Bimodal spectra of nutrient indicators reveal abrupt eutrophication of pine forests

Bimodální spektra indikačních hodnot pro živiny svědčí o náhlé eutrofikaci borů

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Five hundred and eight phytosociological relevés from pine forests on sand, calcareous gravel and rock in NE and S Germany were analysed with respect to the frequency of Ellenberg indicator values of vascular plants for nutrients (N). Principal component analysis revealed that after the average nitrogen value (mN), the distribution shape and modality are the second most important sources of variation in the N-spectra of relevés. Of the five spectral types defined by combinations of mN and modality, the unimodal low nutrient type (66.5%) prevailed, followed by bimodal distributions with many indicators for low and high N-supply, with few in the intermediate classes 4 and 5 (27.4%), whereas spectra with a single mode at high (3.9%) or intermediate (2.2%) N-values were rare. Two explanations for the frequent coexistence of vascular plant indicators of N-deficiency with those indicating eutrophication are discussed: (a) Bimodality may be a consequence of the low capacity of pine forests to sequestre the excess input of anthropogenic nitrogen from the atmosphere, and/or (b) the natural dynamics of humus accumulation and mineralization following disturbance. To avoid misinterpretation of mN, inspection of modality of the N-spectra should be standard practice when analysing pine forest or other long-lived vegetation with low N-sequestration. Predominance of high N- over low N-indicators in relevés may be interpreted as a signal of advanced anthropogenic eutrophication, N-saturation and increased risk of N-leaching to groundwater. Bimodal spectra with prevailing deficiency indicators, on the other hand, may be either due to short-term N-release or indicate the beginning of eutrophication.

Keywords: bioindication, Ellenberg indicator value, phytosociological databank, phytosociological relevés

Introduction

Until recently, nitrogen was viewed as limiting productivity in many terrestrial ecosystems (Ellenberg 1988). The last decades, however, have seen attention shift from N-deficiency towards N-saturation and its harmful consequences for environment and biodiversity. Excess N from combustion of fuels and agriculture contaminates water with nitrate, results in the emission of the greenhouse gas N_2O (Bobbink et al. 1998) and promotes luxurious growth of few dominant plant species at the expense of others (Walker & Preston 2006). As a consequence, N-eutrophication is considered a principal cause of species extinction and biotic homogenization in industrialized countries (Jenssen & Hofmann 2005, Bernhardt-Römermann & Ewald 2006).

Because of the dynamic transitions between several ecosystem compartments, N-supply is difficult to measure directly (Knoepp & Swank 1995), which makes foliar N-concentrations (Van den Burg 1990) or plant species composition (Ellenberg et al. 2001) attractive bioindicators. Thus, systematic increases in average Ellenberg indicator values of plant species for nutrients are attributed to improved N-availability (Van Dobben et al. 1999, Fischer 1999), which implies the gradual replacement of deficiency indicators by species with higher N-demands. As the input of phosphorus into terrestrial forest ecosystems is very low, anthropogenic nitrogen emmissions are a plausible explanation for recent trends in N-values. However, ecosystems like *Pinus sylvestris* forests may rapidly change from deficiency to saturation, because the dominant plants are long-lived, grow slowly and are unable to reduce excess N by uptake (Prietzel & Kölling 1998).

In this contribution, Ellenberg indicator values are used to test, whether eutrophication in Central European pine forests occurs gradually during succession, in which undergrowth species of low nutrient demand are replaced first by those of intermediate requirements and then those that indicate an ample N-supply, or whether ground-dwelling plants reflect a rapid non-linear transition from oligotrophic to eutrophicated states of the forest ecosystems. What should be the consequences of a rapid switch from deficiency to excess for community composition? Persisting deficiency indicators and a few intermediate indicators should be found side by side with eutrophication indicators. The presence of such bimodal indicator spectra in phytosociological relevés of pine forests would support a rapid ecosystem shift. This study presents a test of this hypothesis based on several hundred phytosociological relevés from the major types of pine forest in Central Europe.

Methods and data

Nomenclature of plant taxa follows Wisskirchen & Hauepler (1998), that of syntaxa Rennwald (2000). Phytosociological relevé data from four major pine forest areas, representing the most important terrestrial pine ecosystem types in Germany were collated from the sources listed in the columns of Table 1.

