

Spatial and temporal patterns of Ellenberg nutrient values in forests of Germany and adjacent regions - a survey based on phytosociological databases

Räumliche und zeitliche Muster von Ellenberg-Nährstoffzahlen in Wäldern Deutschlands und angrenzender Gebiete – eine Untersuchung auf Grundlage pflanzensoziologischer Datenbanken

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Abstract

Within the last 30 years the role of nitrogen in Central European forests has changed fundamentally from limiting resource to environmental problem. As the retrospective tracking of nutrient availability by soil chemical and biogeochemical measurements faces serious problems, bioindication based on understorey species composition is indispensable for monitoring broad-scale eutrophication.

Based on a broad survey of more than 100,000 forest vegetation plots accessible in electronic databases from Germany and adjacent countries, we calculated unweighted average Ellenberg nutrient values (mN) as a proxy of plant-available macronutrients. Based on the quantiles of the frequency distribution of mN in a regionally stratified sample, we define five trophic classes, which can be used to compare dimensionless mN values.

We studied spatial patterns of average nutrient values within 17 regions and compared the periods from 1899 to 1975 and 1976 to 2006. After 1975 eutrophic ($mN > 5.67$) and hypertrophic ($mN > 6.28$) conditions were common everywhere except in the Alps and Saxony-Anhalt, but very oligotrophic conditions ($mN < 3.44$) were still widespread in regions with nutrient-poor bedrock. Before 1975 mN of plots had been lower than after 1975 in all but the southeastern regions. Between the pre- and post-1975 data the proportion of hypertrophic plots increased from 5.7 to 11.8%, and that of very oligotrophic plots decreased from 14.6 to 8.3%.

To remove bias resulting from uneven distribution, the dataset was stratified by five tree layer dominance types, period and region and resampled. In pre-1975 plots medians of mN increased in the order *Pinus sylvestris*, *Quercus* spp., *Picea abies*, *Fagus sylvatica* and *Alnus* spp, whereas the increase of mN was highest in forest types with historically low nutrient values. Therefore, the widespread change in mN must be attributed to the pronounced vegetation changes in *Quercus* and *Pinus* stands, indicating the importance of land-use change, i.e. recovery of nutrient cycles after hundreds of years of exploitation through coppicing, grazing and litter use.

The analysis confirms eutrophication as a megatrend of modern vegetation change and demonstrates the high research potential of linking vegetation plot databases across large regions.

Keywords: bioindication, Central Europe, Ellenberg indicator values, eutrophication, nitrogen deposition, soil nutrients, vegetation-plot data

Erweiterte deutsche Zusammenfassung am Ende des Textes

1. Introduction

Within the last 30 years the role of nitrogen (N) in forest ecosystems has changed fundamentally (KREUTZER 1989, BERNHARDT-RÖMERMANN & EWALD 2006). In the 1960s, N was limiting the productivity of many Central European forests (ELLENBERG 1964) and application of N fertilisers was a major focus of forest science (EVERS 1991, ABER 1992). Twenty years later N eutrophication of natural and semi-natural ecosystems was identified as a major threat to biodiversity (ELLENBERG JR. 1985, KUHN et al. 1987, ROST-SIEBERT & JAHN 1988, THIMONIER et al. 1992, ZUKRIGL et al. 1993) and environmental quality (PIERZYNSKI et al. 2005). In contrast to the strong reduction of sulphur pollution since the 1990s (STERN 2005), N eutrophication persists as an unresolved challenge (BOBBINK et al. 1998, SMART et al. 2003, WALKER & PRESTON 2006).

