spp., *Marsilea* spp., *Myriophyllum* spp., *Nymphaea* spp., *Persicaria amphibia*, *Potamogeton* spp., *Ranunculus fluitans*, *Zostera* spp.
- *Bryophytes* – non-aquatic mosses, liverworts and hornworts; examples: *Bazzania* spp., *Dicranum* spp., *Gymnomitrion* spp., *Polytrichum* spp., *Sphagnum* spp.
- *Lichens* – lichenized fungi; examples: *Cladonia* spp., *Parmelia* spp.

3.2 | Phenological optimum

The phenological optimum is defined here as a period when most of the species in the community (or the dominant species in species-poor communities) are flowering. This period usually corresponds to the peak of above-ground biomass in the community. In vegetation dominated by ferns, the phenological optimum corresponds to the period of highest biomass. In vegetation types that have shifted phenological phases for different species groups, more than one phenological optimum is given. For example, temperate deciduous floodplain forests have two phenological optima associated with different life forms: early spring (flowering of spring geophytes and trees) and summer (maximum biomass of tree leaves and flowering and maximum biomass of shade-adapted hemicryptophytes such as *Urtica dioica*). Some types of annual weed or ruderal vegetation may comprise two or three groups of species with the same life form but different phenological optima, resulting in different spring, summer and autumn aspects. Some vegetation types have a long phenological optimum spanning at least two periods defined here. More than one phenological optimum is given in such cases. If spring flowering of deciduous trees or shrubs precedes leaf development, and no other life form is flowering, the time of fully developed foliage (the highest biomass), which usually corresponds with the flowering of other plants, is considered the phenological optimum. The phenological optimum of bryophytes and lichens is not considered.

Phenological optimum categories were defined primarily based on phenological patterns in the Central European lowlands, which roughly correspond to the mean phenological stages in vegetation types across Europe. However, the assessment considers that spring phases start earlier in the Southern European lowlands and later in the Central European mountains and Northern Europe. Because there is little information on the phenological optimum in the phytosociological literature, category assignments were based largely on field experience and the phenology of dominant or other common species in each vegetation type.

Categories:

- *Early spring* – March, April (it can start earlier in Southern European lowlands and end later in Central European mountains and Northern Europe)
- *Late spring* – May (it can start earlier in Southern European lowlands and end later in Central European mountains and Northern Europe)
- *Summer* – June, July, August
- *Autumn* – September, October, November
- *Winter* – December, January, February (it can end in January in the Southern European lowlands)

3.3 | Substrate moisture

Substrate moisture reflects the availability of water to plants during the growing season.

Categories:

- *Dry substrate* is characterized by a low groundwater table and low water-holding capacity; substrates with a higher water-holding capacity that are seasonally very dry due to low precipitation (e.g., clayey soils in the Mediterranean or semidesert areas) are also in this category

- *Mesic substrate* holds a moderate amount of soil moisture throughout the year without pronounced drought or waterlogging
- *Intermittently wet substrate* is occasionally or seasonally flooded with rainwater or has a periodically high groundwater table and then dries out; such conditions occur in continental floodplains, depressions, shallow pans, temporary ponds and streams
- *Moist to wet substrate* is characterized by a permanently high groundwater table that is shallow below the soil surface, at the soil surface, or for some very short period also above the soil surface
- *Water* is the category for the environments in which the water table is above the soil surface for most of the growing season

3.4 | Substrate reaction

Substrate reaction is measured as the pH of soil solution or water. Reaction categories are defined by pH thresholds following USDA (2017). However, only three categories are used because the exact ranges of pH values are unknown for many vegetation types, and the reaction category had to be estimated based on bedrock type and reaction indicator values (Dengler et al., 2023; Tichý et al., 2023) of diagnostic, constant or dominant species for each vegetation type.