Indicator values for nitrogen of vascular plant taxa were taken from Ellenberg et al. (2001). For each relevé the number of N-indicators per class 1 through 9 was determined and expressed as a percentage of all N-indicators. Forty nine relevés from Brandenburg and 18 from Lower Bavaria contained less than five N-indicator taxa and were not included in the analysis. Unweighted averages of N (mN) were computed for relevés.

In order to explore the relationships between indicator proportions, including more complex patterns, the cross-matrix of relevés ($n = 508$) by N-classes was subjected to principal component analysis (PCA) using correlations as cross-products in PC-ORD software (McCune & Mefford 1997). Correlation of mN and individual N-value proportions with the first two PCA-axes were inspected visually in a biplot diagram (Fig. 1, Table 2). Based on this inspection five types of modality of N-spectra were defined. Mean and standard deviation of N-value proportions and of mN within these types were computed and plotted as average spectra.

For each dataset the total list of vascular plant taxa occurring in the respective relevés was queried and taken as the basis of a frequency distribution of N-values in the respective species pool. As a comparison the frequency distribution of N-values for the whole Ellenberg-list of vascular taxa was queried, representing the total species pool of the Central European flora.

Table 1. – Characterization of relevé subsets. Species numbers are mean ± S.D., percentages of the total number of relevés are given in brackets.

Data set	Brandenburg	Lower Bavaria	Munich plain	Bavarian Alps
Source	Heinken & Zippel (1999)	Scheuerer (unpublished)	Schessl (unpublished)	Hölzel (1996), Lorenz (1993), Ketterer & Ewald (1999), Puchner (1998), Herter (1990), Hofmann (1997), queried from BERGWALD databank (Ewald 1995)
Number of relevés	180	99	42	254
Relevés with < 5 N-indicator taxa	49 (27%)	18 (18%)	–	–
Sites	glacial and glaciofluvial sand plains and dunes	recent sand dunes of tertiary sand	glaciofluvial gravel	dolomite and limestone rock and fluvial gravel
Alliance	*Dicrano-Pinion*	*Dicrano-Pinion*	cf. *Erico-Pinion*	*Erico-Pinion*
Associations	*Cladonio-Pinetum*, *Leucobryo-Pinetum*, *Peucedano-Pinetum*	*Leucobryo-Pinetum*, *Peucedano-Pinetum*	*Molinia-Pinus sylvestris* community	*Calamagrostio-Pinetum*
Vascular species richness per relevé	23±9.4	35±21.8	20±8.0	55±16
Number of vascular N-indicators per relevé	10±7.9	14±12.4	14±6.0	34±8.5
Modality type:				
Low (right-skewed)	52 (29%)	43 (53%)	10 (24%)	233 (91%)
High (left-skewed)	2 (1%)	4 (4%)	17 (40%)	–
Median	3 (2%)	1 (1%)	5 (12%)	–
Unimodal low	60 (33%)	32 (32%)	5 (12%)	21 (9%)
Bimodal high	14 (8%)	1 (1%)	5 (12%)	–

To visualize the floristic structure of the communities studied, the three most constant indicators per nutrient value were queried and displayed for each relevé set in a phytosociological constancy table.

Results

The first two PCA-axes accounted for 48% of variation in N-indicator spectra. Axis 1 (33% of variation) represented average nitrogen values (mN), whereas axis 2 separated relevés with high proportions of intermediate indicators (N4, N5) from all others (Fig. 1). Viewing both axes in combination formed the basis for classifying N-spectra into five modality types depicted by symbols in Fig. 1, for which numerical definitions are given in Table 3. While supporting the classification, PCA showed that there are no sharp boundaries but smooth transitions between the modality clusters. In fact, average proportions of N-indicators indicated a certain amount of bimodality even in the low N group, caused by the low incidence of taxa with N = 5.

Table 2. – Results of PCA of the cross-matrix of relevés (n = 508) by Ellenberg nitrogen indicator value classes (N1–N9).

