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RESEARCH ARTICLE

Ellenberg-type indicator values for European vascular plant species

Lubomír Tichý[1] | Irena Axmanová[1] | Jürgen Dengler[2,3,4] | Riccardo Guarino[5] | Florian Jansen[6] | Gabriele Midolo[1] | Michael P. Nobis[7] | Koenraad Van Meerbeek[8,9] | Svetlana Aćić[10] | Fabio Attorre[11] | Erwin Bergmeier[12] | Idoia Biurrun[13] | Gianmaria Bonari[14] | Helge Bruelheide[4,15] | Juan Antonio Campos[13] | Andraž Čarni[16,17] | Alessandro Chiarucci[18] | Mirjana Ćuk[19] | Renata Ćušterevska[20] | Yakiv Didukh[21] | Daniel Dítě[22] | Zuzana Dítě[22] | Tetiana Dziuba[21] | Giuliano Fanelli[11] | Eduardo Fernández-Pascual[23] | Emmanuel Garbolino[24] | Rosario G. Gavilán[25] | Jean-Claude Gégout[26] | Ulrich Graf[7] | Behlül Güler[27] | Michal Hájek[1] | Stephan M. Hennekens[28] | Ute Jandt[4,15] | Anni Jašková[1] | Borja Jiménez-Alfaro[23] | Philippe Julve[29] | Stephan Kambach[15] | Dirk Nikolaus Karger[7] | Gerhard Karrer[30] | Ali Kavgacı[31] | Ilona Knollová[1] | Anna Kuzemko[1,21] | Filip Küzmič[16] | Flavia Landucci[1] | Attila Lengyel[32] | Jonathan Lenoir[33] | Corrado Marcenò[34] | Jesper Erenskjold Moeslund[35] | Pavel Novák[1] | Aaron Pérez-Haase[36] | Tomáš Peterka[1] | Remigiusz Pielech[37,38] | Alessandro Pignatti[11] | Valerijus Rašomavičius[39] | Solvita Rūsiņa[40] | Arne Saatkamp[41,42] | Urban Šilc[16] | Željko Škvorc[43] | Jean-Paul Theurillat[44,45] | Thomas Wohlgemuth[7] | Milan Chytrý[1]

[1]Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic

[2]Vegetation Ecology Research Group, Institute of Natural Resource Sciences (IUNR), Zurich University of Applied Sciences (ZHAW), Wädenswil, Switzerland

[3]Plant Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany

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

[5]Department of Biological, Chemical and Pharmaceutical Sciences and Technologies (STEBICEF), University of Palermo, Palermo, Italy

[6]Faculty of Agricultural and Environmental Sciences, University of Rostock, Rostock, Germany

[7]Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

[8]Department of Earth and Environmental Sciences, KU Leuven, Leuven, Belgium

[9]KU Leuven Plant Institute, KU Leuven, Leuven, Belgium

[10]Department of Botany, Faculty of Agriculture, University of Belgrade, Beograd, Serbia

[11]Department of Environmental Biology, Sapienza University of Rome, Roma, Italy

[12]Vegetation Ecology & Plant Diversity, Albrecht von Haller Institute of Plant Sciences, University of Göttingen, Göttingen, Germany

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

[14]Free University of Bozen-Bolzano, Bolzano, Italy

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

[16]Research Centre of the Slovenian Academy of Sciences and Arts, Jovan Hadži Institute of Biology, Ljubljana, Slovenia

[17]School for Viticulture and Enology, University of Nova Gorica, Nova Gorica, Slovenia
[18]BIOME Lab, Department of Biological, Geological & Environmental Sciences, Alma Mater Studiorum - University of Bologna, Bologna, Italy
[19]Department of Biology and Ecology, Faculty of Science, University of Novi Sad, Novi Sad, Serbia
[20]Faculty of Natural Sciences and Mathematics, Ss. Cyril and Methodius University, Skopje, North Macedonia
[21]M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv, Ukraine
[22]Plant Science and Biodiversity Center, Slovak Academy of Sciences, Bratislava, Slovakia
[23]IMIB Biodiversity Research Institute, University of Oviedo, Mieres, Spain
[24]Climpact Data Science, Nova Sophia - Regus Nova, Sophia Antipolis Cedex, France
[25]Botany Unit, Department of Pharmacology, Pharmacognosy and Botany, Complutense University, Madrid, Spain
[26]Université de Lorraine, AgroParisTech, INRAE, UMR Silva, Nancy, France
[27]Biology Education, Dokuz Eylül University, Buca, Turkey
[28]Wageningen Environmental Research, Wageningen, The Netherlands
[29]Faculté de Gestion, Economie et Sciences, Lille Catholic University, Lille, France
[30]Department of Integrative Biology and Biodiversity Research, University of Natural Resources and Life Sciences Vienna, Vienna, Austria
[31]Burdur Food Agriculture and Livestock Vocational School, Burdur Mehmet Akif Ersoy University, Burdur, Turkey
[32]Centre for Ecological Research, Institute of Ecology and Botany, Vácrátót, Hungary
[33]UMR CNRS 7058 "Ecologie et Dynamique des Systèmes Anthropisés" (EDYSAN), Université de Picardie Jules Verne, Amiens, France
[34]Department of Chemistry, Biology and Biotechnology, University of Perugia, Perugia, Italy
[35]Department of Ecoscience, Section for Biodiversity, Aarhus University, Aarhus, Denmark
[36]Department of Evolutionary Biology, Ecology and Environmental Sciences, University of Barcelona, Barcelona, Spain
[37]Department of Forest Biodiversity, Faculty of Forestry, University of Agriculture in Kraków, Kraków, Poland
[38]Foundation for Biodiversity Research, Wrocław, Poland
[39]Institute of Botany, Nature Research Centre, Vilnius, Lithuania
[40]Faculty of Geography and Earth Sciences, University of Latvia, Riga, Latvia
[41]Conservatoire Botanique National Méditerranéen, Hyères, France
[42]Aix Marseille Université, Université Avignon, CNRS, IRD, UMR IMBE, Marseille, France
[43]University of Zagreb, Faculty of Forestry and Wood Technology, Zagreb, Croatia
[44]Fondation J.-M. Aubert, Champex-Lac, Switzerland
[45]Department of Plant Sciences, University of Geneva, Chambésy, Switzerland

Correspondence
Lubomír Tichý, Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic.
Email: tichy@sci.muni.cz

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Abstract

Aims: Ellenberg-type indicator values are expert-based rankings of plant species according to their ecological optima on main environmental gradients. Here we extend the indicator-value system proposed by Heinz Ellenberg and co-authors for Central Europe by incorporating other systems of Ellenberg-type indicator values (i.e., those using scales compatible with Ellenberg values) developed for other European regions. Our aim is to create a harmonized data set of Ellenberg-type indicator values applicable at the European scale.

