

Methodological Aspects of Using Indicator Values in Biodiversity Analysis

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Abstract—Indicator values are becoming an increasingly popular tool in basic and applied botanical research: more than 55 original phytoindication systems, including about 200 optimal and range scales for various environmental factors, are known. This paper describes seven methods for calculating the phytoindication optimum of a taxonomical list: averaging with weighting by indicators of the taxon's participation (cover, frequency, and activity) and the degree of ecological tolerance amplitude breadth. Optimum and interval indices of ecological consensus are proposed for a quantitative assessment of the level of ecological homogeneity of plant communities and floras. The distinguishing ability of the described methods of environmental calculation and consensus indices were critically compared and assessed in the environmental analysis module of the IBIS 7.2 botanical information system using data from Bashkiria and the Southern Urals at the level of phytocoenoses assigned to four communities and their coenofloras. The possible fields of further use of the results in phytocoenology and floristics are described.

Keywords: indicator value analysis, biodiversity, indicator values, IBIS information system, weighted averaging, environmental consensus index

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INTRODUCTION

Indicative geobotany deals with issues of indirectly determining the characteristics of environment-forming components or phenomena in an ecosystem by phytobiota parameters. The former ones are called indicators, or objects of indication; the latter are called indicators, or subjects of indication. Individual plants (presence, abundance, various anatomical and morphological characteristics, physiological state, and deviations from the norm), and plant communities (their composition, structure, and proportions) may be the indicators. Any properties of ecosystems can be subjects of indication. In practice, ecological factors of climatic, edaphic, or anthropogenic nature are used more often in their role. The phytoindicative information obtained in this way is probabilistic and specific values of the intensity of the indicated factors can be transposed into the generalizing characteristics of the components of the phytobiota itself: plant communities, coenoflora, and floras of various ranks uniting the subjects of indication.

The indirect acquisition of quantified information on the intensity of the main abiotic factors by the parameters of the vegetative cover is the main task of quantitative synecological phytoindication, the main tool of which is ecological (phytoindicative) scales (Ramensky 1938; Ramensky et al., 1956; Ellenberg,

1974; Landolt, 1977; Tsyganov, 1983; Ellenberg et al., 1991; Landolt et al., 2010; Didukh, 2011; etc.).

Historical, critical, and analytical reviews on the phytoindication in general and the use of ecological scales in particular have been published (Nitsenko, 1957; Ramensky, 1971; Viktorov et al., 1962; Viktorov, Remezova, 1988; Tsyganov, 1983; Bulokhov, 2004; Korolyuk, 2007; Zhukova et al., 2010; Zonneveld, 1983; Dydukh and Plyuta, 1994; Dierschke, 1994: ch. 7 (“Gliederung und Ordnung der Vegetation”); Diekmann, 2003).

Among the advantages of an indirect estimation of factors over direct measurements of the physical parameters of the environment, the following points are most often put forward: (1) the use of plants as indicators of habitat conditions provides significant savings in time and money for research; (2) it allows one to obtain an integral, time-smoothed estimate of fluctuating abiotic parameters (Zonneveld, 1983; Diekmann, 1995); (3) it makes it possible to evaluate complex nonacting factors that are not amenable to direct instrumental control (for example, the degree of anthropogenic transformation of habitats); (4) it makes it possible to evaluate factors that are not pronounced at the time of the study (for example, the severity of the winter period by vegetation); and (5) the use of stock geobotanical materials makes it possible to conduct retrospective

studies (for example, one can obtain information about the intensity level of ecotopic environmental factors and reconstruct the climatic parameters for wetland ecosystems using data from a peat deposit).

Significant attention in modern botanical studies is paid to the problems of phytoindication. Scientific interest is focused on assessing the effectiveness of the use of ecological scales outside the model regions (Dierschke, 1994, 1995; Diekmann and Lawesson, 1999; Hill et al., 2000); regionalization, correction and replenishment of scales (Hill et al., 1999; Pignatti et al., 2005; Zarzycki et al., 2002; Korolyuk, 2006; Troeva et al., 2010; Chytrý et al., 2018); and comparing indication results for subjects from various large taxonomic groups (Hill et al., 2007; Ewald, 2009).

The inclusion of an indicator of the statuses of environmental factors in the set of characteristics of plant species is becoming more common when creating integrated online databases (Fitter and Peat, 1994; *BIOLFLOR*, 2002; Nikolić, 2018; *Ecological Flora...* 2019; FloraWeb, 2019; Pladias, 2019; Kattge et al., 2020). Providing the parameters of ecological portraits of individual indicator taxa, such information portals cannot solve the problems of practical mass synecological phytoindication, since it requires their integration with databases on descriptions of vegetation and the corresponding analytical tools.

More than 55 author-defined phytoindicative systems, combining approximately 200 individual scales for various environmental factors, have been identified so far as a result of a critical review of available published and web resources. The geographical coverage, the composition of indicator taxa, the set of factors for which the ecological requirements of plants are determined, and the number of elementary intervals (gradations, points, steps, and indicator groups) allocated on the factor gradient vary significantly among different authors.

