



HAL
open science

Ellenberg-type indicator values for European vascular plant species

Lubomír Tichý, Irena Axmanová, Jürgen Dengler, Riccardo Guarino, Florian Jansen, Gabriele Midolo, Michael Nobis, Koenraad van Meerbeek, Svetlana Aćić, Fabio Attorre, et al.

► **To cite this version:**

Lubomír Tichý, Irena Axmanová, Jürgen Dengler, Riccardo Guarino, Florian Jansen, et al.. Ellenberg-type indicator values for European vascular plant species. *Journal of Vegetation Science*, 2023, 34 (1), pp.e13168. 10.1111/jvs.13168 . hal-04001980

HAL Id: hal-04001980

<https://u-picardie.hal.science/hal-04001980>

Submitted on 24 Feb 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Ellenberg-type indicator values for European vascular plant species**

2

3 **Lubomír Tichý¹ (0000-0001-8400-7741), Irena Axmanová¹ (0000-0001-9440-7976), Jürgen**
4 **Dengler^{2,3,4} (0000-0003-3221-660X), Riccardo Guarino⁵ (0000-0003-0106-9416), Florian Jansen⁶**
5 **(0000-0002-0331-5185), Gabriele Midolo¹ (0000-0003-1316-2546), Michael P. Nobis⁷ (0000-0003-**
6 **3285-1590), Koenraad Van Meerbeek^{8,9} (0000-0002-9260-3815), Svetlana Ačić¹⁰ (0000-0001-6553-**
7 **3797), Fabio Attorre¹¹ (0000-0002-7744-2195), Erwin Bergmeier¹² (0000-0002-6118-4611), Idoia**
8 **Biurrun¹³ (0000-0002-1454-0433), Gianmaria Bonari¹⁴ (0000-0002-5574-6067), Helge Bruelheide^{15,4}**
9 **(0000-0003-3135-0356), Juan Antonio Campos¹³ (0000-0003-4770-0461), Andraž Čarni^{16,17} (0000-**
10 **0002-8909-4298), Alessandro Chiarucci (0000-0003-1160-235X)¹⁸, Mirjana Čuk¹⁹ (0000-0002-8261-**
11 **414X), Renata Čušterevska²⁰ (0000-0002-3849-6983), Yakiv Didukh²¹ (0000-0002-5661-3944),**
12 **Daniel Dítě²² (0000-0001-5251-9910), Zuzana Dítě²² (0000-0002-2895-9024), Tetiana Dziuba²¹ (0000-**
13 **0001-8621-0890), Giuliano Fanelli¹¹ (0000-0002-3143-1212), Eduardo Fernández-Pascual²⁸ (0000-**
14 **0002-4743-9577), Emmanuel Garbolino²³ (0000-0002-4954-6069), Rosario G. Gavilán (0000-0002-**
15 **1022-445x)²⁴, Jean-Claude Gégout²⁵ (0000-0002-5760-9920), Ulrich Graf⁷, Behlül Güler²⁶ (0000-**
16 **0003-2638-4340), Michal Hájek¹ (0000-0002-5201-2682), Stephan M. Hennekens²⁷ (0000-0003-1221-**
17 **0323), Ute Jandt^{15,4} (0000-0002-3177-3669), Anni Jašková¹ (0000-0002-3510-1093), Borja Jiménez-**
18 **Alfaro (0000-0001-6601-9597)²⁸, Philippe Julve²⁹, Stephan Kambach¹⁵ (0000-0003-3585-5837), Dirk**
19 **Nikolaus Karger⁷ (0000-0001-7770-6229), Gerhard Karrer³⁰ (0000-0001-5172-2319), Ali Kavgaci³¹**
20 **(0000-0002-4549-3668), Ilona Knollová¹ (0000-0003-4074-789X), Anna Kuzemko^{1,21} (0000-0002-**
21 **9425-2756), Filip Kůzmič¹⁶ (0000-0002-3894-7115), Flavia Landucci¹ (0000-0002-6848-0384), Attila**
22 **Lengyel³² (0000-0002-1712-6748), Jonathan Lenoir³³ (0000-0003-0638-9582), Corrado Marcenò³⁴**
23 **(0000-0003-4361-5200), Jesper Erenskjold Moeslund³⁵ (0000-0001-8591-7149), Pavel Novák¹ (0000-**
24 **0002-3758-5757), Aaron Pérez-Haase³⁶ (0000-0002-5974-7374), Tomáš Peterka¹ (0000-0001-5488-**
25 **8365), Remigiusz Pielech^{37,38} (0000-0001-8879-3305), Alessandro Pignatti¹¹, Valerijus**

26 **Rašomavičius³⁹ (0000-0003-1314-4356), Solvita Rūsiņa⁴⁰ (0000-0002-9580-4110), Arne Saatkamp^{41,42}**
27 **(0000-0001-5638-0143), Urban Šilc¹⁶ (0000-0002-3052-699X), Željko Škvorc⁴³ (0000-0002-2848-**
28 **1454), Jean-Paul Theurillat^{44,45} (0000-0002-1843-5809), Thomas Wohlgemuth⁷ (0000-0002-4623-**
29 **0894) & Milan Chytrý¹ (0000-0002-8122-3075)**

30

31 *¹Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic*

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

34 *³Plant Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of*
35 *Bayreuth, Bayreuth, Germany*

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

37 *⁵Department of Biological Chemical and Pharmaceutical Sciences and Technologies (STEBICEF),*
38 *University of Palermo, Palermo, Italy*

39 *⁶Faculty of Agricultural and Environmental Sciences, University of Rostock, Rostock, Germany*

40 *⁷Swiss Federal Research Institute WSL, Birmensdorf, Switzerland*

41 *⁸Department of Earth and Environmental Sciences, KU Leuven, Leuven, Belgium*

42 *⁹KU Leuven Plant Institute, KU Leuven, Leuven, Belgium*

43 *¹⁰Department of Botany, Faculty of Agriculture, University of Belgrade, Beograd, Serbia*

44 *¹¹Department of Environmental Biology, Sapienza University of Rome, Roma, Italy*

45 *¹²Vegetation Ecology & Plant Diversity, Albrecht von Haller Institute of Plant Sciences, University of*
46 *Göttingen, Göttingen, Germany*

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

- 48 ¹⁴*Free University of Bozen-Bolzano, Bolzano, Italy*
- 49 ¹⁵*Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg,*
50 *Halle (Saale), Germany*
- 51 ¹⁶*Research Centre of the Slovenian Academy of Sciences and Arts, Jovan Hadži Institute of Biology,*
52 *Ljubljana, Slovenia*
- 53 ¹⁷*School for Viticulture and Enology, University of Nova Gorica, Nova Gorica, Slovenia*
- 54 ¹⁸*BIOME Lab, Department of Biological, Geological & Environmental Sciences, Alma Mater Studiorum -*
55 *University of Bologna, Bologna, Italy*
- 56 ¹⁹*Department of Biology and Ecology, Faculty of Science, University of Novi Sad, Novi Sad, Serbia*
- 57 ²⁰*Faculty of Natural Sciences and Mathematics, Ss. Cyril and Methodius University, Skopje, North*
58 *Macedonia*
- 59 ²¹*M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv, Ukraine*
- 60 ²²*Plant Science and Biodiversity Center, Slovak Academy of Sciences, Bratislava, Slovakia*
- 61 ²³*Climpact Data Science, Nova Sophia - Regus Nova, Sophia Antipolis Cedex, France*
- 62 ²⁴*Botany Unit, Department of Pharmacology, Pharmacognosy and Botany, Complutense University,*
63 *Madrid, Spain*
- 64 ²⁵*Université de Lorraine, AgroParisTech, INRAE, UMR Silva, Nancy, France*
- 65 ²⁶*Biology Education, Dokuz Eylül University, Buca, Izmir, Turkey*
- 66 ²⁷*Wageningen Environmental Research, Wageningen, the Netherlands*
- 67 ²⁸*IMIB Biodiversity Research Institute, University of Oviedo, Mieres, Spain*
- 68 ²⁹*Faculté de Gestion, Economie et Sciences, Lille Catholic University, Lille, France*

69 ³⁰*Department of Integrative Biology and Biodiversity Research, University of Natural Resources and Life*
70 *Sciences Vienna, Vienna, Austria*

71 ³¹*Burdur Food Agriculture and Livestock Vocational School, Burdur Mehmet Akif Ersoy University,*
72 *Burdur, Türkiye*

73 ³²*Centre for Ecological Research, Institute of Ecology and Botany, Vácrátót, Hungary*

74 ³³*UMR CNRS 7058 "Ecologie et Dynamique des Systèmes Anthropisés" (EDYSAN), Université de*
75 *Picardie Jules Verne, Amiens, France*

76 ³⁴*Department of Chemistry, Biology and Biotechnology, University of Perugia, Perugia, Italy*

77 ³⁵*Department of Ecoscience, Section for Biodiversity, Aarhus University, Aarhus, Denmark*

78 ³⁶*Department of Evolutionary Biology, Ecology and Environmental Sciences, University of Barcelona,*
79 *Barcelona, Spain*

80 ³⁷*Department of Forest Biodiversity, Faculty of Forestry, University of Agriculture in Kraków, Kraków,*
81 *Poland*

82 ³⁸*Foundation for Biodiversity Research, Wrocław, Poland*

83 ³⁹*Institute of Botany, Nature Research Centre, Vilnius, Lithuania*

84 ⁴⁰*Faculty of Geography and Earth Sciences, University of Latvia, Riga, Latvia*

85 ⁴¹*Conservatoire Botanique National Méditerranéen, Hyères, France*

86 ⁴²*Aix Marseille Université, Université Avignon, CNRS, IRD, UMR IMBE, Marseille, France*

87 ⁴³*University of Zagreb, Faculty of Forestry and Wood Technology, Zagreb, Croatia*

88 ⁴⁴*Fondation J.-M. Aubert, Champex-Lac, Switzerland*

89 ⁴⁵*Department of Plant Sciences, University of Geneva, Chambésy, Switzerland*

90

91 **Correspondence**

92 Lubomír Tichý, Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská
93 2, 611 37 Brno, Czech Republic. E-mail: tichy@sci.muni.cz

94

95 **Funding information**

96 This research was funded through the 2019-2020 BiodivERsA joint call for research proposals, under the
97 BiodivClim ERA-Net COFUND program, and with the funding organizations Technology Agency of the
98 Czech Republic (SS70010002), the Swiss National Science Foundation SNF (project: FeedBaCks,
99 193907), and the German Research Foundation (DFG BR 1698/21-1, DFG HI 1538/16-1). E.F.P. was
100 supported by the Jardín Botánico Atlántico (SV-20-GIJON-JBA), A.Č., U.Š. and F.K. were funded by
101 Slovenian Research Agency (ARRS P1-0236), I.B. and J.A.C. were funded by the Basque Government
102 (IT1487-22), and SR was funded by the LIFE Integrated Project LIFE19 IPE/LV/000010.

103 **Running title**

104 Ellenberg-type indicator values for European plants

105

106 **Abstract**

107 **Aims:** Ellenberg-type indicator values are expert-based rankings of plant species according to their
108 ecological optima on main environmental gradients. Here we extend the indicator-value system proposed
109 by Heinz Ellenberg and co-authors for Central Europe by incorporating compatible systems developed for
110 other European regions and creating a harmonized dataset of indicator values applicable at the European
111 scale.

112 **Methods:** We collected European datasets of indicator values for vascular plants and selected 13 datasets
113 that used the nine-, ten- or twelve-step scales defined by Ellenberg for light, temperature, moisture,

114 reaction, nutrients and salinity. We compared these values with the original Ellenberg values and used
115 those that showed consistent trends in regression slope and coefficient of determination. We calculated
116 the average value for each combination of species and indicator value from these datasets. based on
117 species co-occurrences in European vegetation plots, we also calculated new values for species that were
118 not assigned an indicator value.

119 **Results:** We provide a new dataset of Ellenberg-type indicator values for 8,908 European vascular plant
120 species (8,168 for light, 7,400 for temperature, 8,030 for moisture, 7,282 for reaction, 7,193 for nutrients
121 and 7,507 for salinity), of which 398 species have been newly assigned to at least one indicator value.

122 **Conclusions:** The newly introduced indicator values are compatible with the original Ellenberg values.
123 They can be used for large-scale studies of the European flora and vegetation or for gap-filling in
124 regional datasets. The

125 European values and the original and taxonomically harmonized regional datasets of Ellenberg-type
126 indicator values are available in Supplementary Information and the Zenodo repository.

127

128 **Introduction**

129 Bioindication of abiotic site conditions from environmental relationships of plant species has a long
130 tradition (Cajander, 1926; Iversen, 1936). Seminal work was done by the German vegetation ecologist
131 Heinz Ellenberg, who published a comprehensive dataset of indicator values for plant species (Ellenberg,
132 1974). These values were based on field observations and partly also measurements, mainly from
133 Germany. Ellenberg defined indicator values for seven abiotic environmental variables: light,
134 temperature, continentality, moisture, soil reaction, nutrient (nitrogen) content, and salinity. While the
135 first three variables relate mainly to above-ground conditions, the last four describe substrate conditions
136 (soil or water). Ellenberg originally defined indicator values for nitrogen content, but later studies
137 suggested that they rather reflect general soil fertility, such as the combined availability of both nitrogen

138 and phosphorus (Boller-Elmer, 1977; Briemle, 1986; Hill & Carey, 1997). Therefore, Ellenberg's original
139 nitrogen values are nowadays more often called nutrient values (Ellenberg et al. 1992).

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

146 Ellenberg's system was inspired in part by the ideas of Cajander (1926), who used associations of plant
147 species to evaluate forest types and productivity, and Iversen (1936), who arranged plants into response
148 groups to environmental variables relevant to plant growth. However, Ellenberg (1948, 1950, 1952) was
149 the first to use numerical codes instead of verbally defined levels of environmental gradients. Ellenberg
150 (1948) also proposed using these codes to calculate community means based on simple species presence,
151 or weighted values based on abundance (i.e., percentage cover in the plot). Subsequently, other authors
152 (e.g., Zólyomi et al., 1967; Zlatník et al., 1970) adopted Ellenberg's concept of bioindication by creating
153 regional systems of indicator values for other parts of Europe. Not only vascular plants but later also
154 bryophytes and lichens were characterized by indicator values following the same system (Ellenberg et
155 al., 1992).

156 Repeatedly updated and refined, Ellenberg indicator values (Ellenberg et al., 1992, 2001; Ellenberg &
157 Leuschner, 2010) are a widely used tool for rapid estimation of environmental conditions without direct
158 measurements (Diekmann, 2003; Holtland et al., 2010). In the Web of Science database, 907 articles with
159 the keywords (including words used in abstracts) 'Ellenberg' AND 'Indicator' were registered between 1
160 January 1974 and 30 June 2022, indicating their importance to plant ecologists. Several studies found a
161 good agreement between community means (weighted or non-weighted) calculated from Ellenberg
162 indicator values and values of environmental variables measured *in situ* (Ellenberg et al., 1992;

163 Herzberger & Karrer, 1992; Hill & Carey, 1997; Ertsen et al., 1998; Schaffers & Sýkora, 2000; Wamelink
164 et al., 2002; Diekmann, 2003; Chytrý et al., 2009; Sicuriello et al., 2014). Some authors also discussed the
165 consistency of indicator values between different geographical areas (Diekmann & Lawesson, 1999;
166 Gégout & Krizova, 2003; Godefroid & Dana, 2007; Wasof et al., 2013). Because Ellenberg's original
167 dataset focused on plants occurring in the western part of Central Europe, other authors proposed
168 indicator values for other European regions. These datasets included many species that were missing from
169 Ellenberg's original dataset and often contained different values for the same species, reflecting shifted
170 optima of their realized niches between regions (e.g. Landolt, 1977; Tsyganov, 1983; Jurko, 1990; Karrer,
171 1992; Borhidi, 1995; Mayor López, 1996; Böhling et al., 2002; Zarzycki et al., 2002; Hill et al., 2004;
172 Pignatti, 2005; Landolt et al., 2010; Didukh, 2011; Chytrý et al., 2018; Domina et al., 2018; Guarino &
173 La Rosa, 2019; Jiménez-Alfaro et al., 2021). Specialized datasets of indicator values for species limited to
174 a specific habitat type but covering large areas were also created (e.g. Hájek et al., 2020 – mires; Dítě et
175 al., 2022 – saline habitats).

