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VCS METHODS ECOINFORMATICS

Ecological Indicator Values for Europe (EIVE) 1.0

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Abstract

Aims: To develop a consistent ecological indicator value system for Europe for five of the main plant niche dimensions: soil moisture (M), soil nitrogen (N), soil reaction (R), light (L) and temperature (T). **Study area:** Europe (and closely adjacent regions). **Methods:** We identified 31 indicator value systems for vascular plants in Europe that contained assessments on at least one of the five aforementioned niche dimensions. We rescaled the indicator values of each dimension to a continuous scale, in which 0 represents the minimum and 10 the maximum value present in Europe. Taxon names were harmonised to the Euro+Med Plantbase. For each of the five dimensions, we calculated European values for niche position and niche width by combining the values from the individual EIV systems. Using T values as an example, we externally validated our European indicator values against the median of bioclimatic conditions for global occurrence data of the taxa. **Results:** In total, we derived European indicator values of niche position and niche width for 14,835 taxa (14,714 for M, 13,748 for N, 14,254 for R, 14,054 for L, 14,496 for T). Relating the obtained values for temperature niche position to the bioclimatic data of species yielded a higher correlation than any of the original EIV systems (r = 0.859). **The database:** The newly developed Ecological Indicator Values for Europe (EIVE) 1.0, together with all source systems, is available in a flexible, harmonised open access database. **Conclusions:** EIVE is the most comprehensive ecological indicator value system for European vascular plants to date. The uniform interval scales for niche position and niche width provide new possibilities for ecological and macroecological analyses of vegetation patterns. The developed workflow and documentation will facilitate the future release of updated and expanded versions of EIVE, which may for example include the addition of further taxonomic groups, additional niche dimensions, external validation or regionalisation.

Abbreviations: EIV = Ecological indicator value; EIVE = Ecological Indicator Values for Europe; EVA = European Vegetation Archive; GBIF = Global Biodiversity Information Facility; i = index for taxa; j = index for EIV systems; L = ecological indicator for light; M = ecological indicator for moisture; N = ecological indicator for nitrogen availability; R = ecological indicator for reaction; T = ecological indicator for temperature.

Keywords

bioindication, ecological indicator value, Ellenberg indicator value, Europe, light, moisture, niche position, niche width, nitrogen, pH, temperature, vascular plant

Introduction

Since the probability of species' occurrence changes predictably along environmental gradients, plant community composition holds valuable information about local environmental conditions. This basic notion, conceptualised as bioindication, has been a subject of research for a long time (see review by Diekmann 2003). In bioindication, individual plant species are assigned so-called ecological indicator values (EIVs) on ordinal scales based on the "optima" or "centres" of their realised ecological niches along given environmental gradients (niche dimensions) (Smart 2000; Diekmann 2003). "Realised niche" refers to the occurrence of species in plant communities under the influence of competition (or facilitation) of co-occurring species, as opposed to the "fundamental niche" describing the occurrence and performance in monoculture (Leibold 1995). In this paper, we use the term "niche position" to denote the central tendency of the distribution of a species even in the case of skewed or bimodal ecological niches. To assess the site conditions of a vegetation plot or a plant community, the EIVs of all species present in that plot or community can be averaged for each niche dimension of interest.

The idea of using the presence of plants to assess site conditions by qualitatively matching the most probable occurrence of plant species with environmental conditions was introduced to vegetation ecology by Cajander (1926) and Iversen (1936). Subsequently, Ellenberg (1950a, 1950b, 1952) introduced the first explicitly quantitative approach within an agricultural context. Comprehensive EIV systems for the vascular plants of larger territories were then independently proposed by Ramensky et al. (1956) for the European part of the former USSR and Ellenberg (1974) for Central Europe. Ramensky et al. (1956) published indicator values for grazing intensity, soil moisture and a combination of soil fertility and salinity, while Ellenberg (1974; new edition by Ellenberg et al. 1991) covered seven ecological variables: light regime, temperature, continentality, moisture, reaction (pH), nutrient status and soil salinity. The high utility of these indicator values led to an expansion to other regions, with more than 30 EIV systems being published so far (Table 1). Some of the more recent EIV systems not only expanded the approach to new regions, but also added other taxonomic groups (e.g. bryophytes, lichens), other niche dimensions (e.g. mowing tolerance, hemeroby, CSR strategy, organic content of the soil, soil texture) or assessed niche width in addition to niche position. Very recently, new systems with a focus on Europe as a whole have been published: Hájek et al. (2020) published niche position, minimum and maximum for hydrological parameters for a compre-

Table 1. Overview of the 31 ecological indicator value systems (EIVs) used to derive the Ecological Indicator Values for Europe (EIVE) 1.0. Further details are provided in Suppl. material 1.

EIVE name	Country or region	Reference(s)	# of vascular plant taxa	Habitat subset of species	M min	M max	M amplitude coding	N min	N max	N amplitude coding	R min	R max	R amplitude coding	L min	L max	L amplitude coding	T min	T max	T amplitude coding
Alps	Switzerland + entire Alps	Graf (unpubl.), updated and augmented from Landolt et al. (2010)	6470	All	1	5	I, II, x	1	5	I, II, x	1	5	I, II, x	1	5	I, II, x	1	5	I, II, x
Austria	Austria	Englisch and Karrer (unpubl.), updated and augmented from Englisch and Karrer (2001)	3253	All	1	12	I, x	1	9	I, x	1	9	I, x	1	9	I, II, x	1	9	I, x
Austria_Pannonian	Austria: wider surroundings of Vienna	Starmühlner and Ehrendorfer (1971)	954	All	1	6	range*	1	3	range*	1	5	range*	1	3	range*	1	3	range*
British_Isles	United Kingdom + Ireland	Hill et al. (2004)	1867	All	1	11	NA	1	9	NA	1	9	NA	1	9	NA	NA	NA	NA
Czech_Republic	Czech Republic	Chytrý et al. (2018)	2972	All	1	11	I, II	1	9	I, II	1	9	I, II	1	9	I, II	1	9	I, II
Czechoslovakia_Ambros	Czech Republic + Slovakia	Ambros (1986)	587	Forests	1	5	NA	NA	NA	NA	1	5	NA	1	5	NA	1	5	NA
Czechoslovakia_Jurko	Czech Republic + Slovakia	Jurko (1990)	2445	All	1	6	range**	1	5	range**	1	5	range**	NA	NA	NA	NA	NA	NA
Germany	Germany + adjacent regions	Ellenberg et al. (1991)	3405	All	1	11	I, II, x	1	9	I, II, x	1	9	I, II, x	1	9	I, II	1	9	I, II
Germany_Dierschke	Germany + adjacent regions	Dierschke and Briemle (2002)	399	Grasslands	1	11	I, x	1	9	I, x	1	9	I, x	NA	NA	NA	NA	NA	NA
Germany_GDR	Germany: former GDR	Frank and Klotz (1990)	1719	All	1	11	NA	1	9	NA	1	9	NA	1	9	NA	1	9	NA
Spain_Asturias	Spain: Asturias	Mayor López (1999)	1842	All	1	5	I, x	1	5	I, x	1	5	I, x	1	5	NA	1	5	I, x
Spain_Cantabria	Spain: Cantabrian Mountains	Jiménez-Alfaro et al. (2021)	1888	All	1	11	NA	1	9	NA	1	9	NA	1	9	NA	1	9	NA
European_Mires	Europe	Hájek et al. (2020)	1771	Mires	1	11	range	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Faroer	Faroe Islands	Lawesson et al. (2003)	126	All	1	11	I, x	1	9	I, x	1	9	I, x	NA	NA	NA	NA	NA	NA
France	France: European part	Julve (2022)	6166	All	1	11	NA	1	9	NA	1	9	NA	1	9	NA	1	9	NA
Georgia	Georgia: Kazbegi district	Nakhutsrishvili and Batastsahvili (unpubl.), updated and augmented from Sakhokia and Khutsishvili (1975) and Nakhutsrishvili et al. (2017)	1116	All	1	6	I, x	1	5	NA	1	5	NA	1	5	NA	1	5	NA
Greece	Greece: South Aegean region	Böhling et al. (2002)	2400	All	1	11	I, II, x	1	9	I, x	1	9	#, I, x	1	9	I, x	1	9	#, I, II
Hungary_Borhidi	Hungary	Borhidi (1995)	2088	All	1	11	NA	1	9	NA	1	9	NA	1	9	NA	0	8	NA
Hungary_Soo	Hungary	Soó (1980)	2159	All	1	5	I, x	1	5	I, x	1	5	I, x	NA	NA	NA	1	5	I, x
Hungary_Zolyomi	Hungary	Zólyomi et al. (1967)	1243	All	0	11	NA	NA	NA	NA	1	5	I, x	NA	NA	NA	1	7	I, x
Italy	Italy	Guarino (unpubl.), updated from Pignatti et al. (2005), Guarino et al. (2012), Domina et al. (2018) and Pignatti et al. (2017–2019)	5585	All	1	11	NA	1	9	NA	1	9	NA	1	9	NA	1	12	NA
Netherlands	Netherlands	Netherlands Central Bureau of Statistics (1993)	1570	All	1	11	NA	1	9	NA	1	9	NA	1	9	NA	1	9	NA
Poland	Poland	Zarzycki (1984), Zarzycki et al. (2002)	2209	All	1	6	range**	1	5	range	1	5	range**	1	5	range**	1	5	range**
Romania	Romania	Bita-Nicolae and Sanda (2011)	3620	All	1	6	NA	NA	NA	NA	1	5	NA	NA	NA	NA	1	5	NA
Serbia	Serbia	Kojić et al. (1997)	2215	All	1	6	NA	1	5	NA	1	5	NA	1	5	NA	1	5	NA
Sweden	Sweden	Tyler et al. (2021)	2422	All	1	12	NA	1	9	NA	1	8	NA	1	7	NA	18	1	NA
Sweden_Diekmann	Sweden: hemiboreal zone	Diekmann (1995)	34	Forests	1	11	I, x	NA	NA	NA	1	9	I, x	1	9	I, x	NA	NA	NA
Slovenia	Slovenia	Košir (1992)	683	Forests	1	11	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Ukraine	Ukraine	Didukh (unpubl.), updated from Didukh (2011)	3326	All	1	23	range	1	11	range	1	15	range	1	9	range	1	17	range
USSR_Ramensky	Former USSR	Ramensky et al. (1956)	1359	All	1	120	range	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
USSR_Tsyganov	Former USSR: hemiboreal zone	Tsyganov (1983)	2122	All	1	23	range	1	11	range	1	13	range	1	9	range	1	17	range

* In the source there are single values, ranges and "x", all of which are now unified to ranges in the logic of the source;

** In the source there are single values, intemediate values, ranges and bimodal distributions, which are now unified to ranges in the logic of the source.

hensive set of vascular plants and bryophytes occurring in mires, while Midolo et al. (2023) derived a set of five disturbance indicators for more than 6,000 European vascular plants. Recently, Tichý et al. (2023) presented a harmonized dataset of six of the original Ellenberg indicator values for almost 9,000 European vascular plant taxa.

