Ellenberg-type indicator values for the Czech flora

Ellenbergovské indikační hodnoty pro českou flóru

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A new dataset of ecological indicator values for species, subspecies and some varieties, hybrids and infrageneric species groups has been compiled for the vascular flora of the Czech Republic. Indicator values for light, temperature, moisture, (soil) reaction, nutrient availability and salinity were assigned to 2275 species and 801 other taxa, using the nine-degree (or 12-degree for moisture and 10-degree for salinity) ordinal scales proposed by Heinz Ellenberg for the flora of Germany. The values are compatible with Ellenberg indicator values, which were used as a baseline, but extensively revised based on our own field observations, literature, comparison with indicator value systems of other countries and an analysis of taxon co-occurrences in vegetation plots from the Czech National Phytosociological Database. Taxa in the Czech flora missing in the original Ellenberg tables were added. Compared with the original Ellenberg's dataset of indicator values, smaller proportions of taxa were classified as extremely basiphilous, extremely oligotrophic or strictly avoiding saline habitats. The revised values were tested by regressing unweighted site mean indicator values against measured environmental variables. In most cases, prediction of environmental conditions was slightly more accurate with the new Czech indicator values than with the original Ellenberg indicator values. The full dataset of indicator values is available in an electronic appendix to this paper.

Keywords: bioindication, Czech Republic, dataset, Ellenberg indicator values, light, moisture, nutrients, reaction, salinity, temperature, vascular plants

Introduction

Ellenberg indicator values for the central-European flora (Ellenberg et al. 1991) are routinely used to rapidly estimate site conditions from species composition, when measured values of environmental variables are not available (Diekmann 2003). In spite of certain limitations (Schaffers & Sýkora 2000, Wamelink et al. 2002, Diekmann 2003, Chytrý et al. 2009, Zelený & Schaffers 2012, Bartelheimer & Poschlod 2016, Berg et al. 2017), they remain a very popular tool in vegetation science and are also used for assessing ecological conditions in invertebrate research (Horsák et al. 2007, Zhai et al. 2015). The main reasons for their popularity include persistent difficulties with exactly measuring

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some environmental variables and absence of environmental measurements in most historical datasets of vegetation plots (Dengler et al. 2011).

Heinz Ellenberg developed his dataset of indicator values based on field observations of realized niches of plant taxa mainly in Germany and the Alps, and partly on evidence from ecological experiments and measurements of environmental variables (Ellenberg et al. 1991). This dataset therefore contains taxa occurring in the western part of central Europe and reflects knowledge of their ecology specific to this region. However, niches of the same taxa can differ between geographic areas. Possible causes of such niche shifts include genetic differences between populations, different availability of suitable habitats, or taxon displacement from suitable habitats by stronger competitors that exist in one area but not in the other (Diekmann & Lawesson 1999, Gégout & Krizova 2003, Coudun & Gégout 2005, Hájková et al. 2008, Wasof et al. 2013, Wagner et al. 2017). For this reason, systems of taxon indicator values were also developed for other areas, including new taxa not occurring in Ellenberg's study area and changing some indicator values to reflect the specific ecology of taxa in the new area. Examples of such systems include Tsyganov (1983) for the hemiboreal zone of European Russia, Borhidi (1995) for Hungary, Zarzycki et al. (2002) for Poland, Hill et al. (2004) for the British Isles, Pignatti et al. (2005) for Italy (see also Guarino et al. 2012 for an update), Landolt et al. (2010) for Switzerland and the Alps and Didukh (2011) for Ukraine.

Some systems of indicator values were also developed in former Czechoslovakia. Regal (1967) published indicator values for the most common meadow plants of Czechoslovakia. Zlatník et al. (1970) provided indicator values for soil nutrient status, soil reaction, soil moisture, topoclimatic conditions and light for a selection of forest species of the Czechoslovak vascular flora. Some of these values were in non-ordered categories, others on ordinal scales of 4–5 degrees, and yet others were combinations of categories and ordinal scales. Ambros (1985, 1986) elaborated a more standardized system, also for a selection of Czechoslovak forest vascular plants, including indicator values for light, temperature, moisture and soil reaction, each with a five-degree scale and in combination with supplementary information expressed in categories. Jurko (1990) provided indicator values for soil moisture, soil reaction and soil nitrogen for most species of the Slovak vascular flora, using five-degree scales and for many species reporting a range instead of a single value. However, none of these systems has received broad acceptance among Czech and Slovak botanists and ecologists. Probable reasons included the restriction of some of these systems to a single vegetation formation, complicated mixing of ordinal values with categories, or of single values with ranges, relatively obscure publication venues that made hardcopies poorly accessible to a broader scientific community and non-existence or non-accessibility of electronic versions of these datasets. Most studies from the Czech Republic employing indicator values used Ellenberg's dataset, assuming a close similarity of species ecology between Germany and the Czech Republic (e.g. Simonová & Lososová 2008, Axmanová et al. 2012, Jírová et al. 2012, Dostál et al. 2013, Čuda et al. 2014, de Bello et al. 2016, Navrátilová et al. 2017). However, values for some taxa of the Czech flora, especially those with their western distribution limit in the Carpathians or in the Pannonian floristic region, were missing in Ellenberg's tables. These taxa were consequently disregarded in analyses, with unknown effects on the results. Although the previous applications of Ellenberg indicator values for the Czech flora seem to provide reliable results in most cases, it is highly desirable to revise the dataset of indicator values for this country, considering potential niche shifts in some taxa, and especially to provide values for missing taxa.

In this paper we provide a new dataset of indicator values for vascular plants of the Czech Republic, which is compatible with Ellenberg indicator values, considering the same factors (light, temperature, moisture, reaction, nutrients and salinity) assessed on the same scales. We compare this dataset with original Ellenberg indicator values and test its performance in bioindication against measured environmental values.

Materials and methods

Revision of the indicator values

The baseline dataset for our work was the last edition of Ellenberg indicator values published as electronic Supplementary Chapter 27 of the 6th edition of Ellenberg's handbook Vegetation Mitteleuropas mit den Alpen (Ellenberg & Leuschner 2010, http://www.utb-shop.de/downloads/dl/file/id/27/zusatzkapitel_zeigerwerte_der_pflanzen_mitteleuropas.pdf). We aimed to preserve the scaling of the values introduced by Ellenberg in order to ensure compatibility with the original Ellenberg values and other systems of indicator values that follow the same scale. We focused on indicator values for light (L), temperature (T), moisture (M), reaction (R), nutrients (N) and salinity (S), which are direct indicators of site conditions (Appendix 1). We did not deal with indicator values for continentality, because they were originally based on an evaluation of species distribution ranges rather than on an assessment of species affinity to site conditions. Moreover, the continentality indicator values involved several inconsistencies in the original Ellenberg compilation, which were recently corrected in a new dataset provided by Berg et al. (2017).