Categories:

- *Acid substrate* has a pH of up to 6.0 and a low base content
- *Slightly acid to neutral substrate* has a pH between 6.0 and 7.3 and a moderate base content
- *Alkaline substrate* has a pH above 7.3 and a high content of calcium or other basic cations

3.5 | Salinity

Salinity refers to the concentrations of soluble salts (especially carbonates, chlorides and sulfates of calcium, magnesium, sodium and potassium) in soil or water. In coastal areas, salinity can be caused by sea surges, tides, storms, salt spray from the sea and the mixing of freshwater and seawater in estuaries. In inland areas, salinity can be high due to mineral-rich springs or salt accumulation in the soil from salt-rich sediments in dry climates with high evaporation. Measurements of salinity are rare; therefore, salinity is usually estimated from the occurrence of indicator plants.

Categories:

- *Non-saline substrate* has no or very low concentrations of soluble salts; the vegetation contains no halophytes
- *Subsaline substrate* has low to moderate concentrations of soluble salts; vegetation is composed of a mixture of halophytes and glycophytes (non-halophytic plants)
- *Saline substrate* has a high concentration of soluble salts; vegetation is dominated by halophytes

3.6 | Nutrient status

Nutrient status refers to the concentration of available nitrogen, phosphorus and potassium in soil or water.

Categories:

- *Oligotrophic* substrate or water has low nutrient availability; vegetation has low productivity; dystrophic environments are also included here
- *Mesotrophic* substrate or water has moderate nutrient availability; vegetation has moderate productivity
- *Eutrophic* substrate or water has a high amount of available nutrients, especially nitrogen and phosphorus; vegetation has high productivity
- *Hypertrophic* substrate or water has a very high amount of available nutrients, often due to anthropogenic eutrophication; vegetation has very high productivity

3.7 | Soil organic matter

Soil organic matter consists of remains of dead plants and animals at various stages of decomposition. The following categories are distinguished according to the relative proportion of mineral or organic components. Aquatic vegetation types that do not root in soil are not classified.

Categories:

- *Poorly developed soil* – rock outcrops, gravel, sand or clay with poorly developed soil
- *Developed mineral soil* – developed soil in which the mineral soil component predominates over the soil organic matter, or both components are represented equally; forest soils with a layer of humus are also included here, provided the mineral component predominates in the topsoil
- *Organic soil* – the organic soil component predominates over the mineral component

3.8 | Vegetation region

Vegetation regions defined here (Figure 1) are large areas with relatively uniform climates and vegetation. These regions partially correspond to other land classification units such as biogeographical regions, ecoregions or biomes (Rivas-Martínez et al., 2004a; Schultz, 2005; EEA, 2016; Mucina et al., 2016; Dinerstein et al., 2017; Bruelheide et al., 2018). However, these classification systems are inconsistent across Europe, differ in the number of units and the location of boundaries between them, and some of them do not consider vegetation as the main classification criterion. Here, we propose a system based mainly on a combination of the Biogeographic and