Axis	Eigenvalue	% variance	Cumulative % variance	Eigenvectors								
				N1	N2	N3	N4	N5	N6	N7	N8	N9
1	2.997	33.3	33.3	–0.20	–0.41	–0.30	0.10	0.27	0.45	0.42	0.35	0.34
2	1.343	14.9	48.3	0.39	–0.19	0.17	–0.65	–0.43	0.09	0.06	0.41	0.06

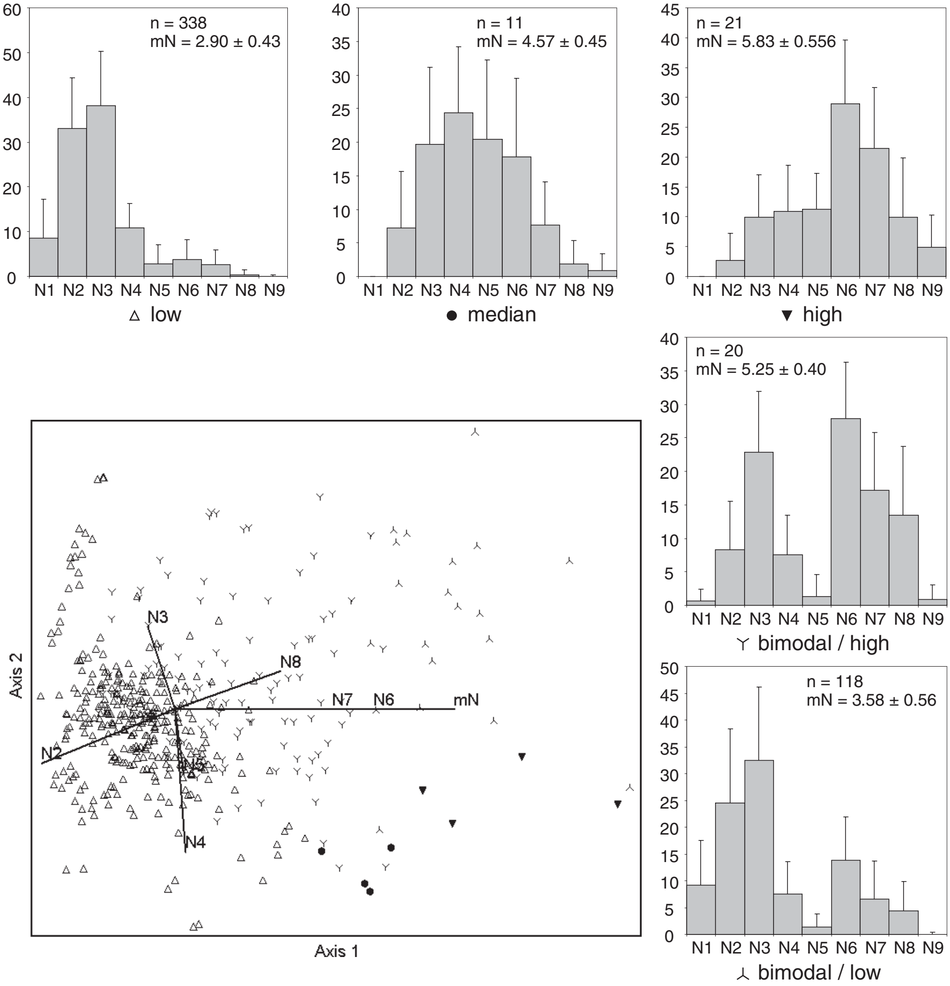

Fig. 1. – Ordination diagram of principal component analysis of N-spectra of pine forest relevés. The proportions of N-classes 1 to 9 are shown as biplot vectors. Five types of modality in N-indicator spectra (see Table 1) are characterized by averages and standard deviations of N-class proportions.

Table 3. – Definitions of modality types of frequency spectra of nitrogen indicator values in relevés.

Type	Definition
Low (right-skewed)	N1–3 > N4–5 and N6–9 < N4–5
High (left-skewed)	N1–3 < N4–5 and N6–9 > N4–5
Median	N1–3 < N4–5 and N6–9 < N4–5
Bimodal/low	N1–3 > N4–5 and N6–9 > N4–5 and N1–3 > N6–9
Bimodal/high	N1–3 > N4–5 and N6–9 > N4–5 and N1–3 < N6–9

The vast majority of relevés exhibited right-skewed (67%) or bimodal (27%) N-indicator distributions (side histograms in Fig. 1). In most relevés of the bimodal type, low N–prevailed over high N-values. There were only a few relevés with a predominance of intermediate (2.2%) or high N-values (3.9%).

Pine forest on sand (*Dicrano-Pinion*) from Brandenburg and Lower Bavaria were similar with respect to the high incidence of bimodal indicator spectra (Table 1) and composition (Table 4). The dataset from the Munich gravel plain was the only one with a predominance of left-skewed N-spectra. The relevés from the Alps (*Erico-Pinion*) have a markedly higher species richness, particularly of calciphilous species and almost an exclusive preponderance of low N-spectra. Gravel plains and Alps had in common mostly indicators of oligotrophic calcareous sites (Table 4).