All scales are divided into two main categories according to the format of environmental information: optimal (point) scales (only the ecological optimum point is indicated for each indicator taxon (Ellenberg et al., 1991, Korolyuk, 2006; Landolt et al., 2010)) and amplitude scales, which indicate the limits of ecological amplitude (Tsyganov, 1983; Didukh, 2011; Frank and Klotz, 1990); the optimum score in this case corresponds to the median. L.G. Ramensky (Ramensky et al., 1956) and the followers of his school (*Metodicheskie ukazaniya...*, 1974; Seledets, 2000, etc.) used in the expansion of the second category to the amplitude optimum format. Such scales are the most informative, since tolerance amplitudes are indicated for several levels of taxon abundance, and the median of amplitude at the highest abundance is considered the optimum point.

Ecological scales on the factors of soil moisture and trophicity are most in-demand in the studies on a phytodiversity, since there is no doubt on their leading role in the formation of the composition and differen-

tiation of phytocoenoses. The statuses¹ of indicators for these factors have been identified by almost all authors, and the maximum number of gradations usually differs on the gradient of these factors.

Unfortunately, researchers, analyzing botanical data, often use ecological scales and do not pay enough attention to the methodological accuracy of their application. Studies in which the authors simply indicate the environmental factor and the author of the scales (for example, in the form of “continentality according to D.N. Tsyganov” or “soil reaction according to H. Ellenberg”) and then immediately operate with digital values, for example, using them for ordinating the descriptions of phytocoenoses or coenoflora in the axes of two factors, clustering objects, are frequent. The reader is left in ignorance about which of the many possible calculation options was used. Apparently, it is understood that there is some kind of “standard” method which simply does not need explanation. At the same time, such an approach is sometimes applied to different types of scales, both amplitude and optimal, within the framework of one study. With a high degree of certainty, we can assume that the authors of such works do not know any other way to obtain phytoindication ecological statuses for taxon lists, except for calculating a simple arithmetic mean value. This is partly explained by the influence of the traditions of the Western European school of phytoindication, which is characterized by point scales. However, the weighting of ecological optima of taxa by the points of the scale of richness-coverage of J. Brown-Blanca can be read in the early works of H. Ellenberg and E. Clapp, and this issue was considered in more detail by Diekmann (1995, 2003). On the other hand, this simple way of calculating average statuses is often the only choice implemented in software (Hennekens and Schaminée, 2001; Tichý, 2002; Landolt et al., 2010). Such a neglect of methodological aspects is especially sad against the background of the efforts that the authors of phytoindication scales spend on their creation, trying to make them as accurate and representative as possible.

The modern arsenal of bioinformatic tools for conducting full phytoindication analysis is rather limited: Turboveg (Hennekens and Schaminée, 2001), Juice (Tichý, 2002), “Phytoindication” (Kleshcheva, 2007); IBIS (Zverev, 2007); EcoScaleWin (Zubkova et al., 2008), and an electronic supplement to Flora Indicativa (Landolt et al., 2010). The botanical information systems have an obvious advantage in the effectiveness of

¹ The term status sensu Korolyuk (2007) means the original indicator value expressed in gradations or fractions of a unit for an indicator taxon on a specific ecological scale. Depending on the type of scale, it is possible to talk about the minimum, optimal, and minimum statuses (all three categories are applicable for amplitude-optimal scales). This term is also used (in the form of “average status”) to denote the ecological optimum of a community or flora equal to the estimated phytoindication value for the list of taxa by the selected factor.

Table 1. Descriptive and phytoindicative characteristics of vegetation according to the moisture factor: level of phytocenoses