176 The increasing number of synthetic and macroecological studies on European vegetation, catalyzed by the
177 launch of the European database of vegetation plots (European Vegetation Archive, EVA; Chytrý et al.,
178 2016), require a coherent system of species-level indicator values. Although regional systems of indicator
179 values have been widely used for a long time, no consensual system of indicator values for European
180 plants has been developed so far. Therefore, we have compiled a harmonized dataset of vascular plant
181 indicator values for light, temperature, moisture, soil (or water) reaction (related to base saturation),
182 nutrients (site productivity), and salinity suitable for a large part of Europe, using the same numerical
183 scales as defined by Ellenberg. In this article, we describe the content of the new dataset and the methods
184 used to compile it.

185

186 **Methods**

187 We compiled a database of thirteen published European datasets of indicator values for vascular plant
188 species defined on the same nine-degree scale (or ten-degree scale for salinity and twelve-degree scale for
189 moisture) as the original Ellenberg indicator values (Ellenberg et al., 1992, 2001). We refer to these
190 datasets as *Ellenberg-type* indicator values. Datasets with scales containing a lower number of degrees,
191 i.e., with a coarser resolution, were not included. If the scale had a higher number of degrees than nine (or
192 ten for salinity or twelve for moisture), we accepted it, provided that: (1) the additional degrees
193 represented an extension of the environmental gradient, while the other degrees retained the same
194 meaning as in the original Ellenberg dataset (e.g. extending the nine-degree temperature scale originally
195 defined for Central Europe to twelve degrees to reflect Mediterranean conditions; Pignatti, 2005) or (2)
196 the additional degrees represented intermediate values on the nine- or twelve-degree scale (e.g. the 17-
197 degree temperature scale and the 23-degree moisture scale in Didukh, 2011). We considered only datasets
198 based entirely or largely on expert knowledge, and excluded those based on values re-calculated from
199 vegetation plots without expert-based assessment of values for individual species (e.g. Lawesson et al.,
200 2003 for the Faroe Islands).

201 The thirteen indicator-value datasets that met the above conditions included: Great Britain (Hill et al.,
202 2000); the Cantabrian Mountains in Spain (Jiménez-Alfaro et al., 2021); France (Julve, 2015);
203 Switzerland and the Alps (Landolt et al., 2010; temperature values only, as the other values use coarser
204 scales than Ellenberg); Germany (Ellenberg et al., 2001, taken from Ellenberg & Leuschner, 2010); Czech
205 Republic (Chytrý et al., 2018); Austria (Karrer, 1992); Hungary (Borhidi, 1995); Ukraine (Didukh, 2011;
206 only the light, temperature and moisture values, as the others cannot be matched to the Ellenberg scales);
207 Italy (Guarino & La Rosa, 2019, a corrected version prepared by R. Guarino for this study); South
208 Aegean region of Greece (Böhling et al., 2002); European mires (Hájek et al., 2020); and saline habitats
209 in Central Europe (Dítě et al., 2022). The scales of these thirteen datasets had twelve degrees for moisture
210 and some of them also for temperature, ten degrees for salinity and nine degrees for the other values.

211 Therefore, we integrated the datasets using twelve-degree scales for temperature and moisture, a ten-
212 degree scale for salinity and nine-degree scales for light, reaction and nutrients.

213 We did not include the indicator values for continentality because they are based on species geographical
214 ranges. Continentality values may have an ambiguous meaning at the local scale since they may correlate
215 with different factors, including seasonal differences in temperature and precipitation, diurnal differences
216 in temperature, annual minimum temperatures and drought. Moreover, Berg et al. (2017) identified
217 methodological weaknesses in the original Ellenberg approach to continentality values, proposed an
218 improved protocol for their compilation, and defined new formally-verified values.

219 We unified the taxonomy and nomenclature of all vascular plant taxa across the thirteen datasets
220 according to the Euro+Med PlantBase (<http://euoplusmed.org>). We merged subspecies, varieties and
221 forms at the species level and removed hybrids and rare alien species (mostly casual neophytes;
222 Richardson et al., 2000). We also merged as ‘aggregates’ those taxonomically related species that are
223 difficult to identify and, therefore, are often misidentified or not identified at all, such as species of the
224 *Achillea millefolium* group in the *Achillea millefolium* aggr. The aggregates used were those defined in
225 the Euro+Med PlantBase (Euro+Med, 2021) and the EUNIS-ESy expert system for EUNIS Habitat
226 Classification (Chytrý et al., 2020). For infraspecific taxa within the same species or species within the
227 same aggregate, we used their arithmetic mean as the indicator value for the species or aggregate to
228 equally weight the indicator values of species in all datasets where the species occurs. In addition, we also
229 calculated the median, minimum, and maximum. Some databases provided indicator values for both
230 individual species and aggregates of species. Although some of these aggregates are not regularly used in
231 vegetation science and do not fit the concept of Euro+Med and EUNIS, we kept them on the list to avoid
232 losing information.

233 The new system of indicator values was prepared by calculating the arithmetic mean for each
234 combination of species and environmental variable across all compatible regional datasets in which an
235 indicator value was defined for the target species. As a first step, we tested whether the indicator values of

236 each of the twelve datasets (other than the original Ellenberg dataset) were compatible with the Ellenberg
237 values. We conducted two comparisons. For the first one, we tested a direct pairwise relationship between
238 the original Ellenberg values (independent variable) for individual species (Ellenberg & Leuschner, 2010)
239 and values for the same species in a different dataset (dependent variable; species-based regression). For
240 the second comparison, we used vegetation plots from the EVA database (Chytrý et al., 2016) to calculate
241 the unweighted means of the original Ellenberg values (independent variable) and indicator values from
242 the other 12 datasets (dependent variable; plot-based regression). A total of 1,790,582 vegetation plots
243 covering a wide range of vegetation types from across Europe were available for this approach. The
244 Russian Federation, Georgia, Armenia, and Azerbaijan were not included due to their peripheral
245 biogeographical location, lack of indicator-value datasets compatible with Ellenberg scales, and low
246 density of plots in the EVA database. Species nomenclature was unified in the same way as in the
247 indicator-value databases (see above). We selected only vegetation plots that contained at least five
248 species with indicator values, both from the original Ellenberg dataset and from other indicator-value
249 datasets, resulting in 622,402 plots for light indicator values, 413,832 for temperature, 615,301 for
250 moisture, 490,617 for reaction, 575,406 for nutrients and 673,141 for salinity.

251 Based on the regression analyses described above, we selected datasets that showed consistent trends in
252 both the direct species-based and indirect plot-based regressions against the original Ellenberg indicator
253 values. In order to compare these trends, we selected two regression characteristics: (a) the coefficient of
254 determination (R^2), which shows the amount of variation in the dependent variable that is explained by
255 the regression. However, the same R^2 can be obtained with vastly different slopes. Therefore, we also
256 adopted (b) the second criterion of the slope, which mainly indicates differences at the ends (extremes) of
257 the indicator value range. Based on the empirical assessment of the regression results, we selected only
258 indicator values for which the regression slope was within the range from 0.5 to 1.2 and R^2 was higher
259 than 0.5. The only exception was the salinity dataset for Central Europe (Dítě et al., 2022), which, in
260 contrast to Ellenberg salinity values, did not include any non-halophytic species.

261 When different indicator values occurred in different datasets for the same species and the same
262 environmental variable, we calculated the mean of these values. If the difference between the minimum
263 and maximum values across all original taxa that were merged into the same species or aggregate was
264 more than three indicator value units across all datasets, and the range crossed the central value (i.e. a
265 value of 5 for the 9-degree scales and a value of 6.5 for the 12-degree scales), we reported no indicator
266 value. The condition of crossing the central degree filtered out generalist species occurring under
267 intermediate conditions, while preserving values for species occurring under more extreme conditions.
268 All indicator values resulting from either the averaging or median calculation that had more than one
269 decimal place were rounded to one decimal place.

270 To assign indicator values to species for which indicator values were not available in any of the datasets
271 but which occurred in at least 50 EVA vegetation plots, we used the method described by Chytrý et al.
272 (2018). First, for each of these target species, we searched for the set of other species that had the most
273 similar occurrence pattern across EVA plots. We measured the degree of co-occurrence of species pairs
274 using the *phi* coefficient of association (Sokal & Rohlf, 1995). For each species with no indicator value,
275 we listed all species with an indicator value that had a similar occurrence pattern (interspecific association
276 of $\phi > 0.1$). If there were at least five such species, we calculated the mean (rounded to one decimal
277 place) of their indicator values and assigned it as the indicator value for the target species with no
278 indicator value. If more than 20 species met these conditions, we considered only the 20 species with the
279 highest *phi* value. If there were fewer than five such species, no new indicator values were calculated.

280 Mean indicator values always have a narrower range than the original scale of indicator values (see Hill et
281 al., 2000), which reduces the compatibility between the newly calculated and original indicator values. To
282 standardize the range of indicator values for species with newly-calculated values, we first calculated
283 indicator values for species that occurred in at least one dataset of indicator values and for which we knew
284 the original indicator values in the regional datasets. For a set of these species, we calculated a linear
285 regression between the values estimated from species co-occurrence (independent variable) and average

286 indicator values from the regional datasets (dependent variable). Then we used the formula of the
287 regression line to adjust indicator values for species with values estimated only from species co-
288 occurrence, i.e., those for which indicator values were not previously available.
289 Any subjective adjustment of indicator values was avoided. However, indicator values for obligatory
290 epiphytic hemiparasites germinating on trees (*Arceuthobium*, *Loranthus* and *Viscum*) were not included in
291 the final list in the case of nutrients, reaction and salinity.
292 We tested the validity of the harmonized indicator values using an example of indicator values for
293 temperature by regressing them on an independent source of gridded temperature data. We calculated
294 unweighted community-mean temperature indicator values across species in each EVA plot that
295 contained at least five species (413,832 plots) and related them to modeled mean summer temperatures
296 from the Chelsa database (Karger et al., 2017; bio10 – daily mean air temperatures of the warmest quarter
297 for the period of 1981–2010). Data processing and analyses were performed using the programs JUICE v.
298 7.1 (Tichý, 2002) and R v. 4.0.3 (R Core Team, 2022).

299

300 **Results**

301 Of the 12 Ellenberg-type indicator-value datasets (i.e., excluding the original Ellenberg dataset), 11 were
302 found to be at least partially compatible with the original Ellenberg dataset (Table 1, Appendix S1) after
303 being tested with species-based regression and plot-based regression (Appendix S2). Outlier datasets that
304 did not meet our compatibility conditions were excluded from further analyses. Indicator values for the
305 Cantabrian Mountains were excluded entirely. For the Southern Aegean dataset, we retained the indicator
306 values for moisture and salinity, but excluded the other values for lack of compatibility. For the Ukrainian
307 dataset, we retained the indicator values for light and moisture, but excluded temperature (thermal climate
308 or thermoregime).

309

310 *Table 1. Regional datasets of Ellenberg-type indicator values used as a potential source for the European*
311 *dataset. Numbers are given where indicator values are present in the source dataset and were considered*
312 *for the calculation. The numbers are, in turn, counts of species or aggregates (after nomenclature*
313 *standardization) with indicator values. ‘NA’ (not accepted) – the indicator value exists, and the authors*
314 *declared that it follows the Ellenberg concept, but it did not meet our compatibility criteria and was*
315 *excluded from further analyses. ‘NC’ (not considered) – indicator value exists, but its concept or scale*
316 *differs from Ellenberg indicator values. ‘–’ – indicator value does not exist in the source dataset.*
317 *Information on the percentage distribution of indicator values across three indicator value ranges within*
318 *each dataset is provided in Appendix S1.*

Source		Light	Temperature	Moisture	Reaction	Nutrients	Salinity
Germany	Ellenberg & 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
South Aegean	Böhling et al. (2002)	NA	NA	1831	NA	NA	1922
Hungary	Borhidi (1995)	2028	2028	2028	2026	2028	2028
Italy	Guarino & La Rosa (2019)	5136	4985	5092	4869	5049	5121
Saline habitats	Dítě et al. (2022)	–	–	–	–	–	335
Switzerland	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

319
320 The final dataset contained 8,908 European vascular plant species with at least one indicator value
321 Indicator values defined for all six environmental variables were defined for 5,398 species. At least one
322 indicator value was newly assigned for 398 species that were not listed in any regional dataset.
323 Correlation matrix, histograms, and the relative frequency of indicator values for species or mean
324 indicator values for vegetation plots with the relationship between each combination of the environmental
325 variables was shown in Fig. 2 and 3.

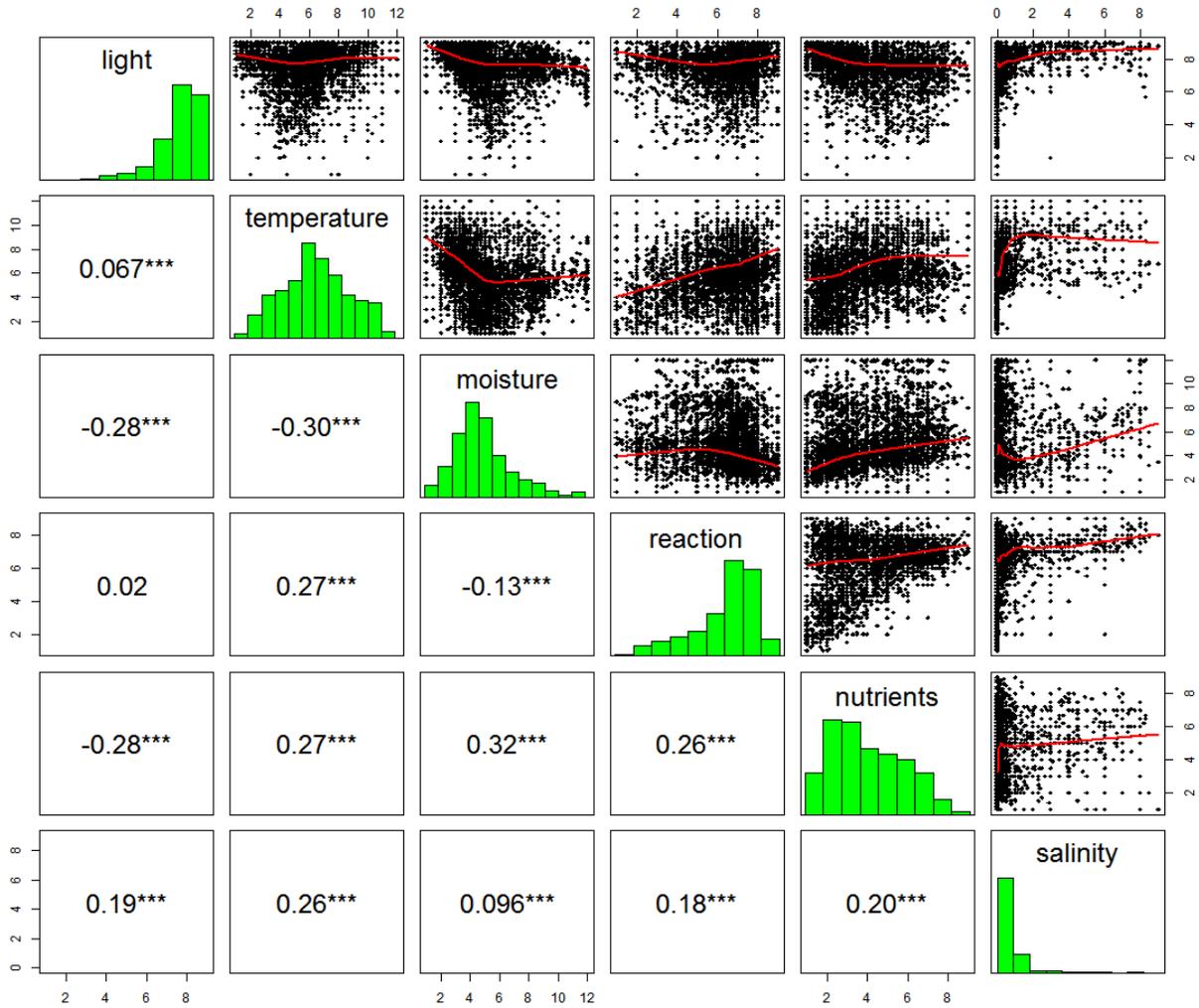
326 The set of 1,790,582 vegetation plots from the EVA database contained 11,161 species of vascular plants
327 after standardizing the nomenclature. Of these, 7,918 (70.9%) had at least one indicator value derived
328 from at least one of the 12 retained datasets or estimated from species co-occurrences. The new indicator
329 values were defined mainly for frequent species. Therefore, at least one indicator value was available for
330 99.7% of all species occurrences in the EVA vegetation plots.