Methods: We collected European data sets of indicator values for vascular plants and selected 13 data sets that used the nine-, ten- or twelve-degree scales defined by Ellenberg for light, temperature, moisture, reaction, nutrients and salinity. We compared these values with the original Ellenberg values and used those that showed consistent trends in regression slope and coefficient of determination. We calculated the average value for each combination of species and indicator values from these data sets. Based on species' co-occurrences in European vegetation plots, we also calculated new values for species that were not assigned an indicator value.

Results: We provide a new data set of Ellenberg-type indicator values for 8908 European vascular plant species (8168 for light, 7400 for temperature, 8030 for

moisture, 7282 for reaction, 7193 for nutrients, and 7507 for salinity), of which 398 species have been newly assigned to at least one indicator value.
Conclusions: The newly introduced indicator values are compatible with the original Ellenberg values. They can be used for large-scale studies of the European flora and vegetation or for gap-filling in regional data sets. The European indicator values and the original and taxonomically harmonized regional data sets of Ellenberg-type indicator values are available in the Supporting Information and the Zenodo repository.

KEYWORDS
bioindication, Ellenberg indicator values, light, moisture, nutrients, reaction, salinity, temperature, vascular plants

1 | INTRODUCTION

Bioindication of abiotic site conditions from environmental relationships of plant species has a long tradition (Cajander, 1926; Iversen, 1936). Seminal work was done by the German vegetation ecologist Heinz Ellenberg, who published a comprehensive data set of indicator values for vascular plant species (Ellenberg, 1974). These values were based on field observations and partly also measurements, mainly from Germany. Ellenberg defined indicator values for seven abiotic environmental variables: light, temperature, continentality, moisture, soil reaction, nutrient (nitrogen) content, and salinity. While the first two variables relate mainly to above-ground conditions, the last four describe substrate (soil or water) conditions. Ellenberg originally defined indicator values for nitrogen content, but later studies suggested that they rather reflect general soil fertility, such as the combined availability of both nitrogen and phosphorus (Boller-Elmer, 1977; Briemle, 1986; Hill & Carey, 1997). Therefore, Ellenberg's original nitrogen values are nowadays more often called nutrient values (Ellenberg et al., 1992), while there are attempts to develop separate indicator values for these two nutrients (Tyler et al., 2021).

Ellenberg indicator values were defined on ordinal scales that characterize the relative position of the centroid of a species' realized one-dimensional niche related to the respective environmental variable. A low value corresponds to the position of the species' optimum towards the lower end of the environmental gradient, whereas a high value corresponds to the position at the higher end. For example, low values of the light scale are assigned to shade-tolerant species, whereas high values are assigned to species that occur in full light.

Ellenberg's system was inspired in part by the ideas of Cajander (1926), who used associations of plant species to evaluate forest types and productivity, and Iversen (1936), who arranged plants into response groups to environmental variables relevant to plant growth. However, Ellenberg (1948, 1950, 1952) was the first to use numerical codes instead of verbally defined levels of environmental gradients. Ellenberg (1948) also proposed using these codes to calculate community means based on species presence and community-weighted means based on species cover-abundances. Subsequently, other authors (e.g., Zólyomi et al., 1967; Zlatník et al., 1970) adopted Ellenberg's concept of bioindication by creating regional systems of indicator values for other parts of Europe. Not only vascular plants but later also bryophytes and lichens were characterized by indicator values following the same system (Ellenberg et al., 1992). Similar systems were developed to indicate disturbance (Briemle & Ellenberg, 1994; Herben et al., 2016; Midolo et al., 2023).

Repeatedly updated and refined, Ellenberg indicator values (Ellenberg et al., 1992, 2001; Ellenberg & Leuschner, 2010) are a widely used tool for rapidly estimating environmental conditions without direct measurements (Diekmann, 2003; Holtland et al., 2010). In the Web of Science database, 907 articles with the keywords (including words used in abstracts) 'Ellenberg' AND 'Indicator' were registered between 1 January 1974 and 30 June 2022, indicating their importance to plant ecologists. Several studies found a good agreement between community means (weighted or non-weighted) calculated from Ellenberg indicator values and values of environmental variables measured *in situ* (Ellenberg et al., 1992; Herzberger & Karrer, 1992; Hill & Carey, 1997; Ertsen et al., 1998; Schaffers & Sýkora, 2000; Wamelink et al., 2002; Diekmann, 2003; Chytrý et al., 2009; Sicuriello et al., 2014). Some authors also discussed the consistency of indicator values between different geographical areas (Diekmann & Lawesson, 1999; Gégout & Krizova, 2003; Godefroid & Dana, 2007; Wasof et al., 2013). Because Ellenberg's original data set focused on plants occurring in the western part of Central Europe, other authors proposed indicator values for other European regions. These data sets included many species that were missing from Ellenberg's original data set and often contained different values for the same species, reflecting shifted optima of their realized niches between regions (e.g. Landolt, 1977; Tsyganov, 1983; Jurko, 1990; Karrer, 1992; Borhidi, 1995; Mayor López, 1996; Böhling et al., 2002; Zarzycki et al., 2002; Hill et al., 2004; Pignatti, 2005; Landolt et al., 2010; Didukh, 2011; Chytrý et al., 2018; Domina et al., 2018; Guarino & La Rosa, 2019; Jiménez-Alfaro et al., 2021; Tyler et al., 2021). Specialized data sets of indicator values for species limited to a specific habitat type but covering large areas were also created (e.g. Hájek et al., 2020 — mires; Dítě et al., 2023 — saline habitats).

The increasing number of synthetic and macroecological studies on European vegetation, catalyzed by the launch of the European database of vegetation plots (European Vegetation Archive, EVA; Chytrý et al., 2016), require a coherent system of species-level indicator values. Although regional systems of indicator values have been widely used for a long time, no consensual system of indicator values for European plants has been developed so far. Therefore, we have compiled a harmonized data set of vascular plant indicator values for light, temperature, moisture, soil (or water) reaction (related to base saturation), nutrients (site productivity), and salinity suitable for a large part of Europe, using the same numerical scales as defined by Ellenberg. In this article, we describe the content of the new data set and the methods used to compile it.