	RNO	SPE	IR	IND	S1	S2	S3	S4	S5	S6	S7	CI	CO
Example 1: <i>Tanacetum vulgare</i> – <i>Hieracium onegense</i> (A1x) vs <i>Carex pallescens</i> – <i>Betula pendula</i> (A2x)													
	A11	66	0.848	56	65.071	64.083	64.343	63.734	63.875	61.0	64.0	0.575	0.902
	A12	50	0.840	42	64.393	63.292	68.123	67.339	64.000	62.0	67.0	0.538	0.898
	A13	77	0.821	64	64.898	63.805	66.051	65.005	63.100	61.0	66.0	0.585	0.907
	A14	75	0.840	63	64.460	63.999	64.953	64.731	65.000	61.0	66.0	0.566	0.902
	A15	75	0.868	66	63.720	63.020	63.185	62.553	64.200	62.0	68.0	0.533	0.903
Average			0.843		64.509	63.640	65.331	64.673	64.035	61.400	66.200	0.560	0.903
	A21	47	0.745	35	68.357	68.149	69.766	69.684	69.167	68.0	68.0	0.602	0.915
	A22	44	0.750	33	66.833	66.417	69.662	69.484	66.875	63.0	69.0	0.543	0.916
	A23	49	0.714	35	64.571	64.060	69.440	69.061	65.125	63.0	68.0	0.583	0.933
	A24	36	0.694	25	66.120	65.155	69.720	69.471	67.125	63.0	69.5	0.560	0.929
	A25	44	0.778	35	66.171	65.700	69.549	69.164	66.500	63.0	69.0	0.544	0.913
	A26	40	0.825	33	68.606	68.648	69.867	69.847	69.750	65.5	71.0	0.570	0.921
Average			0.751		66.777	66.355	69.667	69.452	67.424	64.250	69.083	0.567	0.921
Delta					2.268	2.715	4.336	4.779	3.389	2.850	2.883	0.007	0.019
Example 2: <i>Stachyo sylvaticae</i> – <i>Tilietum cordatae</i> (Fix) vs <i>Lactuca serriola</i> – <i>Aegopodium podagraria</i> (F2x)													
	F11	24	0.833	20	71.600	71.522	70.348	70.076	73.333	71.0	71.0	0.577	0.931
	F12	30	0.833	25	72.260	71.942	70.718	70.582	72.500	72.0	72.0	0.564	0.937
	F13	30	0.833	25	72.060	72.325	70.675	70.604	74.000	71.0	71.0	0.572	0.936
	F14	26	0.923	24	71.063	71.146	70.498	70.300	74.500	74.0	74.0	0.647	0.950
	F15	26	0.815	22	70.000	70.333	70.238	70.052	73.167	71.0	71.0	0.640	0.961
	F16	29	0.867	26	71.250	71.734	70.389	70.220	75.667	75.5	75.5	0.645	0.949
	F17	29	0.793	23	70.870	70.799	70.512	70.291	73.333	70.0	70.0	0.627	0.952
	F18	30	0.833	25	70.320	70.709	71.373	71.249	71.500	71.0	71.0	0.547	0.941
Average			0.841		71.178	71.314	70.594	70.422	73.500	71.938	71.938	0.602	0.944
	F21	53	0.830	44	63.830	65.737	58.574	62.676	67.400	68.5	66.5	0.504	0.902
	F22	59	0.867	52	66.327	68.011	66.576	68.673	70.333	70.0	70.0	0.526	0.902
	F23	70	0.814	57	66.202	67.507	64.140	66.046	69.750	69.0	70.0	0.542	0.916
	F24	63	0.873	55	64.973	66.567	61.336	64.812	68.400	68.5	70.0	0.520	0.899
	F25	62	0.810	51	65.794	67.314	62.395	65.835	69.600	69.0	70.0	0.508	0.902
	F26	69	0.829	58	65.905	67.214	68.319	69.802	69.400	69.0	69.0	0.538	0.914
	F27	61	0.820	50	65.970	67.056	67.224	69.260	68.400	69.0	68.0	0.533	0.905
	F28	62	0.810	51	64.745	66.483	58.637	62.135	69.500	69.0	71.0	0.530	0.907
	F29	67	0.868	59	65.898	66.846	66.918	68.509	69.100	71.0	68.0	0.534	0.911
	F20	64	0.797	51	66.657	68.011	67.460	68.623	70.000	71.0	69.0	0.514	0.908
Average			0.832		65.630	67.075	64.158	66.637	69.188	69.400	69.150	0.525	0.907
Delta					-5.548	-4.239	-6.436	-3.785	-4.312	-2.537	-2.787	-0.077	-0.038

RNO, serial number of relevé; SPE, number of taxa in relevé; IR, proportion of indicator taxa from the number of taxa; IND, number of indicator taxa; S1–S7, average statuses in gradations calculated in seven ways (see explanations in the text); CI, interval compliance index; and CO, optimum environmental compliance index.

phytoindication, since they make it possible to perform the mass processing of taxon lists based on geobotanical databases.

The purpose of this publication is to give an overview of the methods for calculating primary phytoindicative indicators, including those supported by computer technologies, and to show the differences between them and the validity of the criteria for their choice using the concrete examples.

MATERIALS AND METHODS

Since this study is methodological, we used geobotanical material for illustrative purposes only. For the first example, two small arrays of relevés of abandoned

agricultural land of the Bashkir Cis-Urals from (Shirokikh et al., 2017) are used. For the second example, the relevés characterizing indigenous broad-leaved forests and clear-cutting communities of the low-mountain part of the western macroslope of the Southern Urals are taken from (Martynenko et al., 2016). A brief description of the associations presented in these examples is given below. Since the study does not pursue any syntaxonomic goals, species epithets are omitted from syntaxon names and the authors of syntaxons are not given. The reports of Cherepanov (1995) and Ignatov et al. (2006) were used as nomenclature sources. When descriptions were introduced into the IBIS system (Zverev, 2007), an automatic synonymous replacement was performed for some taxa in

accordance with the taxonomic library synchronized with current ecological scales.

The IBIS 7.2 integrated botanical information system was used for the input and selection of relevés (Zverev, 2007). All calculations were performed there; the methods used are described in the Results section. The instrumental capabilities of the module of environmental and phytoindication analysis of the IBIS system have been described earlier (Zverev, 2012a). The software can operate with all types of ecological scales described above; the taxonomic library contains information on taxa-indicators on 70 environmental factors from various author systems. The average statuses of relevés and flora are stored along with other descriptive information and can be reused as surrogate variables (for example, for ordinations of summary tables) or exported for further processing in third-party analytical programs.

RESULTS

Methods for Calculating Average Phytoindication Statuses

Environmental information is used on all indicator taxa that are part of the taxonomic list of coenosis or

flora to obtain a quantitative assessment of the synecological optimum of a plant community or flora of any rank and nature. For brevity, we will call this value the average status (AS) of the list. The methods for obtaining AS illustrated with specific examples are described below. They get end-to-end designations **S1–S7**, which are also used in Table 1 and in the further discussion of the results.

No known unified classification of environmental accounting methods exists. We propose dividing them into three main categories: weighted averaging methods, structural methods, and others. The methods of the first two categories are analyzed in this paper.