Against this background detection and tracking of eutrophication remain major tasks of forest ecosystem monitoring. At intensive monitoring sites such as the European Level II network N deposition, pools and outputs are measured directly (DE VRIES et al. 2003). However, as these observations are too sparse for regionalising N status of forests on the landscape scale, bioindication of eutrophication and associated biodiversity changes based on Ellenberg indicator values for nutrients (ELLENBERG et al. 2001) is a crucial component in extensive monitoring on the European level (LORENZ 1995) and finer scales (SMART et al. 2003, PITCAIRN et al. 2004, SEIDLING & FISCHER 2008, THIMONIER et al. 2011, VERHEYEN et al. 2012).

While the usefulness of average indicator values in detecting spatial patterns of N-deposition and temporal trends in eutrophication is broadly accepted, the lack of calibration against direct chemical measurements hinders the universal acceptance of the method. The problem lies partly in the difficulty to quantify plant-available nitrogen (KNOEPP & SWANK 1995), partly in the superposition of and interaction with the effects of other resources such as phosphorous and potassium (ERTSEN et al. 1998, SCHAFFERS & SYKORA 2000). Indicator plants respond to the availability of N (cumulative sum of NH_4^+ and NO_3^-

concentration in the soil solution) as a limiting resource, for which no standard measurement exists in forest soils. Because standard ecosystem parameters such as concentrations, total amounts, fluxes or ratios of N in atmosphere, throughfall, biomass, soil and seepage are only partial indicators of N availability, their weak bivariate correlations with N values are not surprising. N values are indicators of macronutrient, i.e. N and P availability, which, in unfertilised terrestrial systems, depends on microbial release from soil organic matter (CHAPIN et al. 2002). While some (semi-)terrestrial systems such as calcareous fens may be P-limited (BOYER & WHEELER 1989, PAULI et al. 2002, WASSEN et al. 2005) or N- and P-co-limited (GÜSEWELL et al. 2003), N and P supplies co-vary in most forest ecosystems. As intensive forest monitoring provides no indication of significant P deposition (THIMONIER et al. 2005) and recent P balances are usually negative (ILG et al. 2009), recent eutrophication can be safely attributed to changes in N supply. However, once ecosystems are released from N limitation, P may limit further increases in mN values (GRESS et al. 2007).

In practice, average Ellenberg nutrient values are difficult to compare, because they are not calibrated against straightforward chemical measurements (WAMELINK et al. 2002, PRÖLL et al. 2011) and because averaging compresses the verbally defined ordinal scale of species values given by ELLENBERG et al. (2001). Quantiles of the distribution derived from a large representative dataset can be used to partition the mN scale. Although not a perfectly representative sample of vegetation composition (CHIARUCCI 2007), large phytosociological databases (EWALD 2001, DENGLER et al. 2011) may provide a reasonable approximation of the frequencies of measured mN values if sampling bias is reduced by stratified resampling (KNOLLOVÁ et al. 2005).

In the present research a large database of mN values from forests in Germany and adjacent areas was compiled, the frequency distribution of mN in forest plots was studied and a relative scale for evaluating levels of mN was derived in order to compare regional distributions and to detect temporal trends of mN in forest plots.

As no institutionalised network of phytosociological plot databases exists at this moment (but see DENGLER et al. 2011, JANSEN et al. 2011), the rapid compilation of data was a trial of the feasibility to establish such a cooperation, as intended in the SynBioSys Europe and the European Vegetation Archive projects (SCHAMINÉE & HENNEKENS 2006, EUROPEAN VEGETATION SURVEY 2012).

2. Materials and Methods

In December 2006 owners and managers of known phytosociological databases in the German federal states and neighbouring countries were asked to provide a table containing the following data on forest vegetation plots: Plot-ID, average Ellenberg indicator value for nutrients (mN), number of vascular understorey species in the plot with assigned Ellenberg indicator value for nutrients and year of plot sampling. Data were delivered from the databases shown in Table 1. In France (Alsace, Lorraine), Switzerland (Central Plateau and Jura, Northern Alps), Austria (Northwestern lowlands [regions 7 and 9], Northern front range of the Alps [region 4]) and the Czech Republic (west of the 15th meridian) data use was restricted to the subregions bordering Germany.