Indicator values are widely applied in vegetation science and global change studies. They are suitable to indirectly assess environmental conditions and the drivers of observed vegetation differences in time or space (see review by Diekmann 2003). Several factors can explain the success of their application. First, environmental variables may fluctuate strongly in time and space (e.g. Sercu et al. 2017), making one-time measurements scarcely representative of average conditions or critically limiting extremes (Shipley et al. 2017). Thus, the appropriate assessment of environmental variables often requires repeated measurements (not feasible in many projects) or is costly if to be done across numerous plots. Additionally, measurements obtained at different times and with different techniques and equipment may not be directly comparable. In contrast, the plant species composition of a site is an expression of the species' responses to the prevailing environmental conditions integrated across the study area (e.g. a plot) over longer time periods (several months to several years). Therefore, bioindication using EIVs offers a less time-consuming and cheaper alternative to the direct measurement of local environmental variables (Englisch and Karrer 2001; Diekmann 2003; Didukh 2012; Zelený and Schaffers 2012; Marcenò and Guarino 2015). Finally, most historical vegetation data do not contain measurements of environmental data (Dengler et al. 2011). The ability to reconstruct past environmental conditions from historical relevés (Pignatti et al. 2001; Van Calster et al. 2007; Diekmann et al. 2019) or floristic occurrence data (Finderup Nielsen et al. 2021; Hallman et al. 2022; Scherrer et al. 2022) can thus be very valuable in assessing trends in environmental change and their effects on biodiversity.

However, the bioindication approach as such, and the wide use of EIVs, have also been criticised. One line of criticism holds that indicator values have been assigned to plant species mainly based on expert judgement, rather than on accurate measurements (Wamelink et al. 2002; Diekmann 2003). Secondly, although large regional differences in the niches of species have been demonstrated (Diekmann and Lawesson 1999; Pakeman et al. 2008), EIVs have often been applied outside the region for which they were developed (e.g. Hermy et al. 1999). This could potentially lead to misinterpretations (Godefroid and Dana 2007). Another line of critique has warned against averaging indicator values and subjecting them to parametric statistics, since they were defined on ordinal scales (e.g. Kowarik and Seidling 1989; Möller 1992). However, analysing mean EIVs does not lead to statistical issues, since the arithmetic means of values of any distribution *per se* follow a normal distribution (Central Limit Theorem; see Quinn and Keough 2002). Ewald (2003) demonstrated the robustness of the correlation of weighted mean of EIVs with environmental measurements, even when species lists were incomplete. Finally, the use of environmental information inferred from plant community composition to interpret vegetation patterns and dynamics has been criticised for potential circularity (Zelený and Schaffers 2012). However, these authors and Wildi (2016) demonstrated proper ways to use EIVs in vegetation ecological studies.

Recent trends in ecoinformatics opened opportunities for continental-scale studies of plant community data in Europe. Important developments were the emergence of large-scale vegetation-plot databases like the European Vegetation Archive (EVA; Chytrý et al. 2016) and GrassPlot (Dengler et al. 2018), a European vegetation classification system (EuroVegChecklist; Mucina et al. 2016) and an automated supervised habitat classification for vegetation plots in Europe (Chytrý et al. 2020; Bruelheide et al. 2021). Rapid environmental change over large regions increases the need to perform broad-scale analyses of changes and trends in community composition and environmental conditions (Kempel et al. 2020; Leclère et al. 2020; Hallman et al. 2022). However, most of the large European vegetation-plot databases (e.g. Chytrý et al. 2016) do not contain *in situ* measured environmental data, at least not in easily accessible forms (but see Dengler et al. 2018). Thus, such analyses have to rely on approximate site conditions derived via plot coordinates from modelled geodata (e.g. CHELSA: Karger et al. 2017; SoilGrids: Poggio et al. 2021), but such modelled data are available only for larger grid cells (e.g. 250 m × 250 m for SoilGrids), while soil conditions can change dramatically within metres. Mean EIVs can contribute to solving this challenge by easily linking the wealth of relevé data to abiotic conditions. Scherrer and Guisan (2019) showed that the application of mean EIVs instead of gridded environmental variables doubled the proportion of variance explained in species distribution models, with particularly strong improvements for light and soil conditions. However, the more than 30 national and regional EIV systems lack consistency in scaling and coding of the ecological indicators, as well as in plant nomenclature, impeding analyses at the continental scale. These issues have partly been solved by the recently published pan-European EIV systems (Hájek et al. 2020; Midolo et al. 2023; Tichý et al. 2023) but their coverage of indicators and taxa, respectively, is far from complete. Thus, there is still an urgent need for an integrated and comprehensive EIV system for Europe.

Here, we aim to fill this gap by developing the Ecological Indicator Values for Europe (EIVE), a pan-European ecological indicator value system for the five niche dimensions most often included in the existing EIV systems and most frequently used in ecological analyses. These are the three main substrate variables moisture (M), nitrogen (N) and reaction (R), as well as light (L) and temperature (T). We achieved this by numerically combining all available systems that contained these indicators into a "consensus system". In doing so, we also implemented several novelties that should facilitate the future application of EIVE: (i) all indicators were scaled from 0 to 10 on a continuous interval scale and (ii) for each indicator

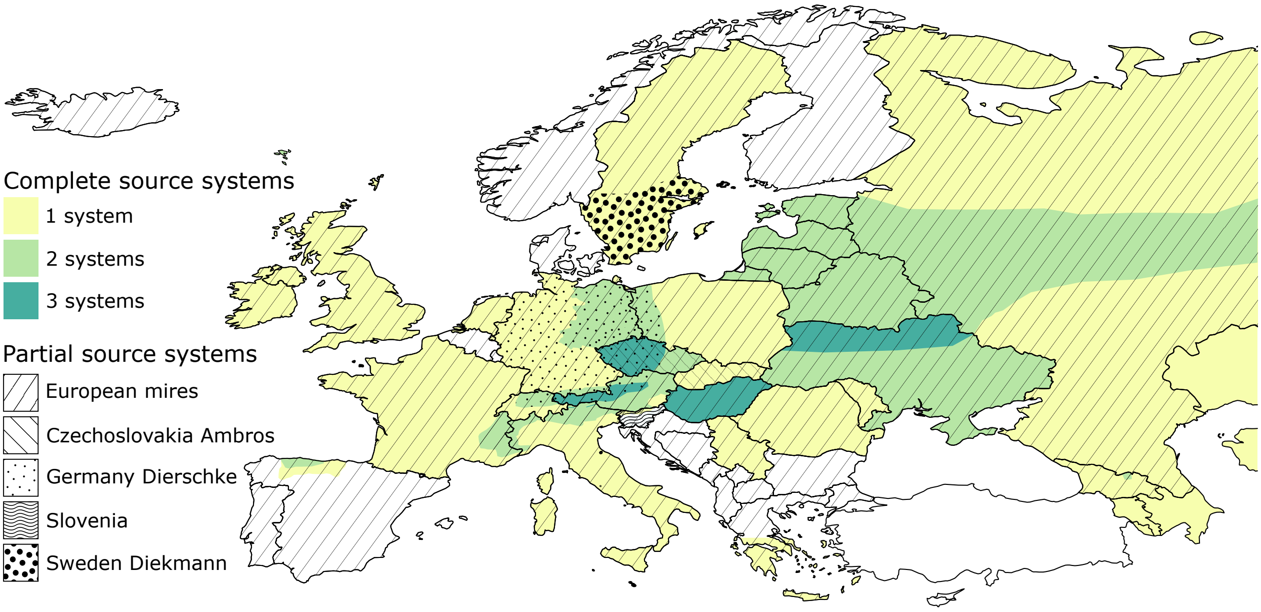

Figure 1. Map of Europe showing the areas covered by ecological indicator value (EIV) systems that were used to derive the Ecological Indicator Values for Europe (EIVE) 1.0. Colours indicate the number of EIV systems covering the complete vascular plant flora. Hatched and dotted areas refer to EIV systems that cover only a subset of specific habitats. Please note that for several EIV systems we could only approximate the geographic scope, as they did not provide a map or precise verbal description. Two EIV systems refer to very small areas that are hardly visible on the European map: the Faroe Islands and the Kazbegi region of Georgia.

we provide one value for niche position and one for niche width. In this paper, we describe the development of EIVE and release version 1.0 as an open access database to initiate a community-based approach for future updates and extensions.

Study area

Our study covers Europe as a whole in the geographic sense, i.e. from the Atlantic Ocean to the Ural and Caucasus Mountains. We also included Georgia, whose placement in either Europe or Asia is disputed, and kept the few species of the Asian part of the former Soviet Union that were included in Ramensky et al. (1956) and Tsyganov (1983). This means that according to Breckle (2002) the mediterranean (IV), oceanic (V), nemoral (VI), continental (VII), boreal (VIII) and arctic (IX) zonobiomes are included. However, given the availability of regional EIV systems (Figure 1), some regions of Europe are covered better than others.

Methods

Source EIV systems

We collected all indicator value systems known to us that contain assessments of plants regarding their niche position (and potentially also niche width) along ecological gradients on numerical scales. Of those, we used the 31 EIV systems that included indicator values of vascular plants for at least one of the five most frequent indicators, namely moisture (M), reaction (R), nitrogen (N), temperature (T) and light (L) (Table 1; further details in Suppl. material 1). We intentionally denote the N indicator as "nitrogen", not as "nutrients" as in some EIV systems. The reason is that existing tests of correlations of mean N EIVs with measured environmental variables mostly reported significant relationships with nitrogen-related measures (C/N ratio, potential N mineralisation) (Ellenberg et al. 1991; Ewald 2003). Moreover, Tyler et al. (2021) defined separate indicators for nitrogen and phosphorus.

If several editions of the same EIV system existed (e.g. Landolt 1977 and Landolt et al. 2010), we used the most recent digitally available version with comprehensive information. In case of multiple independent systems for the same region by different authors (e.g. three EIV systems for Hungary), we included all. In total, we had 31 source systems for M, 24 for N, 28 for R, 33 for L and 23 for T. In Suppl. material 2, we provide all EIV systems of vascular plants that we used with their original and harmonised plant nomenclature (see below) and their original and rescaled values (see below) for the five dimensions considered.