Bimodality in the N-indicators is not a general feature of the Central European flora (Fig. 2), or pine forest species pools (the list of all N-indicators found in a particular relevé set). Only the Brandenburg pool shows a slight and the Munich gravel plain a marked depression in N-classes 4 and 5.

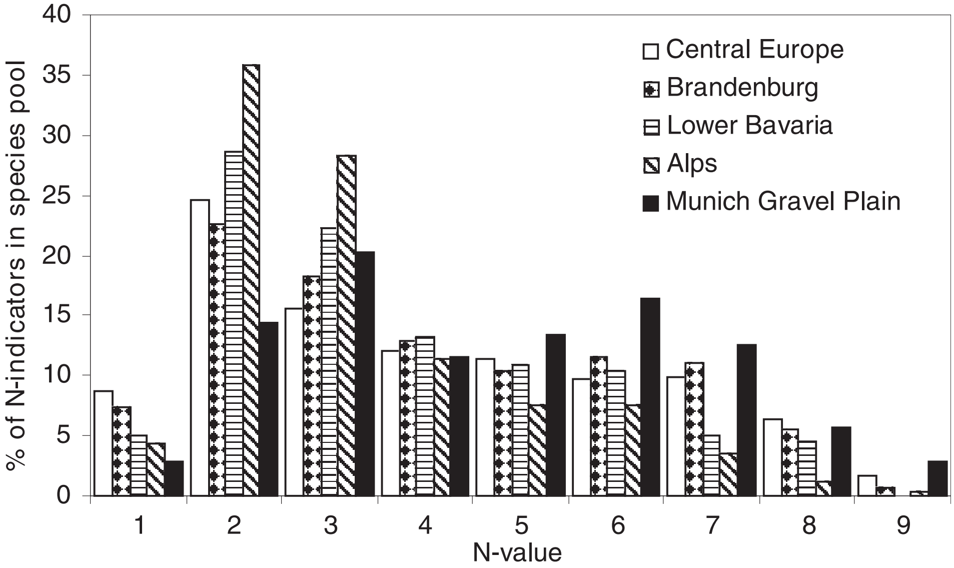

Fig. 2. – Frequency distribution of N-indicator vascular plant taxa in the species pool. Data for Central Europe are based on complete flora given in Ellenberg et al. (2001), for particular regions on total species lists from all relevés.

Table 4. – Constant nitrogen indicator taxa. For each dataset and indicator value the three most frequent taxa are shown. See Table 1 for details of datasets.

	N-value	Brandenburg	Lower Bavaria	Munich Plain	Alps
Number of relevés		180	99	42	254
Sambucus nigra	9	1	.	36	.
Arctium lappa	9	.	.	2	.
Calystegia sepium	9	.	.	2	.
Epilobium angustifolium	8	18	16	.	.
Robinia pseudoacacia	8	8	.	.	.
Senecio sylvaticus	8	7	.	.	.
Senecio ovatus	8	.	6	.	1
Anthriscus sylvestris	8	.	3	.	.
Urtica dioica	8	2	2	31	.
Cirsium vulgare	8	.	.	24	.
Torilis japonica	8	1	.	14	.
Galium aparine	8	1	.	10	.
Eupatorium cannabinum	8	.	.	.	1
Chaerophyllum hirsutum subsp. *villarsii*	8	.	.	.	0
Moehringia trinervia	7	18	2	2	.
Taraxacum officinale agg.	7	9	19	12	.
Arrhenatherum elatius	7	9	23	2	.
Cynoglossum officinale	7	.	4	.	.
Acer pseudoplatanus	7	9	.	33	.
Geum urbanum	7	2	1	26	.
Fraxinus excelsior	7	1	2	17	.
Dryopteris dilatata	7	8	.	14	.
Mercurialis perennis	7	.	.	.	20
Salvia glutinosa	7	.	.	.	11
Listera ovata	7	.	.	.	9
Calamagrostis epigejos	6	44	5	24	.
Fragaria vesca	6	17	34	48	35
Rubus idaeus	6	15	10	86	.
Mycelis muralis	6	11	22	.	1
Galeopsis bifida	6	.	17	.	.
Galeopsis tetrahit	6	11	2	24	.
Brachypodium sylvaticum	6	8	1	52	6
Leontodon hispidus	6	.	6	2	26
Knautia dipsacifolia	6	.	.	.	26
Epipactis helleborine	5	7	6	2	.
Linaria vulgaris	5	2	2	.	.
Calamagrostis arundinacea	5	2	.	.	.
Carex hirta	5	1	4	12	.
Conyza canadensis	5	1	4	.	.
Tilia cordata	5	1	1	36	.
Euonymus europaea	5	.	1	26	.
Potentilla alba	5	.	1	12	.
Prunus avium	5	1	2	12	.
Aposeris foetida	5	.	.	.	14
Hepatica nobilis	5	.	1	.	13
Prenanthes purpurea	5	.	.	.	9
Agrostis tenuis	4	33	21	41	6
Veronica officinalis	4	14	7	2	0
Luzula pilosa	4	12	11	2	.
Hieracium sylvaticum	4	1	30	.	65
Brachypodium pinnatum	4	.	13	.	3
Crataegus monogyna agg.	4	6	1	48	.