Weighted averaging methods for calculating average status. This group of methods exploits the obvious idea that a simple arithmetic mean of the individual optimal statuses of indicator taxa in the list (**S1**, formula (1)) can be more likely to be brought closer to the current AS of the list if we take into account additional parameters of indicator taxa that characterize individual indicator properties of plant species and their degree of participation (intensity) in the composition of coenosis or flora (**S2**, **S3**, and **S4**, formulas (2)–(4)).

$$\bar{S} = \frac{\sum_{j=1}^M S_j}{M} \quad (1)$$

$$\bar{S} = \frac{\sum_{j=1}^M S_j A_j}{\sum_{j=1}^M A_j} \quad (2)$$

$$\bar{S} = \frac{\sum_{j=1}^M S_j U_j}{\sum_{j=1}^M U_j} \quad (3)$$

$$\bar{S} = \frac{\sum_{j=1}^M S_j U_j A_j}{\sum_{j=1}^M U_j A_j} \quad (4)$$

Legend:

\bar{S} is the estimated average phytoindication status (AS) of the community, flora, ecotope, and territory;

M is the number of species having statuses according to the selected factor (the number of indicator species) in the taxonomic list;

S_j is the optimum status of the j th indicator species (median of the amplitude for the highest indicator of species richness in range scales);

U_j is the weighted parameter of the participation of the j th indicator species in the community or representation in the flora;

A_j is the tolerance index of the j th indicator species: the inverse share of the total gradient of the factor occupied by its amplitude.

Weighing by the tolerance index (**S2**, formula (2)) is possible only when one works with range-format scales (amplitude and amplitude-optimum). The meaning of its use is to increase the influence of steno-

topic species on the average phytoindication status and lower the value of wide-amplitude eurytopic indicators. The proposed proportional option for calculating the index of tolerance is $A = k / (S_{\max} - S_{\min} + 1)$, where A is the taxon tolerance index, S_{\max} is its maximal and S_{\min} are minimal statuses, and k is the number of gradations (steps, indicator groups) in the scale (not the only possible one). Weighting the degree of eurytopicity of indicators can be based on disproportionate estimates, for example, on a 5-point scale of “steno-eurybiontism” proposed by Zhukova (2004).

Calculating the proportional tolerance index (**S2** and **S4**), it is important to understand that the amplitude of the indicator taxon begins at the lower boundary of its minimum status and ends at the upper boundary of the maximum status. That is, gradations (steps and points) of the scale are considered not as points on the gradient of the factor, but as minimally discriminated intervals. For example, a stenotopic indicator species *Campanula rotundifolia* L. (min. 2 and max. 3), mesotopic *Gypsophila paniculata* L. (3 and 7), and eurytopic *Chenopodium album* L. (2 and 10) will get tolerance indices equal to $10/2 = 5.00$, $10/5 = 2.00$, and $10/9 = 1.11$, respectively, on the scales of I.A. Tsatsenkin et al. (*Metodicheskie ukazaniya...*, 1974) with a 10-point factor of pasture digression. Such an index of absolute tolerance depends on the number of gradations in the factor. Therefore, it can be normalized to one for the purposes of comparability of the indicator value of species on different scales.

Various quantitative characteristics of the representation of the indicator species, depending on the nature of the list of taxa, can be used as a weight parameter (U_j) in options **S3** and **S4** (formulas (3) and (4)). It is usually presented in relevés as a percentage of projective cover or richness, expressed in ordinate points, or approximated by percent coverage. The weight parameter of each taxon can be represented in floras of various ranks and natures resulting from the nonduplicate merging of single relevés of vegetation by percentage or point occurrence (the proportion of relevés in which the taxon is found), the sum of projective covers, average total or nonzero (relevés with no taxon) by projective cover, point (expert), or estimated activity. The use of the indicator of taxon activity in phytoindication is not a common method; therefore, an additional explanation is required.

The activity of a species is a complex characteristic that shows a measure of the prosperity of a species in a given territory. It is one of the expressions of “weight of a species” in a given flora, its landscape activity (Yurtsev, 1968). The first formula for the quantitative expression of activity was given by Malyshev (1973) with both components of activity, the occurrence and richness of taxa, expressed in point scales. The activity index was calculated by Chepinoga and Rosbakh (2008) analyzing the aquatic flora of the Irkutsk-Cheremkhov Plain, by Telyatnikov (2010) studying the local flora of

the Putorana Plateau, and by Kupriyanov et al. (2018) comparing plant communities of the Karakan Ridge. We do not know any published examples of the use of indicator activity in obtaining average phytoindication statuses. The calculation of the activity of species in the IBIS system for summary lists (coenofloras, partial floras, and local floras) is performed according to formula (5):

$$Act = \sqrt{\frac{C \times 100\%}{N} \frac{\sum_{i=1}^N U_i}{N}} = 10 \sqrt{\frac{CU_{\Sigma}}{N}} \% \quad (5)$$

where Act is the calculated activity of a taxon from the taxonomic summary list, percentage (0–100%);

N is the number of relevés combined in a summary list;

C is the taxon constancy, the absolute number of relevés where the taxon is registered;

U_i is the projective cover of a taxon in an i th relevé;

U_{Σ} is the sum of the projective covers of a taxon in all relevés.

Activity as the weight of a taxon of any summary list can be used for phytoindication both in the form of percentage (as given in formula (5)) and in fractions of a unit. The same is true for occurrence rates or average coverage.