Harmonisation of plant taxonomy

We first split the **original taxon names** as they appeared in the 31 EIV systems into genus name, species epithet, infraspecific epithets, rank-indicating abbreviations (such as subsp., var., aggr.) and taxonomic authorities. Genus names and species epithets were searched for typos and rank-indicating abbreviations standardised to "sect.", "subg.", "aggr.", "subsp.", "nothosubsp.", "var." and "×". Additions like "sensu lato" and "sensu stricto" were retained at this step, but harmonised in spelling to "s. l." and "s. str." to support name interpretation in the following steps. Taxonomic authorities were disregarded, as there is a huge variety of spelling variants and they rarely aid in the discrimination of false vs. correct interpretations. This first step resulted in the assignment of a (preliminary) **harmonised original taxon name**.

In a second step, we retrieved the database underlying the Euro+Med Plantbase with accepted taxon names and all synonymy and parent-child relationships on 2022-03-21 (Euro+Med 2022). When a harmonised original taxon name (not considering s. l. and s. str.) matched an accepted Euro+Med name, this name was assigned as our preliminary **accepted name**; when it matched a synonym in Euro+Med (2022), we assigned it to the accepted Euro+Med name. All other harmonised original taxon names were treated as "unresolved" at this step.

Third, the numerous **"unresolved" names** were all checked by experts to pinpoint reasons for mismatching and treated according to one of the following rules: (a) if the spelling harmonisation of step (1) had failed for some reason, the R code was adjusted; (b) if the reason for the non-match was a typo, such as "*vemalis*" instead of "*vernalis*", an epithet erroneously starting with a capital letter or a name field containing also the synonym ("*Alchemilla baltica=nebulosa*"), the adjustments were made in the harmonised original taxon name; (c) if we, however, came to the conclusion that there was no spelling error, but the name was missing in Euro+Med (2022) completely (as either accepted or synonymic name), we defined additions to Euro+Med (2022).

Our additions fall into four categories and are comprehensively documented with explicit definition of content, taxonomic authorities and the source of the definition where applicable (Suppl. material 3):

(i) **Hybrids** (Suppl. material 3: table S3.1): All hybrids for which indicator values were given in at least one EIV system were accepted and defined by their parents. They were preferentially referred to by a binomen (or trinomen), and only if this was not available as a hybrid formula.

(ii) **"Aggregates"** (here used as a generic term to refer to any formal or informal taxon between species and genus rank; Suppl. material 3: table S3.2): As a basis, we accepted the few aggregates, collective species (coll.) and sections that were accepted in Euro+Med (2022). To these we added all aggregates that occurred in any of the EIV systems and those that are widely used in vegetation science (e.g. from Ehrendorfer 1973; Wisskirchen and Haeupler 1998; Juillerat et al. 2017). We additionally defined ad-hoc aggregates when taxa treated as subspecies in one of the EIV systems had been raised to species rank and, thus, there was no taxon concept available in Euro+Med (2022) to match the former polytypic species. Formal sections were given prevalence over informal aggregates; collective species and enumerations of taxa (e.g. "*Empetrum hermaphroditum + nigrum*") were replaced by aggregates. In cases where several different aggregates with different taxonomic extent had been defined for the same species in different sources, we defined aggregates s.l., with at least one member being an aggregate itself. In conclusion, we accepted four types of supraspecific taxa on three hierarchy levels: (1) aggregates (aggr.), (2) aggregates s.l. (aggr. s.l.) and sections (sect.) and (3) enumeration of sections (one case: *Rubus* sect. *Corylifolii* + *Rubus*). All of them were defined by listing their accepted member taxa of the next-lower rank.

(iii) **Other additional taxa** (Suppl. material 3: table S3.3): These belong mainly to three groups: (1) neophytes (of which only few are included in Euro+Med 2022), (2) recently described or locally endemic taxa not included in Euro+Med (2022) and (3) autonyms of polytypic species. The latter are cases where a taxon is treated as a species with several accepted subspecies in Euro+Med (2022), but the typical subspecies (the autonym) is missing for unknown reasons despite it is often the most widespread subspecies (e.g. *Anthyllis vulneraria* subsp. *vulneraria* and *Chenopodium album* subsp. *album*). Native European species not automatically matched to a Euro+Med taxon were only exceptionally accepted as separate taxa (these could be newly described species or local endemics); we generally rather assumed that these were included in the concept of an accepted Euro+Med taxon, but not included in its list of synonyms in Euro+Med (2022).

(iv) **Additional synonyms** (Suppl. material 3: table S3.4): This file documents all additional synonymic relationships not included in Euro+Med (2022), including those involving "aggregates".

When making additions, we strived for consistency with Euro+Med (2022), respecting the species and genus concepts adopted in this source. For example, the original hybrid taxon name *Chamaecytisus ×versicolor* in one of the EIV systems is treated as *Cytisus ×versicolor* because the genus *Chamaecytisus* in Euro+Med (2022) is included in the genus *Cytisus*. Therefore, this case led to entries both in the "additional synonyms" and the "hybrid definition" file. These four files with the taxonomic additions were used to expand the "taxonomic backbone" of Euro+Med (2022) to something that we call **"Euro+Med augmented"**.

Further, we identified cases in which the same taxon name has been applied to different taxa by different EIV systems. Often the same correctly applied name might refer to a concept of different width (subspecies vs. species, species vs. aggregate, aggregate vs. aggregate s.l.; see Jansen and Dengler 2010). Rather rare are cases of names that have been misapplied in a certain EIV system. When we identified such cases, we documented EIV-specific assignments of the names (**"concept synonyms"**; Suppl. material 3: table S3.5). These assignments were then used at the end of the taxonomic workflow to overrule the preliminary assignments of accepted names in these cases.

We ran the whole automated workflow repeatedly over all combinations of original name and EIV system until only a small number of **unresolved taxa** remained and there were no evident mis-assignments.

Preparation of indicator values from the source EIV systems

The 31 selected EIV systems were checked for entries that were not in accordance with their defined categories of the respective indicators and corrected if needed. Additional symbols, such as "~" for indication of fluctuating water table in the case of M, were removed. We merged indicator values for moisture if they were defined by different growth forms under identical habitat conditions, such as M = 11 and M = 12 in Ellenberg et al. (1991), where 11 means "growing in permanent water, with leaves at or above the water surface" and 12 "growing in permanent water, with leaves below the surface".

For those systems that characterised the niche with minimum and maximum instead of a single number for niche position, we took the arithmetic mean of these two values as the metric of niche position. In four EIV systems, certain taxa had multiple assessments of their relevant indicators (Suppl. material 1). In the case of the EIV systems "Austria" and "Hungary_Soo", which differentiated indicator values of woody taxa according to vegetation layer, we considered only the herb layer indicator. In the case of "USSR_Ramensky" and "Slovenia", which contained different assessments depending on vegetation zone or soil type, we averaged the values per species. If a taxon was given as being "indifferent" (e.g. by the symbol "x"), we took the average indicator value across all taxa in the relevant EIV system as the most plausible assessment of its niche position.

Next, we scaled the raw indicator values of each EIV system (*EIVori*) linearly to a range of 0 to 10, with the idea that 0 should represent the lowest possible and 10 the highest possible value of the respective environmental variable in Europe (Figure 2, step 1). We applied an expert rescaling in case of T and for the dry end of M, when the definitions of the individual EIV system suggested that only part of the full European gradient was covered. For example, in the case of T, this means that one must add three more levels to the classical scale of Ellenberg et al. (1991) to approximately reach the temperature conditions in the southern Mediterranean region, as proposed by Guarino et al. (2012). Likewise, Böhling et al. (2002) proposed that the driest sites in the southernmost Mediterranean areas are one level drier than the most xeric sites in Central Europe on the classical scale of Ellenberg et al. (1991). On the other hand, Böhling et al. (2002) assigned T = 1 to a mean annual temperature that roughly corresponds to the median of mean annual temperatures in Europe, not their minimum. Details of such adjusted "offsets" are documented in Suppl. material 1. By contrast, we assumed *a priori* that the scales in all source EIV systems cover the

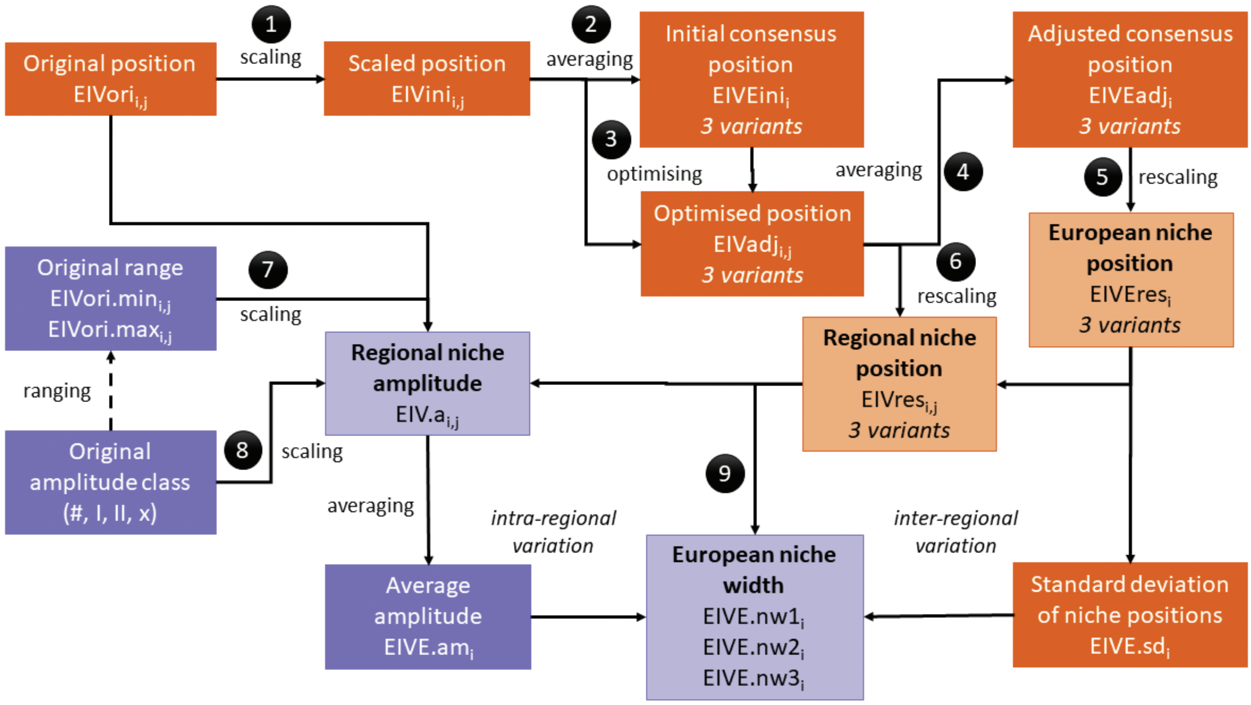

Figure 2. Methodological workflow of deriving EIVE as a consensus system of the 31 EIV input systems. Orange and blue boxes refer to niche position and amplitude/niche width metrics, respectively. White letters refer to input and intermediate metrics, black letters describe the definitive metrics of EIVE 1.0. Numbers denote the steps which are described in more detail in the text.