2 | METHODS

We compiled a database of 13 published European data sets of indicator values for vascular plant species defined on the same nine-degree scale (or 10-degree scale for salinity and 12-degree scale for moisture) as the original Ellenberg indicator values (Ellenberg et al., 1992, 2001). We refer to these data sets as *Ellenberg-type* indicator values. Data sets with scales containing a lower number of degrees, i.e., with a coarser resolution, were not included. If the scale had a higher number of degrees than nine (or 10 for salinity or 12 for moisture), we accepted it, provided that: (1) the additional degrees represented an extension of the environmental gradient, while the other degrees retained the same meaning as in the original Ellenberg data set (e.g. extending the nine-degree temperature scale originally defined for Central Europe to 12 degrees to reflect Mediterranean conditions; Pignatti, 2005) or (2) the additional degrees represented intermediate values on the nine- or 12-degree scale (e.g. the 17-degree temperature scale and the 23-degree moisture scale in Didukh, 2011). We considered only data sets based entirely or largely on expert knowledge and excluded those based on values recalculated from vegetation plots without expert-based assessment of values for individual species (e.g. Lawesson et al., 2003 for the Faroe Islands).

The 13 indicator-value data sets that met the above conditions included: Great Britain (Hill et al., 2000); the Cantabrian Mountains in Spain (Jiménez-Alfaro et al., 2021); France (Julve, 2015); Switzerland and the Alps (Landolt et al., 2010; temperature values only, as the other values use coarser scales than Ellenberg); Germany (Ellenberg et al., 2001, taken from Ellenberg & Leuschner, 2010); Czech Republic (Chytrý et al., 2018); Austria (Karrer, 1992); Hungary (Borhidi, 1995); Ukraine (Didukh, 2011; only the light, temperature and moisture values, as the others cannot be matched to the Ellenberg scales); Italy (Guarino & La Rosa, 2019, a corrected version prepared by R. Guarino for this study); South Aegean region of Greece (Böhling et al., 2002); European mires (Hájek et al., 2020); and saline habitats in Central Europe (Dítě et al., 2023). The scales of these 13 data sets had 12 degrees for moisture and some of them also for temperature, 10 degrees for salinity, and nine degrees for the other values. The Italian values originally also had 12 degrees for light, but we replaced the values 10–12 with 9 and had the result manually checked by the first author of the original data set. Therefore, we integrated the data sets using 12-degree scales for temperature and moisture, a 10-degree scale for salinity and nine-degree scales for light, reaction and nutrients. We did not include the Swedish indicator values for moisture and nitrogen (Tyler et al., 2021), which were expressed on the same scales but published after we completed our calculations.

We omitted the indicator values for continentality because they are based on species' geographical ranges. Continentality values may have an ambiguous meaning at the local scale since they may correlate with different factors, including seasonal differences in temperature and precipitation, diurnal differences in temperature, annual minimum temperatures, and drought. Moreover, Berg et al. (2017) identified methodological weaknesses in the original Ellenberg approach to continentality values, proposed an improved protocol for their compilation, and defined new formally-verified values.

We unified the taxonomy and nomenclature of all vascular plant taxa across the 13 data sets according to the Euro+Med PlantBase (http://europlusmed.org). We merged subspecies, varieties and forms at the species level and removed hybrids and rare alien species (mostly casual neophytes; Richardson et al., 2000). We also merged as 'aggregates' those taxonomically related species that are difficult to identify and, therefore, are often misidentified or not identified at all, such as species of the *Achillea millefolium* group in the *A. millefolium* aggr. The aggregates used were those defined in the Euro+Med PlantBase (Euro+Med, 2021) and the EUNIS-ESy expert system for EUNIS Habitat Classification (Chytrý et al., 2020). Unlike the aggregates defined in some data sets on the national or regional scales, these aggregates are valid at the European scale. For infraspecific taxa within the same species or species within the same aggregate, we used the arithmetic mean of their indicator values as the indicator value for the species or aggregate. In addition, we calculated the median, minimum, and maximum of indicator values for each species and aggregate. Some databases provided indicator values for both individual species and aggregates. Although some of these aggregates are not regularly used in vegetation science, have a regional validity and do not fit the concept of Euro+Med and EUNIS, we kept them on the list to avoid losing information.

The new system of indicator values was prepared by calculating the arithmetic mean for each combination of species and indicator value across all compatible regional data sets in which an indicator value was defined for the target species. As a first step, we tested whether the indicator values of each of the 12 data sets (other than the original Ellenberg data set) were compatible with the Ellenberg values. We conducted two comparisons. For the first one, we tested a direct pairwise relationship between the original Ellenberg values (Ellenberg & Leuschner, 2010) for individual species (independent variable) and values for the same species in a different data set (dependent variable; species-based regression). For the second comparison, we used vegetation plots from the EVA database (Chytrý et al., 2016) to calculate the unweighted means of the original Ellenberg values (independent variable) and indicator values from the other 12 data sets (dependent variable; plot-based regression). A total of 1,790,582 vegetation plots covering a wide range of vegetation types sampled across Europe were used. The territory of Russian Federation, Georgia, Armenia, and Azerbaijan were not included due to their peripheral biogeographical location, lack of indicator-value data sets compatible with Ellenberg scales, and low density of plots in the EVA database. Species nomenclature was unified in the same way as in the indicator-value databases (see above). We selected only vegetation plots that contained at least five species with indicator values, both from the original Ellenberg data set and from other indicator-value data sets, resulting in 622,402 plots for light indicator values, 413,832 for temperature, 615,301 for moisture, 490,617 for reaction, 575,406 for nutrients and 673,141 for salinity.

Based on the regression analyses described above, we selected data sets that showed consistent trends in both the direct species-based and indirect plot-based regressions against the original Ellenberg indicator values. In order to compare these trends, we selected two regression characteristics: the coefficient of determination (R^2) and slope. The coefficient of determination shows the amount of variation in the dependent variable explained by the regression. However, the same R^2 can be obtained with vastly different slopes. Therefore, we also used slope, which mainly indicates differences at the ends (extremes) of the indicator value range. Based on the empirical assessment of the regression results, we selected only indicator values for which the regression slope was within the range from 0.5 to 1.2 and R^2 was higher than 0.5. The only exception was the salinity data set for Central Europe (Dítě et al., 2023), which, in contrast to Ellenberg salinity values, did not include any non-halophytic species.