Unweighted average indicator values for nutrients (mN) were calculated by database managers based on the lists for vascular plant indicators by ELLENBERG et al. (2001), LANDOLT (1977) and HILL et al. (1999). Despite the mathematical problem of averaging ordinal numbers, simple averaging has

Table 1. Sources of plot data used in the survey of mN values; database code from the Global Index of Vegetation-Plot Databases (GIVD, see DENGLER et al. 2011).

Tabelle 1. Quellen der im Überblick von mN benutzten Vegetationsaufnahmen; Datenbank-Code aus dem Global Index of Vegetation-Plot Databases (GIVD, siehe DENGLER et al. 2011).

Region	Database Name/Institution/ GIVD-Code	Database Manager	Indicator Values
Baden-Württemberg	Standorts-Datenbank/Forstliche Versuchsanstalt	J. Kayser, H.-G. Michiels	Ellenberg (2001)
Bavaria*	Naturwaldreservats-Datenbank/LWF	C. Abs, H. Walentowski	Ellenberg (2001)
Bavarian Alps	BERGWALD/Hochschule Weihenstephan-Triesdorf/EU-DE-002	J. Ewald	Ellenberg (2001)
Berlin/Brandenburg	Institute for Forest Science, Eberswalde	M. Jenssen	Ellenberg (2001)
Mecklenburg- Vorpommern	Vegetationsdatenbank Mecklenburg- Vorpommern/Universität Greifswald/EU- DE-001	F. Jansen	Ellenberg (2001)
Saxony-Anhalt	Institute for Forest Science, Eberswalde	M. Jenssen	Ellenberg (2001)
Saxony	TU Dresden-Tharandt, Sachsenforst	S. Conrad	Ellenberg (2001)
Schleswig-Holstein	Vegetat/University of Kiel	M. Breuer	Ellenberg (2001)
Thuringia	Institute for Forest Science, Eberswalde	M. Jenssen	Ellenberg (2001)
Austria Northern alpine fringe	Federal Research and Training Centre Vienna	F. Starlinger	Ellenberg (2001)
Austria Northwestern lowlands	Federal Research and Training Centre Vienna	F. Starlinger	Ellenberg (2001)
Belgium, Flanders	Agency for Nature and Forest	J. Cornelis	Ellenberg (2001)
Belgium, Brussels region	Vrije Universiteit Brussel	S. Godefroid	Hill et al. (1999)
Czech Republic west of the 15 th meridian	Czech National Phytosociological Database/Masaryk University/ EU-CZ-001	M. Chytrý	Ellenberg (2001)
France Alsace/Lorraine	ECOPLANT/ Laboratoire d'Etude des Ressources Forêt-Bois	J.-C. Gégout	Ellenberg (2001)
Netherlands	National Vegetation Database The Netherlands/ALTERRA/EU-NL-001	S.M. Hennekens	Ellenberg (2001)
Switzerland Central Plateau and Jura	Swiss Forest Vegetation Database/WSL/EU-CH-005	T. Wohlgemuth	Landolt (1977)
Switzerland Northern Alps	Swiss Forest Vegetation Database/WSL/EU-CH-005	T. Wohlgemuth	Landolt (1977)

been shown to perform as well as more complex indices and is preferred for simplicity (DIEKMANN 2003). Landolt indicator values, which are defined on a scale from 1 to 5, were rescaled to a range from 1 to 9:

$$\text{Eq. 1. } mN = 1 + (mN_{\text{Landolt}} - 1) * 2$$

In order to avoid unreliable indication, only mN values based on plots with at least five N indicator species were considered. Data tables from the source regions were joined in a MS-Access database and united in one data table, in which every plot was assigned a unique identifier. To avoid bias resulting from uneven distribution of available plots between regions, we estimated the frequency distribution of mN in forest plots based on a random sub-sample of 5,202 plots (306 per region, which is the number

of plots available in the least sampled region). We computed a histogram of mN and quantiles in 10% steps using the R statistical environment (R DEVELOPMENT CORE TEAM 2008, version 2.7.1).