same ranges for the dimensions R, N, L and the wet end of M (but note that, in some EIV systems, the full range of defined values is not actually covered by taxa). With these considerations in mind, the initial EIV value (*EIVini*) of taxon i in the individual EIV system j was derived from the EIV value on the original scale (*EIVori*) as follows:

$$EIVini_{i,j} = EIVini.min_j + (EIVori_{i,j} - EIVini.min_j)\frac{EIVini.max_j - EIVini.min_j}{EIVori.max_j - EIVori.min_j}$$

with

$EIVori_{i,j}$ = original indicator value of taxon i in the respective EIV system j

$EIVini_{i,j}$ = indicator value scaled to a European range of 0 to 10

$EIVori.min_j$ = lowest number that is defined in the respective EIV system

$EIVori.max_j$ = highest number that is defined in the respective EIV system

$EIVini.min_j$ = lowest number scaled to the European range of 0 to 10

$EIVini.max_j$ = highest number scaled to the European range of 0 to 10

If an EIV system after our taxonomic harmonisation contained several taxa that correspond to the same taxon of “Euro+Med augmented”, we assigned the arithmetic mean of the indicator values to the latter. In cases of nested taxa (subspecies in species, species in aggregates) we derived EIV values for the superior level by averaging the EIV values of the member taxa of the next-lower level. This was only done if the taxon at the higher level did not have an EIV value assigned in the source.

Creating a consensus system of niche positions

To derive European values of niche position, we applied three different approaches to combine the scaled EIVs of all systems in which the respective taxon was included: (i) median; (ii) mean and (iii) weighted mean. With our “niche position” we aim to approximate the position on an ecological gradient which roughly separates equal halves of species occurrences. Therefore, niche position differs from realised niche optimum or mode (the environmental conditions under which a species is most frequent and/or reaches the highest cover values), particularly in the case of skewed or bimodal distributions. In the following, we describe the “mean” variant, while the analogous calculations for “median” and “weighted mean” are explained in Suppl. material 4.

The initial indicator value of a taxon i of the European consensus system (*EIVEini*) was derived as follows from the scaled values in the individual EIV systems (*EIVini*) (Figure 2, step 2):

$$EIVEini.m_i = \mathrm{mean}_j(EIVini_{i,j})$$

Using linear regression and correlation coefficients, we evaluated the results of *EIVEini* against all expert-scaled EIV systems (*EIVini*) for each of the five indicators (Suppl. material 5). While many regressions came close to the 1:1 line, most had a shallower slope (Suppl. material 5), meaning that the range of realised environmental conditions in a region was smaller than assumed in the expert-based scaling. Only in two cases (“Ukraine” and “USSR_Tsyganov” for M) the opposite was true (Suppl. material 5). We thus tried to remove the remaining major discrepancies in the concepts of the different EIV systems using an automated linear optimisation (Figure 2, step 3), with a_j and b_j being intercept and slope, respectively, of the regression *EIVEini* vs. *EIVini*. In this way, the values of both *EIVini* and *EIVEini* were iteratively adjusted.

$$EIVadj.m_{i,j} = a_j m_j + b_j m_j \cdot EIVini_{i,j}$$

This numerical procedure standardised all regression lines for *EIVEini* vs. *EIVadj* to lie exactly on the 1:1 line. Subsequently, we created a new consensus system *EIVEadj* from the *EIVadj* values (Figure 2, step 4):

$$EIVEadj.m_i = \mathrm{mean}_j(EIVadj_{i,j})$$

The resulting fit between *EIVEadj* and *EIVadj* was on average better (i.e. the slope was closer to 1) than between *EIVEini* and *EIVini* (Suppl. material 5). When we tried another round of iteration, this resulted in little to no further improvement. Thus, we retained *EIVEadj* for the remaining steps. However, the iteration generally caused a contraction, or very rarely an expansion, of the value range, so that *EIVEadj* did not cover the full intended range of 0 to 10 anymore. To remedy this, a final step of rescaling (Figure 2, step 5) was applied to *EIVEadj* to get *EIVEres* as the European indicator values of niche position:

$$EIVEres.m_i = 10\frac{EIVEadj.m_i - min(EIVEadj.m)}{max(EIVEadj.m) - min(EIVEadj.m}$$

The exact same rescaling was applied to *EIVadj* to get *EIVres* (Figure 2, step 6):

$$EIVres.m_{i,j} = 10\frac{EIVEadj.m_i - min(EIVEadj.m)}{max(EIVEadj.m) - min(EIVEadj.m)}$$

Deriving European niche width indicators

To establish a European indicator of niche width for each taxon in each of the five niche dimensions, we developed a separate workflow for the heterogeneous information in the various EIV systems. While some provided only a niche position, others provided niche width information as a range (minimum and maximum values) or as amplitude classes with two to four levels. If a source EIV system contained categorical niche amplitude information, we harmonised the coding. In Suppl. material 2, amplitude classes are stored as "#" for particularly narrow amplitude, "I" for normal amplitude, "II" for wide amplitude, but not indifferent, and "x" for "indifferent". We considered uncertain information (coded by smaller font in Ellenberg et al. 1991) for the purpose of calculating mean indicator values of a plot as equivalent to a wide amplitude (II).

For the further calculations, we chose the final outcomes of the EIVE niche position calculation, i.e. the rescaled values (*EIVEres*) of the best variant according to the external validation (see below). In EIV systems *j* with range-based niche width coding, we derived the amplitude of taxon *i* ($EIV.a_{i,j}$) as follows (Figure 2, step 7):

$$EIV.a_{i,j} = (EIVori.max_{i,j} - EIVori.min_{i,j}) \cdot \frac{max(EIVres_j) - min(EIVres_j)}{max(EIVori_j) - min(EIVori_j)}$$

If, for a certain taxon in a range-based system, minimum and maximum were the same ($EIVori.max_{i,j} = EIVori.min_{i,j}$), we assigned to $EIV.a_{i,j}$ half of the minimum non-zero amplitude that occurred for other taxa in this system to account for the fact that a niche width of zero does not exist. In case of EIV systems with categorical niche width coding, we assumed standard widths *w* for each of the four categories on the scale of 0 to 10, namely # → 1.25, I → 2.5, II → 5 and x → 7.5 (Figure 2, step 8). In absence of precise definitions (which was the case for most of the sources), we assume that these assignments should generally reflect the intended meaning of the authors, at least their relative relationships. The final amplitude of taxon *i* in EIV system *j* ($EIV.a_{i,j}$) was calculated as follows (note that here *EIVini* and not *EIVori* had to be used as starting point):

$$EIV.a_{i,j} = w\frac{max(EIVres_j) - min(EIVres_j)}{max(EIVini_j) - min(EIVini_j)}$$

To derive European indicators for niche width (Figure 3), we applied three different approaches to combine the rescaled niche position and niche width indicators of all EIV systems (Figure 2, step 9). They were constructed to meet the idea that the niche width at the European level is composed of intraregional and interregional variability in the niches. In the following, we describe the "nw3" variant, while the analogous calculations for "nw1" and "nw2" are explained in Suppl. material 4.

The nw3 indicator was calculated as the sum of the average amplitude of taxon *i* across EIV systems (intraregional variation) and twice the population standard deviation (σ) of the niche position (interregional variation), bounded to a maximum of 10:

$$EIVE.nw3_i = min\left(10, \overline{EIV.a_i} + 2\sigma(EIVres_i)\right)$$

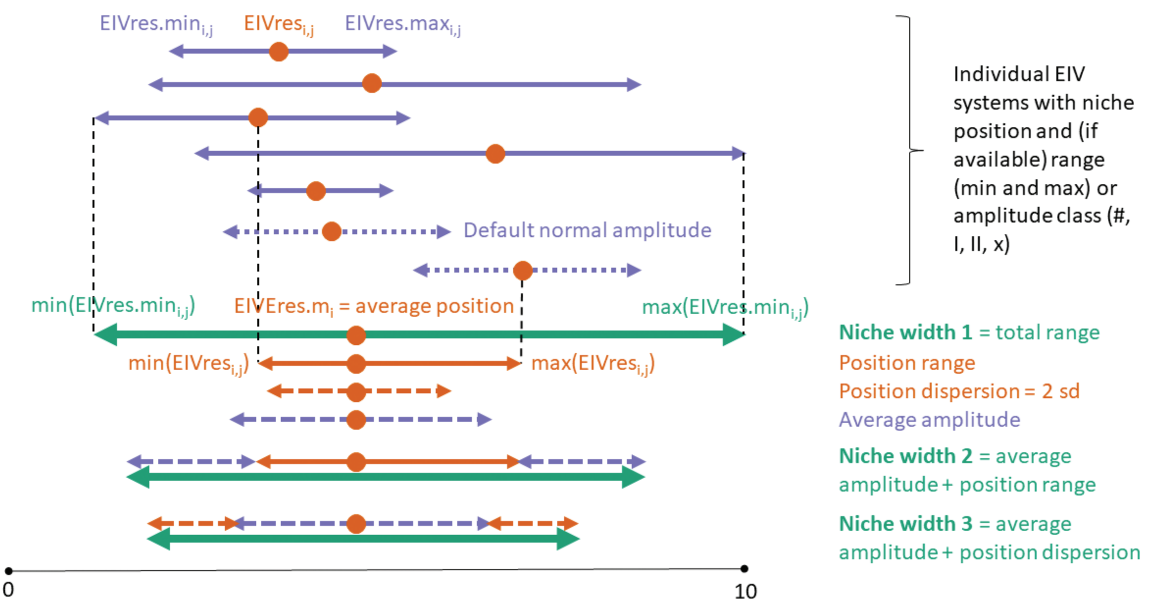

Figure 3. Combining interregional (based on niche position, red) and intraregional (based on niche amplitude, blue) information to derive a composite pan-European indicator of niche width (*EIVE.nw*, green), with three variants (grey). *EIVres* = regional ecological indicator value, rescaled, *EIVEres* = Ecological Indicator Value of Europe, rescaled.