Rhamnus cathartica	4	1	10	43	.
Poa nemoralis	4	2	4	17	.
Carduus defloratus	4	.	.	.	64
Rubus saxatilis	4	.	.	.	31
Avenella flexuosa	3	89	76	.	.
Vaccinium myrtillus	3	35	67	.	15
Carex pilulifera	3	26	2	.	.
Dryopteris carthusiana	3	24	26	43	.
Euphorbia cyparissias	3	8	23	21	8
Brachypodium rupestre	3	.	.	69	39
Hypericum perforatum	3	10	8	24	.
Sesleria varia	3	.	.	.	92
Calamagrostis varia	3	.	.	.	91
Buphthalmum salicifolium	3	.	.	.	86
Melampyrum pratense agg.	2	27	39	.	21
Hieracium pilosella	2	25	29	.	4
Hieracium lachenalii	2	24	10	.	.
Campanula rotundifolia	2	6	29	.	24
Filipendula vulgaris	2	.	.	40	.
Polygala chamaebuxus	2	.	.	14	94
Erica carnea	2	.	.	10	93
Potentilla erecta	2	.	8	24	78
Allium carinatum	2	.	.	12	.
Calluna vulgaris	1	47	70	.	6
Vaccinium vitis-idaea	1	17	42	.	15
Thymus serpyllum	1	13	24	.	.
Galium boreale	1	.	3	14	45
Dorycnium germanicum	1	.	.	12	3
Potentilla incana	1	1	.	2	.
Thymus praecox subsp. *polytrichus*	1	.	.	.	48
Teucrium montanum	1	.	.	.	25

Discussion

The results of this study support the hypothesis that Central European *Pinus sylvestris* forests experience rapid changes in N-availability. Starting from oligotrophic levels on acid sand, calcareous rock and gravel, eutrophication is associated with the abrupt appearance of plants that need quite high amounts of N, bypassing a phase dominated by species with intermediate N-requirements. This may be attributable to (a) the low capacity of these ecosystems to incorporate large quantities of N into stand biomass, and (b) the dynamics of N-immobilization in litter and duff, and pulses of mineralization of these metastable pools (Prietzel et al. 2006).

While showing rapid growth in height in the young stages, mature pine stands increase more slowly in timber volume and biomass than temperate climax forests. In addition, pine foliage, branches and bark contain very little N (Jacobsen et al. 2003). Thus, stands of pine are a less effective buffer against elevated N-inputs than stands of other tree species. As a consequence, a high N-input from the atmosphere more rapidly leads to undesirable effects of N-saturation, such as elevated NO_3-concentrations in seepage, unbalanced nutrition of foliage and eutrophication of ground vegetation. Mellert et al. (2005) found, that seepage water from Bavarian pine forests has either very low or very high, but rarely intermediate nitrate-concentrations. This susceptibility is expressed as a lower critical load for N-input (Sverdrup et al. 1995). From this perspective, the appearance of N-indicators in oligotrophic ground vegetation indicate that this threshold has been exceeded.

However, explanation (b) introduces more complexity. In many pine communities, dry soils with extreme pH-values (acid on sand, alkaline on carbonate rock) and low N-concentrations in the litter limit bioturbation and microbial N-mineralization, and favour accumulation of poorly decomposed organic duff. Despite high C/N-ratios, these surface layers accumulate considerable amounts of N by virtue of their sheer mass. Less stable than the mineral-organic complexes in biologically active A-horizons, these N-stocks are mineralized, as soon as favourable conditions occur during moist weather, stand disturbance or liming. As a natural feature, these sink-source dynamics in humus layers may occur independently of N-input and explain the circumboreal occurrence of N-indicators such as *Epilobium angustifolium* in coniferous forests (Hultén 1971), far from anthropogenic N-sources, following natural disturbance. If dependant on the release from limited internal N-sources, natural eutrophication occurs in rapid, but short pulses, which, due to leaching, leave ecosystems more oligotrophic than before the disturbance.