Considering that the weight of taxa in calculating the AS (**S3** and **S4**) is far from always being the right strategy (Diekmann, 2003): it can change the AS of communities of small species with a sharp dominance of one or two taxa too much, and it also is not suitable for long-term monitoring studies.

To “soften” the effect of weighting the indicator strength of taxa in calculating the AS, their weight can be expressed not in percentage or fractions of a unit, but in the values transformed into ordinated points in the corresponding scales. Therefore, one can use 5- or 10-point scales based on the J. Braun-Blanquet abundance-coverage scale (Ellenberg et al., 1991: 28) or a 9-point geometric scale (Zverev, 2007: 126). In the latter case, differences in indicator strength between dominant and single taxa will be as much as 9-fold, whereas, for a percentage scale, similar differences can even be 400-fold if we take the single presence of a taxon, which is usually indicated in the percentage scale by “+” for 0.25%.

In the double-weighting option (**S4**, formula (4)), depending on the ecological properties of the indicators of the analyzed list, the ecotope (territory) features and the possible succession stage of the plant community or the stage of flora genesis, the weighing components (ecological tolerance of the indicators and their weight characteristics) can have a coordinated multidirectional effect on the change in the AS when compared with simple averaging. In accordance with this, the value of **S4** can deviate even more from the “basic” **S1** than **S2** and **S3** separately, and approach it.

Structural methods for calculating average status.

The table-constraint method (**S5**), proposed and described in detail by Ramenskii et al. (1956), is the most famous structural method for determining AS. It is a modification of the graphical “serif method,” which is unsuitable for mass processing of relevés. The essence of the method is to build the left ends of the ecological amplitudes of indicator species (minimum statuses, or “from” delimiters) in the descending order of their values, and the right ends (maximum statuses, or “to” delimiters) in the ascending order. The crossing point of these sorted series (of two values of the pair) is the desired average status, which is specified, on the recommendation of the author, with two pairs of values above and below the crossing point. An important remark must be made: a real crossing of the sorted left and right borders is possible only in the case of an “environmental conflict”: the presence of a gap zone between the amplitudes of at least a pair of indicator taxa from the list. Formally, such a community does not have a right to exist, since the mean value determined in this way for the selected factor by one of the species will be insufficient and the other excessive for normal life (in accordance with individual environmental requirements). In practice, such a situation is not at all rare. Possible explanations for this are given later after the introduction of environmental compliance indices. In relation to summary lists (floras), the concept of “environmental conflict” is often not applicable at all, since such lists combine indicator taxa that may not grow together with the same values of some environmental factors, especially factors of an ecotopic level. Technically, the calculation of AS using tabular restrictions in the absence of crossing the restrictive series “from” and “to” (that is, in the absence of a gap in amplitudes between taxa) is solved by averaging the values of a certain number of status pairs (usually four or five) from the highest pair.

The minimum “environmental-conflict” line method (**S6**) consists of determining the limiting statuses (the largest minimum status and the smallest maximum status) and the middle of the range that they limit. In the case of an environmental gap (the limiting minimum is greater than the limiting maximum), the middle of the gap zone is calculated as a compromise.

The last method of calculating the AS is the method of crossing the majority of intervals (**S7**). It is close to the previous one and often gives values close or coinciding with **S6** in the absence of an environmental conflict. It consists of finding the middle of the zone of maximum overlap of the ecological amplitudes of all indicator taxa. When there is an environmental conflict, such a maximum overlap can occur on one of the sides of the gap zone. However, two overlapping zones of equal intensity can also occur; then the boundaries of the overlapping zones distant from the gap are averaged.

Among other methods, we should mention the algorithm proposed by Buzuk and Sozinov (2007) for determining the ecological optimum of plant communities based on the use of linear regression analysis of taxon indicators ranked by the breadth of ecological amplitudes on range scales and implemented as a calculation system in MS Excel spreadsheet format. Another method that is not suitable for mass phytoindication and cannot be reproduced without computer support is a graphical method based on the construction of ellipses of the two-dimensional distribution of the indicator probability density in the axes of two environmental factors at once, implemented in the Phytoindication software (Kleshcheva, 2007).

It should be noted that all of the listed methods for calculating AS are suitable for the ecological scales of the amplitude type, while only **S1** and **S3** are applicable for optimum scales, and the **S7** degenerates into a modal gradation in the distribution of all individual optima of the list of indicator taxa.

Environmental Compliance Concept

Even in the case of phytocenoses, where the tolerance amplitudes of all species have a nonzero overlapping zone, we can talk about varying degrees of ecological homogeneity of plant communities. In this case, it is important to have an objective indicator of the degree of this homogeneity/heterogeneity. For this purpose, we proposed several environmental compliance indices (CIs) (Zverev, 1995). Practice has shown that interval CIs (formula (6)), inheriting the idea of the similarity measure of P. Jacquard known from comparative floristry (Jaccard, 1901), turned out to be the most popular and interpreted one. The calculation formula was published (Zverev, 2011), and the calculation of this CI is implemented in the environmental analysis module of the IBIS system:

$$C_{int} = \frac{\sum_{i=1}^n \sum_{j=i+1}^n I_{ij} / (A_i + A_j - I_{ij})}{(M^2 - M) / 2} \quad (6)$$

where C_{int} is the value of the interval consent index;

M is the number of species having statuses according to the selected factor (the number of indicator species) in the taxonomic list;

A_i and A_j are amplitudes (the number of steps or gradations occupied by the species on the gradient of the factor) of i th and j th species, respectively;

I_{ij} is the interval of amplitude overlap for i th and j th species (in steps or gradations).