Comparing EIVE temperature indicators with bioclimate

For one selected niche dimension, the temperature indicator, we validated our three consensus approaches for niche position calculation (median, mean and weighted mean) by comparing their results for species with the bioclimatic characteristics of these species globally. The T indicator was chosen since the temperature niche is relatively easy to calculate from readily available independent data. For this purpose, we correlated the T values of species (not considering other taxonomic ranks) with the temperature characteristics derived from their geographic distributions. These were retrieved from the Global Biodiversity Information Facility portal (GBIF 2022; Suppl. material 6) for 9,446 species (85% of the species in EIVE; if several EIVE species corresponded to the same GBIF species, they were not considered). The corresponding approx. 145 million distribution records were subsequently thinned to one coordinate per species and 30 arc second grid cell to reduce the bias of local oversampling. In addition, occurrences marked as managed in the GBIF database (field EstablishmentMeans) were not used for further analysis. From the remaining approx. 65.8 million coordinates, we extracted for each species nineteen bioclimatic variables from CHELSA V2.1 (Karger et al. 2017, 2021) with the same spatial resolution of 30 arc seconds and calculated the median of each variable. Out of all nineteen bioclimatic variables, the variable bio10, i.e. mean daily mean air temperature of the warmest quarter, showed the highest Pearson correlation with our EIVE-T values (in each of the three variants, see above). Subsequently, we compared the three variants to combine the rescaled individual EIV systems into a European consensus system with bio10 median values, defining the best-performing approach as EIVE 1.0. This system was then used for further comparisons, namely with the T values of the 23 source EIV systems that contained T. Moreover, we also compared EIVE 1.0 with the European T values recently proposed by Tichý et al. (2023). For all comparisons, Pearson correlations were calculated for the subset of species co-occurring in EIVE and the respective EIV system, and the most highly correlated bioclimatic variable was determined for both EIVE and the EIV system. For the evaluation of our three variants to calculate EIVE niche width, we used the same CHELSA bioclimatic data and GBIF coordinates but calculated the interquartile range (IQR) and the standard deviation of bio1 and bio10. The comparison of the EIVE temperature indicator with bioclimate was performed in R (R Core Team 2022) using the R packages rgbif (Chamberlain et al. 2023) and terra (Hijmans 2022).

Results

Data processing

After taxonomic harmonisation, the 31 source EIV systems contained between 34 (Sweden_Diekmann) and 6,470 (Alps) vascular plant taxa with at least one of the five niche dimensions assessed. The combined data comprised 77,795 rows of taxon name × EIV system combinations, corresponding to 14,835 accepted taxa: 22 sections, 60 aggregates s.l., 664 aggregates, 11,148 species, 2,899 subspecies and 42 varieties. Of these, 13,017 were from Euro+Med (2022) while 1,819 were EIVE additions to the taxonomic backbone. Only 22 (0.03%) of all taxon name × EIV system combinations remained unresolved for the time being, meaning that we did not decide whether they are separate taxa or synonyms of other taxa. The European consensus system of the five niche dimensions contains between 13,748 and 14,714 accepted taxa, with an average of 4 and more assessments underlying each EIVE value (Table 2).

Table 2. Accepted taxa, number of assessments (i.e. accepted taxa x EIV systems in which they were assessed) and mean number of assessments on which the consensus values in EIVE 1.0 was based.

Indicator	Accepted taxa	Assessments	Assessments / accepted taxa
M – Moisture	14,714	74,640	5.1
N – Nitrogen	13,748	60,120	4.4
R – Reaction	14,254	65,281	4.6
L – Light	14,054	59,547	4.2
T – Temperature	14,496	63,889	4.4

The iterative workflow to derive EIVE 1.0 clearly improved the congruence of the EIVE scaling to that of the individual EIV systems, as can be seen in an increase of the mean slope of the linear regressions from *EIVEini* vs. *EIVini* to *EIVEres* vs. *EIVres* (Suppl. material 5): the mean slope based on the mean variant for M improved from 0.872 to 0.878, for N from 0.756 to 0.775, for R from 0.709 to 0.722, for L from 0.755 to 0.761 and for T from 0.746 to 0.801 (Suppl. material 5: table S5.1). The iteration particularly brought those EIV systems closer to the 1:1 line that deviated strongest, as can be seen in the strong reduction of the absolute values of the extreme deviations to about one seventh to one half (columns "min diff." and "max. diff." in Suppl. material 5: table S5.1). The various steps of transformation (Figure 3) in most cases caused a contraction of the value ranges of individual EIV systems from *EIVini* to *EIVres* (after simple expert-based rescaling to 0…10; see Suppl. material 5).

Performance of the consensus systems

The Pearson correlation between EIVE-T values and median bio10 values was highest for the calculation variant "mean" (r = 0.859; see Figure 4) and showed minimally lower values for "median" (r = 0.857) and "weighted mean" (r = 0.857). Thus, we accepted the values of the consensus variant "mean" as the niche position indicators in EIVE 1.0 and used them for further comparisons with individual EIV systems. In addition to the bioclimatic

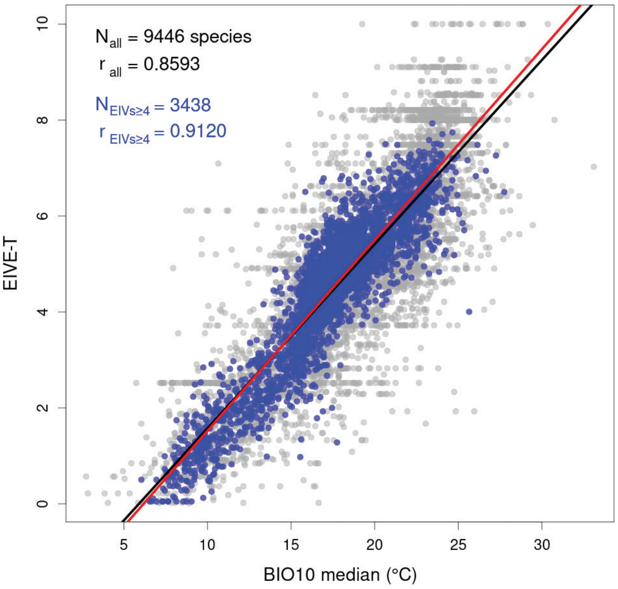

Figure 4. Scatter plot of the temperature indicator T of EIVE 1.0 (mean approach) and median values of the CHELSA bioclimatic variable bio10 (mean daily mean air temperatures of the warmest quarter) at GBIF coordinates of the species. The black line was fitted for all species by least squares linear regression. Species occurring in at least four EIV systems are displayed in blue and the fitted regression line for this species subset is shown in red. Species which were covered by less than four EIV systems are in grey.

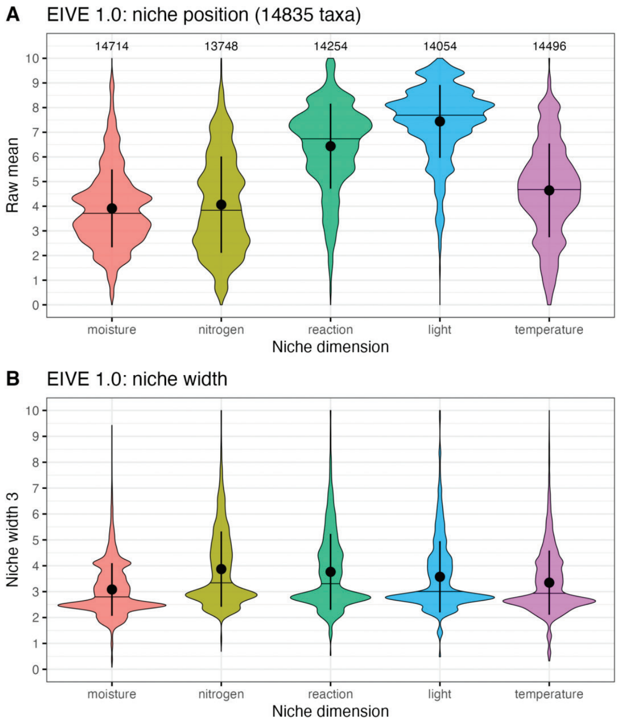

Figure 5. Niche position (A) and niche width (B) distribution of the five niche dimensions in EIVE 1.0. The figure refers to the accepted calculation variants, i.e. "mean" in the case of niche position and "nw3" in the case of niche width. Equal-area violin plots are displayed with median (horizontal line), mean (point) and standard deviation (vertical error bar). The number of taxa for each niche dimension is indicated at the top of the upper plot.

variable bio10, "mean annual air temperature" (bio1) was also frequently identified as the most highly correlated bioclimatic variable for the restricted species subsets "median" (r = 0.857) and "weighted mean" (r = 0.857). Only in two cases did the original EIV-T values show higher correlations with other bioclimatic variables: bio5, i.e. "mean daily maximum air temperature of the warmest month" for "Austria_Pannonian" and bio8, i.e. "mean daily mean air temperatures of the wettest quarter" in the case of "Greece". Correlations of EIVE-T were in general higher than those of both the EIV-T values of the original EIV systems and the European Ellenberg-type indicator values (Tichý et al. 2023) (Table 3).

The distribution of interregional niche width metrics (position range and position standard deviation) was very skewed, with many 0 values, whereas the distribution of intraregional metrics (average amplitude) showed multimodality. However, the three variants of composite niche width metrics showed a more homogeneous distribution (Suppl. material 7: figure S7.1). Therefore, we decided to choose one of these three composite metrics as consensus niche width. The first one ("nw1"), as the total range, generally had the highest values and was very sensitive to extreme position and amplitude values in some individual systems. The second one ("nw2") is partly based on position range and may also be strongly influenced by extreme position values. The third one ("nw3") generally had the lowest values and was less sensitive to extreme regional values. The Pearson correlation between EIVE-T niche width values and the standard deviation of bio1 and bio10 values was higher for variant "nw3" (r = 0.160 and 0.133, respectively) than for the variants "nw2" (r = 0.143 and 0.106) and "nw1" (r = 0.087 and 0.030) (Suppl. material 7: figure S7.2). Thus, we decided to retain "nw3", a composite niche width metric based on intraregional average amplitude and interregional dispersion of niche position, as the niche width indicator in EIVE 1.0.

Properties of EIVE 1.0

Per definition, the five EIVE indicators for niche positions cover the full range of 0 to 10. Plotting the number of plant species in the European species pool on the five niche dimensions revealed characteristic patterns (Figure 5a). EIVE-T showed an almost symmetric distribution of species centred around middle temperatures (EIVE-T ≈ 5), while the remaining four other indicators were asymmetrically distributed. The EIVE distribution was skewed towards higher values in case of EIVE-R and EIVE-L but towards lower values in case of EIVE-M and EIVE-N (Figure 5a). Given that the source EIV systems were all ordinal with mostly only a few categories, it is interesting

Table 3. Highest Pearson correlations between indicator values for temperature and the median values of 19 CHELSA bioclimatic variables extracted at species occurrences (GBIF), comparing the source EIV systems with T values and the Ellenberg-type indicator values by Tichý et al. (2023) with EIVE. For a fair comparison, the bioclimatic variables with the highest correlations were determined separately for both EIV and EIVE indicator values ("best"), and correlations for EIVE ("EIVE cor.") and the other EIV systems ("EIV cor.") were calculated for the same number of species ("Species") co-occurring in EIVE and the respective other system. For each comparison, the higher correlation is indicated in bold, and the difference of the correlations is reported (for naming of EIV systems, see Table 1; BIO1, BIO5, BIO8, BIO10 are CHELSA bioclimatic variables).