We revised and completed Ellenberg indicator values using expert judgement, but also considered information from a statistical assessment in which we linked the original Ellenberg values with the taxon co-occurrence data in the Czech National Phytosociological Database (Chytrý & Rafajová 2003). We used a stratified selection of vegetation plots (i.e. relevés; henceforth called plots) from a dataset containing 30,115 plots belonging to all phytosociological associations as defined in the national vegetation classification (Chytrý 2007–2013). If two or more plots belonging to the same association were available from the same grid cell of 1.25 minutes of longitude × 0.75 minutes of latitude (approximately 1.5 × 1.4 km), only one of them was retained in the database to assure a balanced geographic distribution. Plot data editing and resampling was done using the JUICE 7 program (Tichý 2002). We linked indicator values to those taxa in this vegetation-plot dataset for which they were available in Ellenberg & Leuschner (2010), after resolving synonymous names.

We used two methods of statistical assessment. The first method was based on reciprocal averaging. We calculated the unweighted mean of original Ellenberg indicator values for each plot, and subsequently calculated indicator values for each taxon occurring in the plot dataset using unweighted averaging of the indicator values for plots in which this taxon occurred (reciprocal averaging). Because averaging causes shrinkage of values towards the mean (Hill et al. 2000), the calculated taxon indicator values were shifted to the same median and rescaled to the same range as the original Ellenberg values. For this purpose, we calculated the median (Q_{50}) and the quartiles (Q_{25}, Q_{75}) for grouped data (Woolson & Clarke 2002: 34) for the original Ellenberg indicator values (individual categories on the Ellenberg scale were understood as groups). Statistics for grouped data provide finer estimations than ordinary statistics for non-grouped data. Medians and quartiles calculated in such a way are decimal numbers, which are directly comparable with the recalculated indicator values. We found the median (Q'_{50}) and quartiles (Q'_{25}, Q'_{75}) for the recalculated indicator values and shifted the recalculated indicator values for each taxon by the difference of the two medians ($Q'_{50} – Q_{50}$). As a result, the recalculated values had the same median as the original values. Further, we rescaled the recalculated values by multiplying them by the factor k (for the values in the interval from Q_0 to Q_{50}) or k' (for the values in the interval from Q_{50} to Q_{100}). The value of the factor k was calculated as the ratio of the distances between Q_{25} and Q_{50} between the original Ellenberg indicator values and the recalculated values. The value of the factor k' was calculated analogically using the distances between Q_{50} and Q_{75}. The rescaled data followed the original Ellenberg scale and were comparable with Ellenberg indicator values in their overall distribution, while values of individual taxa could differ.

The second method of statistical assessment assigned each taxon to an indicator value calculated as the mean of Ellenberg indicator values of 10 taxa with the highest degree of co-occurrence with the target taxon (faithful taxa). The degree of co-occurrence was measured using the phi coefficient of association (Sokal & Rohlf 1995: 741, 743) between taxon presences in the vegetation-plot dataset. Both methods assigned new indicator values to all taxa in the dataset, including those not present in the original Ellenberg tables. Statistical assessment of indicator values was computed using functions programmed in the JUICE program (Tichý 2002).

Although the recalculated values provided useful approximations of appropriate indicator values for many taxa, they contained many inconsistencies, especially for rare taxa occurring in a few plots, but also because some gradients are truncated in the Czech Republic (e.g. the temperature gradient because of the absence of high mountains) or values of some factors are not combined with all values of other factors in the Czech territory (e.g. there are almost no base-rich soils in cool mountainous areas). Therefore, the main part of our work was the expert assessment of indicator values. For this purpose, we assigned each taxon of the Czech vascular flora contained in the national standard list (Danihelka et al. 2012) the following values (if available): (i) original Ellenberg indicator values (Ellenberg & Leuschner 2010); (ii) Borhidi indicator values for the Hungarian flora (Borhidi 1995); (iii) Julve indicator values for the French flora (www.telabotanica.org/projets/18/documents/98); (iv) Jurko indicator values for the Slovak flora (Jurko 1990); (v) Pignatti indicator values for the Italian flora (Pignatti et al. 2005); (vi) indicator values calculated based on reciprocal averaging; (vii) indicator values calculated as mean Ellenberg values of faithful taxa

Then each of the first four authors of the current paper separately evaluated the list of Czech flora, considering the above values, information in the Flora of the Czech Republic (Hejný et al. 1988 et seq.), Vegetation of the Czech Republic (Chytrý 2007–2013), other literature sources including those from other countries of central Europe and our own knowledge based on field observations. Particular attention was given to the taxa that differed by two or more degrees between the original Ellenberg value and values from other sources. Each of these four authors proposed six values (L, T, M, R, N, S) for most species and other taxa of the Czech flora. We did not assign values to the taxa for which we did not have sufficient knowledge, especially those from taxonomically difficult (e.g. apomictic) groups and casual alien taxa. In some cases, we only assessed a supraspecific taxon or species aggregate, e.g. *Hieracium alpinum* agg., *Ranunculus auricomus* agg. and sections in the genus *Taraxacum*. We also did not evaluate cultivars and hybrids, except for a few stabilized or common hybrids.

In the expert assessment we considered our own or literature-based knowledge of species ecology in the broader area of central Europe, rather than only in the Czech Republic. For example, several species of limestone outcrops are confined to warm low-altitude areas in the Czech Republic because limestone is very rare at high altitudes, whereas in the Alps or central Carpathians the same species also occur on limestone in cool high-altitude areas. Such species were not assigned high temperature indicator values as an isolated assessment within the Czech Republic might suggest. Because of the relatively rare occurrence of base-rich substrates in the Czech Republic, we paid particular attention to assessing indicator values for reaction, considering species occurrence on calcareous soils outside the country even if the species occurred only on acidic soils in the Czech Republic. Consideration of species ecology outside the Czech Republic also allowed us to assign indicator values to many rare and even some extinct or missing species of the Czech flora.

We assigned values for all the six factors to all evaluated taxa except for parasitic epiphytes of the *Loranthaceae*, for which we did not assign values for moisture, reaction, nutrients and salinity. We also assigned values for taxa with a very broad ecological amplitude for the given factor, usually near the middle of the scale. On this point our approach differed from that of Ellenberg, who did not assign values to such taxa. However, similarly to Ellenberg, we added the symbol “x” to the numerical indicator value for the taxa with broad ecological amplitudes.

After finishing separate evaluations, we compared the indicator values proposed by the four of us and discussed all cases in which our proposal differed by two or more degrees. Then we accepted consensus solutions or a value closest to the mean of the proposed values.

In the final editing, indicator values and the amplitudes were harmonized between species and their respective subspecies, varieties and supraspecific taxa (especially aggregates). In the case of species with a single subspecies occurring in the Czech Republic, the same values were assigned to both the species and subspecies. It has to be noted that these species values may not be valid for another subspecies of this species occurring outside the Czech Republic. In the cases of two or more lower taxa existing within a higher taxon (e.g. species within aggregates, subspecies within species), the indicator values for the higher taxon are usually close to the means of the values of the lower taxa, but if some of the lower taxa are very common and others rare in the country, the value for the higher taxon was set closer to or identical with the value of the most common lower taxon. In the cases of aggregates that contained one species assessed and one species not assessed, the values were given only to the species, not to the aggregate.