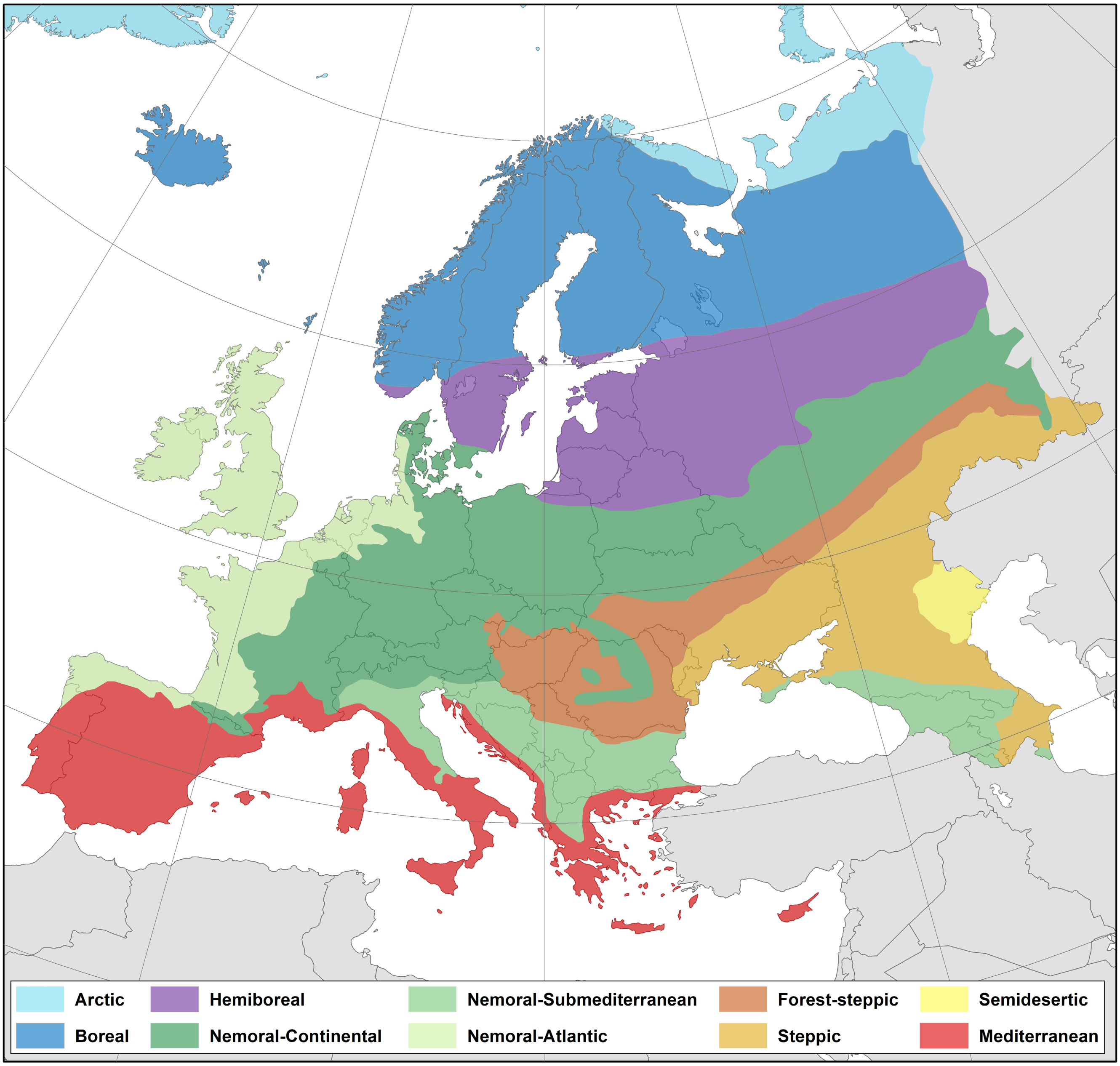

FIGURE 1 European vegetation regions used in the database (an original compilation based on different biogeographical and vegetation maps). The Macaronesian vegetation region is not shown.

Bioclimatic Maps of Europe by Rivas-Martínez et al. (2004a, 2004b), European Biogeographical Regions (EEA, 2016) and Ecoregions by Dinerstein et al. (2017).

The assignment of vegetation types to vegetation regions is partly based on the distribution maps of European alliances (Preislerová et al., 2022). Since these maps do not provide sufficient details, such as point distribution, we also used information from various literature sources and expert knowledge.

Categories (regions):

- *Arctic* – Arctic Biogeographical Region in the northernmost part of the European mainland, Greenland and Svalbard
- *Boreal* – northern part of the Boreal Biogeographical Region in the European part of Russia, Finland, Sweden and Norway (except for the southern parts of these three countries), Iceland and the Faroe Islands
- *Hemiboreal* – southern part of the Boreal Biogeographical Region in the European part of Russia, Estonia, Latvia, Lithuania, Belarus, the Kaliningrad Region of Russia and the adjacent part of Poland, the southern part of Sweden except for the Skåne Peninsula and the southernmost parts of Finland and Norway
- *Nemoral-Atlantic* – Atlantic Biogeographical Region including Ireland, Great Britain, western Denmark, northwestern Germany, Benelux, northern and western France and the northern Iberian Peninsula

