Towards the pan-European bioindication system: Assessing and testing updated hydrological indicator values for vascular plants and bryophytes in mires

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ABSTRACT

Bioindication systems based on the occurrence of plant species are widely used in vegetation science, palaeoecology, community ecology, geographical modelling and global change biology. Although the existing systems are mostly regional, the development of large-scale vegetation databases calls for the establishment of a pan-European indication system. Here we present the first step towards this goal, by assessing indicator values for soil moisture and water table depth in European mires and associated grasslands. For each vascular plant and bryophyte species occurring in 24,091 vegetation-plot records of European mires, we developed an updated system of Ellenberg-like Ecological Indicator Values (EIVs) at the scale of 1–12 (*species optimum*) including ecological valences – minimum value (*drought intolerance*), maximum value (*flooding tolerance*) and range of values (*tolerance*), using both statistical and expert-based approaches for species co-occurrence data. Spearman correlation coefficients, Akaike Information Criterion (AIC) and Akaike weights were used to assess the performance of the updated EIVs against measured soil moisture and water table in two Central-European datasets, and against the proportion of aquatic mollusc species in a European-scale dataset. The updated EIVs performed well in all cases, having stronger correlations with directly measured water table and the combined proportion of aquatic and wetland molluscs than the original EIVs. The original EIVs, however, performed better with soil moisture. In the Central-European datasets, the use of minimum values (*drought intolerances*) of the updated EIVs weighted by species covers and/or tolerances led to the highest correlations with water table in all cases. This improvement of the indication potential on the regional scale is mainly related to the inclusion of bryophytes into the updated EIVs. Our data show that the updated EIVs are beneficial not only when used in the cross-regional or pan-European datasets, but also when water table rather than soil moisture is to be indicated in the regional-scale data, as it occurs frequently in bryological, zoological and protistological research. Overall, this study demonstrates how EIVs can be updated by including previously omitted taxa of vascular plants and bryophytes and adding ecological valences to reflect accurate conditions of natural habitats at the continental scale.

1. Introduction

Bioindication systems based on the occurrence of plant species are widely used in vegetation science (Vild et al., 2018; Rion et al., 2018), palaeoecology (Kuneš et al., 2011; Amesbury et al., 2018), ecosystem ecology (Pakeman et al., 2019), plant and animal community ecology (Diekmann, 2003; Horsák et al., 2007; Rádková et al., 2014), functional ecology (Vojtkó et al., 2017), geographical modelling (Wamelink et al., 2019) and global change biology (Diekmann et al., 2019). The importance of such systems increases with the increasing extent of the study, as the exact values of locally measured environmental parameters are difficult to obtain across large spatial scales. Although

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missing data can be imputed based on the overall species composition (the *MOSS* method, Tichý et al., 2010), this approach requires large datasets with reliably measured environmental variables. Likewise, many techniques in palaeoecology and historical ecology use extensive training datasets, i.e. compositional data associated with directly measured environmental parameters (Mitchell et al., 2008; Amesbury et al., 2018; Šímová et al., 2019). When the exact values of environmental variables are not available or difficult to measure because of their large temporal variation, bioindication systems provide a useful and powerful alternative.

The use of Ecological Indicator Values (EIVs) for individual species or species aggregates is a widespread approach for the estimation of site conditions. In this approach, most plant species are associated with an ordinal value according to their occurrences along the target environmental gradient. The assignment of ordinal values has typically been developed by experts based on the field observations of realized niches of plant species and the evidence from ecological experiments and measurements of environmental variables. The most popular system, involving the EIVs for light, temperature, continentality, soil moisture, soil reaction, nutrient availability, and soil salinity has been established in Germany by Ellenberg et al. (1992). Further, it was established for many other European countries and regions such as Great Britain (Hill et al., 2000; 2007), Hungary (Borhidi, 1995), Poland (Zarzycki et al., 2002), Alps (Landolt et al., 2010), Italy (Guarino et al., 2012), Ukraine (Didukh, 2011) and Czech Republic (Chytrý et al., 2018). However, this approach has never been applied to Iberian and Balkan peninsulas, Mediterranean islands and Fennoscandia, except for local studies (e.g. Mayor, 1999) and some fragmentary reports (https://www.tela-botanica.org/). Outside Europe, the same or similar systems have been locally or regionally developed in North America (Bakuzis, 1959; Wang, 2000), Asia (Naqinezhad et al., 2019), Australia (Ling et al., 2019) and Afrika (Maamar et al., 2018).

The EIV system sorts species on a scale of 1 to 12 (see Hill et al., 2007 for the explanation of individual categories) and when applied, the unweighted or weighted means of these values are calculated for vegetation-plot records or species lists. The extraordinarily high popularity of this system in Central Europe, despite certain limitations with precise ecological interpretations (Raduła et al., 2018; Schaffers and Sýkora, 2000; Wamelink et al., 2002) and statistical testing (Zelený and Schaffers, 2012; Zelený, 2018), is largely caused by persistent difficulties to precisely measure principal ecological factors (Chytrý et al., 2018) and by the absence of measured variables in old vegetation-plot datasets (Navrátilová et al., 2017). Therefore, new methods have been proposed for revisiting EIVs using large databases and observed ecological conditions (e.g. Berg et al., 2017 for continentality).