To illustrate the differences between the new Czech indicator values and the original Ellenberg indicator values, we plotted the former against the latter, fitted a linear regression and compared the regression line with the identity line that would represent no systematic trend in the revision of indicator values. We also compared the adjusted coefficient of determination (r^2) to measure the degree of difference between the original and new system of indicator values. In this case r^2 was adjusted to enable comparison of the amount of variation accounted for by regressions with different numbers of species. The difference between the original and revised system of indicator values was also shown using frequency histograms.

Testing the performance of the revised indicator values against measured variables

To assess the performance of the revised system of indicator values for the Czech Republic, we tested the accuracy of prediction based on unweighted mean indicator values for sites against measured environmental variables, and compared the accuracy between the original Ellenberg indicator values and the new Czech indicator values, using R version 3.4.1 (R Core Team 2017). We used linear regression models and considered two measures of accuracy: coefficient of determination (r^2) and root mean square error of prediction (RMSEP). Increasing value of r^2 indicates a higher accuracy of prediction; it depends on the differences between predicted and observed values and on the slope of the regression. In contrast, RMSEP decreases with a higher accuracy of prediction and it depends only on the differences between predicted and observed values (Mevik & Cederkvist 2004). For all indicator values except reaction, we fitted the relationship of unweighted mean indicator values for sites against measured environmental variables using linear regression. In the case of reaction, we used polynomial regression with third-order polynomials, since the relationship with measured pH is empirically known to be non-linear (e.g. Schaffers & Sýkora 2000).

For testing, we used the following vegetation-plot datasets with measured environmental variables (Table 1):

(i) Light indicator values – dataset **Czech forests**. This dataset was taken from the stratified selection of vegetation plots from the Czech National Phytosociological Database (see above; Chytrý & Rafajová 2003). It comprised forest vegetation plots of a size of 100–400 m^2 with shrub layer cover less than 10%, sampled across the country. In each plot, total cover of tree layer estimated by the author of the plot record was used as a measure of light availability in the understorey.

(ii) Temperature indicator values – dataset **Czech meadows**. This dataset was also taken from the stratified selection of plots from the Czech National Phytosociological Database. It included plots of wet to mesic meadows and mesic pastures of the class *Molinio-Arrhenathereta* sampled across the country and classified by an expert system for automatic vegetation classification developed within the project Vegetation of the Czech Republic (Chytrý 2007–2013). We selected only plots sampled on flat land or slopes of up to 5°. Each plot was assigned a value of mean July temperature from a climatic model based on the interpolated measured values from climatic stations, as used in the Climate atlas of Czechia (Tolasz 2007). Mean July temperature was selected after preliminary tests as it provided better correlations with mean temperature indicator values than other temperature variables. Given that all the plots were from flat treeless areas, we considered their temperature regime as being unaffected by slope, aspect and canopy shading, and thus reasonably well described by macroclimatic data from the atlas.

(iii) Moisture indicator values – dataset **Moravian grasslands**. This dataset included dry to semi-dry grassland plots from southern Moravia and the White Carpathians (Merunková et al. 2012). All of these grasslands were sampled on deep soils on slopes unaffected by a high water table or flooding, therefore precipitation can be considered as a good proxy for moisture availability in this system. Total annual precipitation for plot sites was derived from a climatic model developed for the Climate Atlas of Czechia (Tolasz 2007), based on the measured values from climatic stations.

(iv) Reaction indicator values – dataset **Dyje valley forests**. This dataset included vegetation plots sampled in various types of natural forest vegetation in the Dyje (Thaya) valley on the Czech/Austrian border (Podyjí/Thaytal National Park). The dataset is described by Zelený & Chytrý (2007), however, unlike in that paper, here we used also plots sampled on calcareous soils. In each plot, five samples of mineral soil were taken from a depth of 1–10 cm, mixed and put into distilled water with a weight ratio of soil:water ~2:5. Soil pH was measured in this suspension after 24 hours.

(v) Nutrient indicator values – dataset **Dyje valley forests** as described above. Ratio of soil organic carbon to total nitrogen content (C:N ratio) in the upper 10 cm of mineral soil was used as a proxy for nutrient availability, following Ewald & Ziche (2017), who among several soil variables found this ratio to be the best correlate of Ellenberg indicator values for nutrients.

Table 1. – Datasets used for testing the accuracy of predictions of environmental conditions using the original Ellenberg and Czech indicator values.

Tested indicator value		Light	Temperature	Moisture	Reaction	Nutrients
Dataset		Czech forests	Czech meadows	Moravian grasslands	Dyje valley forests	Dyje valley forests
No. of plots		2371	835	68	104	104
No. of species		902	805	530	324	324
Species with original	no.	765	518	374	231	271
Ellenberg value	%	85	64	71	71	84
Species with Czech	no.	790	668	451	257	303
indicator value	%	88	83	85	79	94
Species with both	no.	672	495	372	230	271
Ellenberg and Czech value	%	75	61	70	71	84

Results

Indicator values were established for 2275 species and 801 other taxa (subspecies, varieties, hybrids, aggregates and sections) of the Czech vascular plant flora (Table 2). For between 1558 (69%, for reaction) and 1832 (81%, for salinity) of these species and between 81 (10%, reaction) and 99 (12%, salinity) of the other taxa indicator values are also in Ellenberg & Leuschner (2010). The species and other taxa present in the new list of indicator values of the Czech flora were especially (i) taxa of the Czech flora with eastern distributions that were not assessed by Ellenberg; (ii) generalist taxa included in Ellenberg's tables but with unassigned indicator value for a given factor; (iii) taxa possibly included in Ellenberg's tables, which we failed to assign because of uncertain correspondence of taxonomic concepts.

The full dataset is available in Electronic Appendix 1 at www.preslia.cz. For each indicator value except salinity, this dataset contains two variants, one with values assigned to all taxa and the other in which values for generalist taxa are replaced by "x".

Table 2. – Number of vascular plant taxa with assigned indicator values for light (L), temperature (T), moisture (M), reaction (R), nutrients (N) and salinity (S) in the new dataset for the Czech flora. Counts are given separately for all taxa with assigned values and after subtraction of generalist taxa (those marked with "x"). No species were considered as generalists for salinity, therefore the counts for salinity are given only once.

	All taxa		Without generalist taxa				
	L, T, M	R, N, S	L	T	M	R	N
All taxa	3076	3071	2899	2852	2954	2597	2883
Species	2275	2273	2146	2135	2194	1973	2150
Subspecies	521	518	496	479	504	419	486
Varieties	101	101	95	90	93	81	92
Hybrids	10	10	10	10	10	10	9
Aggregates and s. lat.	162	162	145	133	146	108	139
Sections	7	7	7	5	7	6	7

Comparing the new indicator values for the Czech flora with the original Ellenberg indicator values (Ellenberg & Leuschner 2010), we found generally high correspondence (adjusted $r^2 = 0.637$ for salinity and between 0.804 and 0.946 for the other factors; Fig. 1). Most taxa retained the original Ellenberg value or differed by just one degree in the new dataset. However, there were some notable deviations in the assessment of individual taxa. For example, Ellenberg assigned a light value of 9 to *Orobanche flava*, a species occurring under dense canopies of broad *Petasites* leaves, usually at the bottom of shaded mountain valleys. We assign this species a value of 5. For moisture, Ellenberg assigned a value of 7 to *Parietaria judaica*, a species growing on dry walls; we assigned it a value of 3. For nutrients, he assigned a value of 8 to *Scirpoides holoschoenus*, a species of oligo- to mesotrophic wet grasslands and fens; we assigned this species a value of 4.