When different indicator values occurred in different data sets for the same species and the same environmental variable, we calculated the mean of these values. If the difference between the minimum and maximum values across all original taxa that were merged into the same species or aggregate was more than three indicator value units across all data sets, and the range crossed the central value (i.e. a value of 5 for the nine-degree scales, a value of 4.5 for the 10-degree salinity scale and a value of 6.5 for the 12-degree scales), we reported no indicator value. The condition of crossing the central degree filtered out generalist species occurring under intermediate conditions while preserving values for species occurring under more extreme conditions. All indicator values resulting from either the averaging or median calculation that had more than one decimal place were rounded to one decimal place.

To assign indicator values to species for which indicator values were not available in any of the data sets but which occurred in at least 50 EVA vegetation plots, we used the method described by Chytrý et al. (2018). First, for each of these target species, we searched for the set of other species that had the most similar occurrence pattern across EVA plots. We measured the degree of co-occurrence of species pairs using the *phi* coefficient of association (Sokal & Rohlf, 1995). For each species with no indicator value, we listed all species with an indicator value that had a similar occurrence pattern (interspecific association of $phi > 0.1$). If there were at least five such species, we calculated the mean (rounded to one decimal place) of their indicator values and assigned it as the indicator value for the target species with no indicator value. If more than 20 species met these conditions, we considered only the 20 species with the highest *phi* value. If there were fewer than five such species, no new indicator values were calculated.

Mean indicator values always have a narrower range than the original scale of indicator values (see Hill et al., 2000), which reduces the compatibility between the newly calculated and original indicator values. To standardize the range of indicator values for species with newly-calculated values, we first calculated indicator values for species that occurred in at least one data set of indicator values and for which we knew the original indicator values in the regional data sets. For a set of these species, we calculated a linear regression between the values estimated from species co-occurrence (independent variable) and average indicator values from the regional data sets (dependent variable). Then we used the formula of the regression line to adjust indicator values for species with values estimated only from species co-occurrence, i.e., those for which indicator values were not previously available.

Any subjective adjustment of indicator values was avoided. However, indicator values for obligatory epiphytic hemiparasites germinating on trees (*Arceuthobium*, *Loranthus* and *Viscum*) were not included in the final list in the case of nutrients, reaction and salinity.

We tested the validity of the harmonized European data set of indicator values using an example of indicator values for temperature by regressing them on an independent source of gridded temperature data. We calculated the unweighted community mean of temperature indicator values across species in each EVA plot that contained at least five species (413,832 plots) and related them to modelled mean summer temperatures from the Chelsa database (Karger et al., 2017; bio10 — daily mean air temperatures of the warmest quarter for the period of 1981–2010). Data processing and analyses were performed using the programs JUICE v. 7.1 (Tichý, 2002) and R v. 4.0.3 (R Core Team, 2022).

3 | RESULTS

Of the 12 Ellenberg-type indicator-value data sets (i.e., excluding the original Ellenberg data set), 11 were found to be at least partially compatible with the original Ellenberg data set (Table 1, Appendix S1) after being tested with species-based regression and plot-based regression (Appendix S2). Outlier data sets that did not meet our compatibility conditions were excluded from further analyses. Indicator values for the Cantabrian Mountains were excluded entirely. For the Southern Aegean data set, we retained the indicator values for moisture and salinity but excluded the other values for lack of compatibility. For the Ukrainian data set, we retained the

TABLE 1 Regional data sets of Ellenberg-type indicator values used as a potential source for the European data set

Data set	Source	Light	Temperature	Moisture	Reaction	Nutrients	Salinity
Germany	Ellenberg and Leuschner (2010)	2478	2191	2407	3778	2315	2495
Austria	Karrer (1992)	1006	724	938	1198	855	1000
Cantabrian Range	Jiménez-Alfaro et al. (2021)	NA	NA	NA	NA	NA	–
Czech Republic	Chytrý et al. (2018)	2191	2194	2194	2192	2192	2194
European mires	Hájek et al. (2020)	–	–	1479	–	–	–
France	Julve (2015)	3815	3763	3750	3758	3764	3792
Great Britain	Hill et al. (2000)	1684	–	1684	1684	1684	1684
Greece (South Aegean)	Böhling et al. (2002)	NA	NA	1831	NA	NA	1922
Hungary	Borhidi (1995)	2028	2028	2028	2026	2028	2028
Italy	Guarino and La Rosa (2019)	5136	4985	5092	4869	5049	5121
Saline habitats	Dítě et al. (2023)	–	–	–	–	–	335
Switzerland/Alps	Landolt et al. (2010)	NC	4380	NC	NC	NC	NC
Ukraine	Didukh (2011)	2877	NA	2895	NC	NC	NC
FINAL		8168	7400	8030	7282	7193	7507

Note: Numbers are given where indicator values are present in the source data set and were used for the calculation. The numbers are, in turn, counts of species or aggregates (after nomenclature standardization) with indicator values. 'NA' (not accepted), the indicator value exists and the authors stated that it follows the Ellenberg concept, but it did not meet our compatibility criteria and was excluded from further analyses; 'NC' (not considered), the indicator value exists, but its concept or scale differs from Ellenberg indicator values; '–', the indicator value does not exist in the source data set. Information on the percentage distribution of indicator value classes within each data set is provided in Appendix S1. The bottom row (FINAL) reports the number of species and aggregates included in the final harmonized European data set.

indicator values for light and moisture, but excluded temperature (thermal climate or thermoregime).

The final data set contained 8,908 European vascular plant species with at least one indicator value. Indicator values for all six environmental variables were defined for 5,398 species. At least one indicator value was newly assigned for 398 species not listed in any regional data set. The matrix of correlations between indicator values and frequency histograms for individual indicator values, both for species and community means calculated for EVA plots, are shown in Figures 2 and 3.

The set of 1,790,582 vegetation plots from the EVA database contained 11,161 species of vascular plants after standardizing the nomenclature. Of these, 7,918 (70.9%) had at least one indicator value derived from at least one of the 12 retained data sets or estimated from species co-occurrences. The new indicator values were defined mainly for frequent species. Therefore, at least one indicator value was available for 99.7% of all species occurrences in the EVA vegetation plots.