The importance of EIVs increases with the increasing size of a dataset and spatial extent of a study. For example, while some local environmental factors such as soil or water nutrient concentration, or hydrology may strongly fluctuate between years or seasons (Tahvanainen et al., 2003; Hájek and Hekera, 2004; Styles and Coxon, 2007; Griffiths et al., 2019), plant species composition is more stable and usually reflects long-term environmental conditions (Jiroušek et al., 2013). Despite that, the currently available EIVs are based on regional (mostly national) data, with no effort made to create a continental system. Here, we focus on hydrological conditions, i.e. soil moisture and water table depth, to develop a pan-European system of EIVs in European mires (springs, fens and bogs). Mires represent extremely endangered ecosystems at the continental (Janssen et al., 2016) and regional (Chytrý et al., 2019) scales. Their species composition and richness are generally governed by water pH/calcium and hydrological gradients (Malmer, 1986; Dierssen and Dierssen, 2001; Rydin and Jeglum, 2013; Peterka et al., 2017; Horsáková et al., 2018), yet the ongoing land use and climate changes disturb their natural hydrology. As the water level and soil moisture decrease (Price, 1997; van Diggelen et al., 2006; Marazzi et al., 2019), the most important ecological functions of mires – such as the capacity to act as global carbon sinks

and refugia for endangered species – are being put at a serious risk (Fenner and Freeman, 2011; Gatis et al., 2016; Robroek et al., 2017). However, hydrological conditions are difficult to measure because of their complexity and fluctuation, and precise long-term direct measurements are therefore available only for a few individual sites (e.g. Laitinen et al., 2008; Jabłońska et al., 2011; Hájek et al., 2013). EIVs therefore still have not gone out of fashion, playing a pivotal role in many recent monitoring, resurvey and restoration studies (e.g. Koch et al., 2017; Navrátilová et al., 2017; Hancock et al., 2018; Johansen et al., 2018). In mire ecosystems, we argue that the extension of EIVs on the European scale is not only possible but urgently needed.

The current development of continental-scale vegetation databases (Chytrý et al., 2016) has emphasized the need for large-scale bioindication systems because measured environmental data are scarce. Peterka et al. (2015, 2017) collected a comprehensive vegetation dataset of European fens, but only the minority of compositional data is associated with *in situ* measured environmental parameters, in most cases with water pH. While climate data for such a large dataset can be obtained from climatic models such as WorldClim (Hijmans et al., 2005) or CHELSA (Karger et al., 2017), and base saturation data can be extrapolated from large data sets of measured pH values, there is no easy way to estimate hydrological conditions. Contrary to pH niches that may differ between distant regions at the continental scale (Hájková et al., 2008), hydrological niches seem to be more stable and evolutionarily deeply ingrained, due to the complex nature of adaptations to high water level, requiring large genomic changes (Crawford, 1996; Jackson and Colmer, 2005) as demonstrated for vascular plants (alpha niche; Ackerly and Cornwell, 2007) and peat mosses (Johnson et al., 2015). Indeed, an important feature of mire vegetation is the key ecological role of bryophytes (Jones et al., 1994; Vitt, 2000). Bryophytes and lichens are however rarely considered in studies using EIVs, partially because available EIVs for bryophytes are scaled differently than those for vascular plants (Ellenberg et al., 2001; Düll et al., 2001; Hill et al., 2004, 2007).

The principal aim of our study is to develop an integrated system of Ellenberg-type EIVs for hydrological conditions, including species optima and tolerances, for European mire bryophyte and vascular plant species using an identical scaling, and to test its validity using independent data. We also include an indication of hydrological niche width (i.e. species tolerances expressed as a range of ordinal values) that could be used for weighting EIVs in a site. Such a consideration of species tolerances has been rarely applied in EIV approaches (but see Košuthová and Šibík, 2013), although it is widely used in palaeoecology (transfer function models; Mitchell et al., 2008; Amesbury et al., 2018). At the regional scale, we aim to test the updated EIVs against directly measured values of water table depth and soil moisture using data from the Czech Republic (Navrátilová et al., 2006; Hájek et al., 2013), and compare the results with those obtained for the original EIVs. At the continental scale, we will use our data on plant and mollusc species composition, covering southern-European to boreal-arctic regions (Horsáková et al., 2018). For this dataset, any direct water table and soil moisture measurements are not available. Therefore, we will use the combined proportion of aquatic and wetland mollusc species in the whole mollusc assemblage as a proxy for hydrological conditions. Specifically, we will test the updated EIVs against this proxy, and determine whether the updated EIVs – including bryophytes and vascular plants occurring outside Central Europe – account for more variation than the original EIVs, limited to Central-European vascular plants.

2. Material and methods

2.1. Compilation of EIVs

The initial source of EIVs for our work was the last edition of the original Ellenberg indicator values for vascular plants and soil moisture (Ellenberg and Leuschner, 2010). At the first step, we linked the

Ellenberg values with the species co-occurrence data in the pan-European dataset of 24,091 vegetation plots compiled by Peterka et al. (2017) for classification of fen vegetation. Because this dataset also includes plots transient to bogs, almost a complete list of European mire species was covered. The species list also contains species spanning to mires from surrounding habitats, having their ecological optima outside mires (i.e. wet and mesic grasslands, springs, heaths, wet tundra etc.). We assigned indicator values to those species in the dataset for which they were available in Ellenberg and Leuschner (2010), after resolving synonymous names. Next, we assigned a new indicator value to all species, using two different methods of statistical assessment. The first method was based on reciprocal averaging as described in Chytrý et al. (2018), calculating the mean of original Ellenberg EIVs for each vegetation plot of the pan-European vegetation dataset of mires. These values were averaged for each species by calculating the mean of EIVs from all plots with the species. Because averaging generally causes shrinkage of values towards the mean (Hill et al., 2000), the final values were rescaled in order to fit the original scale. The second method utilised a similarity between species co-occurrences within the vegetation data. In this case, an indicator value for each species was estimated as a mean of EIVs of ten species with the highest degree of co-occurrence with the target species (faithful species). The degree of co-occurrence was measured using the *phi* coefficient of association (Sokal and Rohlf, 1995) between species presences in the vegetation-plot dataset. Both methods assigned new indicator values to all vascular plant and bryophyte species in the dataset independently, including those not present in the original Ellenberg tables. Plot data editing and statistical assessment of indicator values were conducted in the JUICE 7 program (Tichý, 2002).