In spite of changes in indicator values of some taxa, the frequency distributions of indicator values were very similar to the distribution of the original Ellenberg values, especially for light and moisture (Fig. 2). For temperature, the frequency distributions were also similar, but in the original Ellenberg dataset very many taxa were assigned a value of 6, whereas in the new Czech dataset taxa were more evenly distributed among the categories 5–7. However, frequency distributions of the reaction, nutrient and salinity values revealed systematic differences between Ellenberg's and our assessments. While Ellenberg tended to consider more taxa to be strongly basiphilous, we considered many of these taxa to be slightly basiphilous, neutrophilous or generalists with respect to reaction. In the case of nutrients, Ellenberg assigned many taxa to the lowest categories, evaluating them as oligotrophic. We reclassified many of these taxa, especially dry grassland plants and arable weeds, to higher categories of nutrient requirements. In the case of salinity, Ellenberg considered many taxa as not salt-tolerant, assigning them a salinity value of 0, while we considered 333 such taxa to be slightly salt-tolerant (value 1) and 36 even more salt-tolerant.

The original Ellenberg indicator values and the new Czech indicator values predicted environmental conditions with very similar accuracy in our tests against measured variables. When using the available values for all the species in the plots (except generalists indicated with "x"), i.e. involving on average more species with the new Czech indicator value than those with the original Ellenberg value, predictions with Czech values were slightly worse for light and slightly better for temperature, moisture, reaction and nutrients (Figs 3, 4). The results were very similar when we considered only species that had

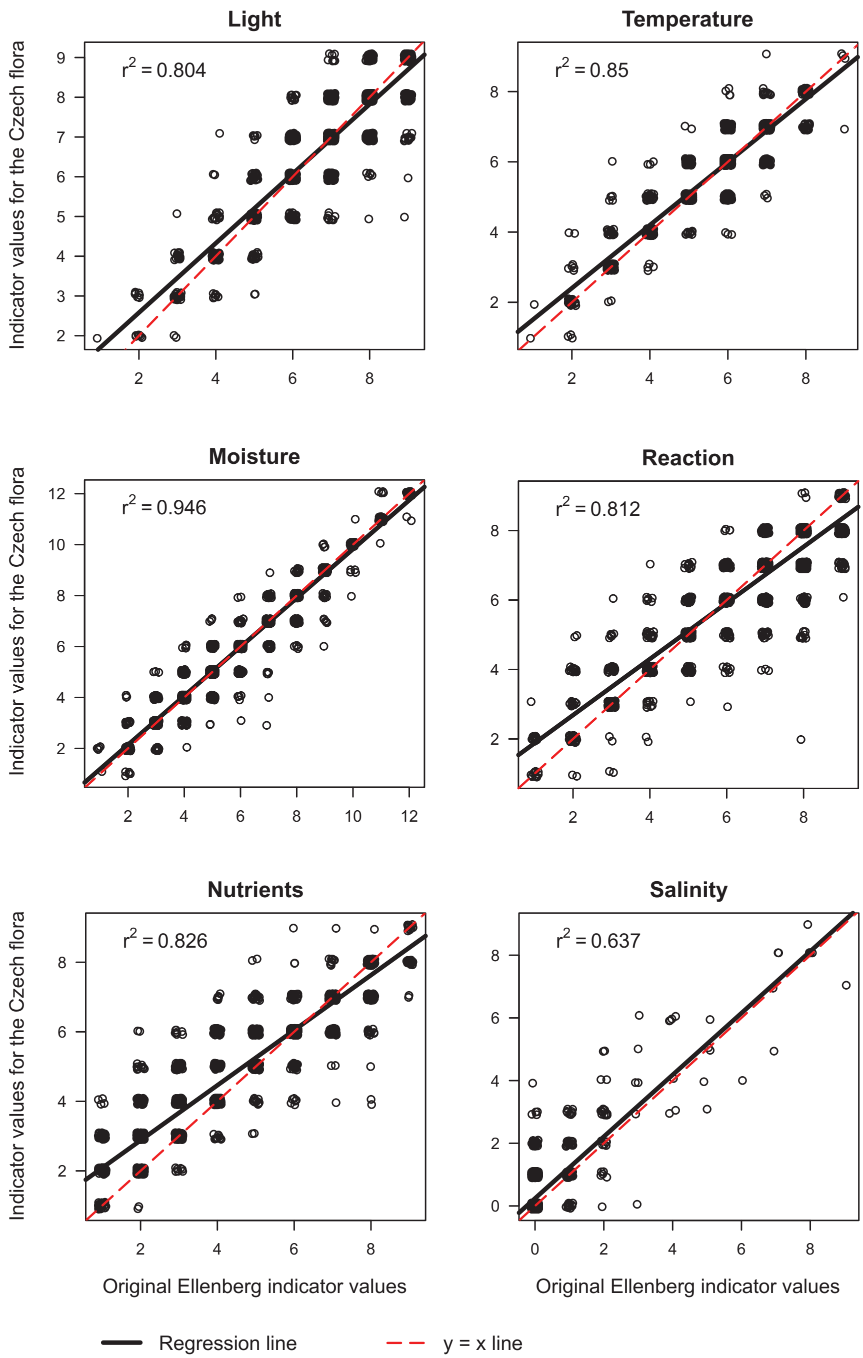

Fig. 1. – Scatter plots comparing the new indicator values for the Czech flora and the original Ellenberg indicator values. Only species (not other taxa) occurring in both datasets were used in comparisons, including 1822 species for light, 1560 for temperature, 1758 for moisture, 1558 for reaction, 1718 for nutrients and 1832 for salinity. Adjusted coefficients of determination (r^2) are shown. The points, corresponding to individual species, are slightly jittered to show the areas with their higher and lower concentrations.