- *Nemoral-Continental* – Pyrenees, eastern France, southeastern Belgium, Luxembourg, eastern and southern Germany, eastern Denmark, Skåne Peninsula, Poland, Czechia, Slovakia, Switzerland, Austria, Italian Alps, northern Slovenia, southwestern Hungary, Ukrainian and Romanian Carpathians, and the nemoral forest zone of Belarus, Ukraine and Russia
- *Nemoral-Submediterranean* – northern Italy except the Alps, southern Slovenia, Croatia, Bosnia and Herzegovina, Serbia, Kosovo, North Macedonia, Montenegro, eastern Albania, Bulgaria, northern part of Greece and European Turkey, southern Crimea, the Greater Caucasus, Georgia, Armenia and western and southern Azerbaijan
- *Forest-Steppic* – the Pannonian Biogeographical Region in southeastern Czechia, southern Slovakia, eastern Austria, Hungary and northern Serbia, the extra-Carpathian parts of Romania, forest-steppe zone in Ukraine, Moldova and Russia, and the mountain fringes of the Southern Urals
- *Steppic* – steppe zone in Ukraine, Moldova and Russia, low-lying areas in the Caucasus countries and the Russian part of the Greater Caucasus
- *Semidesertic* – extremely dry eastern part of the Steppic Biogeographical Region around the Caspian Sea
- *Mediterranean* – Iberian Peninsula except for its Atlantic part and the Pyrenees, southern France, southern and southwestern Italian Peninsula, the coastal areas of the Balkan Peninsula, Greece and all the Mediterranean islands
- *Macaronesian* – Azores, Madeira and Canary Islands

3.9 | Elevational vegetation belt

The elevational vegetation belts reflect the vertical zonation of vegetation in relation to the changing climate with increasing elevation. In the Arctic and Boreal vegetation regions, we distinguish only the Boreo-Arctic lowland and the Boreo-Arctic mountain belts because the distinction between multiple belts is often unclear due to the low timberline in maritime and northern areas. In the Hemiboreal, Nemoral, Forest-Steppic, Steppic and Semidesertic vegetation regions, we distinguish lowland, submontane, montane, subalpine, alpine and subnival belts. In the Mediterranean and Macaronesian vegetation regions, we use the division into Inframediterranean, Thermomediterranean, Mesomediterranean, Supramediterranean, Oromediterranean and Cryomediterranean belts. Each elevational belt may shift up or down in any mountain range or region, depending on local environmental conditions.

Categories:

Boreo-Arctic vegetation belts

- *Boreo-Arctic lowland* – lowland landscape with coniferous forests or a mixture of deciduous and coniferous forests in the Boreal and Hemiboreal vegetation regions or with shrub vegetation, heathlands, grassy tundra, snow beds or arctic desert in the Arctic vegetation region
- *Boreo-Arctic mountain* – mountainous landscape with shrubby vegetation or open deciduous woodlands, heathlands and grasslands in the Boreal or Arctic vegetation regions

Temperate vegetation belts

- *Lowland* – low-altitude landscapes, including the most thermophilous vegetation types in the given area
- *Submontane* – transitional landscapes between lowlands and mountains with deciduous forests
- *Montane* – mountainous landscapes with mixed coniferous-deciduous forests or cool deciduous forests, with an increasing predominance of coniferous forests toward higher elevations or more continental macroclimates
- *Subalpine* – landscapes around the timberline with open coniferous forests, krummholz, heathlands and grasslands around the timberline
- *Alpine* – landscapes above the timberline with grasslands and heathlands
- *Subnival* – landscapes close to the snow line and rocky summits with patchy vegetation dominated by bryophytes and lichens with a low cover of vascular plants

Vegetation belts of the Mediterranean and Macaronesian vegetation regions

- *Inframediterranean* – lowest elevations of Madeira and the Canary Islands with a warm and arid climate; natural vegetation is dominated by low-growing, succulent, thorny or summer-deciduous shrubs
- *Thermomediterranean* – a belt at low elevations, usually near the coast, with potential natural vegetation dominated by evergreen sclerophyllous or microphyllous scrub and forests
- *Mesomediterranean* – a belt characterized by warm summers, mild winters with rare frost and pronounced periods of summer drought, suitable for the cultivation of the olive tree; the natural vegetation of this belt is the evergreen sclerophyllous or laurophyllous forest or sclerophyllous scrub at dry sites
- *Supramediterranean* – a belt at middle elevations with less pronounced summer drought and regular winter frost; the natural vegetation of this belt is mainly broad-leaved deciduous forest; coniferous forests may occur on humid slopes, while sclerophyllous forests or scrub can occur at dry sites
- *Oromediterranean* – a belt below and around the timberline, characterized by heaths and pine and juniper forests
- *Cryomediterranean* – the highest belt of the Mediterranean mountain ranges, located above the timberline; it is characterized by natural grasslands and hedgehog heaths