2.2. New expert-based values

The two statistical estimates of EIVs contained inaccuracies, especially for species with ecological optima outside mires that occurred only in a few plots. Further, the two methods (reciprocal averaging vs similarity between species co-occurrences) produced different outcomes. Besides, several specialised mire plants were missing in our pan-European vegetation dataset, especially Corsican and Iberian endemics and narrow-range northern peat mosses. Therefore, we complemented the list using the diagnostic species of individual EUNIS mire types (Janssen et al., 2016) and the monograph on northern peat mosses (Flatberg, 2013). Finally, we conducted an expert assessment of the complete list of EIVs (M.Há., D.D., T.P., B.J-A., P.H. for all species and a bryologist E.M. for bryophytes) according to our best expertise, considering own empirical or literature-based knowledge of species ecology from across Europe. The statistically estimated values (see above) were used as a guideline, but not as a definite outcome. We further considered other than original Ellenberg EIVs, especially the Hill's EIVs for Atlantic species (Hill et al., 2000), unpublished EIVs for bryophytes compiled by C. Berg (http://www.sci.muni.cz/botany/juice/ELLENB_Christian_Berg_2011_11_1.txt), and other available scales describing moisture demands of species (rescaled to the range of 1–12). The most important additional sources were the moisture scale published by Flatberg (2013) for individual *Sphagnum* species and the scale available at Tela Botanica web pages (https://www.tela-botanica.org/) for southern-European endemic species. In the reviewing process, particular attention was paid to the species that differed by two or more degrees between the original Ellenberg value and values from other sources. For taxonomically difficult groups, we often set the values only for the whole aggregate, or for both the aggregate and the precisely identified species. The mean EIV we set to each species in this way is hereafter called *species optimum*.

For each species, we further estimated their tolerance (niche range), i.e. the minimum and maximum value of EIV (Supplementary Tables S1–S4). The minimum or maximum value, respectively, corresponded to the optimum value of species that are characteristic of the habitat

that represents a niche margin of a target species. For example, if the target species has an optimum in fens, but can sometimes occur in mesic grasslands, the minimum value corresponds to the EIV of those species that show an optimum in mesic grasslands. By analogy, if the target species can occur in aquatic habitats such as lakes or fishponds, the maximum value corresponds to the EIV of aquatic species. These estimates were also based on our expert assessments. The minimum value is hereafter called *drought intolerance*, while the maximum value is called *flooding tolerance*. The wider is the range between minimum and maximum (the species has a broad niche to soil moisture conditions), the lower importance should be given to this species in the EIV system. Therefore, the species tolerances were inverted to weights (natural numbers) that can be used in EIV calculations (higher tolerance = lower weight in averaging).

2.3. Testing the validity of updated EIVs against measured data

We excerpted original data on species composition and repeatedly measured water table dynamics and soil moisture from two regional studies conducted in the Czech Republic (the authors have participated in both of them). The dataset of Hájek et al. (2013), hereafter **heterogeneous dataset**, covered different vegetation types distributed along the entire pH/calcium gradient, from calcareous tufa-forming spring fens to ombrotrophic bogs (but not topogenic fens). The dataset of Navrátilová et al. (2006), hereafter **homogeneous dataset**, covered topogenic fens at fishpond margins along a shorter pH/calcium gradient. From these datasets, we extracted the values of the mean water table, mean autumnal water table (the period of deepest water table drops), water table dynamics (range, standard deviation) and soil moisture (the latter only available for the heterogeneous dataset) in four depths. For the corresponding vegetation plots, we calculated (i) unweighted means of EIVs, (ii) means weighted by percentages of species cover, (iii) means weighted by species tolerances, and (iv) means weighted by both variables (i and ii were calculated for both the original and updated EIVs, iii and iv only for the updated EIVs). Further, we calculated these means for the minimum value (*drought intolerance*, smaller value = higher drought tolerance) and maximum value (*flooding tolerance*) of the updated EIVs. Abundances of plant species were estimated using the nine-grade Braun-Blanquet's scale (van der Maarel, 1979). For each plot, we also calculated the percentage number of vascular plant species from the landscape matrix that enter the fens from the surrounding low-productive habitats, i.e. dry grasslands of the *Festuco-Brometea* phytosociological class and mesic nutrient-poor grasslands of *Nardo-Callunetea* class (for the list of species and class descriptions see Mucina et al., 2016) as an alternative indication of soil moisture (as originally used in Horsáková et al., 2018). These species were however very rare in the homogeneous dataset from topogenic fens, and hence this indication approach was tested only for the heterogeneous dataset.

The relationships between directly measured hydrological data and values derived from the plant species composition were explored using the Spearman correlation coefficient, comparing both the original and updated EIVs, as well as the percentage numbers of matrix-derived plants. All relationships were also explored by simple linear regressions, with direct measurements being used as response variables, and values derived from plant species composition as explanatory variables. The individual models for each of the directly measured variables were compared based on the Akaike's Information Criterion (AIC), with the lower AIC value indicating a better fit of the model (Akaike, 1973). To estimate the probability of each model to represent the best-fitting model, we calculated the values of Akaike weights (Wagenmakers and Farrell, 2004). For the sake of simplicity, only correlation between EIVs and soil moisture in the depth of 10 cm, mean annual water table depth and autumnal water table are shown; water table dynamics showed lower correlation with EIVs in all cases. All calculations and visualisations were conducted in R version 3.5.2 (R Core Team, 2016; https://

www.r-project.org/), using 'vegan' (Oksanen et al., 2017), 'qpcR' (Spiess, 2018), and 'ggplot2' (Wickham, 2016) packages.