Linear regressions between community-mean values for EVA vegetation plots calculated from the new data set of European indicator values for temperature and the mean summer temperature from the Chelsa data set showed a stronger relationship (R^2 = 0.49) than regressions calculated from each regional data set individually (Appendix S3). Community means for temperature values showed negligible differences in slope and coefficient of determination when calculated with or without the species for which the indicator value had been derived from the EVA-based estimations.

4 | DISCUSSION

We created an extensive data set of indicator values for six main environmental variables that affect plant distribution and community composition under natural conditions. This data set covers a large part of Europe and is suitable for European studies of flora and vegetation. Although it does not include all the European species, it contains most of the widespread and common species, and represents the broadest harmonized source permitting sound comparisons. Our indicator values were created by mathematically integrating data from the original Ellenberg values and 11 compatible data sets for other European regions. In addition, we estimated indicator values for species for which no values had been published based on species co-occurrences in vegetation plots from the EVA database.

Alternative approaches to calculating Ellenberg-type indicator values from vegetation plots were proposed by ter Braak and Gremmen (1987) and Hill et al. (2000). They calculated indicator values by reciprocal averaging of community means of species indicator values from vegetation plots. ter Braak and Gremmen (1987) also proposed the maximum likelihood method. However, both methods utilized community means as a source for species' indicator estimation or correction. Our experience from a previous study (Chytrý et al., 2018) shows that the calculation of indicator values for new species from community means can be negatively affected by the fact that a few widespread and common generalist species are found in many plots and account for a relatively high proportion of the total number of species in individual plots. For example, only 477 out of 11,164 vascular plant species in the selection from the EVA database used for this study occur in more than 1% of plots. There are many vegetation plots in which these widespread species are the only species with an indicator value. In the case of temperature, for instance, this concerns 10.4% of all plots. As a result, some specialized species with missing indicator values may receive inappropriate values if only the average values for generalist species are used. Therefore, we suggest using only the values for the most specialized and most similarly distributed species for calculating new indicator values based on vegetation plots. The advantage of the method proposed by Chytrý et al. (2018) and used in this work is that it does not average all species in plots but assigns missing indicator values based on averaging the values for a limited number of species with the most similar co-occurrence patterns. Although this method calculates indicator values only for species that frequently co-occur with other species that already have indicator values, the calculated values are more reliable.

Ellenberg (1974) and other authors defined indicator values on ordinal scales, which has sometimes been criticized (Dierschke, 1994). Ellenberg et al. (2001) argued that at least part of their scales have equidistant segmentation of the interval scale, which allows for calculating community means. ter Braak and Barendregt (1986) showed that community means calculated from indicator values best estimate environmental conditions when each indicator value is the centroid of the symmetric (normally distributed) species response curve to the given environmental variable. Other authors (Pignatti et al., 2001; Marcenò & Guarino, 2015; Wildi, 2016) have also shown that in large data sets, Ellenberg indicator values can be evaluated with parametric tests because they tend to be normally distributed. Because