3.10 | Azonality

Azonality is defined by locally specific substrate or other abiotic conditions that prevent the development of vegetation types that occupy large areas under given macroclimatic conditions (zonal vegetation) and promote the development of specific, localized vegetation types (azonal vegetation). Many azonal vegetation types occur in specific habitats but are confined to a single vegetation zone. Such vegetation types are called intrazonal. Some vegetation types may be zonal in some areas but dependent on local conditions in others, for example, some types of arctic-alpine or mire vegetation are zonal in Northern Europe but confined to locally specific conditions in Central or Southern Europe. Such occurrences are referred to as extrazonal and are also considered here. Some vegetation types are included in more than one category, for example, salt-sprayed coastal cliffs are both Rock and Saline.

Categories:

- *Marine* – sea littoral with sea-grass vegetation
- *Aquatic* – inland freshwater, brackish and saline lakes, ponds and pools
- *Wetland* – places with groundwater permanently or frequently at the level of the soil surface or slightly above it
- *Riverine* – rivers, streams and streambeds that may be subject to short-term flooding; both vegetation in the water and on the banks is considered here
- *Shallow soil* – places with soils that dry out frequently or quickly, have low nutrient levels and do not buffer the chemical reaction of the bedrock
- *Rock* – outcrops and cliffs without soil that are stressed by lack of water and extreme temperatures; vegetation develops patchily in rock crevices, on ledges and terraces
- *Scree* – an unstable mixture of rock fragments of various sizes that are moved downward by gravity
- *Eroded slope* – non-rocky steep slopes that are heavily affected by erosion processes
- *Sand* – coastal or inland sandy habitats with low water storage and low nutrient content
- *Ultramafic and heavy-metal soil* – outcrops or shallow soils on peridotite, ophiolite, serpentinite, and other rocks that contain high concentrations of heavy metals such as Fe, Mn, Cu, Cr, Ni, Pb, Co, and Cd, which are toxic to many plant species; heavy-metal soils on mine dumps are also included
- *Gypsum* – outcrops of hydrated calcium sulfate with a hard surface crust that is difficult for plants to penetrate; gypsum soils are often poor in macronutrients and dry out due to heavy water runoff
- *Saline* – habitats affected by high concentrations of soluble salts (carbonates, chlorides and sulfates of calcium, magnesium, potassium and sodium) in the soil or water
- *Snowbed* – arctic and alpine habitats where snow melts much later than in the surrounding area, resulting in a short growing season and locally increased moisture
- *Alpine or Cryomediterranean, wind-exposed* – high-mountain (alpine or Cryomediterranean, or less frequently subalpine or Oromediterranean) or arctic (less frequently subarctic) sites exposed to wind; in winter, the wind blows away snow and exposes vegetation to frost; in summer, wind causes desiccation
- *Zonal* – vegetation types other than those defined above that occur over large areas and reflect macroclimate rather than a particular substrate or other local abiotic conditions; fringe vegetation that develops at the boundary between forests and herbaceous vegetation on widespread soil types is also included here despite its linear nature; this category is included here as a complement to the azonality categories to provide an attribute to all the alliances

3.11 | Successional status

The successional status reflects the position of vegetation types in the successional series from early-successional stages that occur after the emergence of new habitats (primary succession) or after a major stand-replacing disturbance (secondary succession). Some vegetation types are assigned more than one successional stage because they may have different successional statuses in different climatic zones (e.g., some types of scrub can be late-successional under dry climates and mid-successional under wet climates).