2.4. Testing the validity of updated EIVs at the continental scale

To test the applicability of the updated EIVs in Europe, we used our continental-scale dataset of plant and mollusc species composition recorded between 2001 and 2016 at a total of 551 fen sites across Scandinavia, Baltic region, Bohemian Massif, Western Carpathians, Eastern Carpathians, Alps including pre-Alps, Jura Mts., and the Balkans. As no direct water table or soil moisture measurements were available for this dataset, we extracted a proxy for hydrological conditions from the mollusc species composition (see further for details). We are aware of potential drawbacks of such estimation, mainly because mollusc diversity is driven by other than hydrological factors such as calcium availability (e.g. Horsák, 2006). However, we previously found aquatic molluscs to be useful indicators of waterlogging (Horsáková et al., 2018), thus providing a possibility to test the performance of the updated EIVs relative to the original EIVs in our continental-scale data. The majority (373) of the sites were used and described in Horsáková et al. (2018). In the present study, we also included fen grasslands transient from undisturbed fens to wet meadows of the *Calthion palustris* alliance to extend the range of the hydrological gradients. Strongly acidic sites with no mollusc species were excluded from the analyses, as well as the sites with water conductivity of below 100 μS/cm and with less than two mollusc species, leaving a total of 516 analysed sites. This was done to at least partially account for the fact that aquatic species are generally more tolerant to acidic conditions (Lodge et al., 1987; Horsák and Hájek, 2003), while the majority of European terrestrial snails avoids calcium-poor habitats (Horsák, 2006; Nekola, 2010). Thus, the absence of terrestrial snails at calcium-poor mire sites is inevitable even when the moisture of these sites is high (Horsák, 2006). For this dataset, we calculated both unweighted and weighted means of EIVs, their minima and maxima, in the same manner as described in the previous chapter, and we also calculated the percentage of matrix-derived plant species that enter the fens from the surrounding low-productive habitats (see above).

From the data on mollusc species composition, we compiled a list of 53 species (out of 140) that can be classified as either aquatic or strongly hygrophilous species restricted to wetland habitats based on the classification made by Lisický (1991) and Juřičková et al. (2014), which was slightly updated based on our European-scale data on fen mollusc assemblages (Horsáková et al., 2018). For the full list see Supplementary Table S5. For each plot, we calculated the percentage number of aquatic and wetland species combined out of all mollusc species recorded in the plot, as an alternative indication of moisture conditions (the higher the water table, the higher the percentage of aquatic and wetland mollusc species). The relationships between mollusc indicators and values derived from the plant species composition (again listing different types of EIVs, and percentage number of matrix-derived plants) were explored using Spearman correlation coefficients, AIC values and Akaike weights as described above.

3. Results

The new indicator values were established for 2064 taxa (2001 species and 63 aggregates), out of which 552 are bryophytes. They are listed in Supplementary Table S1 and, along with the most frequently used synonyms, in Supplementary Tables S2 (csv file), S3 (text file for JUICE and R software with EIVs) and S4 (text file for JUICE and R software with weights based on species tolerances). The scale 1–12 corresponds to the original Ellenberg's system, explained in Ellenberg et al. (1992) and Hill et al. (1999). Most of the species showed the optimum (mean) values of 5 and 6 (Fig. 1), i.e. they represent mesic species entering mire vegetation from the surroundings. Many species, however, showed the values of 7 and 8, while the group of species with

their optima in aquatic environments (values of 10 and higher) was less numerous. The most frequent minimum value (*drought intolerance*) was 5, while the most frequent maximum value (*flooding tolerance*) was 7 (Fig. 1).

3.1. Validity of updated EIVs against measured data

In the heterogeneous dataset (Table 1), mean water table correlated poorly (r_s = 0.23) with the original unweighted EIVs, while their weighting by covers slightly improved the relationship (r_s = 0.38). A higher correlation was obtained for the updated EIVs but mainly when weighted by covers (0.52) or by both covers and tolerances (0.57). Minimum (*drought intolerance*) and maximum (*flooding tolerance*) values correlated even more strongly with water table than mean values but only when weighted by covers (0.62 for minima, 0.53 for maxima) or both covers and tolerances (0.66 for minima, 0.57 for maxima). The autumnal water table was more strongly correlated with the updated EIVs than with the original EIVs, and it also reached higher correlations with EIVs than mean annual water table in virtually all cases (Table 1). Soil moisture in 10 cm reached the highest correlation with the original EIVs weighted by covers (0.59), but correlated moderately also with updated EIVs, reaching the values of > 0.45 in all cases (Table 1). The percentage of matrix-derived plant species was more strongly correlated with soil moisture (−0.48) than with mean (−0.27) and autumnal water table (−0.28). In terms of the AICs of linear regression models, the minima of updated EIVs weighted by species covers and tolerances represented the best predictors of both mean water table (Akaike weight w_i = 0.892) and autumnal water table (Akaike weight w_i = 0.885), while soil moisture was best-predicted by original EIVs weighted by covers (Akaike weight w_i = 0.948; Table 1).

In the homogeneous dataset from topogenic fens (Table 2) the use of updated EIVs improved the correlation with mean water table from 0.53 to 0.61 (for unweighted mean values), and the strongest correlation was obtained for *drought intolerance* (minima of updated EIVs) weighted by species tolerances (0.64). The correlations with autumnal water table were lower than correlations with the mean water table in all cases. In terms of the AICs, the minima of updated EIVs weighted by species tolerances were the best predictors of both mean water table (Akaike weight w_i = 0.817) and autumnal water table (Akaike weight w_i = 0.647; Table 2).