To remove the bias in mN caused by uneven distribution of forest types, we selected plots with dominance of the following tree taxa: *Fagus sylvatica*, *Quercus robur* et *petraea*, *Pinus sylvestris*, *Picea abies* and *Alnus* spp. and assigned plots to strata by unique combinations of tree dominance, period and region. After assessing the representation of strata we randomly resampled the database to create a balanced dataset with equal numbers of pre- and post-1975 plots per dominant tree species within each region.

We detected temporal changes by comparing distributions and averages of mN found in plots recorded up to the year 1975 and after, which we defined as a turning point in the scientific perception of nitrogen supply in forests. We tested alternative splits at 1965 and 1985. Comparisons between periods were drawn by calculating the test statistic U (Mann Whitney test, STAT SOFT 1984–2005) on the whole dataset as well as on individual regions (Table 1), except for three regions where only post-1975 plots were available. Comparisons were also performed on the subsample stratified by tree dominance. Based on the stratified subsample, a smooth trend (LOESS function in stats package of statistical environment R) was fitted to the scatter of mN values over time.

As attributes derived from a species composition matrix, average Ellenberg indicator values have been shown to yield biased results in significance testing (ZELENÝ & SCHAFFERS 2012). Because we had only assembled mN values calculated by database owners, modified testing by permutation (JANSEN et al. 2011, ZELENÝ & SCHAFFERS 2012) based on the whole compositional matrix was unfeasible. We therefore report test statistics and coefficients without giving levels of significance in this contribution.

3. Results

The database contained a total of 100,873 plots (matrix A), from which four subsets of plots were obtained by excluding unsuitable plots, by selecting plots with certain dominant tree species and by evenly resampling (sub-)sets of plots (Fig. 1).

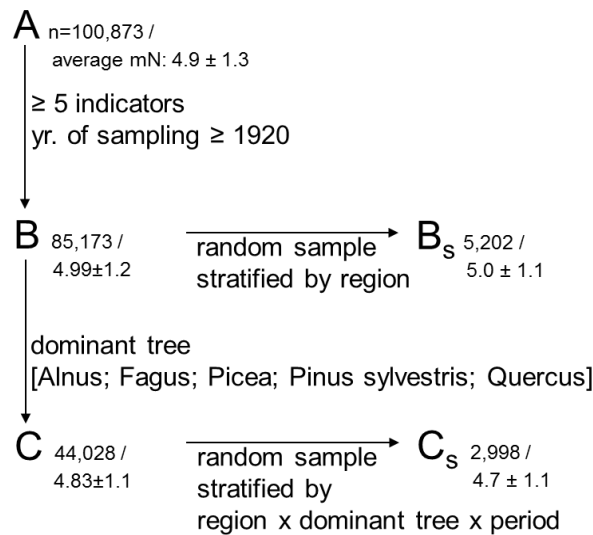


Fig. 1. Flow of subsampling showing respective dataset size, average and standard deviation of mN.

Abb. 1. Ablauf der Bildung von Teilstichproben mit jeweiliger Datensatzgröße, Mittelwert und Standardabweichung von mN.

The distribution of mN in the regionally balanced set B_s (Fig. 2) was slightly skewed towards higher values (skewness -0.40 ± 0.03). The 10, 30, 70 and 90% quantiles were derived as threshold values to distinguish very oligotrophic, oligotrophic, mesotrophic, eutrophic and hypertrophic plots.

In matrix B ($n = 85,173$) a linear trend of mN ($R^2 = 0.019$, $b = 0.010$) was detected, suggesting an average increase of mN by 0.9 units since 1920. LOESS regression suggested a steady, $\pm$ linear trend (Fig. 3).