The potential of passive bioindication to differentiate between alternative causes and processes of eutrophication is obviously limited. However, it is reasonable to regard bimodal indicator spectra as a specific signature of dynamics in N-availability in oligotrophic ecosystems like pine forests. The most frequent bimodal type with mainly oligotrophic taxa probably comprises both natural, short-term sink-source dynamics with transient appearance of N-indicators as well as the initial stages of eutrophication by N-input. Bimodal spectra with mainly high N-indicators more likely represent advanced eutrophication and incipient ecosystem change.

Pine forests with persistent high nutrient requiring undergrowth must be regarded as artificial systems brought about by athmospheric N input (Hofmann 1994). The negative consequences of N-saturation may be alleviated by it favouring deciduous tree species with a greater capacity for N-uptake (Dully et al. 2002).

According to the relevé sets analysed, eutrophication is most advanced in the gravel plain pine forests, where oligotrophic plant species occur as mere relics (Table 1). In fact, Mellert et al. (2005) measured high NO_3-concentrations in the seepage from several comparable sites throughout Bavaria. On Brandenburg and Lower Bavarian sands both eutrophicated and oligtrophic stands appear to be widespread, while alpine pine forests show few signs of eutrophication. Such comparisons may be biased by the preferential sampling of communities that fit the well-known syntaxa of oligotrophic pine forest at the expense of eutrophicated stands. However, there is no reason to believe that phytosociologists have oversampled communities with bimodal N-spectra. The proportions of bimodal and high N-spectra must therefore be regarded as conservative estimates.

While several studies have addressed bimodal species responses in ecological gradients and their consequences for calibrating Ellenberg indicator values (ter Braak et al. 1987, Diekmann 1995), within-relevé bimodality of indicator values has received little attention (Botta-Dukát & Ruprecht 1999/2000, Diekmann 2003). Apart from their special potential for process detection, bimodal spectra have obvious implications for the use of Ellenberg's indicator values. The occurrence of bimodal spectra undermines the use of averages and results in intermediate values in the absence of actual intermediate indicators.

Checks of spectra and modality of indicator frequencies in vegetation relevés should therefore become standard practice (see Durwen 1982), at least where pine forest or other long-lived vegetation is involved.

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Souhrn

Práce na základě 508 fytocenologických snímků analyzuje indikační hodnoty pro živiny v borových lesích severovýchodního a jižního Německa. Analýza základních komponent ukázala, že tvar distribuce a modalita spekter Ellenbergových indikačních hodnot pro dusík byly po průměrné hodnotě druhým nejvýznamnějším zdrojem variability v datech. Na základě průměrné hodnoty a modality bylo vymezeno pět typů spekter; převládalo unimodální rozdělení s nízkou hodnotou pro živiny (65 %), častý byl i bimodální typ s koncentrací indikátorů pro vysoký nebo nízký obsah dusíku (27.4 %). Unimodální spektra s převahou druhů indikujících vysoký (3.9 %) nebo střední (2.2%) obsah dusíku v půdě byla vzácná. Práce diskutuje dvě možná vysvětlení koexistence rostlin indikujících nedostatek dusíku nebo naopak eutrofizaci studovaných společenstev. Bimodalita může být důsledkem omezené kapacity borových lesů sekvestrovat nadbytečný dusík z atmosféry, nebo se může jednat o přirozenou dynamiku akumulace humusu a následnou mineralizaci po disturbanci. Analýza modality distribučních spekter indikačních hodnot by se měla stát standardní součástí jejich interpretace, neboť závěry založené na pouhých průměrných hodnot mohou být při studiu borových lesů nebo jiných dlouhověkých společenstev s omezenou sekvestrací dusíku mylné. Převahu indikátorů pro vysoké hodnoty lze interpretovat jako známku pokročilé antropogenní eutrofizace, saturace dusíkem a zvýšeného nebezpečí jeho vyplavování do podzemních vod. Bimodální spektra s převahou indikátorů nízkého obsahu dusíku mohou být důsledkem krátkodobého uvolnění dusíku ze systému nebo známkou začínající eutrofizace.

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