3.2. Validity of updated EIVs at the continental scale

In the European dataset, the use of unweighted means of updated EIVs slightly improved the correlation with the percentage number of aquatic and wetland mollusc species when compared to the original EIVs (0.62 versus 0.57), and the regression model with unweighted means of updated EIVs was also the best-fitting model (Akaike weight w_i = 0.985; Table 3). Neither weighting nor using drought or flooding intolerances instead of conventional values improved the correlations. The percentage number of matrix-derived plants reached a relatively high correlation with the percentage of aquatic and wetland molluscs as well (−0.50).

3.3. Practical application of updated EIVs

Updated EIVs (both unweighted and weighted by covers) reached consistently higher correlation coefficients when compared to the original EIVs across all datasets and all hydrological variables except for soil moisture (Fig. 2). However, the strength of the relationship between means of updated EIVs (weighted or unweighted; *drought intolerances*, *flooding tolerances*, conventional values) and directly measured or by molluscs indicated hydrological conditions differed according to the variable to be predicted, as well as the dataset scale and coverage (Tables 1–3). For a simple visual overview, we made a schematic summary of our results showing the performance of the updated vs
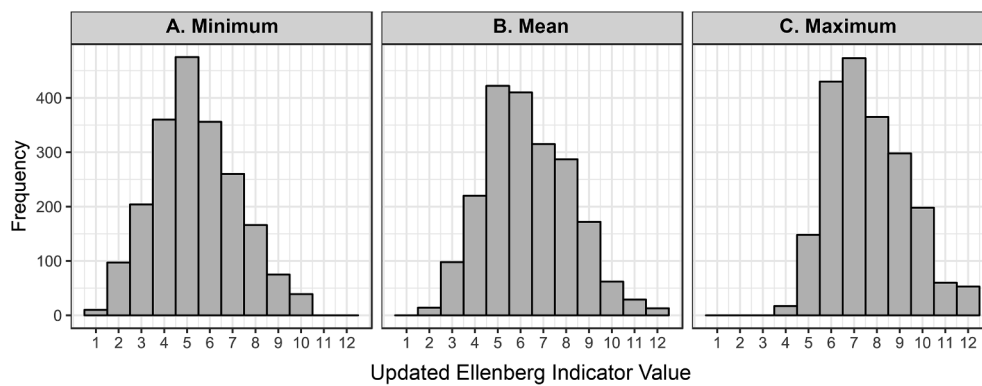
Fig. 1. Histograms of absolute frequencies of updated Ecological Indicator Values for hydrological conditions. A: minimum value (*drought intolerance*), B: mean value (*species optimum*), C: maximum value (*flooding tolerance*).

Table 1

Spearman correlations (r$_s$) between the original and updated EIVs, percentage numbers of matrix-derived vascular plant species (see Methods) and directly measured hydrological variables for the heterogeneous vegetation dataset (ombrotrophic bogs to calcareous spring fens; Hájek et al., 2013), i.e. mean water table depth, mean autumnal water table, and soil moisture in 10 cm. AIC values of all models (calculated using single linear regressions) and Akaike model weights (w$_i$) are shown next to the correlation coefficients for the corresponding relationships. The best-fitting model (i.e. the one with the highest Akaike weight) is highlighted by grey colour for each of the hydrological variables. *Abbreviations*: Mean EIV = *Species optimum*, Min EIV = *Drought intolerance*, Max EIV = *Flooding tolerance*.

		Water table			Autumnal water table			Soil moisture in 10 cm		
		r$_s$	AIC	w$_i$	r$_s$	AIC	w$_i$	r$_s$	AIC	w$_i$
Original EIVs										
Unweighted		0.23	765.9	<0.001	0.39	773.6	<0.001	0.54	864.5	0.005
Weighted by covers		0.38	752.5	<0.001	0.46	767.8	<0.001	0.59	854.0	0.948
Updated EIVs										
Unweighted	Mean	0.35	756.9	<0.001	0.47	765.0	<0.001	0.54	865.3	0.003
	Min	0.39	755.4	<0.001	0.52	760.7	<0.001	0.57	862.9	0.011
	Max	0.25	764.7	<0.001	0.40	772.7	<0.001	0.50	871.1	<0.001
Weighted by covers	Mean	0.52	737.6	0.001	0.55	754.7	<0.001	0.55	863.1	0.010
	Min	0.62	727.0	0.104	0.65	740.1	0.114	0.45	873.8	<0.001
	Max	0.53	745.0	<0.001	0.53	762.9	<0.001	0.54	862.8	0.012
Weighted by tolerances	Mean	0.36	757.7	<0.001	0.48	766.0	<0.001	0.52	866.2	0.002
	Min	0.42	753.9	<0.001	0.53	760.0	<0.001	0.55	864.9	0.004
	Max	0.27	765.5	<0.001	0.41	773.7	<0.001	0.48	872.1	<0.001
Weighted by covers & tolerances	Mean	0.57	733.7	0.004	0.59	751.2	<0.001	0.50	867.6	0.001
	Min	0.66	722.7	0.892	0.68	736.0	0.885	0.46	872.7	<0.001
	Max	0.57	738.9	<0.001	0.56	758.3	<0.001	0.51	865.9	0.002
% no. of matrix species		-0.27	762.1	<0.001	-0.28	782.5	<0.001	-0.48	869.6	<0.001

original EIVs in response to different directly measured variables in each dataset (Fig. 3).