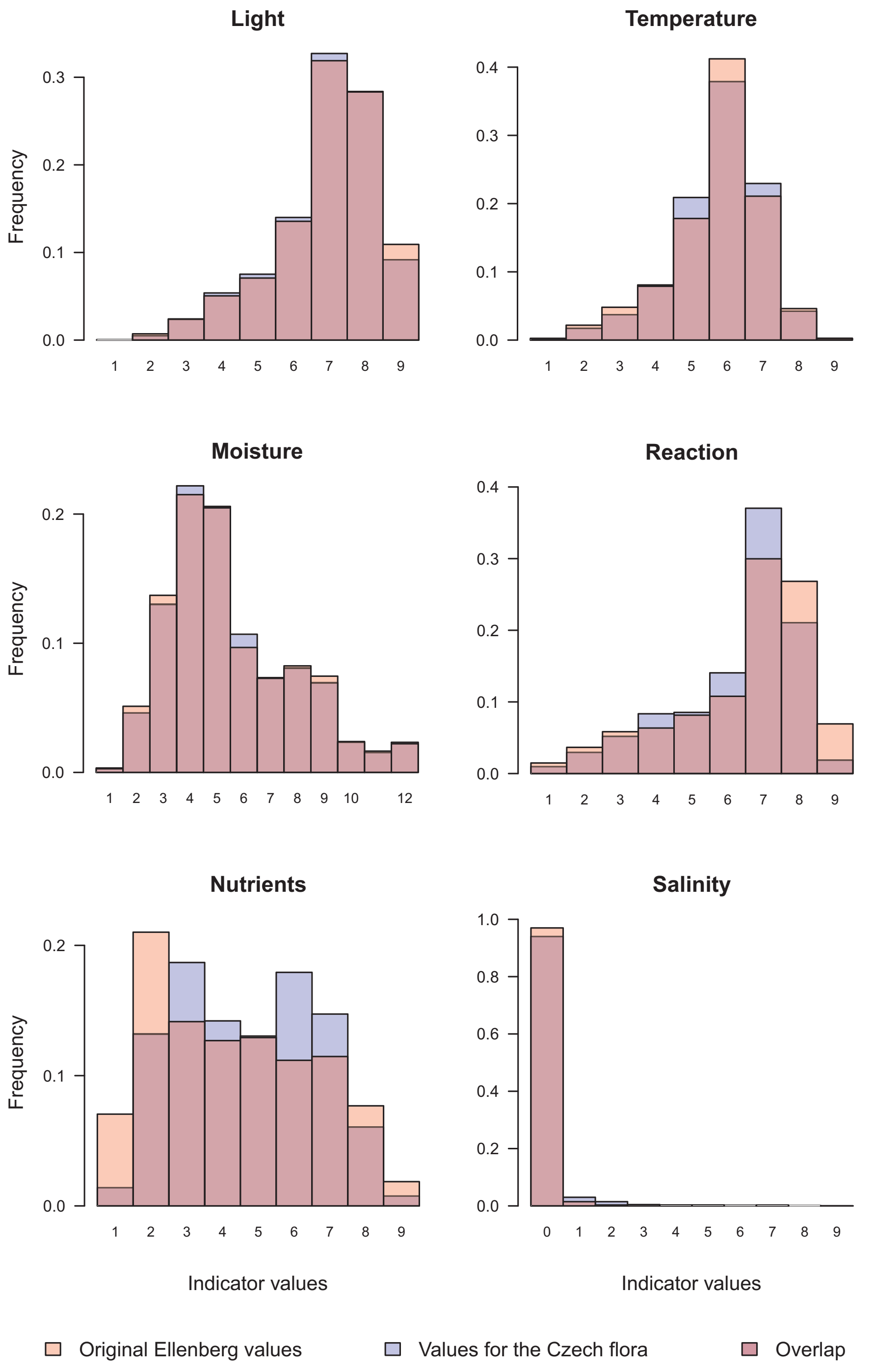

Fig. 2. – Histograms of relative frequencies of the new indicator values for the Czech flora and the original Ellenberg indicator values. Only species (not other taxa) occurring in both datasets were used in comparisons (see Fig. 1 for numbers of cases).

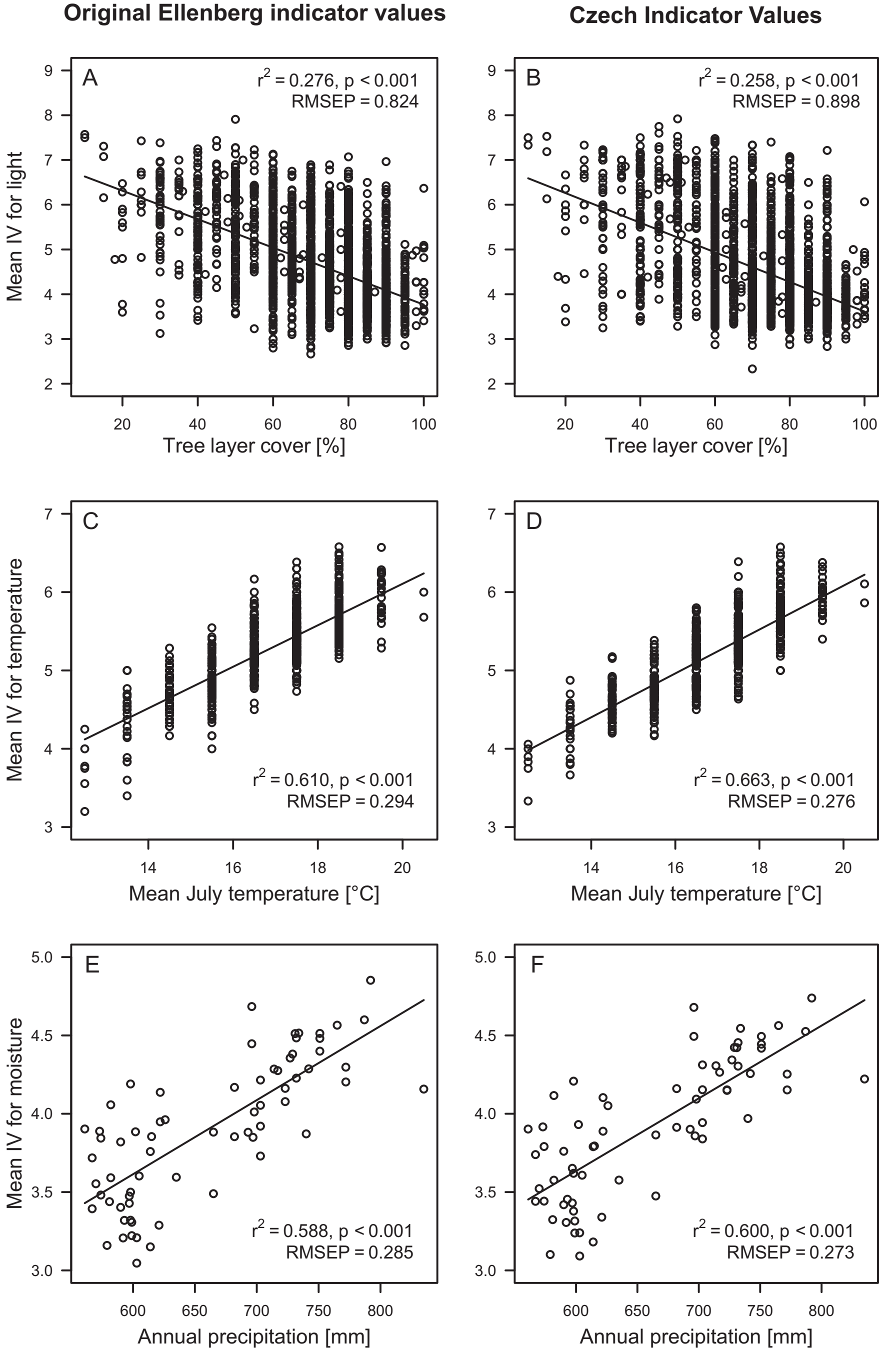

Fig. 3. Comparison of the accuracy of prediction of environmental variables (forest understorey light, temperature and moisture) using the original Ellenberg indicator values (left column) and the new Czech indicator values (right column). In all cases, unweighted site mean indicator values were linearly regressed against measured environmental variables. More accurate prediction is indicated by higher values of r^2 and lower values of RMSEP.