331 Linear regressions between plot mean values calculated from the new dataset of European values for
332 temperature and the mean summer temperature from the Chelsa dataset showed a stronger relationship
333 ($R^2 = 0.49$) than regressions calculated from each regional dataset taken individually (Appendix S3).
334 Community means for temperature values showed negligible differences in slope and coefficient of
335 determination when calculated with or without the the species for which the value is derived from the
336 EVA-based estimations.

337

338 **Discussion**

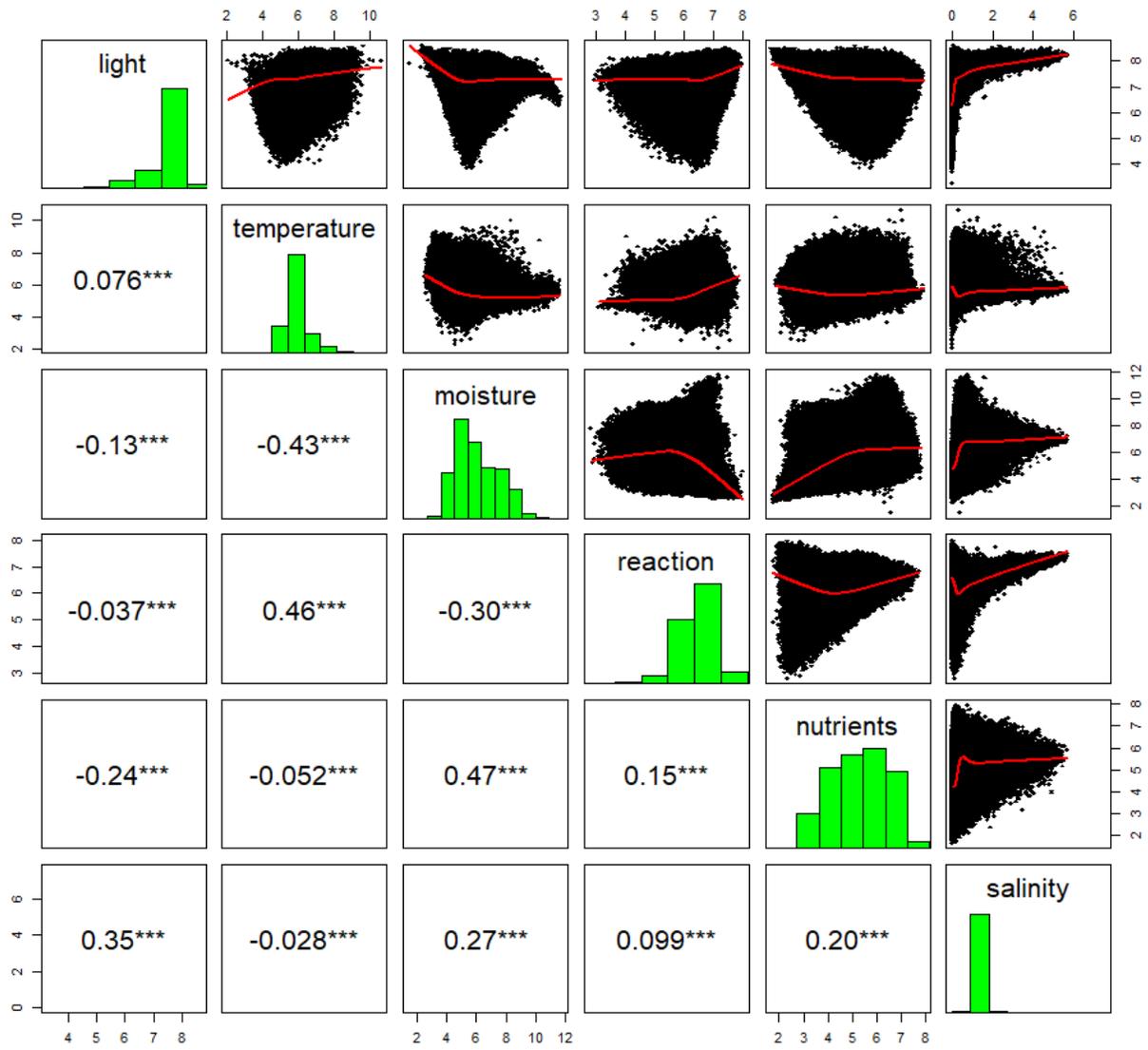
339 We created an extensive dataset of indicator values for six main environmental variables that affect plant
340 distribution and community composition under natural conditions. This dataset covers a large part of
341 Europe and is suitable for European studies of flora and vegetation. Although it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



347

348 *Fig. 1: Correlation matrix of Ellenberg-type indicator values for Europe. Histograms on the diagonal*
 349 *show the relative frequency of species for a particular value along the environmental gradient, boxes*
 350 *below the diagonal show Pearson correlation coefficients with their significance, and scatter plots above*
 351 *the diagonal show the distribution of species in a pairwise comparison between two corresponding*
 352 *indicators (each black dot represents one species)..*

353



354

355 *Fig. 2: Correlation matrix of community means of Ellenberg-type indicator values for Europe calculated*
 356 *for EVA vegetation plots. Histograms on the diagonal show the relative frequency of plots for a particular*
 357 *value along the environmental gradient, boxes below the diagonal show Pearson correlation coefficients*
 358 *with their significance, and scatter plots above the diagonal show the distribution of vegetation plots in a*
 359 *pairwise comparison between two corresponding indicators (each black dot represents one vegetation*
 360 *plot).*

361

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

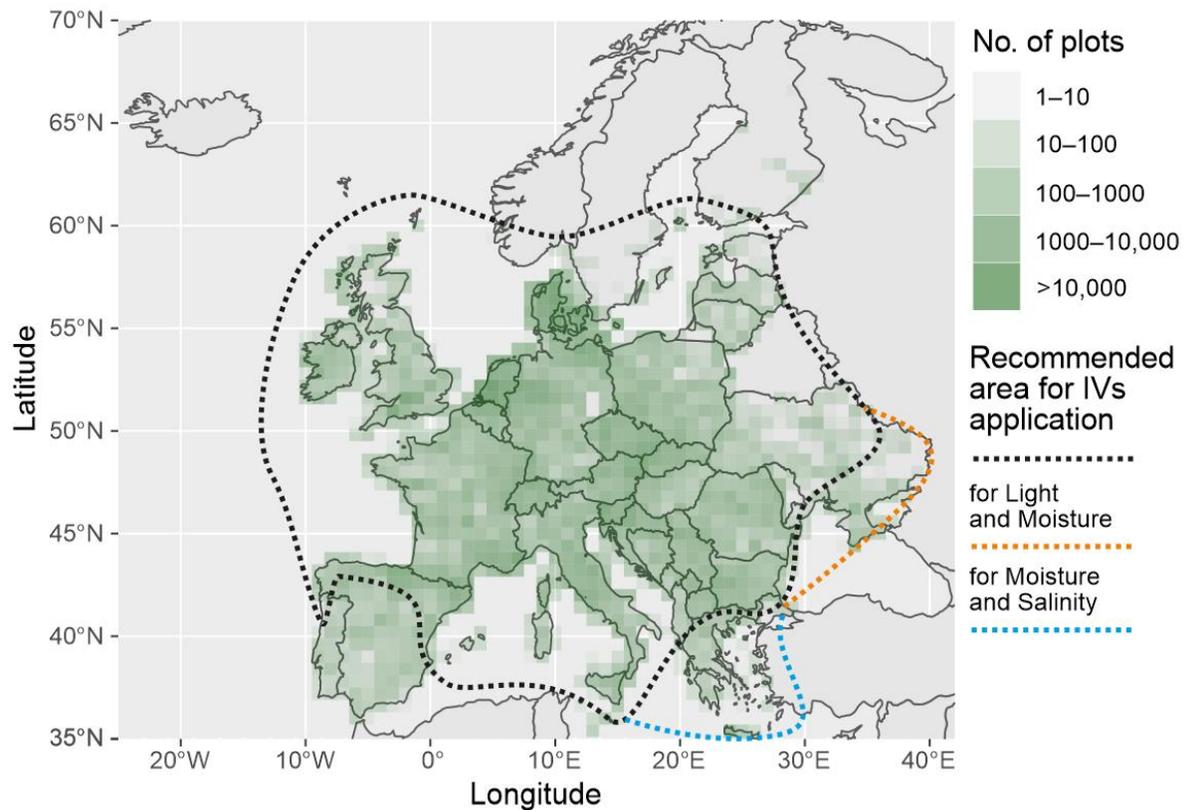
382 Ellenberg (1974) and other authors defined indicator values on ordinal scales, which has sometimes been
383 criticized (Dierschke, 1994). Ellenberg et al. (2001) argued that at least part of their scales have
384 equidistant segmentation of the interval scale, which allows calculating community means. ter Braak &
385 Barendregt (1986) showed that community means calculated from indicator values best estimate
386 environmental conditions when each indicator value is the centroid of the symmetric (normally

387 distributed) species response curve to the given environmental variable. Other authors (Pignatti et al.,
388 2001; Marcenò & Guarino, 2015; Wildi, 2016) have also shown that in large datasets, Ellenberg indicator
389 values can be evaluated with parametric tests because they tend to be normally distributed. Because many
390 recent studies have also estimated environmental conditions using community means (e.g. Ahl et al.,
391 2021; Baumann et al., 2021; Dwyer et al., 2021; Jaroszewicz et al., 2021), we considered all scales of
392 published indicator values to be interval scales. Differences among published sources were smoothed by
393 calculating means with decimal precision. The new dataset of indicator values retains the range of the
394 original Ellenberg scales of nine, ten or twelve degrees, so it is compatible with other datasets defined on
395 the same scales.

396 As our indicator-value dataset is prepared for broad-scale analyses, it uses a relatively coarse taxonomic
397 resolution at the level of species or, in some cases, species aggregates. However, different subspecies of
398 the same species or different narrowly-defined species within an aggregate may differ substantially in
399 their ecological requirements for some environmental variables (e.g. Landolt et al., 2010). Therefore, for
400 some species or aggregates in our dataset, no indicator value was given for some environmental variables.
401 As a result, only 4,946 (44.3%) of the vascular plant species occurring in the EVA vegetation plots had an
402 indicator value for all six environmental variables. Another reason for the relatively low number of such
403 species was that we used only six datasets that contained indicator values for less than six environmental
404 variables compatible with the Ellenberg scales (Hill et al., 2000; Böhling et al., 2002; Landolt et al., 2010;
405 Didukh, 2011; Hájek et al., 2020; Dítě et al., 2022).

406 The original Ellenberg values had been estimated primarily by expert knowledge. Cornwell & Grubb
407 (2003) demonstrated that Ellenberg species values for different environmental conditions are often not
408 independent. They found a significant rank correlation for the relationship between nutrients and moisture
409 ($r_s = 0.362$, $p = 0.001$), which is also found in our harmonized dataset (Fig. 1). Similar trends of the
410 relationship between environmental factors can be seen in Fig. 2, where we compared unweighted
411 community means calculated for vegetation plots of the EVA database. The reason of partial

412 intercorrelations between indicators for individual species is not so obvious as for community means, in
413 which the problem is much more evident because the indication of ecological factors is related to exact
414 site conditions. However, comparing Fig. 1 and Fig. 2, the interpretation of inter-correlations is not trivial.
415 Independent verification of the validity of our dataset of indicator values in relation to accurately
416 measured local environmental variables is difficult because there are no standardized measurements of
417 local conditions at the European scale at the sites where the vegetation was sampled. The only exception
418 is temperature, which has both local and macroscale components considered in the indicator values.
419 Therefore, the community mean indicator values can be compared with interpolated data from
420 temperature measurements at climate stations. Such data represent macroclimate, but Ellenberg (1974)
421 also derived temperature indicator values from species occurrence in altitudinal belts in Germany and the
422 Alps. There was a strong relationship between mean summer temperatures from the Chelsa database
423 (Karger et al., 2017) and community mean temperature indicator values for vegetation plots from the
424 EVA database. However, we did not account for differences in local conditions, such as slope, aspect and
425 shading from trees, shrubs and adjacent topographic features, which can affect local temperatures but are
426 not available for all vegetation plots. Community means calculated from directly assigned indicator
427 values and those calculated using species co-occurrences showed negligible differences in R^2 values
428 (Appendix S3), largely due to the robustness of calculating community means, as also shown in Ewald
429 (2003). Species with indicator values calculated based on species co-occurrences represented only about
430 3% of the species in the EVA database, and these were mainly rare species.



431

432

Fig. 3: Europe divided into a grid of 0.6° for latitude and 1° for longitude. Shades of green represent the

433

density of 413,705 georeferenced vegetation plots from the EVA database that contain at least five

434

species with indicator value for each environmental variable: light, temperature, moisture, reaction,

435

nutrients and salinity. The black dotted line defines the approximate area, for which we recommend

436

using the dataset of indicator values for all environmental variables. The orange dotted line indicates an

437

additional area where light and moisture values can be safely used, and the blue-dotted line is an

438

additional area where moisture and salinity values can be safely used.

439

440

The 12 regional datasets of species indicator values integrated into our unified dataset cover most of

441

central and western Europe. However, their reliability decreases with distance from their area of origin

442

(Herzberger & Karrer, 1992; Englisch & Karrer, 2001; Coudun & Gégout, 2005; Godefroid & Dana,

443

2007), as some species may change their realized niche or be represented by genotypes adapted to

444 different fundamental niches (ecotypic adaptation; Hájková et al. 2008). For example, the niche width of
445 some European species increases northward, making Ellenberg indicator values less applicable in
446 northern Europe (Diekmann, 1995; Hedwall et al., 2019). In contrast, some species shift and narrow their
447 niche toward the edges of their distribution range (Papuga et al., 2018) relative to their center of
448 distribution (Englisch & Karrer, 2001). This is consistent with our comparisons of regional datasets,
449 which showed the largest deviations from the original Ellenberg values for datasets from regions that are
450 geographically and climatically farthest away from Germany, e.g. the Cantabrian Mountains in Spain
451 (Jiménez-Alfaro et al., 2021) and the South Aegean region of Greece (Böhling et al., 2002). It is also
452 likely that local endemics, e.g., in the Cantabrian Mountains and the Aegean region, outcompete species
453 with broader geographic ranges from a part of the full realized niches of the latter, resulting in a shift of
454 their environmental requirements and the narrowing of the realized niche. Therefore, we did not (or only
455 partially) consider these datasets from distant areas. As a result, we consider the new dataset of indicator
456 values to be mainly representative of Central and Western Europe, and southern and eastern adjacent
457 biogeographical areas (Fig. 3). For the Mediterranean region, especially for the Iberian Peninsula, Greece,
458 Turkey and probably also southeastern Ukraine, new systems of ecological indicator values need to be
459 developed, based on local observations, expert knowledge and careful comparisons with indicator values
460 already established in other parts of Europe.