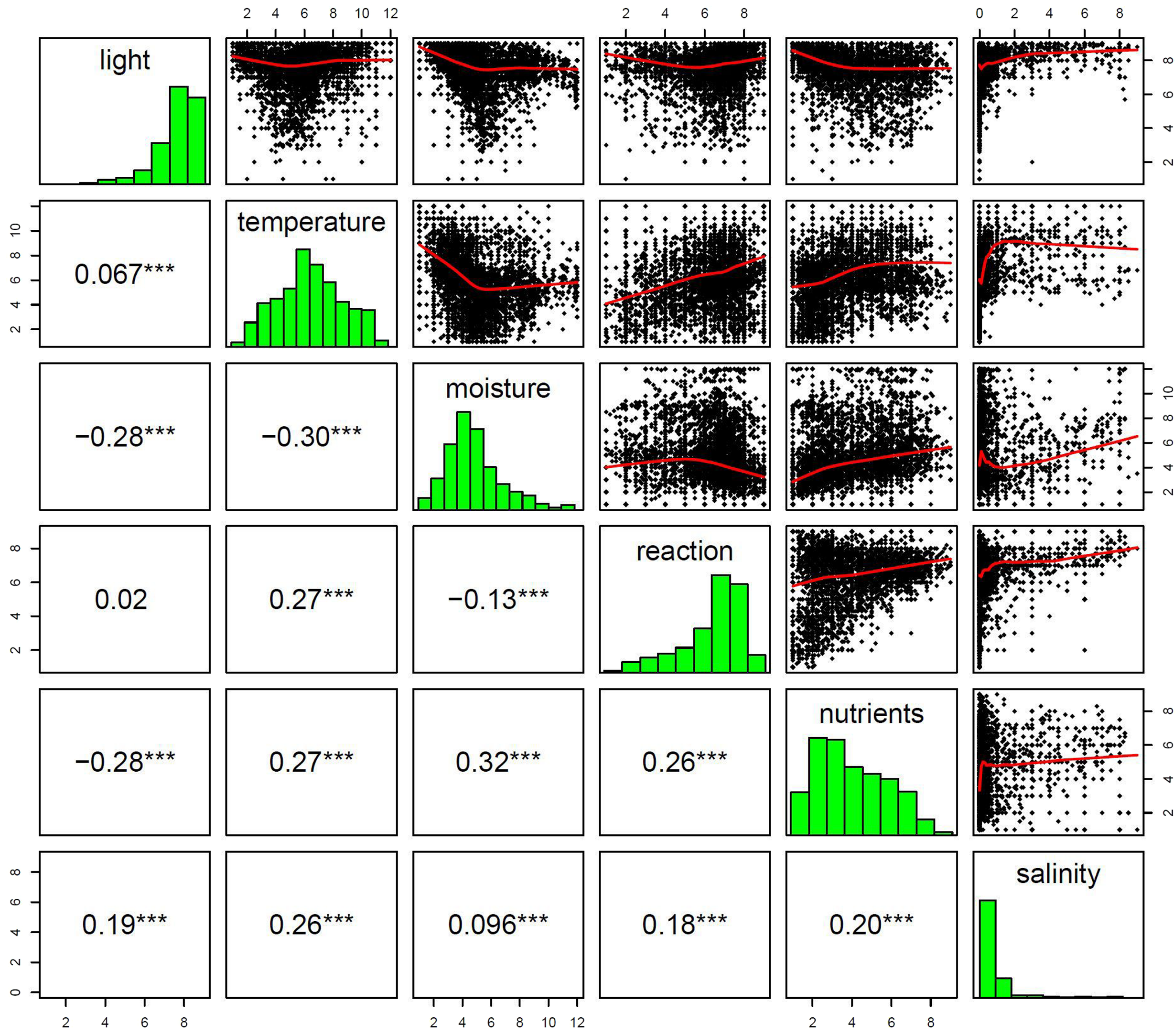

FIGURE 1 Correlation matrix of Ellenberg-type indicator values for Europe. Histograms show the relative frequency of species for a particular value along the environmental gradient. Boxes below the diagonal show Pearson correlation coefficients with their significance, and scatter plots above the diagonal show the distribution of species in a pairwise comparison between two corresponding indicators (each black dot represents one species). ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$.

many recent studies have also estimated environmental conditions using community means (e.g. Ahl et al., 2021; Baumann et al., 2021; Dwyer et al., 2021; Jaroszewicz et al., 2021), we considered all scales of published indicator values to be interval scales. Differences among published sources were smoothed by calculating means with decimal precision. The new data set of indicator values retains the range of the original Ellenberg scales of nine, 10 or 12 degrees, so it is compatible with other data sets defined on the same scales.

As our indicator-value data set is prepared for broad-scale analyses, it uses a relatively coarse taxonomic resolution at the level of species or, in some cases, species aggregates. However, different subspecies of the same species or different narrowly-defined species within an aggregate may differ substantially in their ecological requirements for some environmental variables (e.g. Landolt et al., 2010). Therefore, for some species or aggregates in our data set, no indicator value was given for some environmental variables. As a result, only 4,946 (44.3%) of the vascular plant species occurring in the EVA vegetation plots had an indicator value for all six environmental variables. Another reason for the relatively low number of such species was that only a half of the data sets contained indicator values for less than six environmental variables compatible with the Ellenberg scales (Hill et al., 2000; Böhling et al., 2002; Landolt et al., 2010; Didukh, 2011; Hájek et al., 2020; Dítě et al., 2023).

The original Ellenberg values had been estimated primarily by expert knowledge. Cornwell and Grubb (2003) demonstrated that

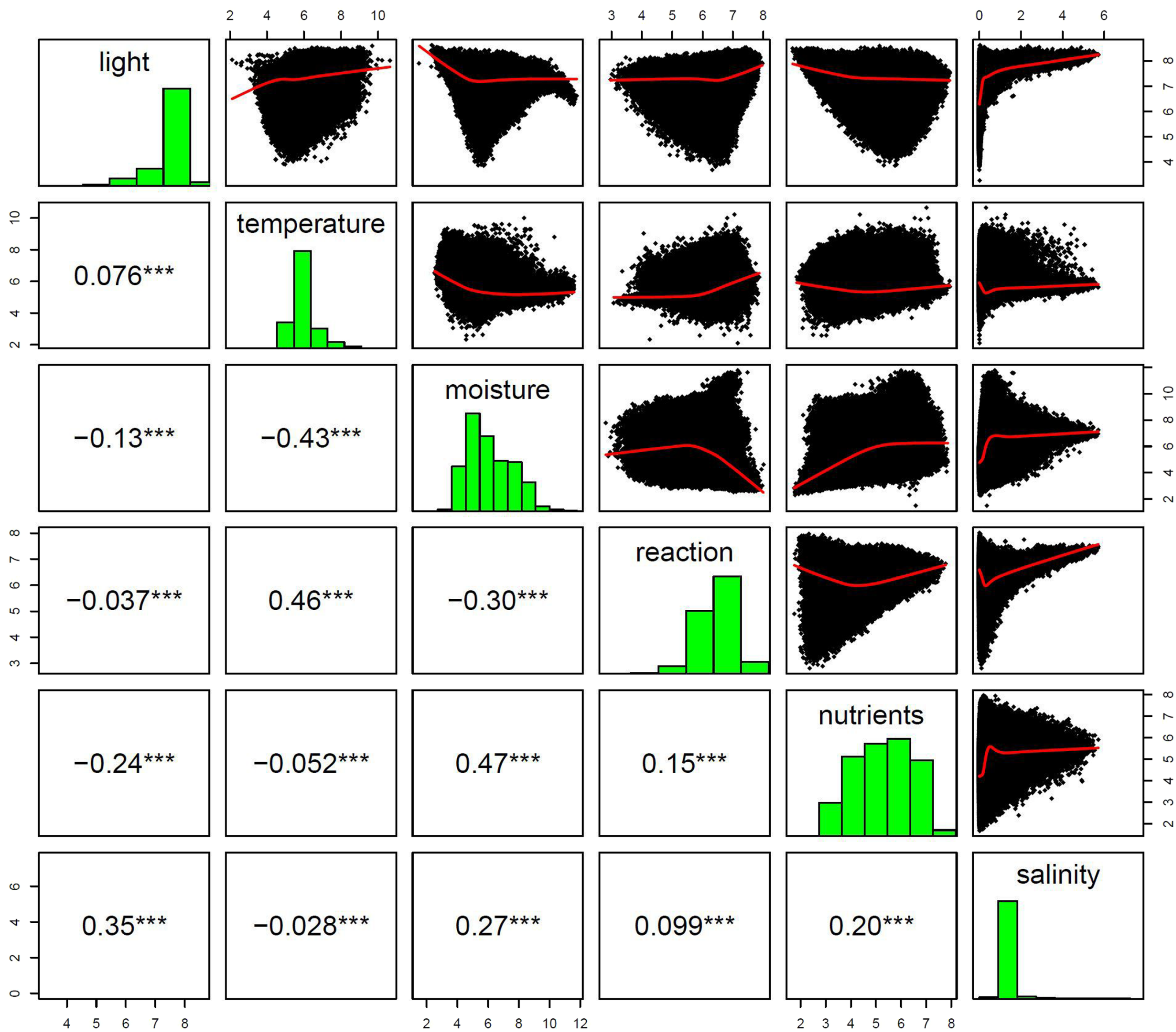

FIGURE 2 Correlation matrix of the community means of Ellenberg-type indicator values for Europe calculated for EVA vegetation plots. Histograms show the relative frequency of plots for a particular value along the environmental gradient. Boxes below the diagonal show Pearson correlation coefficients with their significance, and scatter plots above the diagonal show the distribution of vegetation plots in a pairwise comparison between two corresponding indicators (each black dot represents one vegetation plot). ***, $p<0.001$; **, $p<0.01$; *, $p<0.05$.