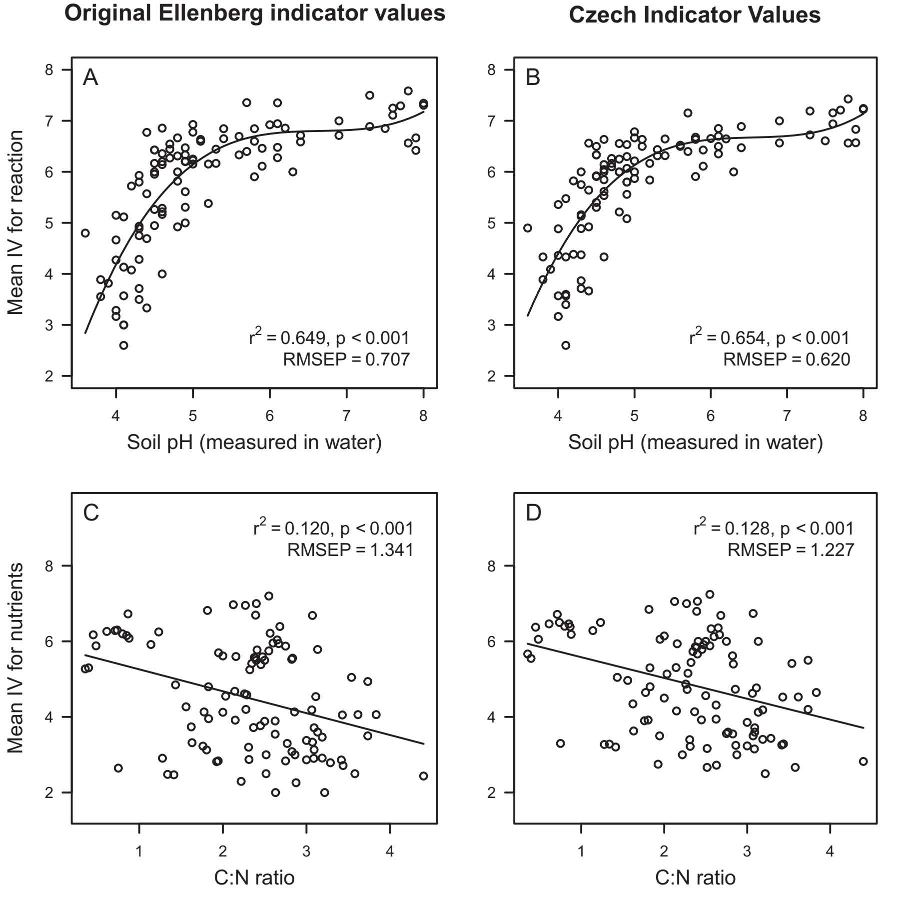

Fig. 4. Comparison of the accuracy of prediction of environmental variables (soil pH and soil C:N ratio as a measure of nutrient availability) with the original Ellenberg indicator values and the new Czech indicator values. In both cases, unweighted site mean indicator values were regressed against measured environmental variables, using third-order polynomial function for reaction and linear function for nutrients. More accurate prediction is indicated by higher values of r^2 and lower values of RMSEP.

a numerical value in both the original Ellenberg and the new Czech dataset, and excluding generalists with "x" (results not shown). In this case, predictions with Czech values were slightly better than with Ellenberg values for all factors except moisture; for moisture they were slightly worse if evaluated using r^2 but slightly better when evaluated using RMSEP.

Discussion

Main properties of the new dataset of Czech indicator values

The new dataset of ecological indicator values for the Czech flora presented here has the following properties: (i) It includes most taxa of the Czech vascular flora, many of which are absent in the datasets compiled by Heinz Ellenberg, mainly because they are absent or rare in Germany and the Alps. (ii) It gives indicator values for six factors (light, temperature, moisture, reaction, nutrients and salinity), and considers the ecology of individual taxa in the Czech Republic, other parts of central Europe and partly also beyond. (iii) It preserves the original Ellenberg scale, making this dataset compatible with others that follow the same scale (Borhidi 1995, Pignatti et al. 2005, Ellenberg & Leuschner 2010, www.tela-botanica.org). (iv) It shows some systematic differences from the original Ellenberg dataset in the assessment of reaction values (fewer taxa considered strongly basiphilous), nutrient values (fewer taxa considered oligotrophic) and salinity values (more taxa considered tolerant of slightly saline conditions). (v) For each taxon evaluated, except parasitic epiphytes, an indicator value is assigned for each of the six factors. However, generalist species, which should be excluded from the calculations of site mean values, are marked by "x".

Frequency distributions of indicator values

The frequency distributions of indicator values for particular environmental factors within a regional flora reflect the history of the evolution and migration of this flora. For example, Ewald (2003) interpreted the strongly left-skewed distribution of the Ellenberg indicator values for reaction as a legacy of the evolution of this flora on base-rich soils that prevailed in Europe in the Pleistocene. These distributions indicate that the Czech (and central-European) flora is biased not only towards a relatively high number of basiphilous, but also towards light-demanding and xerophilous taxa, and less so towards thermophilous taxa. Species adapted to saline habitats make up a very small proportion of this flora.

The frequency distributions of indicator values reflect collective ecological properties of the current species pools, and are therefore relevant for biogeographical considerations. However, the shapes of the frequency distributions may be influenced by the subjectivity of the assessment. In our case it is illustrated by the differences between the original Ellenberg dataset and our new Czech dataset in the assessment of the reaction, nutrient and salinity values.

The higher number of species assessed by Ellenberg as strongly basiphilous (R values of 8 and 9) can be due to purely subjective reasons. Ellenberg followed the tradition of central European vegetation science, which may overemphasize the acid-calcareous contrast and neglect intermediate habitats by establishing concepts of vicariant syntaxa of acidophilous and basiphilous vegetation (Mucina et al. 2016). In contrast to the left-skewed distribution of Ellenberg values for reaction, Lawesson (2003) found fairly balanced numbers of acidophilous and basiphilous species in the Danish forest flora based on pH measurements. However, there can also be an objective ecological explanation of this difference. In the more oceanic and precipitation-rich areas of Germany and Switzerland, where Ellenberg made most of his field observations, soils on bedrocks of intermediate base status tend to be leached, therefore many base-demanding species may be confined to limestone bedrock. In the more continental areas in the Czech Republic, especially in its dry lowland areas, soils on medium base-rich rocks retain more basic cations. Therefore, the same species that in western Europe are restricted to limestone can occur here both on limestone and medium base-rich rocks. This explanation is partly supported by Gégout & Krizova (2003) who found that forest species that behave as neutrophilous to basiphilous in the Vosges Mts in eastern France tend to be acidophilous in Slovakia.