EIV system	Species	EIV based bioclimate selection				EIVE based bioclimate selection			
		best	EIV cor.	EIVE cor.	difference	best	EIV cor.	EIVE cor.	difference
Alps	4253	BIO10	0.8611	**0.8969**	+0.0358	BIO10	0.8611	**0.8969**	+0.0358
Austria	2291	BIO10	0.8649	**0.9152**	+0.0503	BIO10	0.8649	**0.9152**	+0.0503
Austria_Pannonian	835	BIO5	0.5945	**0.7864**	+0.1919	BIO10	0.5933	**0.7975**	+0.2042
Czech_Republic	2024	BIO10	0.7859	**0.8469**	+0.0610	BIO10	0.7859	**0.8469**	+0.0610
Czechoslovakia_Ambros	364	BIO10	0.7157	**0.8798**	+0.1641	BIO10	0.7157	**0.8798**	+0.1641
France	3171	BIO1	0.8028	**0.8756**	+0.0728	BIO1	0.8028	**0.8756**	+0.0728
Georgia	897	BIO1	0.3603	**0.6994**	+0.3391	BIO1	0.3603	**0.6994**	+0.3391
Germany	2561	BIO10	0.8473	**0.9014**	+0.0541	BIO10	0.8473	**0.9014**	+0.0541
Germany_GDR	1089	BIO10	0.6982	**0.8084**	+0.1102	BIO10	0.6982	**0.8084**	+0.1102
Greece	1906	BIO8	**0.5801**	0.3972	-0.1829	BIO1	0.5067	**0.8249**	+0.3182
Hungary_Borhidi	1844	BIO10	0.704	**0.7914**	+0.0874	BIO10	0.704	**0.7914**	+0.0874
Hungary_Soo	1825	BIO10	0.5936	**0.7991**	+0.2055	BIO10	0.5936	**0.7991**	+0.2055
Hungary_Zolyomi	1038	BIO10	0.6176	**0.8139**	+0.1963	BIO10	0.6176	**0.8139**	+0.1963
Italy	4718	BIO1	0.8304	**0.8916**	+0.0612	BIO1	0.8304	**0.8916**	+0.0612
Netherlands	1128	BIO10	0.5837	**0.7583**	+0.1746	BIO1	0.5457	**0.7619**	+0.2162
Poland	1874	BIO10	0.7943	**0.9042**	+0.1099	BIO10	0.7943	**0.9042**	+0.1099
Romania	2856	BIO10	0.7225	**0.8610**	+0.1385	BIO10	0.7225	**0.8610**	+0.1385
Serbia	1947	BIO10	0.7114	**0.8622**	+0.1508	BIO10	0.7114	**0.8622**	+0.1508
Spain_Asturias	1596	BIO10	0.7091	**0.8634**	+0.1543	BIO1	0.7013	**0.8700**	+0.1687
Spain_Cantabria	1641	BIO1	0.5599	**0.8623**	+0.3024	BIO1	0.5599	**0.8623**	+0.3024
Sweden	2035	BIO1	0.8789	**0.8811**	+0.0022	BIO1	0.8789	**0.8811**	+0.0022
Ukraine	2520	BIO1	0.7731	**0.8231**	+0.0500	BIO10	0.7528	**0.8506**	+0.0978
USSR_Tsyganov	1815	BIO1	0.7187	**0.7665**	+0.0478	BIO10	0.7132	**0.8078**	+0.0946
Tichý et al. (2023)	6160	BIO1	0.8752	**0.8839**	+0.0087	BIO10	0.8516	**0.8862**	+0.0346

that the resulting value distribution of the EIVE indicators was rather smooth, as would be expected for an interval-scaled variable. Only EIVE-M had two main modes at 3.3 and 4.3, while EIVE-L had a main mode at 8.2 and a subordinate mode at 9.5, but even in these cases the modes were not clearly separated.

The selected EIVE niche width measure based on both intra- and interregional variation showed remarkably similar patterns across the five niche dimensions (Figure 5b). All distributions were strongly skewed towards narrow niche width, with a pronounced main mode of the value distribution somewhere between 2.5 and 2.9 (Figure 5b). The potential value range up to 10 was (almost) covered only by a small number of taxa in all indicators. The mean EIVEnw values were lowest for moisture (3.2) and highest for nitrogen and reaction (3.8). The value distribution was smooth, as would be expected for an interval-scaled variable. Only EIVEnw-M had a subordinate mode at 4.2 in addition to the main mode at 2.5 (Figure 5b).

Database

The main part of the EIVE 1.0 database is a table with (1) the accepted taxon names, (2) the taxon rank, (3) the source of the taxon concept (Euro+Med, EIVE addition, unresolved) and then for each of the five niche dimensions (M, N, R, L, T) (4) the niche position value (e.g. EIVE-M for moisture), (5) the niche width indicator (e.g. EIVE-M.nw) and (6) the number of source EIV systems on which the consensus values were based (EIVE-M.n) (Suppl. material 8). Further, we provide all source EIV systems with their original and harmonised taxon names and the corresponding name in our taxonomic backbone, together with the original and rescaled niche position and, where available, niche width information (Suppl. material 2). Finally, our documentation of all taxonomic deviations from Euro+Med (2022) forms part of the database (Suppl. material 3).

In addition to the online appendix of this paper, the EIVE 1.0 database is available at https://zenodo.org/record/7534792. The R code to derive EIVE from the source files and to produce the figures and statistics of this papers is available upon request from F.J. A source file to be used for the calculation of mean EIVEs in the software JUICE (Tichý 2002) is provided at: https://www.sci.muni.cz/botany/juice/?idm=10. An interactive tool to compare regional EIVs with the European variants for niche position and niche width is available as a Shiny App at https://data.loe.auf.uni-rostock.de/EIVE.

Discussion

Content of EIVE 1.0

EIVE 1.0 provides assessments of ecological niche position and niche width for a total of 14,835 vascular plant taxa, including 11,148 at species rank. In terms of taxa covered, EIVE 1.0 is thus the most comprehensive ecological indicator value system published so far. In comparison, the most extensive source system of EIVE, Landolt et al. (2010), contains 6,471 vascular plant taxa. Compared to the supranational Ellenberg-type indicator values developed in parallel by Tichý et al. (2023) with 8,908 accepted vascular plant taxa, EIVE has a 67% larger coverage (Table 4). While the exact number of vascular plant taxa occurring in Europe in the geographic sense is not known, we judge that a majority are included in EIVE 1.0, as we combined many national and regional EIV systems, most of them aiming at comprehensive coverage of the vascular plant flora of their focal territory. In comparison, Flora Europaea (Tutin et al. 1964–1980) enumerated 11,557 accepted species in Europe (but this number excludes most neophytes and any species described after the publication). Moreover, most of the countries lacking a dedicated EIV system host very few species that do not occur in neighbouring countries (e.g. Iceland, Norway, Finland, Denmark). We expect areas with non-negligible fractions of missing taxa to be concentrated in Mediterranean Iberia and the Balkan Peninsula.

We decided to include five indicators in EIVE 1.0, namely the three soil-related indicators, moisture, nitrogen and reaction, as well as light and temperature. We selected these five because – apart from continentality and salinity – they have the highest coverage in the 31 available EIV systems addressing multiple particularly important dimensions of the ecological niches of plants at the same time. Continentality and salinity could be calculated with our approach relatively easily. However, we refrained from this step for the time being because we believe that, in their current form, these two indicators would not be compatible with the rest of the system. For continentality, Berg et al. (2017) highlighted the challenges of the current assessments and proposed an alternative approach, although this is not yet available for a large fraction of the European vascular plant flora.

The majority of the source EIV systems had no information on niche width (e.g. Ambros 1986; Frank and Klotz 1990; Hill et al. 2004; Julve 2022), or distinguished only between species with definitive indicator values and "indifferent" species (e.g. Zólyomi et al. 1967; Mayor López 1999) (Table 1). However, a considerable number of EIV systems did actually provide information on niche amplitudes by explicitly listing minima and maxima on the niche axes (e.g. Ramensky et al. 1956; Tsyganov 1983; Didukh 2011; Hájek et al. 2020) or systematic coding of three or four niche-width categories (Böhling et al. 2002; Landolt et al. 2010). However, EIVE is the first indicator value system to provide a systematic and consistent assessment of niche width. Interestingly, our calculation approach "nw3" performed best in terms of external validation for the temperature niche axis. This might be explained by the fact that using twice the standard deviation instead of the total range of niche positions across EIV systems (as in "nw1" and "nw2") suppresses extreme outliers, which could be typos in the source systems (e.g. EIV-L = 9 for *Abies alba* on the 9-step scale in Frank and Klotz 1990). In addition to niche position, niche width is the second main parameter to describe an ecological niche, thus making the characterisation of the ecological behaviour of species more comprehensive. Beyond that, we predict that by taking niche width into account when calculating mean ecological indicator values, one could improve prediction at the plot scale. In the past, this has often been attempted using a yes/no approach, i.e. disregarding species with the widest niches (those assessed as indifferent or "x"), but we judge that a weighting approach accounting for continuous variation in niche width will improve predictions. There is hardly any

Table 4. Major differences between the two new ecological indicator value systems for Europe.

Criterion	Tichý et al. (2023)	EIVE 1.0 (this paper)
Geographic coverage	Focus on temperate Europe plus Italy; coverage varying between indicators	Europe as a whole (in the geographic sense), extending slightly to adjacent areas
Regional EIV systems used	12 (only those directly compatible with the original Ellenberg scales)	31
Number of accepted taxa	8,908*	14,835
Number of species	8,679*	11,148
Treatment of infraspecific taxa	No	Yes, as far as accepted in Euro+Med (2022)
Indicators included	M, N, R, S, L, T	M, N, R, L, T
Scaling of indicators	Mostly 1–9, but M and T 1–12 and S 0–9	All 0–10
Values of indicators	Interval scale, but prevalence of integers	Interval scale
Handling of indicator values that do not reflect the ecological niche but growth form or physiological niches	Maintained as in Ellenberg et al. (1991)	M values that differed only in growth form (such as 11 and 12 in Ellenberg et al. 1991) were merged
Coding of niche width	Not available	Available for all indicator values and all species on an interval scale
Calculation of European indicator values	Mean of included EIV systems	Mean of all available EIV systems after rescaling to the common 0-10 scale
Use of species co-occurrence data from the European Vegetation Archive (EVA)	EVA was used to add 431 species not covered in any of the included EIV systems	Not used

* According to M. Chytrý (pers. comm.) the number of 8,908 "species" given in Tichý et al. (2023) actually does not mean species but accepted taxa including aggregates.

experience on how such a weighting approach could best be applied, but Hájek et al. (2020) recently showed that it generally improves prediction. Hence, the niche width values reported in EIVE have potential to improve plot-level weighting of indicator values in the future.