4. Discussion

4.1. Novelty and potential of the pan-European EIVs

By assessing the updated hydrological EIVs for European mire plants, we present the first step towards the establishment of a pan-European bioindication system. As we retained the 12-grade scale of the original Ellenberg's values (Ellenberg et al., 1992), we made the updated pan-European indicator values for bogs and fens comparable with other Ellenberg-type EIVs (Borhidi, 1995; Hill et al., 2004; Ellenberg and Leuschner, 2010; Chytrý et al., 2018). However, contrary to the majority of EIVs, our list of species is not restricted to one or a few neighbouring countries, but it includes mire species from the whole of Europe. Moreover, except for values for vascular plants, the dataset includes values for bryophytes, an important functional group in wetland habitats (Jones et al., 1994; Singh et al., 2019). We believe that although EIVs have been predominantly utilised in local and regional studies, their application at the continental scale is warranted. Currently, the collection of national and regional electronic databases of vegetation-plot observations in a single data repository named European Vegetation Archive (EVA; Chytrý et al., 2016) contains more than 1.5 M plots in a standardized format and covers more or less proportionally the whole European area (accessed 22nd May 2019). Approximately 6.5% (more than 90,000 of the classified plots) of the database content was identified by the EuroVegChecklist Expert System (see Mucina et al., 2016) as the vegetation of the *Scheuchzerio palustris-Caricetea fuscae* or *Oxycocco-Sphagnetea* classes. Our updated and extended indication system thus has a huge potential for future large-scale studies, because it is virtually impossible to conduct direct ecological measurements for continental-scale datasets. This is particularly true for hydrological conditions, such as water level and soil moisture, that

Table 2

Spearman correlations (r_s) between the original and updated EIVs and directly measured hydrological variables for the homogeneous dataset (topogenic fens; Navrátilová et al., 2006), i.e. mean water table depth and mean autumnal water table. AIC values of all models (calculated using single linear regressions) and Akaike model weights (w_i) are shown next to the correlation coefficients for the corresponding relationships. The best-fitting model (i.e. the one with the highest Akaike weight) is highlighted by grey colour for each of the hydrological variables. Abbreviations: Mean EIV = Species optimum, Min EIV = *Drought intolerance*, Max EIV = *Flooding tolerance*.

		Water table			Autumnal water table		
		r_s	AIC	w_i	r_s	AIC	w_i
Original EIVs							
Unweighted		0.53	521.6	0.013	0.42	567.6	0.012
Weighted by covers		0.49	529.6	<0.001	0.42	574.0	<0.001
Updated EIVs							
Unweighted	Mean	0.61	519.5	0.037	0.52	562.7	0.137
	Min	0.61	517.6	0.095	0.52	563.6	0.088
	Max	0.47	536.0	<0.001	0.41	574.5	<0.001
Weighted by covers	Mean	0.55	529.3	<0.001	0.47	571.8	0.001
	Min	0.53	532.3	<0.001	0.41	575.0	<0.001
	Max	0.45	540.5	<0.001	0.39	577.3	<0.001
Weighted by tolerances	Mean	0.61	519.6	0.035	0.50	563.2	0.107
	Min	0.64	513.3	0.817	0.54	559.6	0.647
	Max	0.48	533.2	<0.001	0.41	573.2	0.001
Weighted by covers & tolerances	Mean	0.59	525.2	0.002	0.50	569.7	0.004
	Min	0.57	527.0	0.001	0.45	571.7	0.002
	Max	0.52	533.4	<0.001	0.46	573.3	0.001

Table 3

Spearman correlations (r_s) between the original and updated EIVs, percentage numbers of matrix-derived vascular plant species (see Methods) and percentage numbers of aquatic and wetland mollusc species from the continental-scale dataset (Horsáková et al., 2018). AIC values of all models (calculated using single linear regressions) and Akaike model weights (w_i) are shown next to the correlation coefficients for the corresponding relationships. The best-fitting model (i.e. the one with the highest Akaike weight) is highlighted by grey colour. Abbreviations: Mean EIV = Species optimum, Min EIV = *Drought intolerance*, Max EIV = *Flooding tolerance*.

		Proportion of aquatic and wetland mollusc species		
		r_s	AIC	w_i
Original EIVs				
Unweighted		0.57	4494.8	<0.001
Weighted by covers		0.49	4559.2	<0.001
Updated EIVs				
Unweighted	Mean	0.62	4440.0	0.985
	Min	0.60	4449.2	0.010
	Max	0.62	4450.9	0.004
Weighted by covers	Mean	0.47	4551.0	<0.001
	Min	0.34	4605.4	<0.001
	Max	0.48	4552.9	<0.001
Weighted by tolerances	Mean	0.61	4454.9	0.001
	Min	0.59	4460.7	<0.001
	Max	0.59	4473.9	<0.001
Weighted by covers & tolerances	Mean	0.45	4563.8	<0.001
	Min	0.33	4613.1	<0.001
	Max	0.45	4568.9	<0.001
% No. of matrix species		-0.50	4564.3	<0.001

are tightly associated with seasonal weather fluctuations. Thus, even if those were theoretically measured at the same time at a continental scale, the regional weather would differ. To conduct repeated measurements over several vegetation periods for thousands of plots located over the entire continent is clearly unrealistic. Therefore, the use of indicator values provides the most feasible solution. Another novelty of the presented EIVs is the application of species tolerances. In the original EIVs, species with broader ecological niches along the moisture gradient (e.g. *Anthoxanthum odoratum, Briza media, Rumex acetosa*) received no value. In the field of mire ecology, these species, however, indicate well the shifts from undisturbed mires towards other habitats (such as wet or intermittently wet meadows) and mirror negative successional changes (van Diggelen et al., 2006; Horsáková et al., 2018). Inclusion of these species into the analysis with their certain under-representation, together with using *drought intolerances* (minima) instead of mean values of EIVs, may improve interpretation of hydrological conditions, as also suggested by the strong correlations of the updated EIVs with measured water table depths.