The frequency of plots assigned to trophic levels varied by region. Figure 4 shows the regional pattern for the 62,586 post-1975 plots. Eutrophic and hypertrophic plots constituted considerable proportions in all regions, except the southernmost ones (Switzerland, Bavarian Alps) and in Saxony-Anhalt.

According to the Mann-Whitney test, average mN of plots in the whole dataset was higher after 1975 (mean: 5.09) than before 1975 (mean: 4.73, $u' = -24.04$). The magnitude of the test statistic decreased if earlier (1965: -21.44 , 1955: -19.25) or later (1985: -19.96) splits were defined. Three regional datasets (Baden-Württemberg, Bavarian lowlands and Schleswig-Holstein) contained only plots from after 1975. Of the remaining 14 regional datasets nine had higher mN after 1975, three (Thuringia, western Czech Republic and Austrian

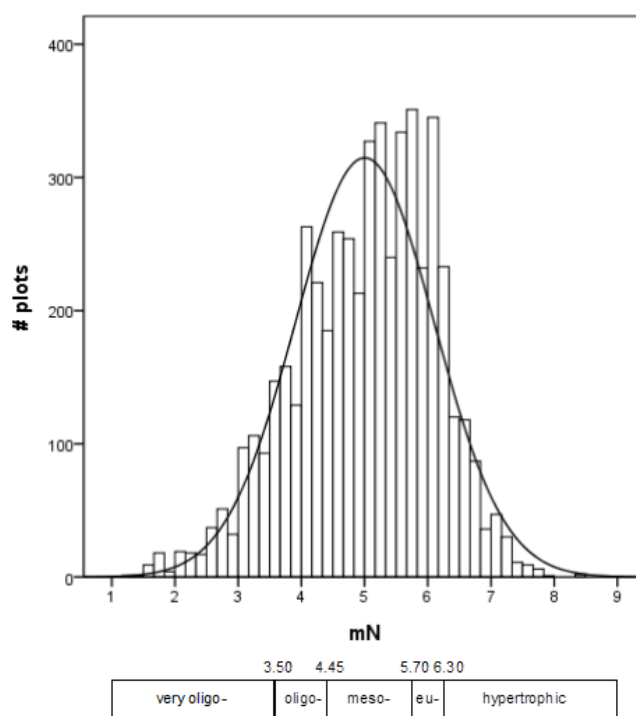


Fig. 2. Frequency distribution of mN in a random sub-sample of 5,202 forest plots (306 per region) containing 5 or more N indicators of the Ellenberg list; quantiles (10, 30, 70, 90%) define five trophic levels.

Abb. 2. Häufigkeitsverteilung von mN in einer zufälligen Teilstichprobe (306 Aufnahmen pro Region) von 5202 Waldaufnahmen mit mindestens 5 Zeigerarten der Ellenberg-Liste; die Quantile (10, 30, 70 und 90%) definieren die fünf Trophiebereiche.