461 Although the primary motivation for our work was to create a dataset of Ellenberg-type indicator values
462 that can be used for broad-scale international studies of macroecological patterns of the European flora
463 and vegetation, this dataset can also be used in local studies. Its advantage is that it retains the traditional
464 Ellenberg scales. Thus, if a local study uses a regional system of Ellenberg-type indicator values from a
465 nearby region, our harmonized European dataset can be used to add values for species that are missing
466 from the regional system but occur in the study area. It is likely that most regional systems of indicator
467 values provide more accurate estimates of site conditions in their region than the European dataset, which
468 is based on averaging indicator values from different regions. For example, species that behave as

469 generalists on the European scale and thus were not assigned an indicator value in the European dataset
470 may have narrower niches and be good indicators in particular regions. Therefore, it is reasonable to
471 continue to use regional systems of indicator values for local studies in regions where such systems exist.
472 Nevertheless, if local studies from different regions use the European system of indicator values, their
473 results can be directly compared. The next step would be to test the explanatory power of the new
474 indicator values to predict measured climate and soil variables in plots.

475

476 **Acknowledgements**

477 We thank Cajo ter Braak for helpful comments on the manuscript, Jan Divišek for the first version of the
478 climate data used for testing, and database custodians and all researchers who collected the vegetation-
479 plot data stored in the EVA database.

480

481 **Author contributions**

482 LT and MC conceived the research idea; IA standardized the nomenclature and prepared the data; RG
483 revised the Italian indicator values; LT proposed analyses and performed all calculations; LT, MC and IA
484 wrote the text; GM helped visualize the appendices; all authors commented on the manuscript.

485

486 **Data availability statement**

487 The vegetation-plot data used in this study are stored in the European Vegetation Archive database (EVA;
488 <http://euroveg.org/eva-database>) under project number 142, product (a). Tables of original indicator
489 values for each region and harmonized indicator values for Europe can be downloaded from the Zenodo
490 repository (<https://doi.org/10.5281/zenodo.6984813>), where also the future updates will be available.

491

492 **Supporting information of the paper**

493 **Appendix S1.** Percentages of indicator values in regional datasets selected as a potential source for a
494 harmonized European dataset of indicator values.

495 **Appendix S2.** Evaluation of 12 regional systems of ecological indicator values based on their relationship
496 to Ellenberg indicator values.

497 **Appendix S3.** Comparison of mean Ellenberg-type indicator values for temperature calculated for
498 vegetation plots and mean summer temperature for plot locations obtained from climatic datasets.

499

500 **References**

501 Ahl, L., Aas, G., Walentowski, H., Höltnen, A.M. & Feulner, M. (2021) Niche differentiation between
502 *Malus sylvestris* and its hybrid with *Malus domestica* indicated by plant community, soil and light.
503 *Journal of Vegetation Science*, 32, e13078. <https://doi.org/10.1111/jvs.13078>

504 Baumann, M., Dittrich, S., Körner, M. & von Oheimb, G. (2021) Temporal changes in the ground
505 vegetation in spruce forests in the Erzgebirge (Ore Mountains) — bryophytes are better indicators
506 of the impact of liming and of sulphur and nitrogen deposition than the herb layer. *Applied*
507 *Vegetation Science*, 24, e12598. <https://doi.org/10.1111/avsc.12598>

508 Berg, C., Welk, E. & Jäger, E.J. (2017) Revising Ellenberg's indicator values for continentality based on
509 global vascular plant species distribution. *Applied Vegetation Science*, 20, 482–493.
510 <https://doi.org/10.1111/avsc.12306>

511 Böhling, N., Greuter, W. & Raus, T. (2002) Zeigerwerte der Gefäßpflanzen der Südägäis (Griechenland)
512 (Indicator values of vascular plants in the South Aegean (Greece)). *Braun-Blanquetia*, 32, 1–108.

- 513 Boller-Elmer, K.C. (1977) Stickstoff-Düngungseinflüsse von Intensiv-Grünland auf Streu- und
514 Moorwiesen. *Veröffentlichungen des Geobotanischen Institutes der Eidg. Tech. Hochschule,*
515 *Stiftung Rübel, in Zürich*, 63, 1-103. <https://doi.org/10.3929/ethz-a-000123290>
- 516 Borhidi, A. (1995) Social behaviour types, the naturalness and relative ecological indicator values of the
517 higher plants in the Hungarian flora. *Acta Botanica Hungarica*, 39, 97–181.
- 518 Briemle, G. (1986) Vergleich der Stickstoff-Mineralisation mit der N-Zahl Ellenberg's am Beispiel einer
519 Streuwiese im Alpenvorland – Erste Erfahrungen mit zweijährigen Nmin- Untersuchungen
520 (Comparison of nitrogen mineralization with Ellenberg's N-value using the example of a litter
521 meadow in the foothills of the Alps – first experiences with two-year Nmin investigations). *Natur*
522 *und Landschaft*, 61, 423–427.
- 523 Cajander, A.K. (1926) The theory of forest types. *Acta Forestalia Fennica*, 29, 1–108.
524 <https://doi.org/10.14214/aff.7193>.
- 525 Chytrý, M., Hejcman, M., Hennekens, S.M. & Schellberg, J. (2009) Changes in vegetation types and
526 Ellenberg indicator values after 65 years of fertilizer application in the Rengen Grassland
527 Experiment, Germany. *Applied Vegetation Science*, 12, 167–176. [https://doi.org/10.1111/j.1654-](https://doi.org/10.1111/j.1654-109X.2009.01011.x)
528 [109X.2009.01011.x](https://doi.org/10.1111/j.1654-109X.2009.01011.x)
- 529 Chytrý, M., Hennekens, S.M., Jiménez-Alfaro, B., Knollová, I., Dengler, J., Jansen, F. et al. (2016)
530 European Vegetation Archive (EVA): an integrated database of European vegetation plots. *Applied*
531 *Vegetation Science*, 19, 173–180. <https://doi.org/10.1111/avsc.12191>
- 532 Chytrý, M., Tichý, L., Dřevojan, P., Sádlo, J. & Zelený, D. (2018) Ellenberg-type indicator values for the
533 Czech flora. *Preslia*, 90, 83–103. <https://doi.org/10.23855/preslia.2018.083>
- 534 Chytrý, M., Tichý, L., Hennekens, S.M., Knollová, I., Janssen, J.A.M., Rodwell, J.S. et al. (2020) EUNIS
535 Habitat Classification: Expert system, characteristic species combinations and distribution maps of
536 European habitats. *Applied Vegetation Science*, 23, 648–675. <https://doi.org/10.1111/avsc.12519>

- 537 Cornwell, W.K. & Grubb, P.J. (2003) Regional and local patterns in plant species richness with respect to
538 resource availability. *Oikos*, 100, 417–428. <https://doi.org/10.1034/j.1600-0706.2003.11697.x>
- 539 Coudun, C. & Gégout, J.-C. (2005) Ecological behaviour of herbaceous forest species along a pH
540 gradient: a comparison between oceanic and semicontinental regions in northern France. *Global
541 Ecology and Biogeography*, 14, 263–270. <https://doi.org/10.1111/j.1466-822X.2005.00144.x>
- 542 Didukh, Ya.P. (2011) *The ecological scales for the species of Ukrainian flora and their use in
543 synphytoindication*. Kyiv: Phytosociocentre.
- 544 Diekmann, M. (1995) Use and improvement of Ellenberg's indicator values in deciduous forests of the
545 Boreo-nemoral zone in Sweden. *Ecography*, 18, 178–189. [https://doi.org/10.1111/j.1600-
0587.1995.tb00339.x](https://doi.org/10.1111/j.1600-
546 0587.1995.tb00339.x)
- 547 Diekmann, M. (2003) Species indicator values as an important tool in applied plant ecology – a review.
548 *Basic and Applied Ecology*, 4, 493–506. <https://doi.org/10.1078/1439-1791-00185>
- 549 Diekmann, M. & Lawesson, J.E. (1999) Shifts in ecological behaviour of herbaceous forest species along
550 a transect from northern central to North Europe. *Folia Geobotanica*, 34, 127–141.
551 <https://doi.org/10.1007/BF02803080>
- 552 Dierschke, H. (1994) *Pflanzensoziologie: Grundlagen und Methoden (Plant sociology: principles and
553 methods)*. Stuttgart: Ulmer. 683 pp.
- 554 Dítě, D., Šuvada, R., Tóth, T. & Dítě, Z. (2022) Inventory of halophytes in central Europe. *Preslia*,
555 (reviewed).
- 556 Domina, G., Galasso, G., Bartolucci, F. & Guarino, R. (2018) Ellenberg Indicator Values for the vascular
557 flora alien to Italy. *Flora Mediterranea*, 28, 53–61. <https://doi.org/10.7320/FIMedit28.053>

558 Dwyer, C., Millett, J., Pakeman, R.J. & Jones, L. (2021) Environmental modifiers of the relationship
559 between water table depth and Ellenberg's indicator of soil moisture. *Ecological Indicators*, 132,
560 article 108320. <https://doi.org/10.1016/j.ecolind.2021.108320>

561 Ellenberg, H. (1948) Unkrautgesellschaften als Mass fuer den Säuregrad, die Verdichtung und andere
562 Eigenschaften des Ackerbodens. *Berichten der Landtechnik*, 4, 130–146.

563 Ellenberg, H. (1950) *Landwirtschaftliche Pflanzensoziologie. I. Unkrautgemeinschaften als Zeiger für*
564 *Klima und Boden (Agricultural Plant Sociology. I. Weed communities as indicators of climate and*
565 *soil)*. Stuttgart: Ulmer. 141 pp.

566 Ellenberg, H. (1952) *Landwirtschaftliche Pflanzensoziologie. II. Wiesen und Weiden und ihre*
567 *standörtliche Bewertung (Agricultural Plant Sociology. II. Meadows and pastures and their site*
568 *assessment)*. Stuttgart: Ulmer. 143 pp.

569 Ellenberg, H. (1974) Zeigerwerte der Gefäßpflanzen Mitteleuropas (Indicator values of vascular plants in
570 Central Europe). *Scripta Geobotanica*, 9, 1–97.

571 Ellenberg, H. & Leuschner, C. (2010) Zeigerwerte der Pflanzen Mitteleuropas (Indicator values of
572 vascular plants in Central Europe). In: Ellenberg H. & Leuschner, C., *Vegetation Mitteleuropas mit*
573 *den Alpen (Vegetation of Central Europe including the Alps)*. 6th ed. Stuttgart: Ulmer. 1334 pp.
574 <https://doi.org/10.36198/9783825281045>.

575 Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. (1992) Zeigerwerte von
576 Pflanzen in Mitteleuropa. (Indicator values of plants in Central Europe) 2nd ed. *Scripta*
577 *Geobotanica*, 18, 1–258.

578 Ellenberg, H., Weber, H.E., Düll, R., Wirth, V. & Werner, W. (2001) Zeigerwerte von Pflanzen in
579 Mitteleuropa (Indicator values of plants in Central Europe). 3rd ed. *Scripta Geobotanica*, 18, 1–
580 262.

581 Englisch, T. & Karrer, G. (2001) Zeigerwertssysteme in der Vegetationsanalyse – Anwendbarkeit, Nutzen
582 und Probleme in Österreich (Indicator value systems in vegetation analysis - applicability, utility
583 and problems in Austria). *Berichte der Reinhold-Tüxen-Gesellschaft*, 13, 83–102.

584 Ertsen, A.C.D., Alkemade, J.R.M. & Wassen, M.J. (1998) Calibrating Ellenberg indicator values for
585 moisture, acidity, nutrient availability and salinity in the Netherlands. *Plant Ecology*, 135, 113–124.

586 Euro+Med (2021) *Euro+Med PlantBase – the information resource for Euro-Mediterranean plant*
587 *diversity*. Available at <http://ww2.bgbm.org/EuroPlusMed/> [accessed 2021]

588 Ewald, J. (2003) The sensitivity of Ellenberg indicator values to the completeness of vegetation relevés.
589 *Basic and Applied Ecology*, 4, 507–513. <https://doi.org/10.1078/1439-1791-00155>

590 Gégout, J.C. & Krizova, E. (2003) Comparison of indicator values of forest understory plant species in
591 western Carpathians (Slovakia) and Vosges Mountains (France). *Forest Ecology and Management*,
592 182, 1–11. [https://doi.org/10.1016/S0378-1127\(03\)00068-9](https://doi.org/10.1016/S0378-1127(03)00068-9)

593 Godefroid, S. & Dana, E.D. (2007) Can Ellenberg's indicator values for Mediterranean plants be used
594 outside their region of definition? *Journal of Biogeography*, 34, 62–68.
595 <https://doi.org/10.1111/j.1365-2699.2006.01582.x>

596 Guarino, R. & La Rosa, M. (2019) Digital Italian Flora (Italian). In: Pignatti, S., Guarino, R. & La Rosa,
597 M. (Eds), *Flora d'Italia*, 2nd edition. Bologna: Edagricole, Edizioni Agricole di New Business
598 Media.

599 Hájek, M., Dítě, D., Horsáková, V., Mikulášková, E., Peterka, T., Navrátilová, J. et al. (2020) Towards
600 the pan-European bioindication system: Assessing and testing updated hydrological indicator
601 values for vascular plants and bryophytes in mires. *Ecological Indicators*, 116, article 106527.
602 <http://dx.doi.org/10.1016/j.ecolind.2020.106527>

603 Hájková, P., Hájek, M., Apostolova, I., Zelený, D. & Dítě, D. (2008) Shifts in the ecological behaviour of
604 plant species between two distant regions: evidence from the base richness gradient in mires.
605 *Journal of Biogeography*, 35, 282–294. <https://doi.org/10.1111/j.1365-2699.2007.01793.x>

606 Hedwall, P.-O., Brunet, J. & Diekmann, M. (2019) With Ellenberg indicator values towards the north:
607 Does the indicative power decrease with distance from Central Europe? *Journal of Biogeography*,
608 46, 1041–1053. <https://doi.org/10.1111/jbi.13565>

609 Herzberger, E. & Karrer, G. (1992) Test der internen Konsistenz ökologischer Zeigerwerte am Beispiel
610 der Vegetationsaufnahmen der Österreichischen Waldboden-Zustandsinventur (Test of the internal
611 consistency of ecological indicator values using the example of vegetation plots of the Austrian
612 forest soil status inventory). *FBVA-Berichte*, 70, 93–102.

613 Hill, M.O. & Carey, P.D. (1997) Prediction of yield in the Rothamsted Park Grass Experiment by
614 Ellenberg indicator values. *Journal of Vegetation Science*, 8, 579– 586.
615 <https://doi.org/10.2307/3237210>

616 Hill, M.O., Roy, D.B., Mountford, J.O. & Bunce, R.G.H. (2000) Extending Ellenberg's indicator values
617 to a new area: an algorithmic approach. *Journal of Applied Ecology*, 37, 3–15.
618 <https://doi.org/10.1046/j.1365-2664.2000.00466.x>

619 Hill, M.O., Preston, C.D. & Roy, D.B. (2004) *PLANTATT – Attributes of British and Irish plants: status,*
620 *size, life history, geography and habitats*. Huntingdon: Centre for Ecology & Hydrology.

621 Holtland, W.J., ter Braak, C.J.F. & Schouten, M.G.C. (2010) Iteratio: calculating environmental indicator
622 values for species and relevés. *Applied Vegetation Science*, 13, 369–377.
623 <https://doi.org/10.1111/j.1654-109X.2009.01069.x>

624 Iversen, J. (1936) Biologische Pflanzentypen als Hilfsmittel in der Vegetationsforschung. Ein Beitrag zur
625 ökologischen Charakterisierung und Anordnung der Pflanzengesellschaften (Biological plant types

626 as tools in vegetation research. A contribution to the ecological characterization and arrangement of
627 plant communities). *Meddelelser fra Skalling Laboratoriet Kobenhavn*, 4, 1–224.

628 Jaroszewicz, B., Borysowicz, J. & Cholewińska, O. (2021) Forest floor plant diversity drives the use of
629 mature spruce forests by European bison. *Ecology and Evolution*, 11, 636–647.
630 <https://doi.org/10.1002/ece3.7094>

631 Jiménez-Alfaro, B., Carlón, L., Fernández-Pascual, E., Acedo, C., Alfaro-Saiz, E., Alonso Redondo, R. et
632 al. (2021) Checklist of the vascular plants of the Cantabrian mountains. *Mediterranean Botany*, 42,
633 e74570. <https://doi.org/10.5209/mbot.74570>

634 Julve, P. (2015) *Baseflor. Index botanique, écologique et chorologique de la flore de France (Baseflor.*
635 *Botanical, ecological and chorological index of the flora of France)*. Available at
636 <http://philippe.julve.pagesperso-orange.fr/catminat.htm> [accessed 2022].