4.2. Ecological meaning of EIVs for hydrological conditions

An important point is the interpretation of results based on EIVs — what is the ecological meaning of the mean EIVs? Do they express soil moisture, as originally implied by Ellenberg et al. (1992), or rather water table depth? Using direct measurements, Schaffers and Sýkora (2000) indeed demonstrated that the expert-based Ellenberg EIVs correlate with soil moisture, best with the lowest moisture content in summer. Likewise, across studies, EIVs also correlated with the depth to water table (Schaffers and Sýkora, 2000), especially in compositionally homogeneous datasets corresponding to a single vegetation class (Wamelink et al., 2002).

Our results support that the original EIVs may effectively indicate both soil moisture as well as water table depth, with the latter requiring a homogeneous dataset as suggested already by Wamelink et al. (2002).
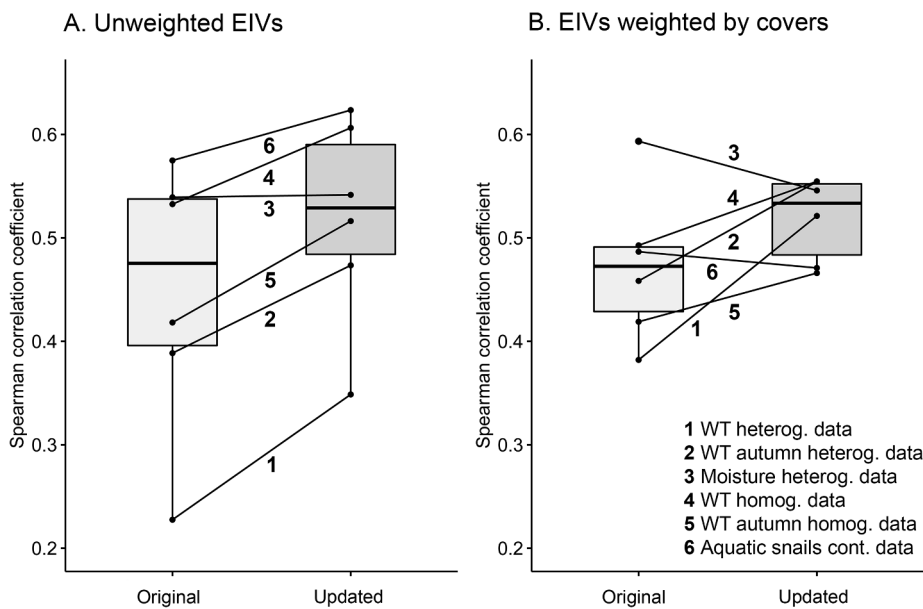
A. Unweighted EIVs

B. EIVs weighted by covers

1 WT heterog. data
2 WT autumn heterog. data
3 Moisture heterog. data
4 WT homog. data
5 WT autumn homog. data
6 Aquatic snails cont. data

Fig. 2. Box-and-whisker plots based on the correlation coefficients between the original and updated EIVs (A: unweighted means, B: means weighted by covers) and directly measured hydrological conditions or indicated by molluscs (water table, autumnal water table, soil moisture and percentage number of aquatic and wetland mollusc species) across all datasets explored, i.e. heterogeneous (Hájek et al., 2013), homogeneous (Navrátilová et al., 2006) and continental dataset (Horsáková et al., 2018). Correlations with the same hydrological variable are connected to highlight the increase/decrease in the correlation when comparing the updated and original EIVs.
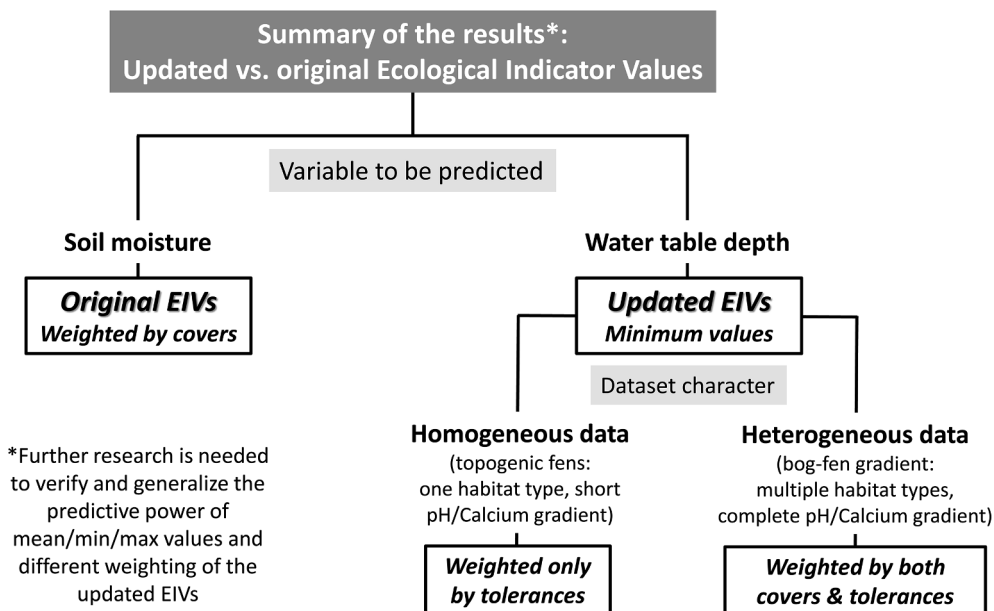

Fig. 3. Schematic summary showing the performance of updated vs. original EIVs tested at the regional scale (Czech Republic) in our study. The diagram considers the variable to be predicted and the nature of each dataset used for the EIVs calculation.