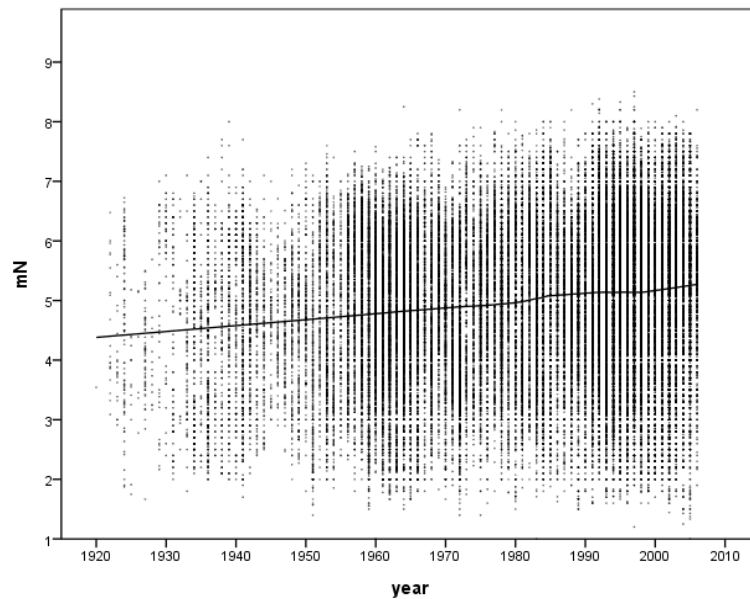


Fig. 3. Temporal trend of mN in the whole data set shown as a scatter plot with LOESS fit; 4,038 plots from Saxony from 1905 were excluded to avoid distortion of the trend by a single region.

Abb. 3. Zeitlicher Trend von mN im Gesamtdatensatz als Streudiagramm mit LOESS-Anpassung; 4.038 Aufnahmen von 1905 aus Sachsen wurden ausgeschlossen, um Verzerrungen des Trends durch eine einzelne Region zu vermeiden.

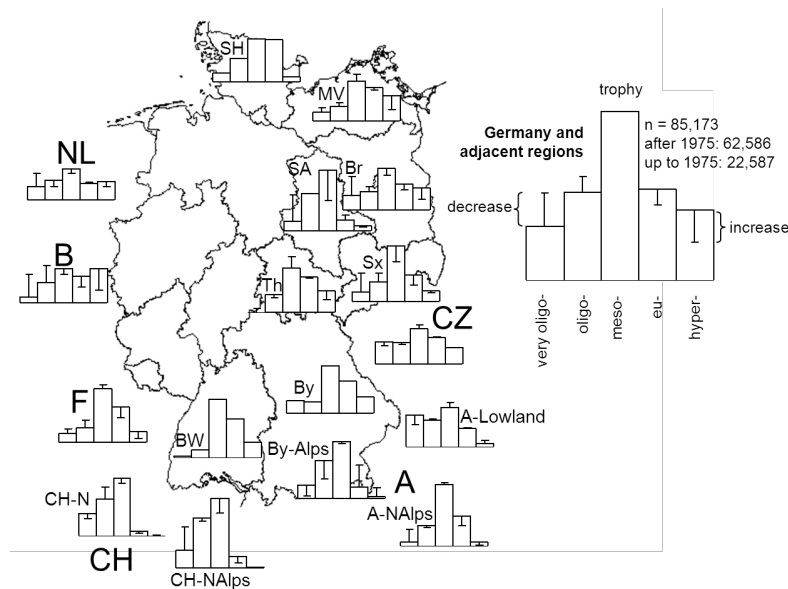


Fig. 4. Frequency of trophic classes in post-1975 plots (matrix B) and its change compared to pre-1975 plots differentiated by region.

Abb. 4. Häufigkeit der Trophiestufen in den nach 1975 angefertigten Aufnahmen (Matrix B) und Veränderungen gegenüber dem Zeitraum vor 1975.

Northern Alps) showed small changes and only two (Austrian lowland and Bavarian Alps) had lower mN after 1975 (Table 2). Correspondingly, the proportion of very oligotrophic and oligotrophic plots decreased, whereas the proportion of eutrophic and hypertrophic plots increased in the whole dataset and in most subregions (Fig. 2). In the whole dataset the proportion of hypertrophic plots more than doubled from 5.65% before to 11.83% after 1975, whereas the percentage of very oligotrophic plots fell from 14.59% to 8.3%.

Availability of plots was highly uneven between regions, forest types and sampling periods (Table 3), which was attributable to the history of contributing databases and uneven distribution of tree species (e.g. *Pinus*, *Alnus* and *Quercus* more frequent in lowlands, *Fagus* and *Picea* in uplands). Consequently, the potential of stratified resampling was restricted by bottlenecks in plot numbers within strata. Resampling intensity per forest type and region followed the period with the lowest numbers, in which all plots were selected, whereas random selection was applied in the complementary period. As a consequence, the resampled dataset contained equal numbers of plots per forest type and period, but not per region.