637 Jurko, A. (1990) *Ekologické a socioekonomické hodnotenie vegetácie [Ecological and socioeconomic*
638 *assessment of vegetation (Slovak)]*. Bratislava: Príroda.

639 Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W. et al. (2017) Climatologies
640 at high resolution for the earth's land surface areas. *Scientific Data*, 4, 170122.
641 <https://doi.org/10.1038/sdata.2017.122>

642 Karrer, G. (1992) Österreichische Waldboden-Zustandsinventur. Teil VII: Vegetationsökologische
643 Analysen (Austrian forest soil status inventory. Part VII: Vegetation ecology analyses).
644 *Mitteilungen Forstliche Bundesversuchsanstalt Wien*, 168, 193–242.

645 Landolt, E. (1977) Ökologische Zeigerwerte zur Schweizer Flora (Ecological indicator values for the
646 Swiss flora). *Veröffentlichungen des Geobotanischen Institutes der Eidg. Tech. Hochschule,*
647 *Stiftung Rübel, in Zürich*, 64, 1–208.

648 Landolt, E., Bäumler, B., Erhardt, A., Hegg, O., Klötzli, F., Lämmli, W. et al. (2010) *Flora indicativa –*
649 *Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen (Flora*

650 *indicativa - Ecological indicator values and biological features for the flora of Switzerland and the*
651 *Alps*). Bern: Haupt Verlag.

652 Lawesson, J.E., Fosaa, A.M. & Olsen, E. (2003) Calibration of Ellenberg indicator values for the Faroe
653 Islands. *Applied Vegetation Science*, 6, 53–62. <https://doi.org/10.1111/j.1654-109X.2003.tb00564.x>

654 Marcenò, C. & Guarino, R. (2015) A test on Ellenberg indicator values in the Mediterranean
655 evergreen woods (*Quercetea ilicis*). *Rendiconti Lincei. Scienze Fisiche e Naturali*, 26, 345–356.
656 <https://doi.org/10.1007/s12210-015-0448-8>

657 Mayor López, M. (1996) *Indicadores ecológicos y grupos socioecológicos en el Principado de Asturias*
658 *(Ecological indicators and socio-ecological groups in the Principality of Asturias)*. Oviedo:
659 Universidad de Oviedo.

660 Papuga, G., Gauthier, P., Pons, V., Farris, E. & Thompson, J.D. (2018) Ecological niche differentiation in
661 peripheral populations: a comparative analysis of eleven Mediterranean plant species. *Ecography*,
662 41, 1650–1664. <https://doi.org/10.1111/ecog.03331>

663 Pignatti, S., Bianco, P.M., Fanelli, G., Guarino, R., Petersen, L. & Tescarollo, P. (2001) Reliability and
664 effectiveness of Ellenberg's indices in checking flora and vegetation changes induced by climatic
665 variations. In: Walter, G.R., Burga, C.A. & Edwards, P.J. (Eds), *Fingerprints of climate changes:
666 adapted behaviour and shifting species ranges*, New York: Springer, pp. 281–304.
667 <https://doi.org/10.1002/joc.871>

668 Pignatti, S. (2005) Valori di bioindicazione delle piante vascolari della flora d'Italia (Bioindicator values
669 of vascular plants of the flora of Italy). *Braun-Blanquetia*, 39, 1–97.

670 R Core Team (2022) *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation
671 for Statistical Computing. URL: <https://www.R-project.org/>

672 Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000)
673 Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, 6,
674 93–107. <https://doi.org/10.1046/j.1472-4642.2000.00083.x>

675 Schaffers, A.P. & Sýkora, K.V. (2000) Reliability of Ellenberg indicator values for moisture, nitrogen and
676 soil reaction: a comparison with field measurements. *Journal of Vegetation Science*, 11, 225–244.
677 <https://doi.org/10.2307/3236802>

678 Sicuriello, F., De Nicola, C., Dowgiallo, G. & Testi, A. (2014) Assessing the habitat conservation status
679 by soil parameters and plant ecoindicators. *iForest*, 7, 170–177. <https://doi.org/10.3832/ifor0963->
680 007

681 Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*, 3rd edition. New York: Freeman.

682 ter Braak, C.J.F. (1987) *Unimodal models to relate species to environment*. Agricultural mathematics
683 Group, Wageningen. <http://edepot.wur.nl/201452>.

684 ter Braak, C.J.F. & Barendregt, L.G. (1986) Weighted averaging of species indicator values: its efficiency
685 in environmental calibration. *Mathematical Biosciences*, 78, 57–72. <https://doi.org/10.1016/0025->
686 5564(86)90031-3

687 ter Braak, C.J.F. & Gremmen, N.J.M. (1987) Ecological amplitudes of plant species and the internal
688 consistency of Ellenberg's indicator values for moisture. *Vegetatio*, 69, 79–87.

689 Tichý, L. (2002) JUICE, software for vegetation classification. *Journal of Vegetation Science*, 13, 451–
690 453. <https://doi.org/10.1111/j.1654-1103.2002.tb02069.x>

691 Tsyganov, D.N. (1983) *Phytoindication of ecological regimes in the mixed coniferous-broad-leaved*
692 *forest subzone* (Russian). Moskva: Nauka.

693 Wamelink, G.W.W., Joosten, V., van Dobben, H.F. & Berendse, F. (2002) Validity of Ellenberg indicator
694 values judged from physico-chemical field measurements. *Journal of Vegetation Science*, 13, 269–
695 278. <https://doi.org/10.1111/j.1654-1103.2002.tb02047.x>

696 Wasof, S., Lenoir, J., Gallet-Moron, E., Jamoneau, A., Brunet, J., Cousins, S.A.O. et al. (2013) Ecological
697 niche shifts of understorey plants along a latitudinal gradient of temperate forests in northwestern
698 Europe. *Global Ecology and Biogeography*, 22, 1130–1140. <https://doi.org/10.1111/geb.12073>

699 Wildi, O. (2016) Why mean indicator values are not biased. *Journal of Vegetation Science*, 27, 40–49.
700 <https://doi.org/10.1111/jvs.12336>

701 Zarzycki, K., Trzcińska-Tacik, H., Róžański, W., Szelağ, Z., Wołek, J. & Korzeniak, U. (2002)
702 Ecological indicator values of vascular plants of Poland. Kraków: W. Szafer Institute of Botany,
703 Polish Academy of Sciences.

704 Zlatník, A., Križo, M., Svrček, M. & Manica, M. (1970) Lesnická botanika speciální (Forestry botany).
705 Praha: Státní zemědělské nakladatelství.

706 Zólyomi, B., Baráth, Z., Fekete, G., Jakucs, P., Kárpáti, I., Kovács, M. et al. (1967) Einreihung von 1400
707 Arten der ungarischen Flora in ökologische Gruppen nach TWR-Zahlen (Classification of 1400
708 species of the Hungarian flora in ecological groups following the TWR numbers). *Fragmenta*
709 *Botanica Musei Historico-naturalis Hungarici*, 4, 101–142.

710

711 **Supporting information of the paper**

712 Tichý, L. et al. (2022) Ellenberg-type indicator values for European vascular plant species. *Journal of*
 713 *Vegetation Science*.

714 **Appendix S1. Percentages of indicator values in regional datasets selected as a potential**
 715 **source for a harmonized European dataset of indicator values.**

716 Percentages are given where indicator values are present in the source dataset and were included in the
 717 calculation. Three categories (cat1, cat2, cat3) express percentages of species (or aggregates, after
 718 nomenclature standardization) in three indicator value ranges – 1.0–3.0; 3.1–6.9; 7.0–9.0 (7.0–12.0 for
 719 temperature and moisture). ‘NA’ (not accepted) – the indicator value exists, and the authors stated that it
 720 follows the Ellenberg concept, but it did not meet our compatibility rules and was excluded from further
 721 analyses. ‘NC’ (not considered) – the indicator value exists, but its concept or scale differs from the
 722 Ellenberg indicator values. ‘–’ – the indicator value does not exist in the source dataset.

Source		Light	Temperature	Moisture	Reaction	Nutrients	Salinity
		%	%	%	%	%	%
		1-3 3-7 7-9	1-3 3-7 7-12	1-3 3-7 7-12	1-3 3-7 7-9	1-3 3-7 7-9	0-3 3-7 7-9
Germany	Ellenberg & Leuschner (2010)	3 21 76	19 57 24	18 54 28	7 57 36	48 34 18	98 1 1
Austria	Karrer (1992)	2 24 74	24 57 17	13 57 30	6 57 37	46 32 22	97 2 1
Cantabrian Range	Jiménez-Alfaro et al. (2021)	NA	NA	NA	NA	NA	–
Czech Republic	Chytrý et al. (2018)	3 27 70	5 68 17	19 55 36	7 36 57	33 47 20	98 1 1
European mires	Hájek et al. (2020)	–	–	5 53 42	–	–	–
France	Julve (2015)	1 17 82	20 47 33	9 66 25	9 37 54	31 50 19	90 6 4
Great Britain	Hill et al. (2000)	1 21 78	–	10 58 32	7 41 52	38 47 15	97 3 0
South Aegean	Böhling et al. (2002)	NA	NA	31 54 15	NA	NA	96 3 1
Hungary	Borhidi (1995)	3 24 73	2 58 40	28 34 36	2 35 63	41 42 17	98 1 1
Italy	Guarino & La Rosa (2019)	2 18 80	14 38 48	42 42 16	12 44 44	52 37 11	98 1 1
Saline habitats	Dítě et al. (2022)	–	–	–	–	–	44 55 1
Switzerland	Landolt et al. (2010)	NC	18 34 48	NC	NC	NC	NC
Ukraine	Didukh (2011)	1 17 82	NA	1 77 22	NC	NC	NC
FINAL		1 15 84	12 42 46	27 59 14	9 40 51	49 43 8	96 3 1

723

724

725

726 **Supporting information of the paper**

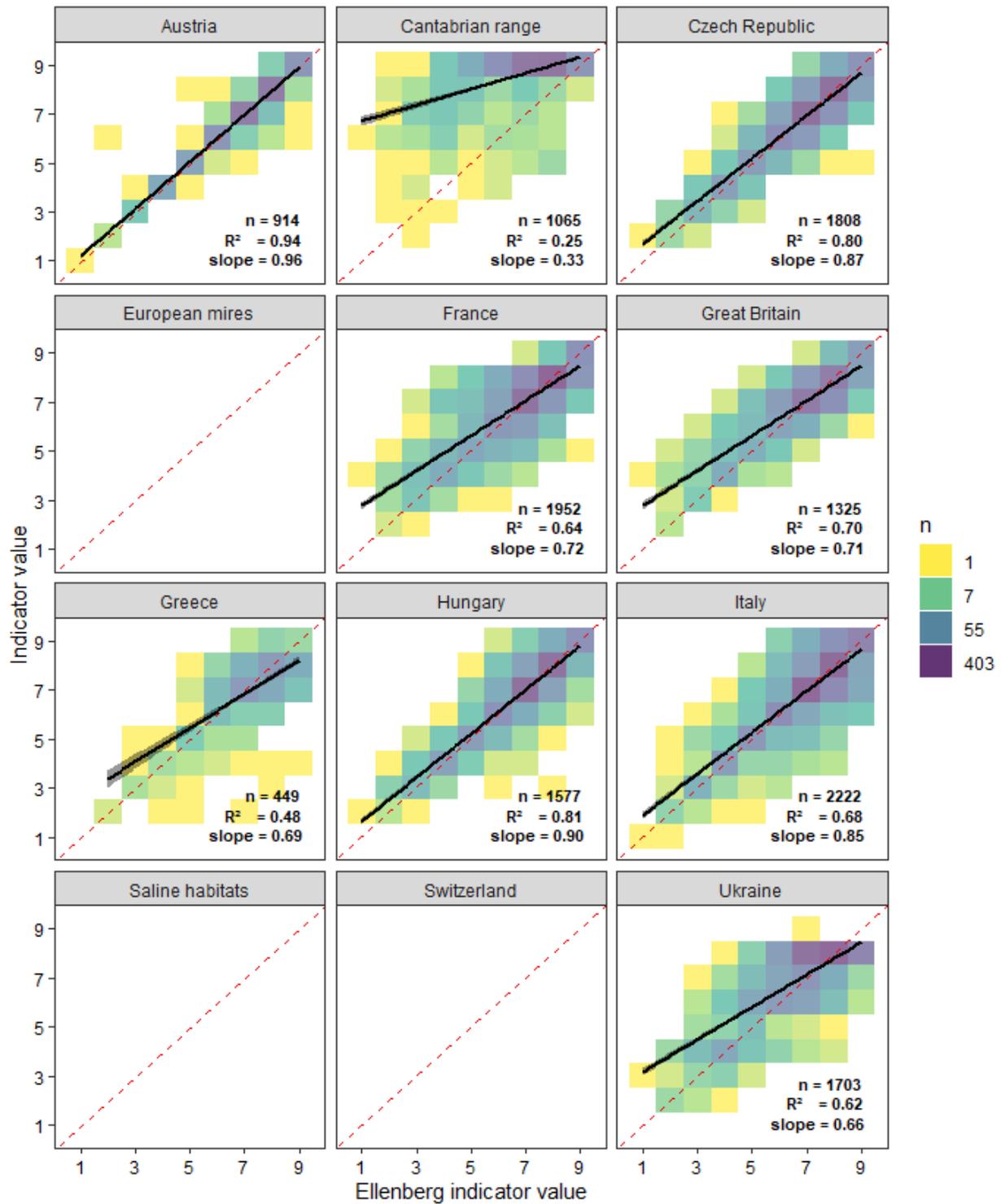
727 Tichý, L. et al. (2022) Ellenberg-type indicator values for European vascular plant species. *Journal of*
728 *Vegetation Science*.