As for the updated EIVs, the inclusion of bryophytes and weighting by species covers or tolerances (or both) may improve correlation with the water table, making the updated EIVs applicable for indicating both soil moisture and water table depth, even in heterogeneous datasets. Contrary to vascular plants that are predominantly affected by redox conditions in the rooting zone (Crawford, 1996; de Mars and Wassen, 1999; Wheeler, 1999), bryophytes respond more closely to the water table *per se*, because of their different tolerances to submergence or desiccation (Hájek and Vicherová, 2014; Borkenhagen and Cooper, 2018). Submergence not only sorts semi-aquatic from terrestrial bryophyte species but also modulates the effect of calcium toxicity by supplying toxic calcium directly to the apical, photosynthetically active parts of bryophytes (Granath et al., 2010; Vicherová et al., 2015). From this perspective, the effect of water table exceeds the effect of soil moisture that reflects the conditions below the bryophyte layer.

Further, our results show autumnal water table depth to correlate more strongly with EIVs than mean water table in the heterogeneous

dataset. In the original study of this dataset conducted by Hájek et al. (2013), similar results were obtained, showing that the compositional variation also correlates better with the autumnal water table. The authors explained the result by an autumnal water level decline as a trigger for the translocation of starch reserves downwards to the overwintering roots, where they serve as energy sources for anaerobic respiration in the following spring and summer periods (Crawford, 1996). On the other hand, the updated EIVs, which include bryophytes, even improved the correlations, suggesting that also bryophytes respond to the autumnal water table. The explanation may be that while summer declines of the water table are common, the compositional shifts towards more mesic vegetation occur predominantly in the sites where water table remains low for a long time.

The effort to obtain the strongest possible correlation between EIVs and water table is not only an academic exercise because to distinguish between soil moisture and water table depth might be very important in several applications. EIVs are often used for an indication of ecological

conditions affecting invertebrates dwelling in the surface layer of fens, such as terrestrial snails (Horsák et al., 2007; Schenková et al., 2012), clitellates (Bojková et al., 2011) and other macroinvertebrate taxa (Rádková et al., 2014). These taxonomic groups, along with some other small organisms living in apical parts of mosses such as protists (Mitchell et al., 2008), are clearly affected by water table depth rather than soil moisture in the rooting zone. The updated EIVs better reflected the proportion of aquatic and wetland species in a molluscan community than the original ones, at least partially because they involve bryophytes responding predominantly to the depth to the water table.

4.3. Use of species tolerances in EIVs

Our study further shows that using *drought intolerances* (minimum values) instead of *moisture optima* (means) can improve the bioindication of hydrological conditions in mire habitats. In other words, the occurrence and cover of species predominantly occupying drier habitats than mires well indicate water table and soil moisture. In line with this, the number of matrix-derived drought-tolerant plant species of nutrient-poor habitats also reached high correlations with soil moisture and hydrological conditions indicated by aquatic and wetland mollusc species. This result advocates the use of the percentage number of matrix-derived plant species as an alternative proxy for soil moisture or water table, as already suggested in the continental-scale study of Horsáková et al. (2018). The *drought intolerances* seem to work better in the EIV-based bioindication than *flooding tolerances* or *moisture optima*, because many species of flooded habitats, typically tall sedges, may persist temporal drought because of their extensive belowground clonal organs, while the species from drier habitats cannot survive in permanently waterlogged mires because of anoxia, low nutrient availability and impossibility to germinate (Crawford, 1996; Wheeler, 1999). In other words, the occurrence of grassland species in a mire better indicates low water levels than the occurrence of reed and tall sedge species does high water levels. Incorporating species tolerances may hence be a useful way how to improve plant bioindication systems such as EIVs.

5. Conclusions and practical implications

Here we proposed and tested an updated system to indicate the hydrological conditions (water table depth and soil moisture) in European mires and similar habitats using the vegetation-plot data. Contrary to the original Ellenberg EIVs, our updated EIVs consider all species occurring in European mires, including many boreal, arctic, Balkan or Iberian species that were not included in previous regional assessments. Besides, our updated EIVs include bryophytes, a group of a high bioindication potential in wetlands, scaled on the same range of values (1–12) as vascular plants. In our updated EIVs we also assigned tolerances to the individual species, i.e. the minimum and the maximum value of the ecological amplitude expressed at the ordinal scale 1–12. Our direct tests of the performance of the updated EIVs showed that they are significantly beneficial not only in the continental-scale datasets but also in the regional datasets when water table rather than soil moisture is to be indicated. In such cases, the minimum values of the updated EIVs weighted by species abundances (i.e., species covers in the vegetation-plot data) or species tolerances (ecological amplitudes) perform best. Based on our study, the calculations of updated EIVs may require different types of weighing depending on the dataset character (see Fig. 3). When water table is to be indicated in a relatively homogeneous dataset, covering a single, rather uniform habitat type, weighting only by species tolerances may produce the most accurate results. For a heterogeneous dataset, covering compositionally different habitats, weighting by both species cover and tolerances may perform best. However, the generalization of these results has to be left for future researchers. This study demonstrates the possibility to combine

expert and statistical assessment for (i) providing a comprehensive characterization of EIVs for all species occurring in one habitat at the continental scale and (ii) developing a new system of EIVs that equals or in many cases improves the indicator value of original EIVs. Such progress will allow calibration of large vegetation databases with environmental data and accelerate continental-scale ecological syntheses.

CRediT authorship contribution statement

Michal Hájek: Conceptualization, Investigation, Methodology, Writing - original draft, Writing - review & editing. **Daniel Dítě:** Conceptualization, Investigation. **Veronika Horsáková:** Data curation, Formal analysis, Visualization, Methodology, Writing - original draft, Writing - review & editing. **Eva Mikulášková:** Investigation. **Tomáš Peterka:** Investigation, Formal analysis, Writing - original draft. **Jana Navrátilová:** Resources, Investigation. **Borja Jiménez-Alfaro:** Investigation, Writing - original draft, Writing - review & editing. **Petra Hájková:** Investigation. **Lubomír Tichý:** Software, Formal analysis, Methodology. **Michal Horsák:** Resources, Formal analysis, Methodology, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106527.

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