Categories:

- *Early-successional* – vegetation developed at recently or frequently intensively disturbed sites (e.g., river bars, trampled sites, and arable fields) or in newly created habitats (e.g., bottoms of drained water bodies, clearings, lava fields and mining sites); it is dominated by short-lived species and may undergo a directional change toward vegetation with a higher proportion of long-lived species; examples include annual-dominated weed or ruderal vegetation
- *Mid-successional* – vegetation on developed soils that undergoes a directional change; however, in many cases, further succession is prevented by periodic disturbances of moderate or low severity (e.g., floods, avalanches, wind, mowing, grazing and burning); long-lived species predominate over short-lived species; examples include scrub and perennial grasslands in areas where the potential vegetation is a forest
- *Late-successional* – vegetation that does not undergo directional changes and is not influenced by strong or regular disturbance; it is usually dominated by long-lived plant species and is in dynamic equilibrium with local climate and soil; examples include forests, but also scrub or grasslands in dry or cold climates
- *Blocked primary succession* – vegetation at sites where extreme soil conditions (e.g., rocks, cliffs, scree, walls, gypsum) or other adverse factors (e.g., strong and constant wind) prevent the development to later successional stages; such sites are dominated by long-lived species adapted to extreme conditions

3.12 | Naturalness

Naturalness expresses the degree to which vegetation has been formed by natural processes or under human influence. Forest vegetation types are considered natural here, although they have been under human influence for centuries or millennia, and specific forest stands can be considered semi-natural or even anthropogenic. Some types of grassland or scrub may occur naturally at some sites, while their formation at other sites has been caused by human management. Such vegetation types are classified into more than one category.

Categories:

- *Natural* vegetation has developed without human intervention and has not been severely disturbed by humans for a long time; managed forests and old plantations of site-native trees are also included, provided that the composition of their tree, shrub and herb layers corresponds to natural forests
- *Semi-natural* vegetation develops from natural vegetation as a result of long-term and regular management by humans, for example, mowing, grazing or burning; such activities have altered vegetation structure and species composition that differ from natural vegetation; vegetation consists mainly of native species that regenerate without direct human intervention; subcategories include:
  - *Meadow* – regularly or irregularly mown grasslands
  - *Pasture* – regularly or occasionally grazed grasslands or scrub but not grazed forests (except for open patches in wooded pastures, which are included here)
  - *Burned* – irregularly burned vegetation, especially scrub
  - *Disturbed, unmanaged* – vegetation at sites that had been disturbed and altered by human activities (e.g., quarries, sod removal sites, military activities, spoil heaps and forest clearings) and then left unmanaged, resulting in secondary succession
- *Anthropogenic* vegetation occurs in habitats created by human activities and intensively managed or disturbed by humans; alien species are common and may dominate in some types. Subcategories include:
  - *Weed* – weed vegetation on arable and other cultivated lands
  - *Ruderal* – vegetation at uncultivated sites that are frequently or were recently disturbed by human activities
  - *Neophyte-dominated* – woody and herbaceous vegetation dominated by neophytes, either planted or spontaneously established

4 | RESULTS

The complete database of vegetation attributes is included in Appendix S1. A summary of the number of alliances assigned to each attribute is in Table 1. It shows that perennial non-graminoid herbs are the most common life form in European vegetation types. Most alliances have their phenological optimum in summer and occur on mesic or dry, alkaline, non-saline, mesotrophic substrate, typically mineral soil. The Mediterranean region hosts the largest number of alliances. Most alliances are found at low elevations and develop in zonal habitats. The most typical azonal habitats are related to shallow soil. Most alliances represent mid-successional and natural vegetation.

TABLE 1 Number of alliances assigned to individual attributes. Alliances assigned to more than one attribute for the same variable are counted more than once; therefore, the total number of alliances across all attributes of each variable is higher than the total number of alliances.