729 **Appendix S2. Evaluation of 12 regional systems of ecological indicator values based on**
730 **their relationship to Ellenberg indicator values**

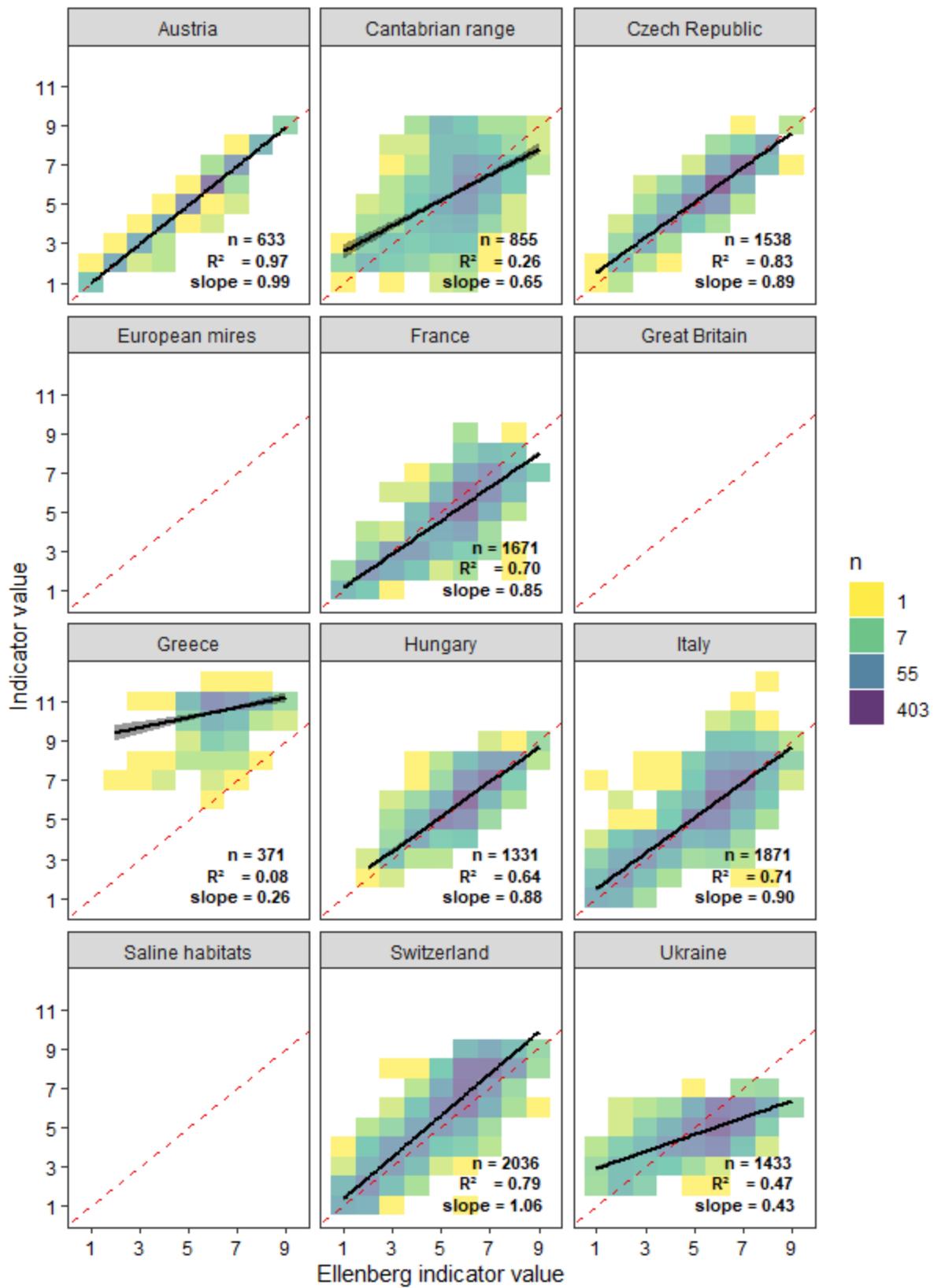
731 **A. Direct comparisons based on species indicator values**

732 Fig. 1A–F: Comparison of regional datasets of indicator values for Austria, Cantabrian Mountains, Czech
733 Republic, European mires, France, Great Britain, Greece, Hungary, Italy, Saline habitats, Switzerland and
734 the Alps, and Ukraine with Ellenberg indicator values (Germany; Ellenberg & Leuschner, 2010). Most
735 values are scaled from 1 to 9, but the range is broader (from 1 to 12) for temperature (Greece and Italy)
736 and moisture (all datasets).