Ellenberg species values for different environmental conditions are often not independent. For example, they found a significant rank correlation for the relationship between nutrients and moisture ($r_s = 0.362$, $p = 0.001$), which is also found in our harmonized data set (Figure 1). Similar trends of the relationship between environmental factors can be seen in Figure 2, where we compared unweighted community means calculated for vegetation plots of the EVA database. The reason for the significance of most partial correlations between indicator values for individual species is not so obvious as for community means, in which the indication of ecological factors is not related to the species, but related directly to site conditions.

Independent verification of the validity of our data set of indicator values in relation to measured local environmental variables is difficult because there are no standardized measurements of local environmental conditions at the European scale at the sites where the vegetation was sampled. The only exception is temperature, which has both local and macroscale components considered in the indicator values. Therefore, the community-mean indicator values can be compared with interpolated data from temperature measurements at climate stations. Such data represent macroclimate, but Ellenberg (1974) also derived temperature indicator values from species' occurrence in altitudinal belts in Germany and the Alps. There was a strong relationship between mean summer temperatures from the Chelsa database (Karger et al., 2017) and community-mean temperature indicator values for vegetation plots from the EVA database. However, we did not account for differences in local conditions, such as slope, aspect, and shading from trees, shrubs, and adjacent topographic features, which can affect local temperatures but are not available for all vegetation plots. Community means calculated from directly assigned indicator values, and those calculated using species co-occurrences showed negligible differences in R^2 values (Appendix S3), as also shown in Ewald (2003). Species with indicator values calculated based on species co-occurrences represented only about 3% of the species in the EVA database, and these were mainly rare species.

The 12 regional data sets of species indicator values integrated into our unified data set cover most of Central and Western Europe. However, their reliability decreases with distance from their area of origin (Herzberger & Karrer, 1992; Englisch & Karrer, 2001; Coudun & Gégout, 2005; Godefroid & Dana, 2007), as some species may change their realized niche or be represented by genotypes adapted to different fundamental niches (ecotypic adaptation; Hájková et al., 2008). For example, the niche width of some European species increases northward, making Ellenberg indicator values less applicable in Northern Europe (Diekmann, 1995; Hedwall et al., 2019). In contrast, some species shift and narrow their niche towards the edges of their distribution range (Papuga et al., 2018) relative to their centre of distribution (Englisch & Karrer, 2001). This is consistent with our comparisons of regional data sets, which showed the largest deviations from the original Ellenberg values for data sets from regions that are geographically and climatically farthest away from Germany, e.g., the Cantabrian Mountains in Spain (Jiménez-Alfaro et al., 2021) and the South Aegean region of Greece (Böhling et al., 2002). It is also likely that local endemics in these marginal regions outcompete species with broader geographic ranges from

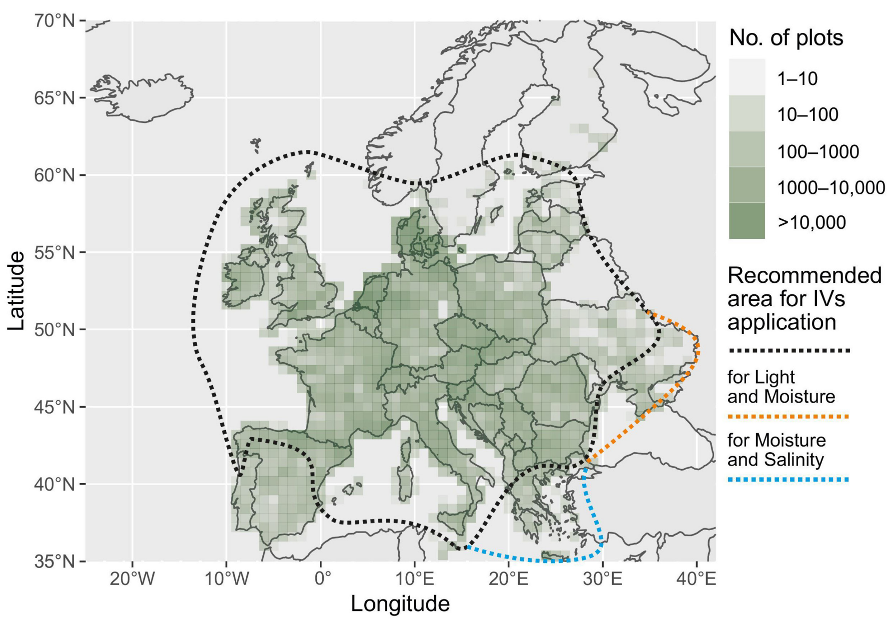

FIGURE 3 Recommended area for application of the harmonized European data set of Ellenberg-type indicator values. Europe is divided into a grid of 0.6° for latitude and 1° for longitude. Shades of green represent the density of 413,705 georeferenced vegetation plots from the EVA database that contain at least five species with an indicator value for each environmental variable: light, temperature, moisture, reaction, nutrients, and salinity. The black dotted line defines the approximate area for which we recommend using the data set of indicator values for all environmental variables. The orange dotted line indicates an additional area where light and moisture values can be safely used, and the blue-dotted line is an additional area where moisture and salinity values can be safely used.

a part of their fundamental niche, resulting in the narrowing of the realized niche. Therefore, we did not consider or only partially used these data sets from distant areas. As a result, we consider the new data set of indicator values to be mainly representative of Central and Western Europe, Italy and adjacent areas (Figure 3). For the Iberian Peninsula, Greece, Turkey and other areas, new systems of ecological indicator values need to be developed based on local observations, expert knowledge and careful comparisons with indicator values already established in other parts of Europe.