The stratified comparison of pre- and post-1975 plots demonstrates that mN has systematically increased in all tree-layer dominance types, while dominance types systematically differed in average levels (Fig. 5) as well as in the rate of temporal change (difference in medians *Quercus*: 0.60 > *Pinus*: 0.44 > *Picea*: 0.45 > *Fagus*: 0.14 > *Alnus*: 0.09). The increase of mN after 1975 remained visible in the stratified dataset as a whole, as well as in the majority of regions with the exception of France (Table 2, last column). The apparent decrease of mN in the Bavarian Alps became less marked, but remained after stratification.

Regression detected a linear trend of mN against time in the stratified data ($R^2 = 0.015$, $B = 0.007$).

4. Discussion

The delimitation of mN levels based on quantiles of the frequency distribution in forest plots is a straightforward and useful result of our survey. It makes it possible to evaluate Ellenberg values for nutrients from local and regional studies against a broad, representative background. The proposed levels lend themselves not only to defining classes for map legends, but also to interpreting frequency distributions and their changes over time. The reference is based on 20th century data. In that period there were forest stands in which only indicators of extremely poor conditions existed (mN = 1.0), but no such extreme stands on the hypertrophic side of the gradient (maximum mN = 8.3) – a disparity that may change as eutrophication advances. As pointed out by WAMELINK et al. (2002, 2003) a universal scale across plant formations (WITTE & VON ASMUTH 2003) may not be advisable. Therefore, for forest vegetation the trophic classes should only be used if the tree layer cover exceeds 30%. To avoid random effects in mN estimation we propose to exclude plots in which less than five plant taxa have an N-value assigned to them. Attention should also be paid to the possibility of bimodal frequency distributions of indicator values within plots, which can occur in pine forests (EWALD 2007) and possibly other vegetation types undergoing rapid pulses of nutrient availability.

The spatial and temporal trends detected in our broad dataset deserve further investigation, for which the following discussion may set the stage.

We interpret spatial patterns against the background of coarse-scale maps of throughfall deposition (LORENZ et al. 2006) and bedrock (ANONYMUS 1993). At the coarse scale consi-

Table 2. Summary of plot data and mN in regions; negative Mann Whitney test statistic denotes increase between the periods before and after 1975.
Tabelle 2. Zusammenfassung der Vegetationsaufnahmen und ihrer N-Zeigerwerte nach Regionen; negative Mann Whitney-Teststatistik bezeichnet Zunahme zwischen den Perioden vor und nach 1975.