Thus, the interval CI is an average measure of similarity between all indicator taxa in the list whose attributes are segments of the gradient of the environmental factor that they occupy.

As was shown above, the steps in the amplitude phytoindication scales are not points, but they corre-

spond to a unit interval: a nonzero segment on the factor gradient. If one species has an amplitude ranging from 2 to 7 steps and the second species has an amplitude ranging from 7 to 11, it means that the interval of their overlap is one step. The interval CI has limits of variation from 0 to 1. A zero value means a situation where all plants in the relevé do not overlap. Obviously, such an extreme value in theory is possible only for very small-sized communities. This CI reaches its maximum value with full coincidence of the amplitudes of tolerance of all taxa. The interval CI can be represented in other modifications if other binary similarity indices are used instead of the Jacquard similarity measure.

It is clear that the interval CI is not suitable for assessing the ecological homogeneity of plant communities in the case of using optimal phytoindication scales. For such scales, an optimal (point) CI is proposed (formula (7)):

$$C_{opt} = 1 - \frac{\sum_{i=1}^n \sum_{j=i+1}^n |O_i - O_j|}{(k-1)(M^2 - M)/2}, \quad (7)$$

where C_{opt} is the value of consent point index;

M is the number of species having statuses according to the selected factor (the number of indicator species) in the taxonomic list;

k is the number of gradations (steps, indicator groups) in the scale;

O_i and O_j are the value of optimum (number of indicator group) of the i th and j th species, respectively.

Thus, the optimum CI is an average measure of the relative distance between the optimum statuses of all taxa in the list, and it is suitable for any type of ecological scale. It has the same limits of variation as the interval CI, 0...1. However, it turns to zero only in one extreme case: when the list includes only two taxa occupying extreme positions on the gradient of the factor and reaching the maximum value of IC if the optima of all indicators coincide.

Low values of environmental compliance indices, as well as extreme cases, “gaps” in the general ecological gradient of the plant community (the phenomenon of environmental conflict described above), can be explained by several reasons that should be combined into two groups:

“Exogenous” reasons are not related to the characteristics of a particular phytocenosis: (i) low quality (errors) of the phytoindication scale itself: incorrect determination of tolerance limits, most often narrowing the environmental amplitudes due to insufficient representativeness of the model sampling of vegetation relevés: not all ecotopes were covered by a sufficient number of relevés;

(ii) shift in optimums and change in tolerance amplitudes for a part of the plants: manifestation of a regional effect (geographic and climatic shift) when using scales developed for a different model territory, often caused by the fact that one limiting factor comes to the fore in the new conditions (the principle of limiting factors of Liebig–Blackman–Shelford); for example, the phenomenon of “physiological dryness” in the tundra zone;

(iii) methodological errors in the relevés, the influence of individual characteristics of individual researchers;

(iv) errors in taxonomic attribution and synchronization: different taxa appear under the same names in scales and relevés (usually careless reconciliation of synonyms when using scales developed for other territories, distribution of the characteristics of a typical subspecies to other subspecies, etc.).

“Endogenous” reasons, reflecting the properties of a particular phytocenosis:

(i) complex highly heterogeneous plant community (for example, hillock bogs) and other manifestations of the vertical structure, when indicators from different tiers are in very different conditions according to the indicated factor;

(ii) the manifestation of the seasonal dynamics of the environmental factor (for example, the factor of illumination in deciduous forests in the spring and summer);

(iii) phytocenosis is in a state of active succession (for example, postfire demutation) and other manifestations of long-term dynamics;

(iv) a high degree of ecotope disturbance: as a result, not all ecological niches are occupied and the participation of pioneer or random species is significant;

(v) the role of mosses and lichens is great in the community, the mechanism of influence of the studied factor on which (and, as a result, their reaction) differs from those in higher plants (Ewald, 2009; Ellenberg et al., 1991; Landolt et al., 2010).

The list of possible reasons given, of course, is not exhaustive. It is also worth noting that usually there will be several possible explanations for the reduction of consent indices at the same time.

The use of CIs can be promising as a refinement parameter for the classification and ordination of vegetation and the study of the structure and dynamics of plant communities.

Comparative Analysis of the Calculation of Phytoindication Characteristics by Various Methods

The illustrative material consisted of 29 complete relevés divided into two examples, each having two arrays representing associations that can be conditionally attributed in pairs to the multidirectional succession stages of one type of vegetation (Table 1).

Example 1. The vegetation of abandoned agricultural land of the Bashkir Cis-Urals is presented (Shirokikh et al., 2017). A1 array, 5 relevés: basal community *Tanacetum vulgare*–*Hieracium onegense* (Artemisietalia/Origanetalia vulgaris). Array A2, 6 relevés: basal community *Carex pallescens*–*Betula pendula* (Fagetalia sylvaticae). The assignment of the first basal community to the two higher units is caused by the transitional nature of the site in accordance with the deductive method of Kopečky and Hejný (1974). The same observation is relevant for the second example. Array A1 represents open (meadow) multispecies (the average number of species in the relevé is 68.6; the volume of coenoflora is 113 species) communities, which actively overgrow with the stand in the absence of anthropogenic impact and form small-species (the average number of species in the relevé is 43.3; the volume of coenoflora is 87 species) communities (array A2) with a dominance of birch, in which the grass cover is very thin due to significant shading by the canopy.