Although the primary motivation for our work was to create a data set of Ellenberg-type indicator values that can be used for broad-scale international studies of macroecological patterns of the European flora and vegetation, this data set can also be used in local studies. Its advantage is that it retains the traditional Ellenberg scales. Thus, if a local study uses a regional system of Ellenberg-type indicator values from a nearby region, our harmonized European data set can be used to add values for species that are missing from the regional system but occur in the study area. It is likely that most regional systems of indicator values provide more accurate estimates of site conditions in their region than the European data set, which is based on averaging indicator values from different regions. For example, species that behave as generalists on the European scale and thus were not assigned an indicator value in the European data set may have narrower niches and be good indicators in particular regions. Therefore, it is reasonable to continue to use regional systems of indicator values for local studies in regions where such systems exist. Nevertheless, if local studies from different regions use the European system of indicator values, their results can be directly compared.

AUTHOR CONTRIBUTIONS

Lubomír Tichý and Milan Chytrý conceived the research idea; Irena Axmanová standardized the nomenclature and prepared the data; Riccardo Guarino revised the Italian indicator values; Lubomír Tichý proposed analyses and performed all calculations; Lubomír Tichý, Milan Chytrý and Irena Axmanová wrote the text; Gabriele Midolo helped visualize the data presented in the appendices; all authors commented on the manuscript.

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DATA AVAILABILITY STATEMENT

The vegetation-plot data used in this study are stored in the European Vegetation Archive database (EVA; http://euroveg.org/eva-database) under project number 142, product (a). Tables of original indicator values for each region and harmonized indicator values for Europe can be downloaded from the Zenodo repository (https://doi.org/10.5281/zenodo.7427088), where future updates will also be available. A user-friendly data set for analyses that combines Ellenberg-type indicator values developed here with disturbance indicator values for European plants developed by Midolo et al. (2023) can be downloaded at https://floraveg.eu/download/. Ellenberg-type indicator values in a format for the JUICE program (Tichý 2002) are available at https://sci.muni.cz/botany/juice/?idm=10.

ORCID

Lubomír Tichý https://orcid.org/0000-0001-8400-7741
Irena Axmanová https://orcid.org/0000-0001-9440-7976
Jürgen Dengler https://orcid.org/0000-0003-3221-660X
Riccardo Guarino https://orcid.org/0000-0003-0106-9416
Florian Jansen https://orcid.org/0000-0002-0331-5185
Gabriele Midolo https://orcid.org/0000-0003-1316-2546
Michael P. Nobis https://orcid.org/0000-0003-3285-1590
Koenraad Van Meerbeek https://orcid.org/0000-0002-9260-3815
Svetlana Aćić https://orcid.org/0000-0001-6553-3797
Fabio Attorre https://orcid.org/0000-0002-7744-2195
Erwin Bergmeier https://orcid.org/0000-0002-6118-4611
Idoia Biurrun https://orcid.org/0000-0002-1454-0433
Gianmaria Bonari https://orcid.org/0000-0002-5574-6067
Helge Bruelheide https://orcid.org/0000-0003-3135-0356
Juan Antonio Campos https://orcid.org/0000-0003-4770-0461
Andraž Čarni https://orcid.org/0000-0002-8909-4298
Alessandro Chiarucci https://orcid.org/0000-0003-1160-235X
Mirjana Ćuk https://orcid.org/0000-0002-8261-414X
Renata Ćušterevska https://orcid.org/0000-0002-3849-6983
Yakiv Didukh https://orcid.org/0000-0002-5661-3944
Daniel Dítě https://orcid.org/0000-0001-5251-9910
Zuzana Dítě https://orcid.org/0000-0002-2895-9024
Tetiana Dziuba https://orcid.org/0000-0001-8621-0890
Giuliano Fanelli https://orcid.org/0000-0002-3143-1212
Eduardo Fernández-Pascual https://orcid.org/0000-0002-4743-9577
Emmanuel Garbolino https://orcid.org/0000-0002-4954-6069
Rosario G. Gavilán https://orcid.org/0000-0002-1022-445X
Jean-Claude Gégout https://orcid.org/0000-0002-5760-9920
Behlül Güler https://orcid.org/0000-0003-2638-4340

Michal Hájek https://orcid.org/0000-0002-5201-2682
Stephan M. Hennekens https://orcid.org/0000-0003-1221-0323
Ute Jandt https://orcid.org/0000-0002-3177-3669
Anni Jašková https://orcid.org/0000-0002-3510-1093
Borja Jiménez-Alfaro https://orcid.org/0000-0001-6601-9597
Stephan Kambach https://orcid.org/0000-0003-3585-5837
Dirk Nikolaus Karger https://orcid.org/0000-0001-7770-6229
Gerhard Karrer https://orcid.org/0000-0001-5172-2319
Ali Kavgacı https://orcid.org/0000-0002-4549-3668
Ilona Knollová https://orcid.org/0000-0003-4074-789X
Anna Kuzemko https://orcid.org/0000-0002-9425-2756
Filip Küzmič https://orcid.org/0000-0002-3894-7115
Flavia Landucci https://orcid.org/0000-0002-6848-0384
Attila Lengyel https://orcid.org/0000-0002-1712-6748
Jonathan Lenoir https://orcid.org/0000-0003-0638-9582
Corrado Marcenò https://orcid.org/0000-0003-4361-5200
Jesper Erenskjold Moeslund https://orcid.org/0000-0001-8591-7149
Pavel Novák https://orcid.org/0000-0002-3758-5757
Aaron Pérez-Haase https://orcid.org/0000-0002-5974-7374
Tomáš Peterka https://orcid.org/0000-0001-5488-8365
Remigiusz Pielech https://orcid.org/0000-0001-8879-3305
Valerijus Rašomavičius https://orcid.org/0000-0003-1314-4356
Solvita Rūsiņa https://orcid.org/0000-0002-9580-4110
Arne Saatkamp https://orcid.org/0000-0001-5638-0143
Urban Šilc https://orcid.org/0000-0002-3052-699X
Željko Škvorc https://orcid.org/0000-0002-2848-1454
Jean-Paul Theurillat https://orcid.org/0000-0002-1843-5809
Thomas Wohlgemuth https://orcid.org/0000-0002-4623-0894
Milan Chytrý https://orcid.org/0000-0002-8122-3075

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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. Percentages of indicator values in regional data sets selected as a potential source for a harmonized European data set of indicator values.

Appendix S2. Evaluation of 12 regional systems of Ellenberg-type indicator values based on their relationship to Ellenberg indicator values.

Appendix S3. Comparison of mean Ellenberg-type indicator values for temperature calculated for vegetation plots and mean summer temperature for plot locations obtained from climatic data sets.

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