Ellenberg also considered more species as oligotrophic (N values of 1 and 2) than we did in our assessment of the Czech flora. One reason for this difference is that we assigned slightly higher nutrient values to species of dry habitats such as dry grasslands, because these habitats do contain considerably more nutrients than truly oligotrophic habitats such as bogs or siliceous outcrops in precipitation-rich mountain areas. However, these nutrients are taken up by plants mainly after rain, whereas in dry periods their acquisition is restricted by drought. We also tended to assign higher values than in Ellenberg's tables to weeds of nutrient-poorer arable land. Although some weed species are confined to sites that are relatively poor within the context of arable habitats, still all arable habitats are richer in nutrients than some non-arable habitats. Doing this, we tried to reduce the dependence of the indicator values on vegetation types as pointed out by Wamelink et al. (2002). Another reason for the difference in nutrient values between Ellenberg's tables and our assessment can be that these two datasets were based on experiences of landscapes with different nutrient statuses. Ellenberg mainly used his field observations of plant species ecology in the 1940s–1960s (the first edition of his indicator value dataset was published in 1974; Ellenberg 1974). At that time, nutrient export from the central-European landscape was still relatively large due to extensive grazing and hay-cutting, while atmospheric nutrient deposition was low. In contrast, our own experience is from the last decades, when many formerly managed habitats have been abandoned, resulting in litter and nutrient accumulation. Artificial nutrient inputs from mineral fertilizers and atmospheric deposition also increased considerably (Ewald et al. 2013). As a result, many species that were previously confined to oligotrophic sites have probably shifted or extended their niche to nutrient-richer habitats in the current nutrient-rich landscape. Actually, Ellenberg himself mentioned this issue already in the 1991 edition of his dataset (Ellenberg et al. 1991).

Finally, our assessment systematically differs from Ellenberg tables in the indicator values for salinity. Ellenberg's scale for salinity differs from the other scales in using a value of 0 for glycophytes, i.e. salt intolerant species. Actually, by far the largest proportion of central-European plant taxa belong to this category. However, our field observations and vegetation-plot data indicate that more than 300 species considered by Ellenberg as glycophytes can actually occur in saline habitats, although they are more common in non-saline habitats. Therefore, we assigned low non-zero indicator values to these species. This difference in the assessment can partly be caused by the fact that Ellenberg et al. (1991) considered only salinity in coastal habitats bordering the North and Baltic Seas based on the proposal of Scherfose (1990). On sea coasts, salinity is due mainly to sodium chloride, whereas in the inland saline habitats in the Czech Republic, salinity is due mainly to calcium and magnesium sulphates from mineral springs, while further to the southeast in the Pannonian Basin the main sources of salinity are sodium and potassium carbonates (Vicherek 1973). The Czech salinity indicator values therefore consider salinity due to various ions of soluble salts.

Accuracy of prediction based on the Czech indicator values

We tested the new Czech indicator values by regressing unweighted site mean values against measured environmental variables for each factor except salinity for which we did not have an appropriate test dataset. In most cases, Czech values gave slightly better predictions than the original Ellenberg values, but the improvement measured by the coefficient of determination (r^2) was only 5% in the case of temperature and around 1% in the case of other values. In the case of light, the accuracy was slightly lower when all values were used and slightly higher when only the species occurring in both datasets were used. The prediction of the availability of light in forests can be somewhat influenced by the fact that Ellenberg considered conditions with fully developed foliage and assigned low light values to vernal forest geophytes, which grow and flower before leaf flushing, whereas we assigned these species higher light values. Although our approach better characterizes the autecology of these species, inclusion of original Ellenberg values in the calculations of site mean values can result in their better correlation with canopy cover measured at the peak of the growing season, which was the variable used for testing in our case.

Our tests also show that for most factors the relationship between the site mean indicator values and the measured environmental variables is well described by a linear function. An exception is the reaction value, which has a pronounced non-linear pattern. This pattern was already described by Schaffers & Sýkora (2000) who argued that Ellenberg reaction values only correlate with pH for acidic conditions, while in near-neutral and basic conditions they mainly reflect calcium concentration.

Some practical recommendations

Indicator values for sites are usually calculated as arithmetic means of indicator values for species and other taxa occurring at those sites. From a strictly statistical point of view this is problematic due to the ordinal nature of indicator values, therefore alternative ways of calculating site indicator values have been proposed (Botta-Dukát & Ruprecht 2000, Schaffers & Sýkora 2000). In spite of these issues, mean values are still preferred by most users, probably because they are usually clearly ecologically interpretable and the potential error due to averaging is small relative to other confounding factors (ter Braak & Barendregt 1986, ter Braak & Gremmen 1987, Hill & Carey 1997, Ertsen et al. 1998, Hill et al. 2000, Schaffers & Sýkora 2000, Wamelink et al. 2002). We also have good experience of using site mean indicator values, e.g. in our tests against measured environmental values, and recommend the use of these averages.

However, the accuracy of the estimates of site conditions can be influenced by the fact that ecological generalists, i.e. taxa that are poor indicators of ecological conditions, are given the same weight in calculations as ecological specialists (ter Braak & Gremmen 1987). Ellenberg resolved this issue in a simple way, by assigning the non-numerical value “x” to such species, thus excluding them from the calculations of mean values. We have assigned numerical values to all species, including generalists, for which the value is the mean value of their broad ecological range. Although such values are useful for autecological characterization of individual species, they may decrease the accuracy of prediction of environmental conditions based on site mean indicator values. This is because the indicator values for generalists are usually in (or near) the middle of the scale, and as a result they tend to shift the site mean indicator values towards the middle of the scale. Consequently, the range of the site mean indicator values is compressed and prediction of site conditions becomes less reliable. We made various tests (results not shown) of the accuracy of the prediction against measured environmental variables, including and excluding generalists, and the accuracy usually decreased when the generalists were included. Therefore, in Electronic Appendix 1 we provide two variants of each indicator value, except for salinity. The variables L, T, M, R, N and S contain numerical values for all taxa, while in the variables Lx, Tx, Mx, Rx and Nx the numerical value is replaced by "x" for generalists. In any calculation of site mean indicator values, we recommend to use the latter set of variables and consider "x" as missing values. We did not define any generalists for salinity, therefore the mean site indicator values for salinity should be calculated using the variable S; in this case it is important that the zero values are included in the calculations.

See www.preslia.cz for Electronic Appendix 1, the dataset of Czech indicator values, which is also included in the new Pladias Database of the Czech Flora and Vegetation (www.pladias.cz).