Taxonomic scope and concepts

We decided to follow the nomenclature and taxonomic concepts of the Euro+Med PlantBase (Euro+Med 2022) as much as possible, as this was considered the most complete and authoritative taxonomic database covering all of Europe. However, most of our sources were based on national and older taxonomic references. Many discrepancies could be corrected automatically with our R code based on the lists of synonymous names included in the Euro+Med database. However, some species (mostly neophytes and hybrids) found in our source lists were absent from Euro+Med (2022) and thus had to be added manually using other sources. Such handling may introduce errors, but all of the taxa we added are fully documented (Suppl. material 3) and may thus easily be reassigned in future versions of EIVE if errors are encountered and reported.

Combining the EIVs of lower-rank taxa to obtain EIVs for species or species aggregates is another issue that may warrant some more work in future versions of EIVE, and which may be greatly facilitated by expected future results of ongoing projects such as the "Atlas Florae Europaeae" (Jalas and Suominen 1972 et seq.). Ideally, EIVs for such aggregates, as well as for species comprising several subspecific taxa, should consider the relative geographic range and population size of the different included subordinate taxa, but since such sufficiently detailed and authoritative information is currently not available for all taxa, we decided to calculate EIVs for taxa of higher rank by simply averaging niche positions across all subordinate taxa. Although this method is admittedly suboptimal, it is simple and transparent, and it does not introduce any hidden errors caused by faulty biogeographic information. When considered appropriate for particular purposes (e.g. regional studies), the EIVs for these aggregate taxa can easily be re-calculated by individual users from the EIVs we provide for subordinate taxa. Furthermore, we only applied the aggregation when the source EIV system did not provide EIVs for the higher level itself.

Instead of aiming at an unachievable "perfect" taxonomic backbone, we developed decent and well-documented solution. With only 0.03% "unresolved" combinations of original taxon name × EIV systems, our rate is almost surely lower than that of pure taxonomic databases, such as Euro+Med (2022) or WFO (2022). We also worked intensively on concept synonymy (Jansen and Dengler 2010), i.e. cases where the exactly same name refers to a different taxonomic content in different EIV systems. While typical taxonomic matching software is not able to address this crucial point, our experts overwrote the automatic assignments with their expertise for 1,413 original taxon name × EIV system combinations (Suppl. material 3: table S3.5), leading to a content-wise much better match. While such a work essentially never can be completed, our documentation facilitates the detection of errors and inconsistencies by users, who are welcome to report such issues to the lead author for taxonomy (J.D.). In the forthcoming releases of EIVE, such issues can then be easily updated in our automated workflow in parallel to a continuous adjustment to up-to-date taxonomic concepts in Europe.

Performance of EIVE 1.0

While it was beyond the scope of this paper to test the prediction accuracy of mean indicator values based on EIVE 1.0 for specific environmental variables, our exemplary validation using the temperature indicator showed a strong positive correlation between EIVE-T values and independent estimates of the temperature niche based on CHELSA bioclimate variables and GBIF occurrence records. Moreover, the correlation between our EIVE-T and bio10 or bio1 median values turned out to be better than that of any of the original EIV systems, albeit only slightly better than the system of Tichý et al. (2023), which also covers large parts of Europe (but was based on only six source systems for T, compared to 23 in the case of EIVE 1.0). The superior correlation of our combined system might be unexpected at first glance, given the fact that ecological responses of species can shift along geographic gradients and regional indicator values may thus be expected to capture the regional species' preferences better. While this pattern needs to be confirmed by testing the correlations of mean EIVE vs. mean EIV values against measured environmental factors of vegetation plots in regional contexts, a test doing so with a "beta version" of EIVE, based on a much smaller number of source EIV systems than EIVE 1.0, found indeed a superiority of the EIVE approach over the regional EIV system in the majority of datasets with measured soil variables (volumetric water content, C/N ratio and pH in H_2O; Moeys 2020).

One explanation for the good performance of EIVE might be that each of the included EIV systems is best understood as a single expert assessment, and every expert necessarily over- or underestimates niche positions of many species equivalent to "random measurement errors". The more such independent assessments are combined, the closer they should get to reality, which is supported in our comparison (Figure 4) by a higher correlation for species occurring in at least four lists (r = 0.912 compared to the overall correlation r = 0.859). This effect might also explain why a combination of 23 systems (EIVE-T 1.0) performed better than that of only six systems (Tichý et al. 2023). Another explanation could be that by combining EIVs from a larger part of the geographic range of a species, we obtain a better estimate of the niche of the species as a whole, at least for temperature. While clearly advantageous for studies at broad geographic scales, the latter possible explanation may suggest that the regional EIV systems may still perform better within their individual geographic ranges. However, determining whether and when this is the case will require extensive testing (but see Moeys 2020).

Limitations of EIVE 1.0

We present a mathematically derived combination or "consensus system" of 31 individual EIV systems. One could thus argue that we are inheriting the limitations of the regional EIV systems, mainly being based on expert assessments rather than on statistical analyses of *in situ* measured environmental variables. While it was beyond the scope of this article to conduct comprehensive tests against measured environmental variables at the European scale, the often-demonstrated close relationship between mean regional EIVs and measured environmental variables (Ellenberg et al. 1991; Schaffers and Sýkora 2000; Ewald 2003; Lawesson 2003; Wamelink et al. 2022) and the indications that EIVE performs at least as well as the existing EIV systems (Moeys 2020; Table 3) support the general validity of the approach.

Another limitation of EIVE is that, given the unequal spatial distribution of source EIV systems (Figure 1), the suitability and validity of EIVE will likely vary between regions. On the one hand, Figure 4 suggests that EIVE indicator values become more reliable if they are based on more source EIV systems. On the other hand, it is likely that in certain parts of Europe the average fraction of species per plot that have assigned values in EIVE 1.0 will be lower, and thus the predictions based on mean EIVE values might be less reliable (Ewald 2003). This potential limitation should mainly affect the Mediterranean parts of the Iberian Peninsula and the central parts of the Balkan Peninsula.

Lastly, while we are expanding the characterisation of the ecological niche of species to two parameters per niche dimension, i.e. niche position and niche width, and thus go beyond the majority of existing EIV systems, one could still consider this too simplistic. While these two parameters can be statistically defined for species response curves along environmental gradients of any shape, they provide incomplete descriptions in case of skewed or bimodal distributions (Jansen and Oksanen 2013). Since the EIV source systems practically never contained more precise information on response curves (except very rare cases that indicated bimodality), our consensus approach did not allow to derive such information for EIVE 1.0 (but see below for future plans).

Potential of EIVE 1.0

The main motivation for the creation of EIVE was the demand to have plot-based assessments of environmental conditions carry a broader set of meaningful predictors in macroecological studies of vegetation plots. Since the largest vegetation-plot databases globally, EVA (Chytrý et al. 2016) and sPlot (Bruelheide et al. 2019), do not provide *in situ* measured environmental variables (except slope aspect, inclination and elevation), researchers were hitherto forced to find "work-arounds". The main approach was to use modelled environmental data for grid cells. This is well-established for climate data, e.g. WorldClim (Fick and Hijmans 2017) and CHELSA (Karger et al. 2017), but less developed and explored for other environmental variables, some of which may be expected to show more local variation. Therefore, the majority of continental-scale studies of vegetation in Europe, be it macroecological studies (e.g. Thuiller et al. 2005; Boonman et al. 2021; Dembicz et al. 2021) or characterisation of vegetation units (e.g. Marcenò et al 2018, 2019; Bonari et al 2021) restricted themselves to coarsely gridded climate data, despite extensive knowledge that soil variables and disturbance regime are at least as decisive in shaping plant community composition. In one of the few attempts thus far to include gridded data of other environmental variables in a broad-scale analysis of vegetation-plot data, such as soil properties, Bruelheide et al. (2018) found a very low predictive power. This was probably driven by the fact that the global or continental geodatasets have modelled, not measured variables, and they are provided at resolutions of ca. 1 km for climate (Karger et al. 2017; but see Haesen et al. 2021) and 250 m for soil variables (Poggio et al. 2021), while microclimate (Pincebourde and Salle 2020) and soil conditions (Sercu et al. 2017) can change drastically within a few metres. Thus, EIVE can support the development of better models of vegetation properties – such as species richness or species composition – in Europe and might motivate vegetation ecologists on other continents to develop similar systems. As recently shown by Scherrer and Guisan (2019) in a regional context, the predictive power of species distribution models improved considerably when fed with mean plot-based EIVs vs. modelled gridded environmental variables.

While the usefulness of EIVE at the continental scale is evident, EIVEcan also be meaningful for local to national studies. Despite the fact that we found 31 EIV systems for this study, country-specific EIV systems are still missing for most European countries. For some EIV systems, such as Poland (Zarzycki et al. 2002) and Slovenia (Košir 1992), the complexity of the coding/symbology largely prevented automated use for calculation of mean indicator values and, thus, researchers tended to prefer EIV systems from neighbouring areas. Here, EIVE offers two solutions: one can either use the European EIVE indicators or use the regional EIV indicators in their harmonised and ready-to-use editions also provided in the EIVE database (Suppl. material 2).

This taxonomic "backbone" is another central feature of EIVE and is provided open access to facilitate further improvements in a well-documented manner. While the EIVE backbone for vascular plants is based on Euro+Med (2022), the most comprehensive and up-to-date European checklist currently available, it aims to overcome some shortcomings of the current Euro+Med Plantbase with the addition of taxa that are regularly recorded by vegetation ecologists. The most important are (a) formal and informal taxa between species and genus level (aggregates and sections), (b) hybrids and (c) neophytes. Beyond that, we also aimed at solving some apparent mistakes in Euro+Med (2022), e.g. when one aggregate member was not assigned to an aggregate or when the typical subspecies (autonym) was not listed despite Euro+Med (2022) ostensibly considering the species as polytypic, containing several other subspecies. We even implemented a solution for cases where the same name refers to different taxonomic concepts in different EIV systems or countries, namely taxa of different width (see Jansen and Dengler 2010). In fact, we now provide something that comes close to what Dengler et al. (2012) proposed under the name "EuroSL". There have been previous attempts to address the multitude of different names and taxonomic concepts of European plants in ways that can be incorporated into automated workflows, e.g. in JUICE (Tichý 2002) or R. Most prominently, Chytrý et al. (2020) presented a system that allows aggregating different taxon names into higher units within EUNIS-ESy, an expert system for the determination of habitat types from the species composition of vegetation plots. This system is now increasingly applied in European vegetation studies, including the European Ellenberg-type indicator values by Tichý et al. (2023). The advantage of this system is that it interprets individual names in a national or regional context, considering how they were largely used in vegetation sampling. However, this system does not differentiate between synonyms, subordinate taxa, taxon concepts of different width, misapplied names and typos. In contrast, our system separates all these different cases and documents them. We suggest that it can be used in European projects independent from the indicator values and, in combination with the regionally interpreted taxon names from the EUNIS-ESy, might help the big European vegetation-plot databases such as EVA (Chytrý et al. 2016) and GrassPlot (Dengler et al. 2018) to provide their content in a more harmonised way in the future. Our documented additions to Euro+Med (2022) are also an invitation to the team of the Euro+Med Plantbase to incorporate these taxa or a subset of these directly in future releases of their database.