Example 2. The opposite phytocenotic situation in broad-leaved forests of the low-mountain part of the western macroslope of the Southern Urals is presented (Martynenko et al., 2016). Array F1, 8 relevés: indigenous mixed broad-leaved forest ass. *Stachyo sylvaticae*–*Tilietum cordatae*. Array F2, 10 relevés: basal community *Lactuca serriola*–*Aegopodium podagraria* (Artemisietalia/Fagetalia). The communities included in the second massif (F2) are formed approximately 3 years after the deciduous broad-leaved indigenous forest (F1) in the summer and represent one of the stages of restorative succession with severe disturbance of the soil cover. A significant enrichment with synanthropic species, which occupy the vacated regenerative niches, occurs in this case. The average number of species in communities sharply increases from 28.0 to 63.0, and the volume of coenoflora increases from 50 to 123 species.

The stress of at least several abiotic factors, including the mode of moistening, should naturally change with succession changes, which are illustrated by these examples. To illustrate it, we chose the amplitude-optimal humidification scale (Ramenskii et al., 1956), which allows one to calculate all seven options for calculating the average status and both indices of environmental compliance. The high proportion of indicator taxa in relevés (75–84%) and coenofloras (79–86%), as well as the territorial compatibility of scales and study areas, makes this choice justified. The choice of a multigradation (120 steps) scale is also convenient, because all changes in the average statuses of humidification regimes between arrays (delta), expressed in the tables in steps, are close to those in percentage, which makes the estimation of the shifts more visual. The reduction of vertical tiers relevant for A2 and F1 arrays with tree canopy was performed before phytoindication analysis, the results of which are presented in Table 1 for communities and in Table 2 for

coenoflora. Standard errors of mean values (Table 1) are not indicated, since the samplings are completely presented.

DISCUSSION

The scales of L.G. Ramenskii were developed, first and foremost, for the ecological assessment of forage lands. Therefore, the classification of moisture regimes was made for meadow communities. According to this classification, almost all averaged ASs and the majority of ASs of individual relevés fall into the wet-meadow humidification mode (Ramensky et al., 1956). The main trend, which was expected in connection with changes in the tree layer (increase in the AS by moisture in the first pair A1–A2 and decrease in the second pair F1–F2), was quite expressive. However, the differences (deltas) in the average values over the description arrays differ significantly in this case, depending on the chosen method for calculating the AS.

Two close structural methods, S6 and S7, behave the least stably. Moreover, the greatest differences between them are obtained for species-rich communities of the A1 massif. An analysis of the individual ecological spectra of these relevés stably reveals the presence of a wide asymmetric environmental gap in the amplitudes of tolerance. Several types of indicators, strongly shifted on the moisture scale to the “dry” part of the gradient, are relatively “responsible” for other types. In this case, a larger overlap of the amplitudes is observed in the right-hand part of the gradient, which results in such a noticeable excess of S7 status over S6 status for these communities, whereas these two methods show very consistent results in other arrays.

In the first example, the differences between the averaging (S1–S4) methods are not as great; the greatest delta is shown by S4: double weighting turned out to be unidirectional for the overgrowing process. Close values of AS are obtained using the table constraint method (S5). In the second example, the S3 method showed the maximum decrease in moisture content for humidification, while S2 did not lead to such sharp changes in CIs. It is obvious that the relatively dry-loving species, occupying the vacant niches after deforestation, had rather wide amplitudes, which allowed the more moisture-loving stenotopic species to “balance” their indicator effect.

Changes in average consent indices also fit into the idea of the nature of the changes. A slight increase in environmental homogeneity is recorded for example 1 during the overgrowth of meadow coenoses. A more significant decrease in CIs is observed for example 2 after serious disturbances associated with logging. The optimum sensitivity in the first case is shown by the optimal CI and by the interval CI in the second case. For the second example, this is confirmed at the level of coenoflora. Such differences are probably caused by

Table 2. Descriptive and phytoindicative characteristics of vegetation according to the moisture factor: level of coenofloras

	CNO	RELS	SPE	IR	IND	S3-F	S3-C	S3-A	CI	CO
Example 1: <i>Tanacetum vulgare</i> – <i>Hieracium onegense</i> (A1) vs <i>Carex pallescens</i> – <i>Betula pendula</i> (A2)										
Delta	A1	5	113	0.841	95	64.497	65.252	64.698	0.539	0.904
	A2	6	87	0.793	69	66.791	69.679	67.945	0.552	0.915
						2.294	4.427	3.247	0.013	0.011
Example 2: <i>Stachyo sylvaticae</i> – <i>Tilietum cordatae</i> (F1) vs <i>Lactuca serriola</i> – <i>Aegopodium podagraria</i> (F2)										
Delta	F1	8	50	0.860	43	71.189	70.508	70.389	0.559	0.938
	F2	10	123	0.789	97	65.664	64.208	64.911	0.504	0.907
						–5.526	–6.300	–5.478	–0.056	–0.031

CNO, serial number of coenoflora; RELS, number of relevés in a coenoflora; SPE, number of taxa in a coenoflora; IR, share of indicator taxa from the general list of taxa; IND, number of indicator taxa; S3-F, S3-C, and S3-A, average statuses in the gradations of the scale, calculated by the method of average and weighted by occurrence (S3-F), average coverage (S3-C), and activity of taxa (S3-A); CI, interval environmental compliance index; and CO, optimum environmental compliance index

a more active participation of synanthropic species with sufficiently wide and asymmetric tolerance amplitudes relative to the optimums in the overgrowth of tree cuts. Moreover, the optimal status of taxa does not always coincide with the median in the widest amplitude of the minimum abundance-coverage in the amplitude-optimum format of the scales.