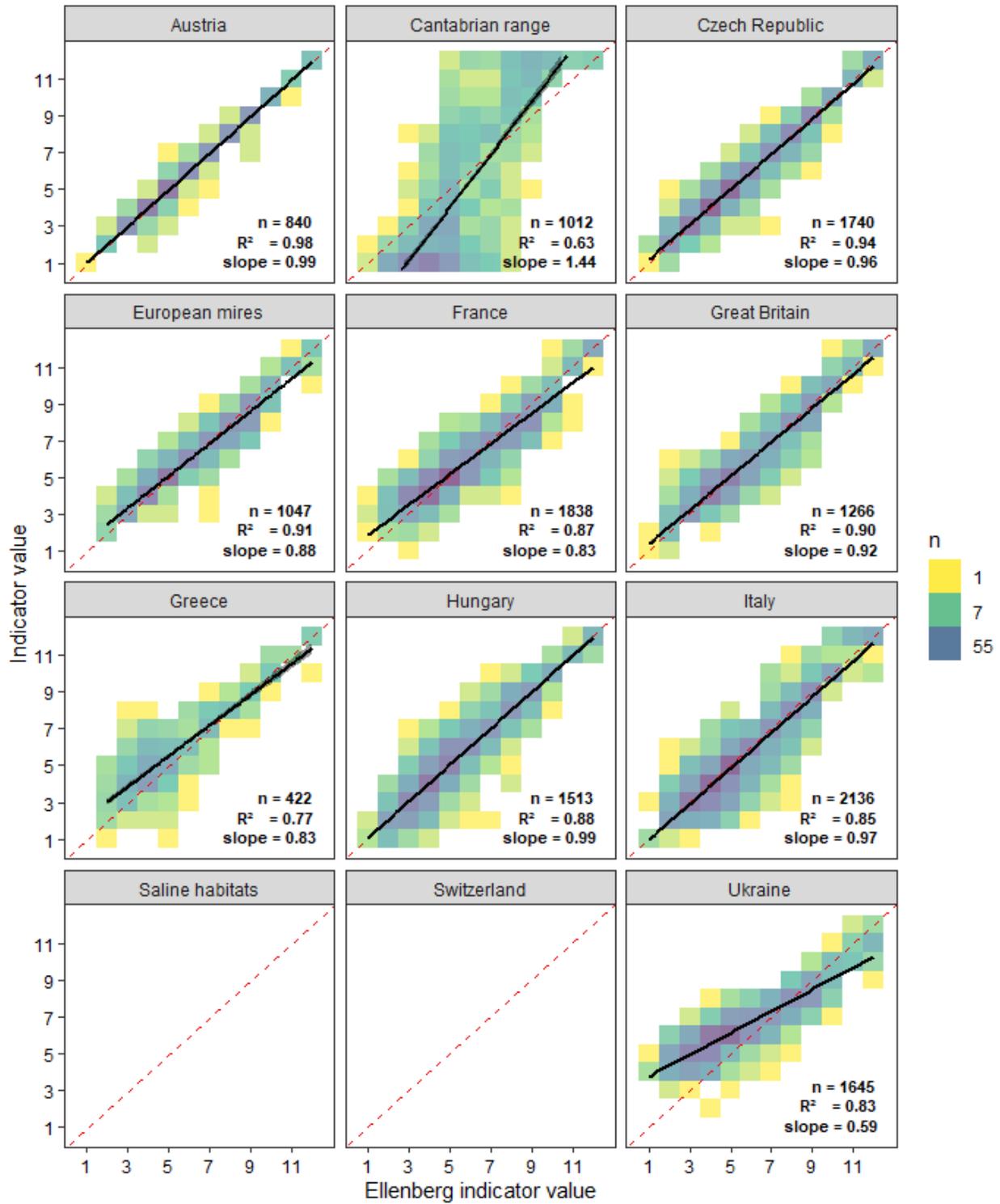
A. Light



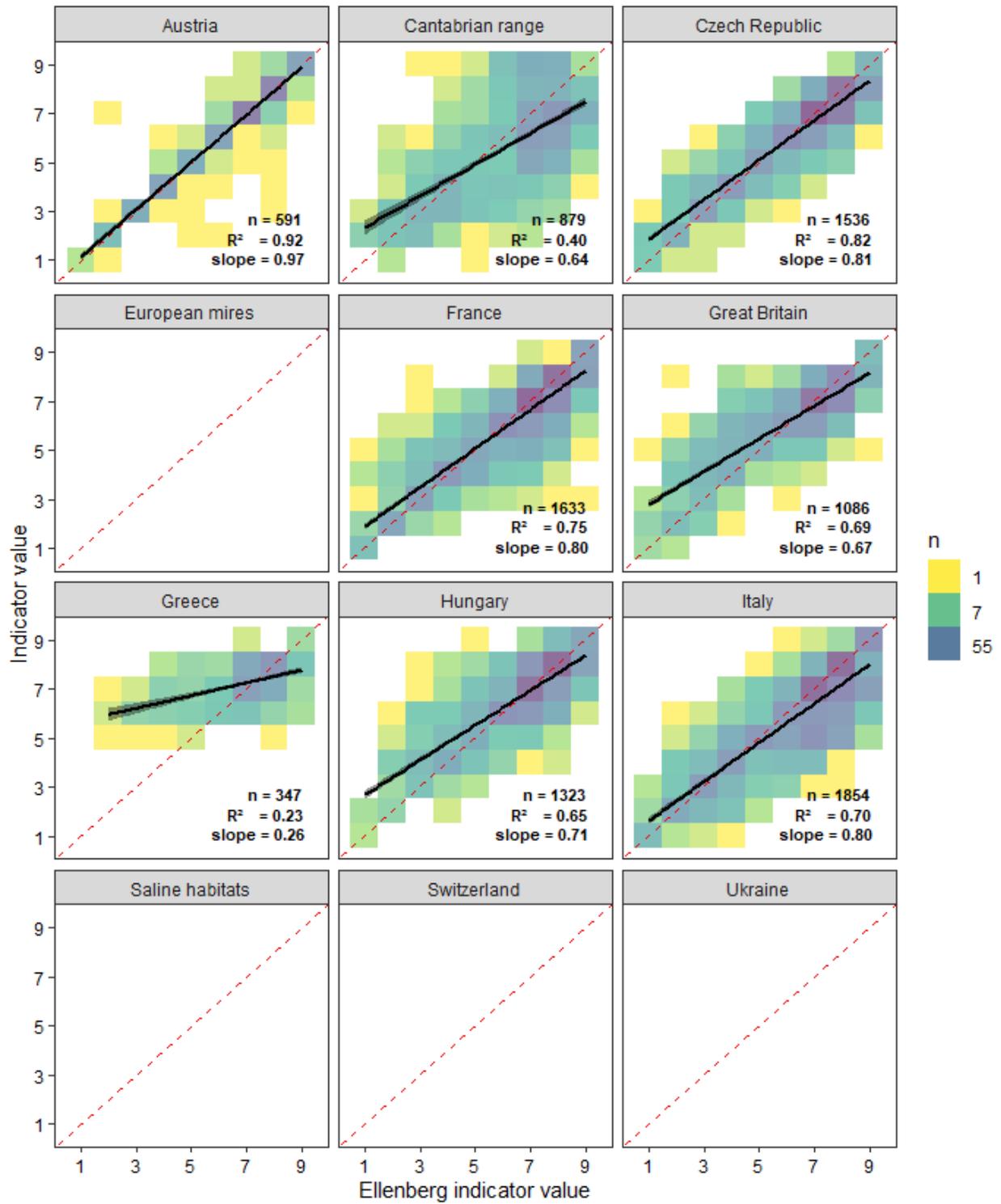
B. Temperature



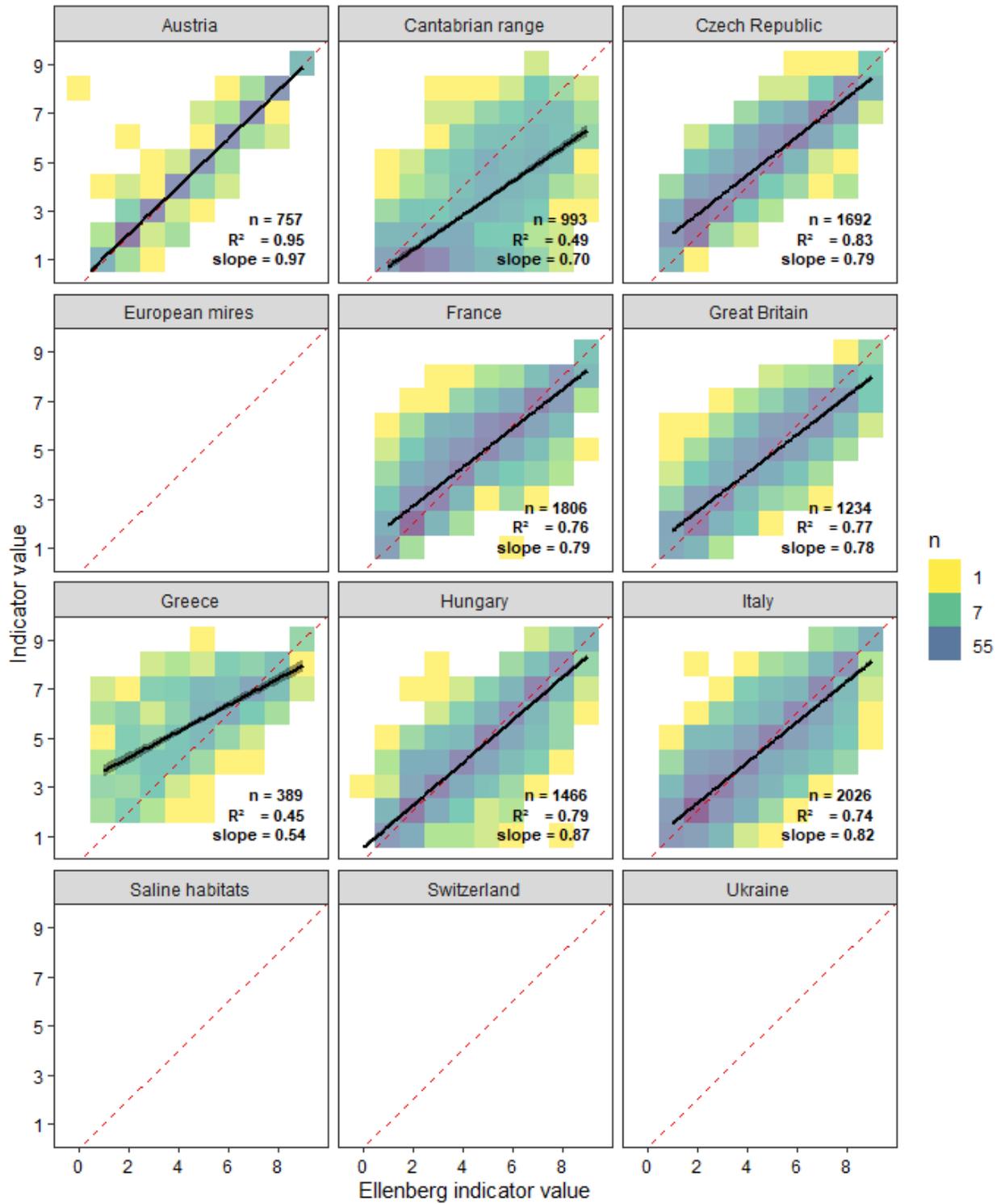
C. Moisture



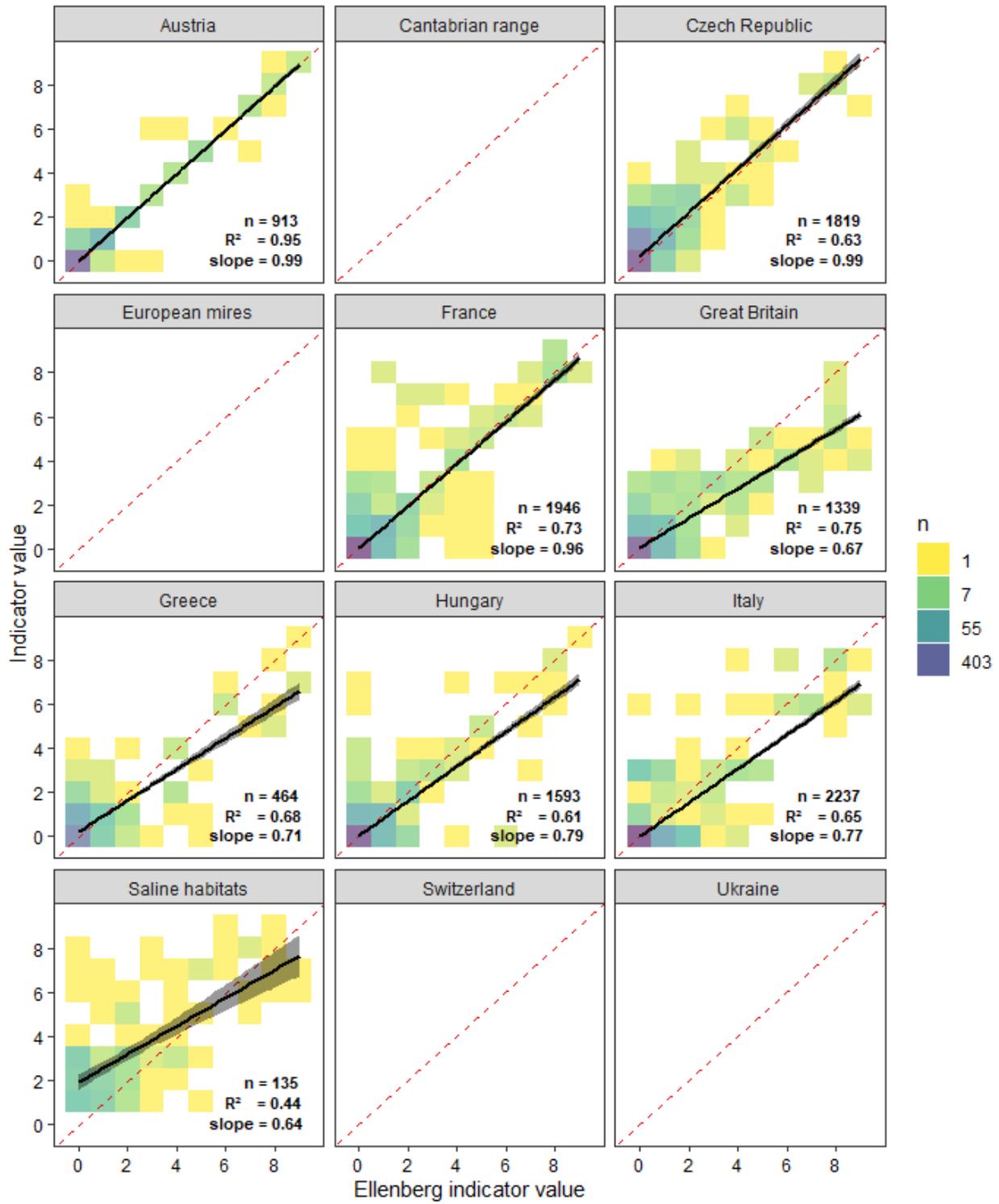
D. Reaction



E. Nutrients



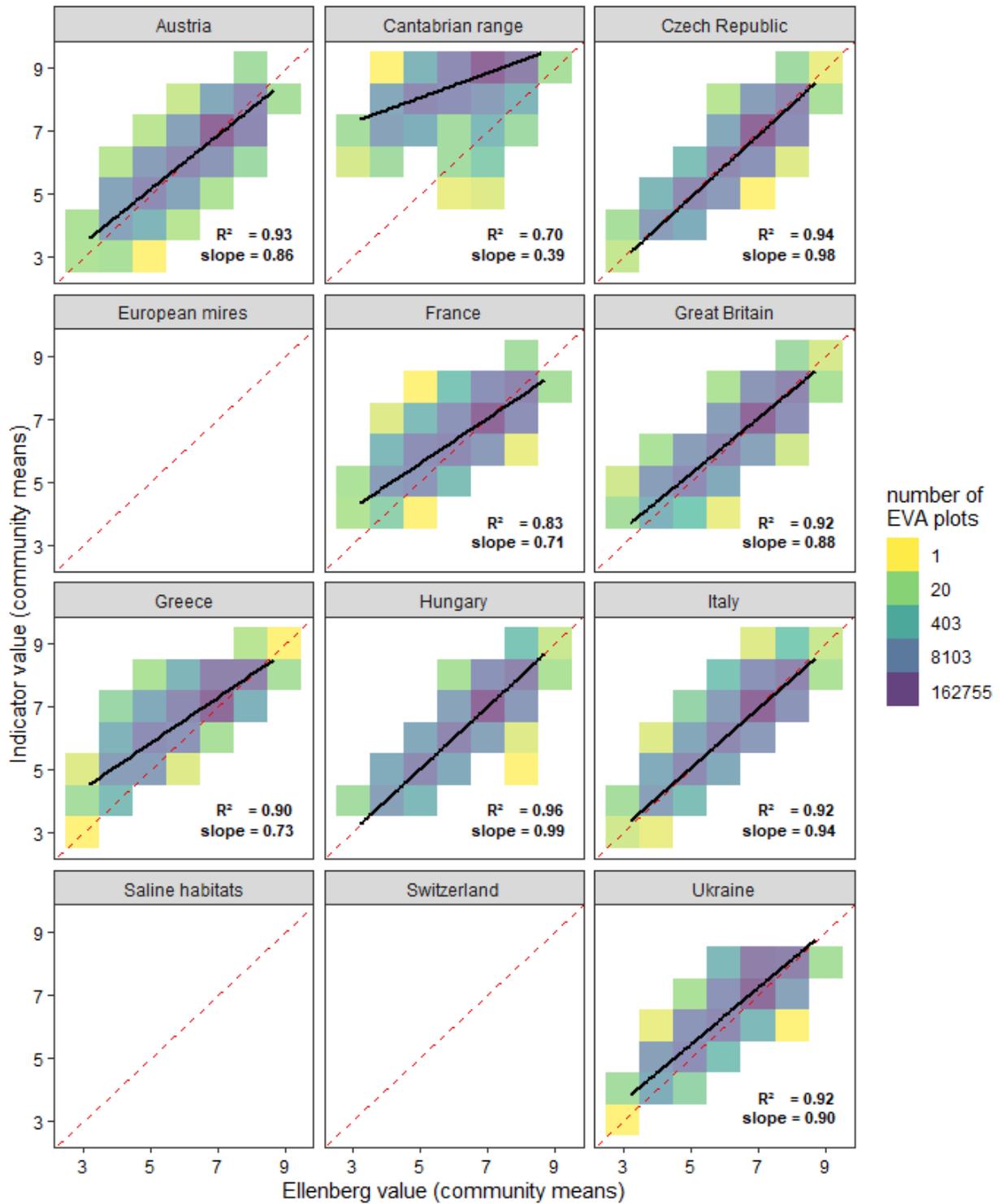
F. Salinity



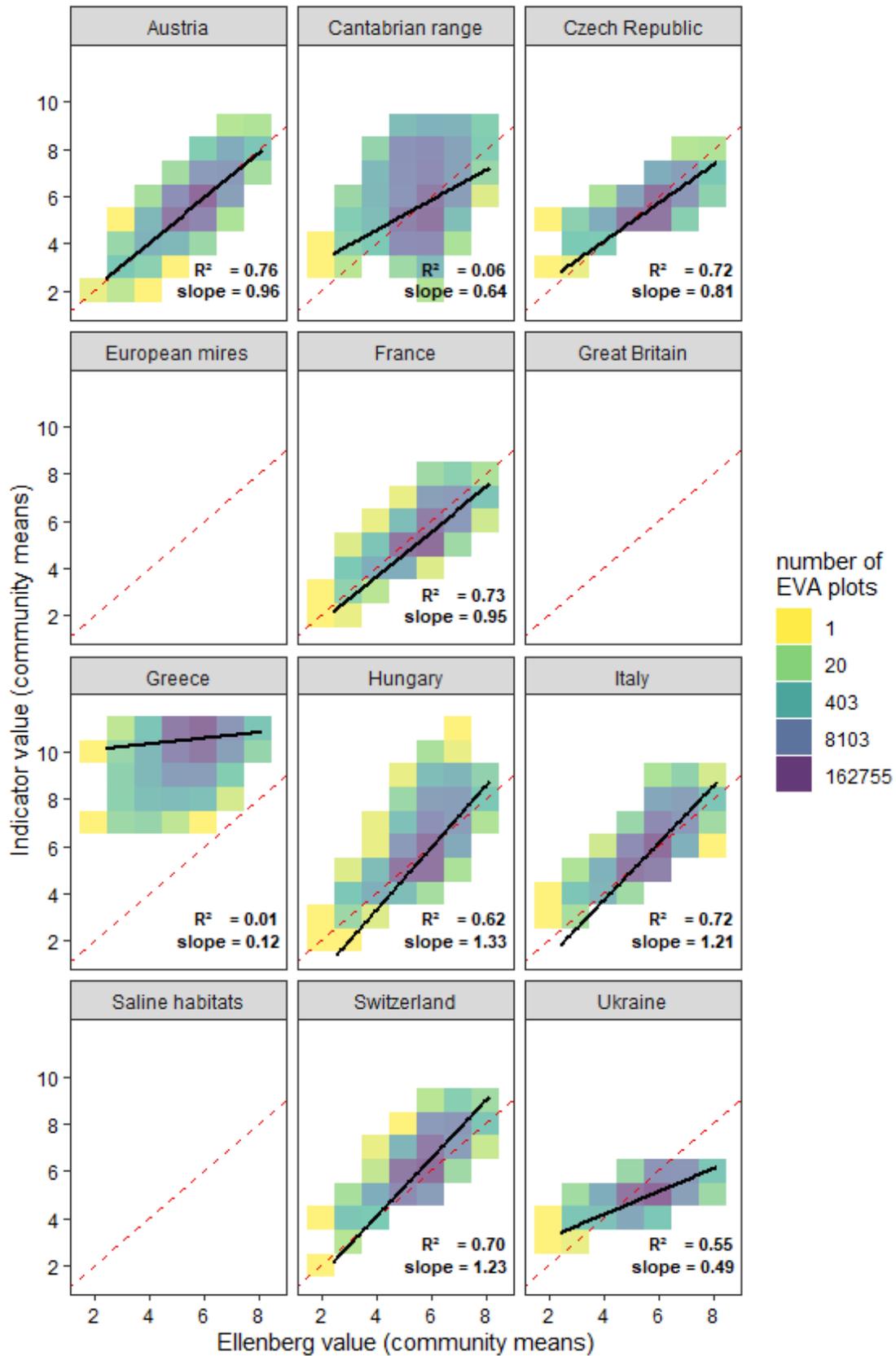
743 **B. Indirect comparisons based on mean indicator values for vegetation plots**

744 Fig. 2A–F: The relationships between the unweighted community means for light, temperature, moisture,
745 reaction, nutrients and salinity calculated for individual vegetation plots using the different regional
746 systems of indicator values and the original Ellenberg indicator values. The dataset includes 622,402 plots
747 for light, 413,832 plots for temperature, 615,301 plots for moisture, 490,617 plots for reaction, 575,406
748 plots for nutrients and 673,141 plots for salinity from the EVA database; calculations were performed
749 only for plots containing at least five species with the respective indicator value.