Future plans for EIVE

With this publication, the first version (1.0) of the Ecological Indicator Values for Europe is released. At the same time, this is the start of an open-ended, community-based endeavour that calls for continuous future updates. All raw data and derived data of EIVE are published open access with a CC BY 4.0 licence, while the R code is available upon request, meaning that everyone is free to use, modify or expand the current system as long as proper credit is given to this publication. We plan to launch a website to host all these materials, possibly within the framework of the European Vegetation Survey (http://euroveg.org/). While everybody is free to develop new systems based on EIVE 1.0, we plan to establish a committee whose responsibility will be to release future official versions of EIVE. Here, we envisage a workflow similar to the EVC Committee (http://euroveg.org/evc-committee) that releases official modifications of the EuroVegChecklist (Mucina et al. 2016) once they are approved by a majority (e.g. Biurrun and Willner 2020).

A first and self-evident step is to expand the current consensus system to additional taxonomic groups and additional indicators. Non-vascular taxa in the vegetation are known to often be particularly sensitive to environmental conditions and thus suitable for bioindication (Cislaghi and Nimis 1997; Kirschbaum and Wirth 1997; Frahm 2001). Accordingly, terricolous bryophytes and lichens are included in several of the EIV systems used here (Ramensky et al. 1956; Tsyganov 1983; Ellenberg et al. 1991; Hill et al. 2004; Landolt et al. 2010; Didukh 2011; Hájek et al. 2020). In addition to these two groups, Julve (2020) also covers *Charophyceae*. Moreover, there are also specific EIV systems for bryophytes (Dierßen 2001; Simmel et al. 2021) and lichens (Wirth 2010; Dingová Košuthová and Šibík 2013). Obvious candidates for additional ecological indicators are salinity (S) and continentality (C). Other potentially useful niche dimensions contained in one or several EIV systems and thus essentially accessible with our approach to derive a European consensus system are moisture variability (Ramensky et al. 1956; Tsyganov 1983; Landolt et al. 2010; Didukh 2011), soil phosphorus (Tyler et al. 2021), heavy metals in soil (Ellenberg et al. 1991; Landolt et al. 2010), soil humus content (Landolt et al. 2010), soil aeration (Landolt et al. 2010; Didukh 2011), air humidity (Tsyganov 1983; Didukh 2011), cryoclimate (Didukh 2011), snow layer duration (Odland and Munkejord 2008), mowing or grazing intensity (Dierschke and Briemle 2002; Landolt et al. 2010; Tyler et al. 2021), anthropogenic influence (or hemeroby) (Frank and Klotz 1990; Landolt et al. 2010) and CSR strategy (Frank and Klotz 1990; Thompson et al. 1993; Landolt et al. 2010).

A second step would be to use the compositional data of the nearly two million vegetation plots from the European Vegetation Archive (EVA; Chytrý et al. 2016), combined with reciprocal averaging (e.g. Hill et al. 2000) or a similar technique (Tichý et al. 2023), to increase the internal consistency of the current EIVE version and to add new taxa from EVA that are not included in any of the regional EIV systems. Combining EIVE with EVA would also allow the connection of *ad hoc* metrics of niche position and niche width to concrete statistical definitions. Further, other attributes of the ecological niches of species, such as minimum, maximum, skewness or bimodality could be determined systematically. It would even be possible to derive complete response curves for each species along each niche dimension, allowing for the ecological characterisation of a site not by averaging the EIVs of the occurring species, but by multiplying these probability curves.

While for pan-European analyses, a single set of continent-wide indicator values appears to be the most practical solution, it should be acknowledged that the ecological niches of species do change across large geographic distances. Some species might change their niche position (Diekmann 1995; Goedecke et al. 2019), while others decrease (Šilc et al. 2014) or increase their niche width from the centre to the margins of their distributional range (unpubl. observ. J.D.: various species appear to have a wider R niche in the hemiboreal than in the nemoral zone). However, up to now, there has been only limited empirical evidence and vague theoretical expectations regarding the changes of ecological niches of species along geographic gradients. Here, EIVE, together with the vegetation-plot data from EVA, would offer the unique chance to explore how frequent such changes are, and whether there are prevailing patterns. Moreover, in a second step, one could complement the pan-European indicator values of EIVE with separate sets of indicator values for the major biogeographic regions in Europe, which then could be used with higher predictive power in regional studies.

In this paper, we derived a European indicator value system without direct link to environmental variables – apart from the external validation of EIVE-T values with GBIF data. In the future, it would be important to conduct such validations with measured or at least independently modelled environmental variables for the other indicators as well. For the light indicator (L), the EVA database might provide suitable proxies, such as slope, aspect and inclination and tree and shrub layer cover (for a possible approach, see Tichý et al. 2023). By contrast, for the soil indicators, EVA lacks well-curated and readily available *in situ* measured environmental variables, such as pH value, C/N ratio or average depth of the water table. However, other vegetation-plot databases that are specialised in this field, such as the Ecological Conditions Database (Wamelink et al. 2012) and GrassPlot (Dengler et al. 2018), can provide the relevant data. Here, one could ask whether and how species cover should be used in the calculation of mean indicator values of a plot: not at all (i.e. only presence/absence), fully (i.e. weighting by % cover) or an intermediate solution (e.g. square root transformed cover) (Käfer and Witte 2004). Finally, one can test which is the best approach to include the now available numeric niche-width information into the calculation of the mean indicator values of a plot: not at all, using a threshold, using inverse weighting or using an even more sophisticated approach.

Conclusions and outlook

In terms of geographical and taxonomic coverage, as well as number of included source systems, EIVE 1.0 is the most comprehensive system of ecological indicator values developed so far. While it was beyond the scope of this paper to test its link to measured environmental site conditions, the high correlation of our EIVE-T values with modelled temperature conditions over the species distribution ranges indicates the general validity of the approach and shows that creating a consensus system from many source systems can even increase their performance. Compared to many, if not all, previous indicator value systems in Europe or parts of Europe, EIVE comes with several methodological novelties that likely will increase the utility of the system: (i) consistent range of 0 to 10 for all niche dimensions; (ii) interval (continuous) instead of ordinal (semi-quantitative) scaling; (iii); provision of both niche position and niche width and (iv) removal of logical inconsistencies, such as the fact that many systems assigned different M values for species that grow in the same habitat but have different morphology.

With these qualities, we are convinced that EIVE 1.0 will open new analytical avenues and become an important tool for vegetation ecologists, conservation biologists, species distribution modellers and macroecologists working on the European vegetation and flora. The implementation of EIVE is facilitated by the fact that the system, its underlying data and R scripts are provided freely. EIVE is an open-source, community-based database that will be released with fixed version numbers following improvements Therefore, readers are invited to send to the lead authors information about overlooked, new or updated EIV systems of any taxonomic group of plants and any niche dimensions, as well as any suggestions for further improvements.

Data availability

The Ecological Indicator Values for Europe (EIVE) 1.0 and the data underlying their derivation are freely available in the Supporting material and in a permanent repository at https://www.doi.org/10.5281/zenodo.7534792.

Author contributions

The idea of the database and paper was conceived by J.D., the database was prepared by E.H., F.J., K.V.M. and J.D., while F.J. and F.G. set up the analytical procedures in R. F.J. implemented the automated taxonomic assignment, which was refined by J.D., O.C., T.T., G.K., R.G. and T.R. M.N. ran the comparisons with GBIF and CHELSA data. J.D. led the writing, with major contributions from K.V.M., K.M., M.N., F.G., R.G., T.T, H.H.B. and M.J.S. The map was prepared by K.V.M. and the conceptual figures by F.G. Harmonised data from several regional EIV systems were contributed by I.A., M.C., L.T., G.K. and J.D., while all remaining co-authors contributed their national EIV system in digital format, partly with unpublished updates, and helped with their interpretation. All authors checked, improved and approved the manuscript.

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Supplementary material

Supplementary material 1
Detailed overview of the 31 ecological indicator value systems (EIVs) used to derive the Ecological Indicator Values for Europe (EIVE) 1.0 (*.pdf).
Link: https://doi.org/10.3897/VCS.98324.suppl1

Supplementary material 2
The analysed 31 EIV systems with original and harmonised plant nomenclature and original and rescaled indicator values for M, N, R, L and T (*.xlsx).
Link: https://doi.org/10.3897/VCS.98324.suppl2

Supplementary material 3
Documentation of additions to and modifications of the taxonomic backbone from Euro+Med (2022) in EIVE 1.0 (*.xslx).
Link: https://doi.org/10.3897/VCS.98324.suppl3

Supplementary material 4

Methodological details of the calculations of the three variants of niche position (median, mean, weighted mean) and the three variants of niche width (nw1, nw2, nw3) (*.pdf).

Link: https://doi.org/10.3897/VCS.98324.suppl4

Supplementary material 5

Documentation of the stepwise approach to derive the European consensus system of niche positions *EIVEres* (EIVE 1.0) from the individual EIV source systems after initial rescaling (*EIVini*) (*.pdf).

Link: https://doi.org/10.3897/VCS.98324.suppl5

Supplementary material 6

Bioclimate statistics of the species used for EIVE evaluation, and the corresponding DOIs of the GBIF occurrence downloads (*.xlsx).

Link: https://doi.org/10.3897/VCS.98324.suppl6

Supplementary material 7

Comparison of different metrics of niche width regarding the resulting value distributions and the correlations with GBIF derived bioclimatic variables. (*.pdf).

Link: https://doi.org/10.3897/VCS.98324.suppl7

Supplementary material 8

EIVE 1.0 indicator values for niche position and niche width of M, N, R, L and T (*.xlsx).

Link: https://doi.org/10.3897/VCS.98324.suppl8

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