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Souhrn

Článek představuje nový soubor ekologických indikačních hodnot pro druhy, poddruhy, variety, běžné hybridy a vnitrorodové druhové skupiny flóry cévnatých rostlin České republiky. Indikační hodnoty pro světlo (L), teplotu (T), vlhkost (M), (půdní) reakci (R), dostupnost živin (N) a salinitu (S) byly stanoveny pro 2275 druhů a 801 dalších taxonů pomocí stupnic vytvořených Heinzem Ellenbergem pro německou a alpskou flóru. Nové indikační hodnoty jsou proto srovnatelné s Ellenbergovými indikačními hodnotami, které byly použity jako základ, ale byly rozsáhle revidovány na základě terénní zkušenosti autorů, literatury, srovnání se systémy indikačních hodnot jiných zemí a analýzy dat o společném výskytu druhů ve fytocenologických snímcích z České národní fytocenologické databáze. Dále byly doplněny taxony české flóry nezahrnuté v Ellenbergových tabulkách. Hlavním rozdílem oproti Ellenbergovým indikačním hodnotám je menší počet taxonů klasifikovaných jako silně bazifilních, extrémně nenáročných na živiny a striktně se vyhýbajících zasoleným stanovištím. Nové indikační hodnoty pro českou flóru byly testovány srovnáním nevážených průměrných indikačních hodnot ve fytocenologických snímcích s měřenými proměnnými prostředí. Ve většině případů byl odhad stanovištních podmínek o něco málo přesnější než odhad pomocí původních Ellenbergových indikačních hodnot. Nové indikační hodnoty jsou volně stažitelné jako elektronická příloha tohoto článku. V této příloze sloupce L, T, M, R, N a S obsahují hodnoty pro všechny taxony, zatímco sloupce Lx, Tx, Mx, Rx a Nx mají u taxonů s širokou ekologickou amplitudou nahrazenu numerickou hodnotu hodnotou „x". Při výpočtu průměrných hodnot pro lokality nebo fytocenologické snímky doporučujeme taxony s hodnotou „x" pro daný faktor vynechat, čímž se zlepší přesnost odhadu podmínek prostředí.

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Appendix 1. – Verbal definitions of the scales of Ellenberg indicator values (English translation of the German original from Ellenberg & Leuschner 2010, with slight modifications) and practical comments on the application of individual scales.

Light (scale 1–9)
For trees, the values relate to juveniles occurring in the herb and shrub layers. Trees occurring in the tree layer and parasitic epiphytes (*Loranthus* and *Viscum*) should be excluded when calculating site mean values.

1 – deep shade plant, occurring where the incident diffuse radiation is less than 1% of that in an open area, rarely at more than 30%
2 – between 1 and 3
3 – shade plant, usually occurring where the incident diffuse radiation is less than 5% of that in an open area, but also at sunnier sites
4 – between 3 and 5
5 – semi-shade plant, only exceptionally occurring in full light, but usually at more than 10% of the diffuse radiation incident in an open area
6 – between 5 and 7; rarely at less than 20% of diffuse radiation incident in an open area
7 – half-light plant, mostly occurring at full light, but also in the shade up to about 30% of diffuse radiation incident in an open area
8 – light plant, only exceptionally occurring at less than 40% of diffuse radiation incident in an open area
9 – full light plant, occurring only in fully irradiated places, not at less than 50% of diffuse radiation incident in an open area

Temperature (scale 1–9)

1 – cold indicator, only in high mountain areas, i.e. the alpine and nival belts
2 – between 1 and 3 (many alpine species)
3 – cool indicator, mainly in subalpine areas
4 – between 3 and 5 (especially high montane and montane species)
5 – moderate heat indicator, from lowland to montane belt, mainly in submontane-temperate areas
6 – between 5 and 7 (lowland and colline species)
7 – heat indicator, occurring in relatively warm lowlands
8 – between 7 and 9
9 – extreme heat indicator, restricted to warmest sites in southern central Europe

Moisture (scale 1–12)
Unlike Ellenberg, we did not use non-numeric symbols "~" for indicators of strongly alternating moisture and "=" for indicators of flooding. Parasitic epiphytes (*Loranthus* and *Viscum*) should be excluded when calculating site mean values.

1 – strong drought indicator, viable at sites that frequently dry out and confined to dry soils
2 – between 1 and 3
3 – missing on damp soil
4 – between 3 and 5
5 – indicator of fresh soils, focus on soils of average moisture, missing on wet soils and on soils that frequently dry out
6 – between 5 and 7
7 – humidity indicator, focus on well moistened, but not wet soils
8 – between 7 and 9
9 – wetness indicator, focus on often soaked, poorly aerated soils
10 – aquatic plant that survives long periods without soil flooding
11 – aquatic plant rooted under water, but at least temporarily with leaves above the surface, or a plant floating on the water surface
12 – permanently or almost permanently submerged aquatic plant

Reaction (scale 1–9)

1 – indicator of strong acidity, never occurring in slightly acidic to alkaline conditions
2 – between 1 and 3
3 – acidity indicator, occurring mainly in acidic conditions, exceptionally in neutral conditions
4 – between 3 and 5
5 – indicator of moderate acidity, occurring rarely in strongly acidic as well as in neutral to alkaline conditions
6 – between 5 and 7
7 – indicator of slightly acidic to slightly basic conditions, never occurring in very acidic conditions
8 – between 7 and 9, occurring mostly in calcium-rich conditions
9 – base and lime indicator, always occurring in calcium-rich conditions

Nutrients (scale 1–9)
Ellenberg related this scale primarily to nitrogen, although admitting that in many cases the values better describe general nutrient availability, including also availability of phosphorus (Ellenberg et al. 1991). As it is difficult to separate the effect of these nutrients in observational studies, we refer to nutrients instead of nitrogen.

1 – occurring at nutrient-poorest sites
2 – between 1 and 3
3 – occurring at nutrient-poor sites more frequently than at average sites and exceptionally at rich sites
4 – between 3 and 5
5 – occurring at moderately nutrient-rich sites, and less frequently at poor and rich sites
6 – between 5 and 7
7 – occurring at nutrient-rich sites more often than at average sites and only exceptionally at poor sites
8 – pronounced nutrient indicator
9 – concentrated at very nutrient-rich sites

Salinity (scale 0–9)
Ellenberg related this scale to chloride content, which is typical of coastal habitats. For inland habitats, in which salinity is also caused by other salts such as sulphates and carbonates, we refer to general salt content. The zero values should be included in calculations of site mean values.

0 – not salt tolerant, glycophyte
1 – salt tolerant, mostly on low-salt to salt-free soils, but occasionally on slightly salty soils
2 – oligohaline, often on soils with very low salt content
3 – β-mesohaline, mostly on soils with low salt content
4 – α/β-mesohaline, mostly on soils with low to moderate salt content
5 – α-mesohaline, mostly on soils with a moderate salt content
6 – α-meso/polyhaline, on soils with moderate to high salt content
7 – polyhaline, on soils with a high salt content
8 – euhaline, on soils with a very high salt content
9 – euhaline to hypersaline, on soils with a very high and in dry periods extremely high salt content