Variables (in bold) and attributes	No. of alliances
Dominant life form	
Coniferous trees	60
Broad-leaved deciduous trees	87
Broad-leaved evergreen trees	27
Palms	3
Coniferous shrubs	59
Broad-leaved deciduous shrubs	165
Broad-leaved evergreen shrubs	82
Microphyllous shrubs and small trees	27
Broom shrubs	34
Dwarf shrubs	257
Woody lianas	22
Perennial graminoids	524
Perennial non-graminoid herbs	691
Ferns	39
Succulents	69
Annual graminoids	74
Annual non-graminoid herbs	149
Floating aquatic plants	5
Rooted aquatic plants	19
Bryophytes	197
Lichens	71
Phenological optimum	
Early spring	158
Late spring	615
Summer	869
Autumn	71
Winter	9
Substrate moisture	
Dry substrate	550
Mesic substrate	551
Intermittently wet substrate	137
Moist to wet substrate	190
Water	44
Substrate reaction	
Acid substrate	445
Slightly acid to neutral substrate	561
Alkaline substrate	729
Salinity	
Non-saline substrate	952
Subsaline substrate	157

(Continues)

TABLE 1 (Continued)

Variables (in bold) and attributes	No. of alliances
Saline substrate	80
Nutrient status	
Oligotrophic	681
Mesotrophic	707
Eutrophic	174
Hypertrophic	6
Soil organic matter	
Poorly developed soil	461
Developed mineral soil	728
Organic soil	45
Vegetation region	
Arctic	52
Boreal	125
Hemiboreal	150
Nemoral-Atlantic	286
Nemoral-Continental	388
Nemoral-Submediterranean	417
Forest-Steppic	189
Steppic	136
Semidesertic	20
Mediterranean	552
Macaronesian	120
Elevational vegetation belt	
Boreo-Arctic lowland	198
Boreo-Arctic mountain	37
Lowland	478
Submontane	285
Montane	264
Subalpine	177
Alpine	93
Subnival	27
Inframediterranean	36
Thermomediterranean	319
Mesomediterranean	331
Supramediterranean	304
Oromediterranean	92
Cryomediterranean	14
Azonality	
Marine	7
Aquatic	22
Wetland	137
Riverine	135
Shallow soil	294
Rock	206
Scree	135
Eroded slope	72
Sand	112
Ultramafic and heavy-metal soil	44
Gypsum	10
Saline	139
Snowbed	23
Alpine or Cryomediterranean, wind-exposed	24
Zonal	378
Successional status	
Early-successional	285
Mid-successional	505
Late-successional	332
Blocked primary succession	226
Naturalness	
Natural	879
Semi-natural (Meadow)	61
Semi-natural (Pasture)	249
Semi-natural (Burned)	27
Semi-natural (Disturbed, unmanaged)	235
Anthropogenic (Weed)	34
Anthropogenic (Ruderal)	90
Anthropogenic (Neophyte-dominated)	35

5 | OUTLOOK

The database of structural, ecological and biogeographical attributes of European vegetation alliances is the first comprehensive compilation of standardized data on European vegetation types. It provides information that was largely missing or provided inconsistently in EuroVegChecklist and other sources. The use of standardized variables and attributes makes it possible to query the database using a combination of different criteria to identify specific sets of alliances with similar structure, ecology and biogeography. Through the crosswalks between the EuroVegChecklist classification and EUNIS Habitat Classification (Chytrý et al., 2020), it can also help characterize European habitat types. Consequently, this database broadens the options for using the phytosociological classification system by researchers and practitioners and for students and non-specialists to learn and understand this system. In the future, it will be desirable to focus on collecting quantitative data on alliance attributes in a standardized manner to improve the current expert-based estimates with more reliable information.

AUTHOR CONTRIBUTIONS

Milan Chytrý conceived the idea. Zdenka Preislerová, Corrado Marcenò and Milan Chytrý prepared the draft list of variables and attributes and the first version of the database. Ondřej Hájek drew

the map. All the other authors commented on the previous versions of the variables/attributes and the database. Zdenka Preislerová, with contributions from Milan Chytrý, prepared the updated versions of the database. Milan Chytrý, with contributions from Zdenka Preislerová, wrote the text. All authors commented on the text and the database and approved the final version.

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DATA AVAILABILITY STATEMENT

The data set described in this article is published as Appendix S1. Future versions of this data set will be available online in the Download section of the FloraVeg.EU database (https://floraveg.eu/download/) and in the Zenodo repository (https://doi.org/10.5281/zenodo.10563021).

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SUPPORTING INFORMATION

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

Appendix S1. A database of structural, ecological and biogeographical attributes of European vegetation alliances in a spreadsheet format.

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