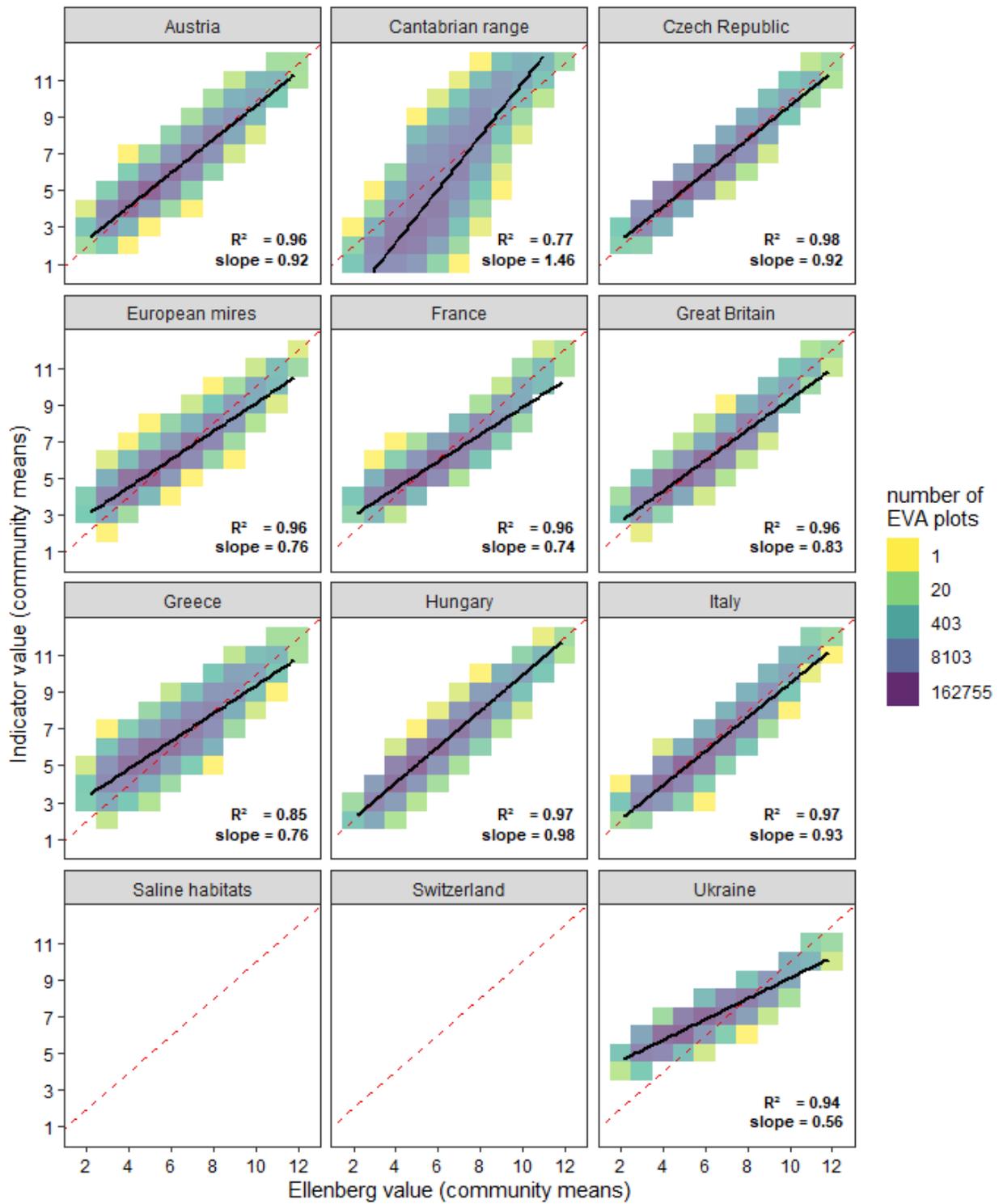
A. Light



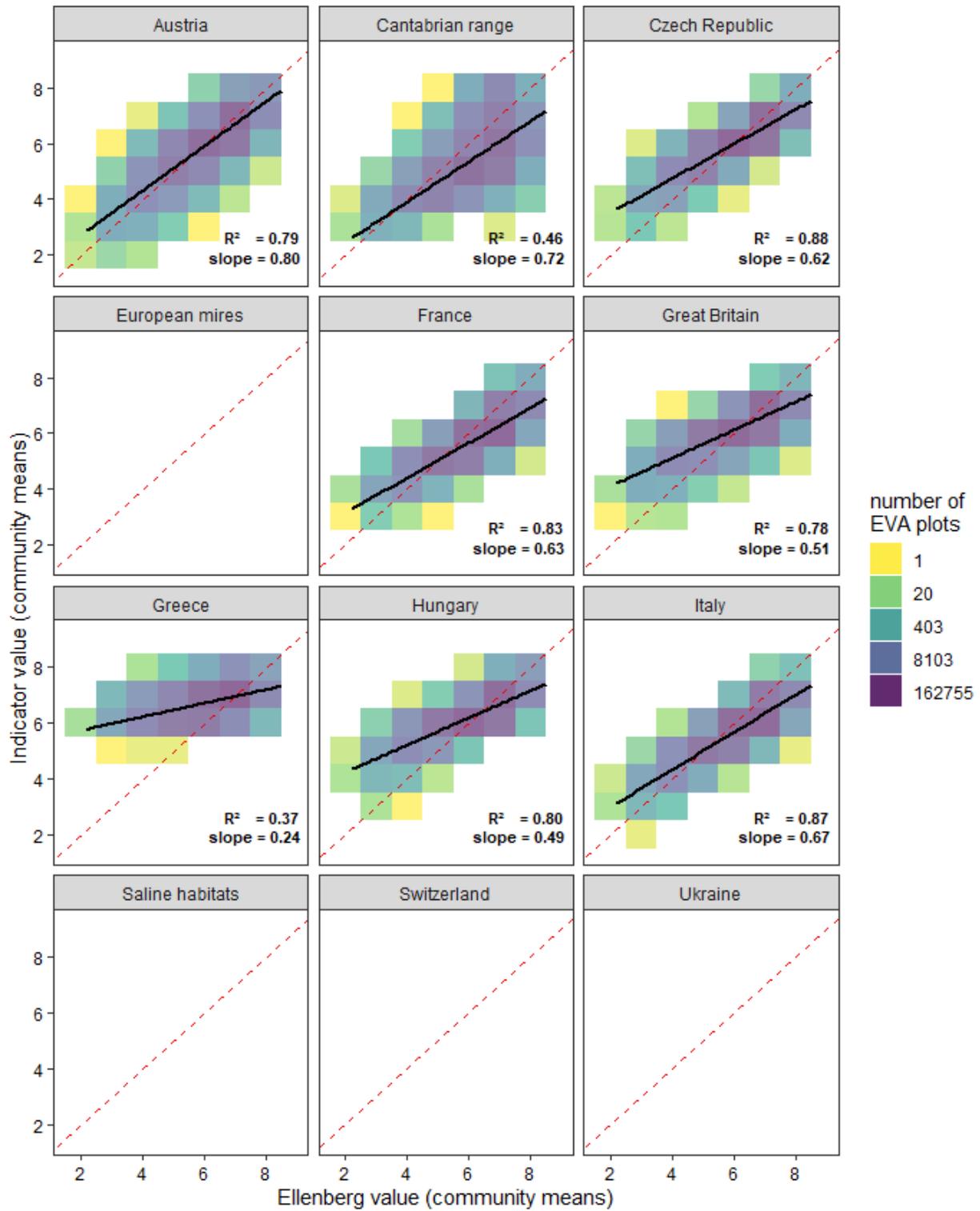
B. Temperature



C. Moisture



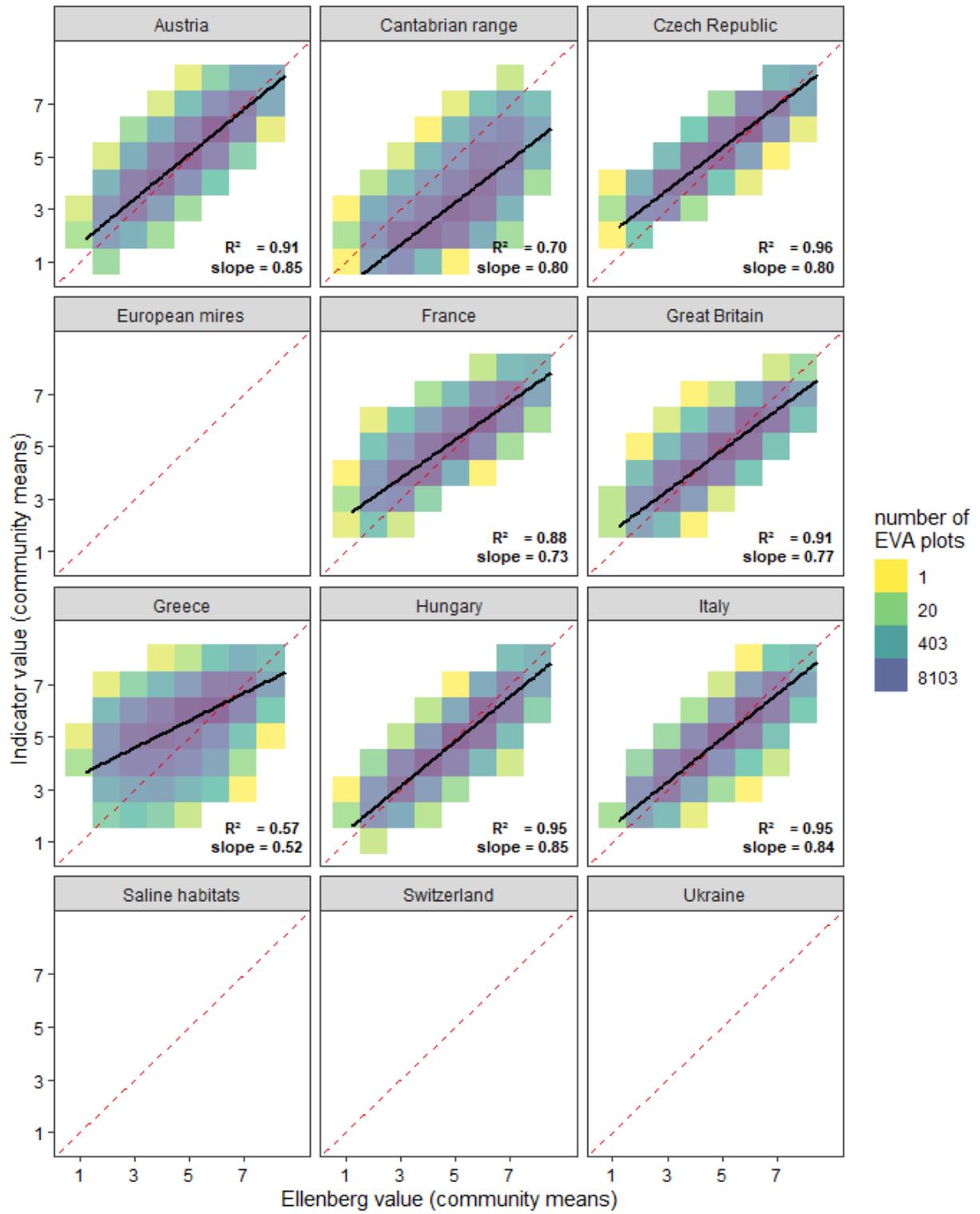
D. Reaction



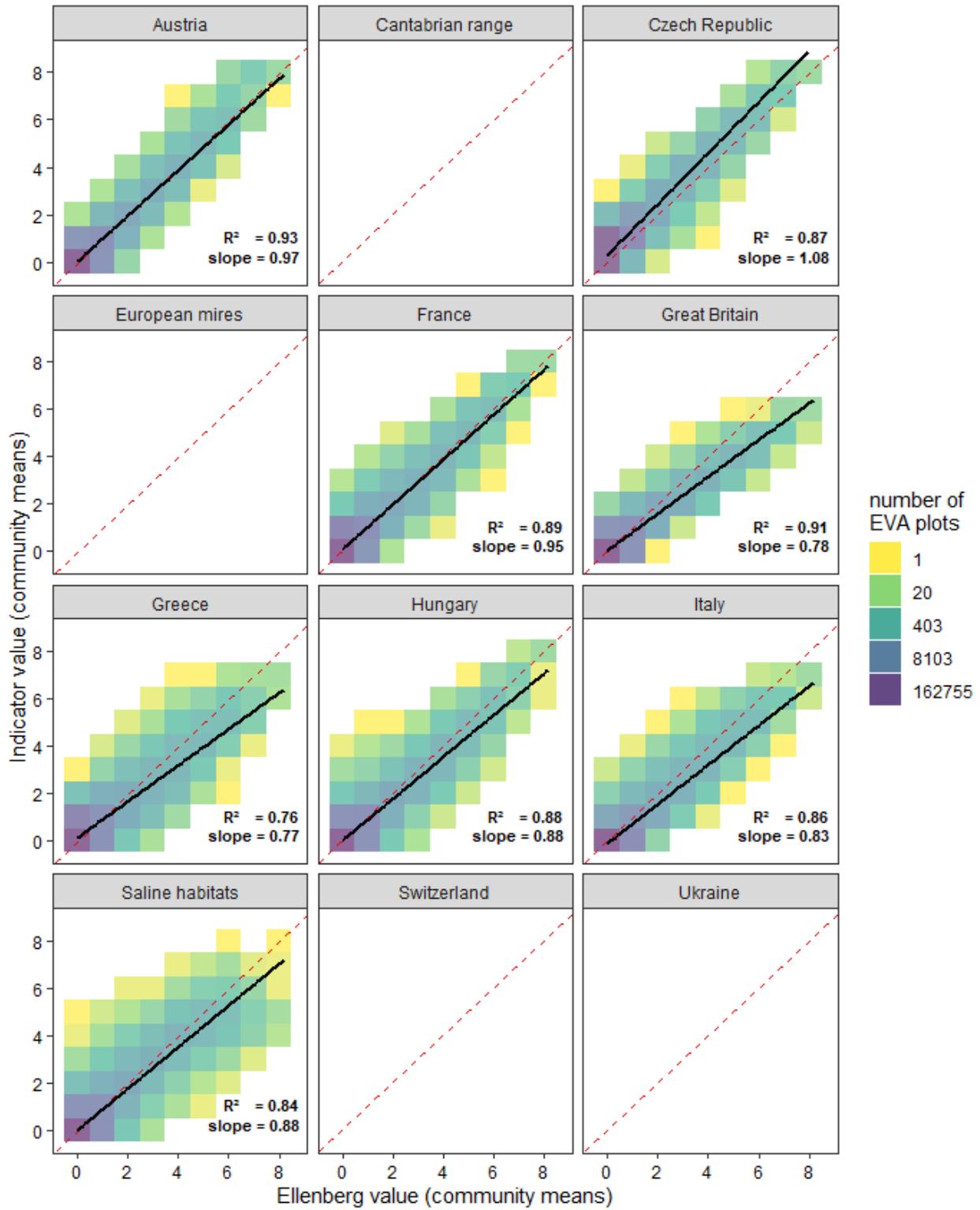
753

754

E. Nutrients



F. Salinity



756

757

758

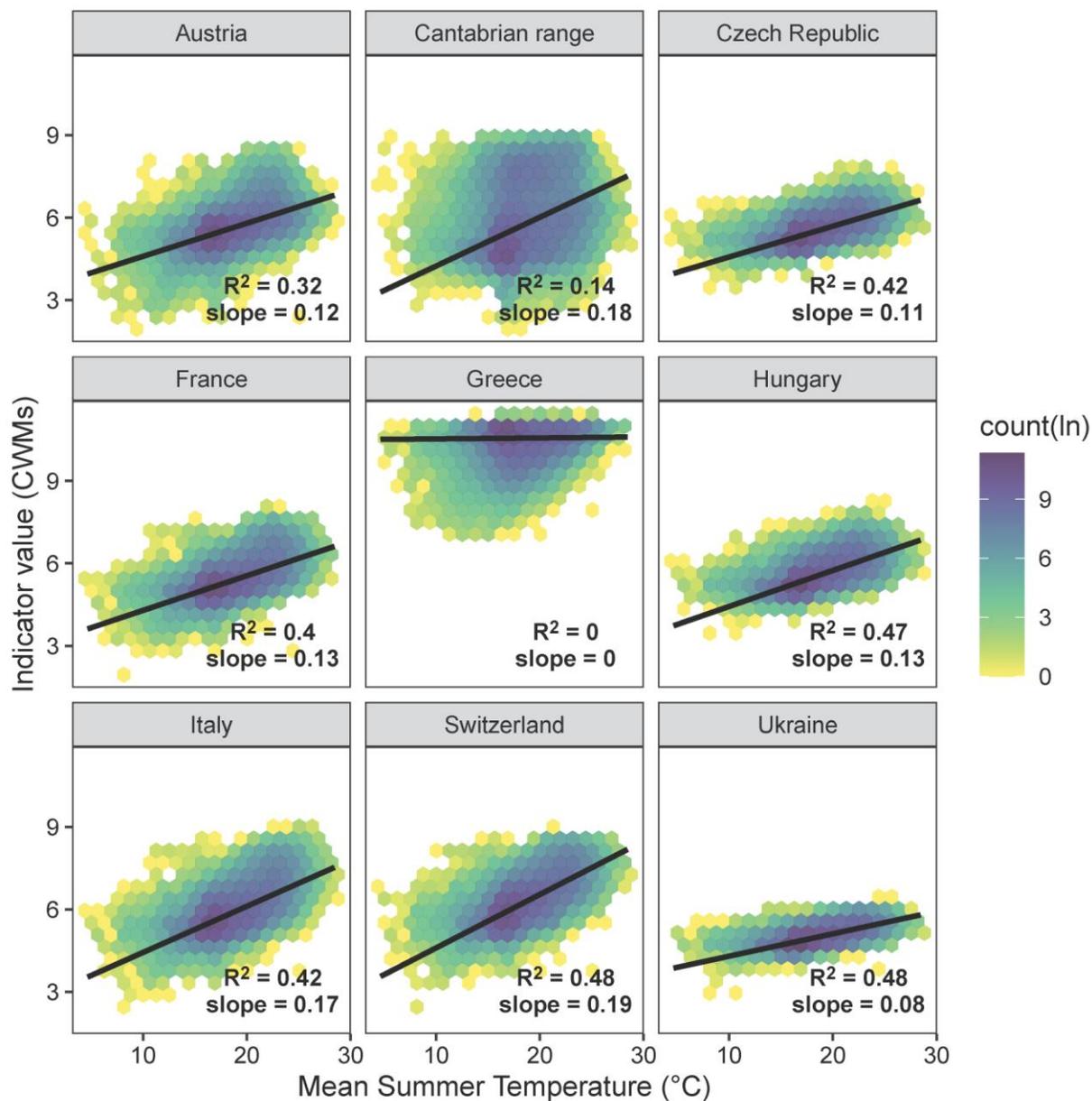
759 **Supporting information of the paper**

760 Tichý, L. et al. (2022) Ellenberg-type indicator values for European vascular plant species. *Journal of*
761 *Vegetation Science*.

762 **Appendix S3. Comparison of mean Ellenberg-type indicator values for temperature**
763 **calculated for vegetation plots and mean summer temperature for plot locations obtained**
764 **from climatic datasets.**

765 **A. Source datasets.**

766 Fig. 1: Comparisons are based on 364,104 georeferenced plots from the EVA database (subset of the
767 dataset selected for comparison of unweighted community means for temperature in Appendix S2B) that
768 contain at least five species with the Temperature indicator value.



769

770

771 **B. Harmonized Ellenberg-type indicator values for Europe.**

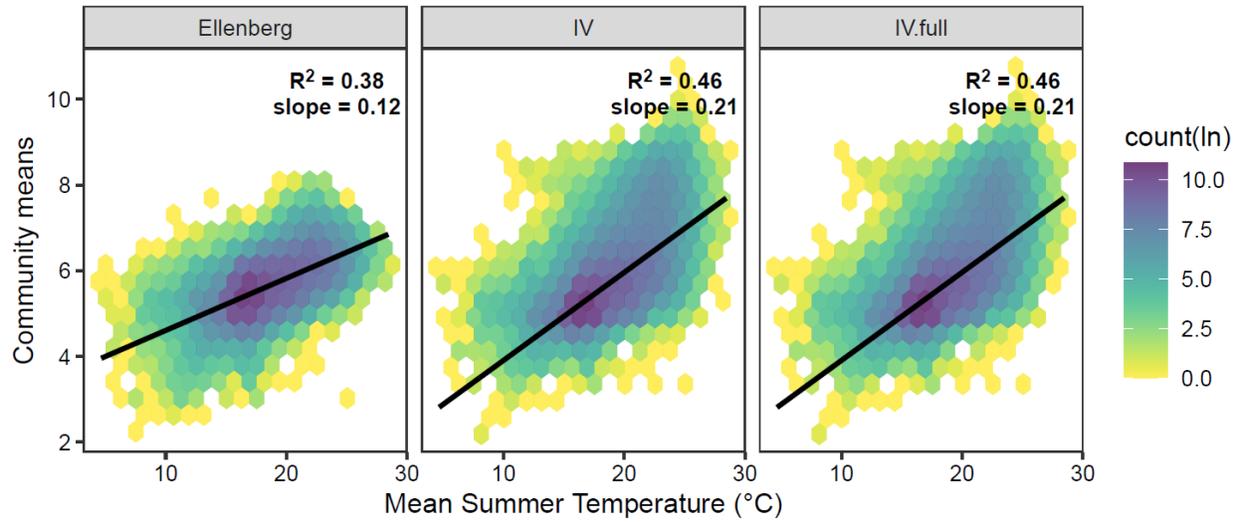
772 Fig. 2: The dataset included 364,104 georeferenced plots and 8,146 species from the EVA database

773 similarly as in Appendix S2. (IV) Unweighted community means for temperature were calculated using

774 5,196 species with temperature indicator value in at least one regional dataset. (IV.full) Unweighted

775 community means for temperature were calculated using 5,553 species with temperature indicator value

776 defined in at least one regional dataset or estimated using a similar distribution for species for which
777 indicator value was not defined in any regional dataset.



778

779

780

781