The weighting of taxa by tolerance indices was turned off to establish a differences between AS, depending on the used weight parameter of taxa (occurrence S3-F, average coverage S3-C, and activity S3-A) at the level of coenofloras, so that the effect of one of the three weight indicators is manifested. Changes in vegetation characteristics between arrays A1 and A2 are less contrasting and relatively balanced in the first example. Therefore, a “compromise” activity indicator leads to intermediate AS values between those when weighed by occurrence and average coverages. The same nature of the relationship between the weight parameters is noted for the F2 array in the second example. The use of activity gives the extreme most “dry” CI value for the primary forest (F1). An explanation for this case can be found by analyzing the head part of the species spectrum of this coenoflora. Field balm (*Glechoma hederacea* L.: optimum moisture status: 64; weight indicators (occurrence, average coverage, and activity in %): 100.0; 1.125; 10.607) bypasses the activity of a more moisture-loving and plentiful, but less constant, common hazel (*Corylus avellana* L.: 69; 62.5; 2.24; 9.35). The difference in the activity-ranked spectrum of coenoflora between these species is 4 positions, which leads to an indicative value of CIs for moisturizing.

Tables 1 and 2 did not include the results of the initial analysis, which was performed in the IBIS environmental module with default settings, implying the use of all indicator taxa for which there are data in the scales. The obvious deviation of the initial results from the expectations in the second (“forest”) example for

methods S2, S4, and S6 led to a critical check of the composition of coenoflora. One of the species, the giant bellflower (*Campanula latifolia* L.), had a marker of incomplete data, but participated in the process of phytoindication along with other species. This bellflower is notable, because it has a unique (for moderate abundance) amplitude from 55° to 56° (the humidification scale of L. G. Ramenskii), which turns it into an extreme pseudostenotope. Humidification ASs using the tolerance index weighting were underestimated in 7 relevés, including *Campanula latifolia*. This reduction reached 5 or more steps. The error in the calculations would be even more dramatic if this species were abundant in these coenoses. For example, the ecological amplitude of *Campanula latifolia* occupies 26% of the total moisture gradient on the scales of Tsyganov (1983) calculated for the same territory. It is known that the scales in the system of L.G. Ramenskii are not complete. The work on them was interrupted by the death of the author himself, and for many taxa there was not enough material to confidently assess their environmental preferences. The incompleteness of the data on the humidification scale is relatively small: 7.63% of indicators have only predefined statuses or open amplitudes (no limiting status). A similar indicator of the alluviality scale is 90.52%, which makes it simply inoperative, if one works with a small number of indicator taxa. So much space was given to this example to draw attention to the errors that may occur during mass phytoindication processing under conditions of an uncritical attitude to the list of indicator taxa. The capabilities of software for processing huge arrays of descriptions can only exacerbate this problem.

Interested readers can draw other conclusions from the exposed material on their own by referring to the source study. There are synoptic tables in both publications; community description tables are also available for the first example.

CONCLUSIONS

Choosing the method appropriate for the nature of the data and the uniform calculation of the average phytoindication statuses for an array of relevés or floras is necessary, but it is only the initial stage for a series of further analytical processing of the material. Average statuses can be used for a multivariate analysis of botanical data as surrogate abiotic variables. Individual taxon statuses can serve as the basis for generalization of summary tables (Zverev, 2012a). Among the possible tasks that are solved using phytoindication characteristics, we list the following:

(i) calculating the ecological correlations between the breadth of the ecological amplitudes of indicator taxa and their occurrence, average coverage, and activity of taxa in the arrays of relevés;

(ii) creating the ecological spectra of communities and floras on scales of any type;

(iii) calculating the probabilistic ecological profiles of communities and floras on scales of the amplitude format (Zverev, 2012b);

(iv) constructing the ecograms (radar schemes) for the visualization of multidimensional ecological ranges as separate taxa of various ranks (Shurupova et al., 2017; Shchegoleva, Zverev, 2019), as well as communities or floras of any nature and scale;

(v) calculating the ecological distances between taxonomic lists, including in a multifactor ecological space;

(vi) performing a hierarchical or nonhierarchical cluster analysis based on environmental parameters and the use of environmental distances in the problems of vegetation classification (Zverev, 2012b);

(vii) conducting indirect ordination of communities and floras by their environmental parameters, including two-dimensional ordination with the possible construction of isopleths;

(viii) using combined environmental parameters based on several environmental factors for ordination;

(ix) using the regression analysis for indirect assessment of the tension of one environmental factor by other factors (for example, assessing habitat disturbance by factors of moisture, trophicity, and illumination);

(x) accumulating the phytoindication statuses in large databases of relevés for correcting and regionalizing existing ecological scales.

Effectively implementing all these tasks is impossible without the use of modern information systems that have both means of managing vegetation data and analytical tools for the use of phytoindication scales.

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