Region	# plots	# > 5	mN with > 5 indicators					before 1975				after 1975				standardised U	
			min	mean	s. d.	max	# plots	mean	s. d.	# plots	mean	s. d.	All	stratified			
whole dataset	101,047	89,784	1.00	4.99	1.20	8.50	26,126	4.73	1.21	62,586	5.10	1.19	-38.80	-14.84			
Baden-Württemberg (BW)	5,536	4,097	2.20	5.55	0.76	7.86				4,097	5.55	0.76					
Bavaria (Ba)	1,559	1,439	1.00	5.18	1.24	7.80				1,439	5.18	1.24					
Bavarian Alps (B-Alp)	3,424	3,412	1.63	4.74	0.91	7.09	681	5.27	0.83	2,731	4.60	0.88	17.04	3.67			
Berlin/Brandenburg (Br)	6,947	6,072	1.40	4.84	1.33	7.67	3,047	4.50	1.37	3,025	5.18	1.20	-18.90	-11.07			
Mecklenburg-Vorpommern (MV)	7,768	7,192	1.40	5.30	1.14	8.14	2,579	5.07	1.14	4,613	5.43	1.12	-13.10	-5.95			
Sachsen-Anhalt (SA)	1,015	956	2.00	4.61	0.97	7.92	233	4.28	1.13	723	4.72	0.88	-5.60	-5.95			
Saxony (Sx)	8,112	7,109	1.57	4.89	1.19	8.25	4,405	4.77	1.29	2,7	5.10	0.99	-9.21	-7.95			
Schleswig-Holstein (SH)	2,642	2,303	2.40	5.19	0.95	7.00				2,303	5.19	0.95					
Thuringia (Th)	2,453	2,343	2.13	5.35	0.86	7.29	2,245	5.35	0.85	98	5.44	0.92	-1.45	1.23			
Austria Northern alpine fringe (A-Alp)	306	306	2.45	4.97	0.90	6.60	184	4.88	0.96	122	5.10	0.80	-1.55	-2.43			
Austria Northwestern lowlands (A-Low)	766	729	1.50	4.59	1.17	7.33	469	4.69	1.11	260	4.40	1.26	2.76	1.18			
Belgium (B)	6,591	5,258	2.00	5.30	1.20	8.50	641	4.57	1.23	3,77	5.48	1.15	-16.88				
Czech Republic W 15th meridian (CZ)	4,077	3,803	1.20	4.93	1.32	7.86	1,602	4.97	1.31	2,201	4.90	1.33	1.65	-1.05			
France Alsace/Lorraine (F)	2,708	2,356	2.00	5.18	0.96	7.83	441	4.90	0.97	1,915	5.25	0.95	-7.06	-1.47			
Netherlands (NL)	36,614	32,08	1.60	5.03	1.31	8.30	3,85	4.78	1.45	28,097	5.07	1.29	-10.89	-7.94			
Switzerland midland and Jura (CH-CP)	5,648	5,589	1.57	4.37	0.78	7.25	3,693	4.35	0.76	1,896	4.39	0.82	-2.34	-2.69			
Switzerland Northern Alps (CH-Alp)	4,707	4,652	1.00	4.39	0.87	6.66	2,056	4.20	0.87	2,596	4.55	0.83	-13.50	-2.24			

Table 3. Representation of canopy dominance types in the datasets before and after 1975, differentiated by region; bold figures indicate "bottlenecks" in plot availability.**Tabelle 3.** Regionale Repräsentanz der Typen von Baumschicht-Dominanz in den Datensätzen vor und nach 1975; fett gedruckte Zahlen bezeichnen den jeweiligen „Flaschenhals“ der Aufnahmeverfügbarkeit.

dominant period	A- Lowland	A- NAIps	B	CH-N	CH- NAIps	CZ- W15merid	D- BaWue	D-Ber- Brand	D-By- Alps	D-By- Alps	D-MV	D-Sa- Anh	D-SH	D-Sx	D- Thuer	F	NL	total
<i>Alnus</i>	pre	20	3	24	53	55		269		34	450	23	334		23	313		1315
	post	13		9	13	22	65	34	539	28	33	1479	30	205	118	8	14	2365
<i>Fagus</i>	pre	55	62	1063	308		178		599		56	1062	7	1035		1563	74	81
	post	30	56	225	285	512	137	484	415	628	251	1064	21	996	322	75	320	845
<i>Picea</i>	pre	116	76	279	304		97		24		228	26		262		104	12	7
	post	65	38	346	317	153	866	73	117	957	61	1	5	254		157	505	1335
<i>Pinus sylvestris</i>	pre	86	15	120	124	9		1274			349	133		322		13	17	235
	post	21	2	150	95	44	50	697	46	22	486	501	43	127		60	1702	1805
<i>Quercus</i>	pre	12		198	54	57		468			182	22		312		158	115	1406
	post	27	3	57	67	257	89	71	492	68	463	65	379	305		663	8366	2688
total		282	192	1528	1566	710		3746		634	4138	372	2248		166	436	4084	20102

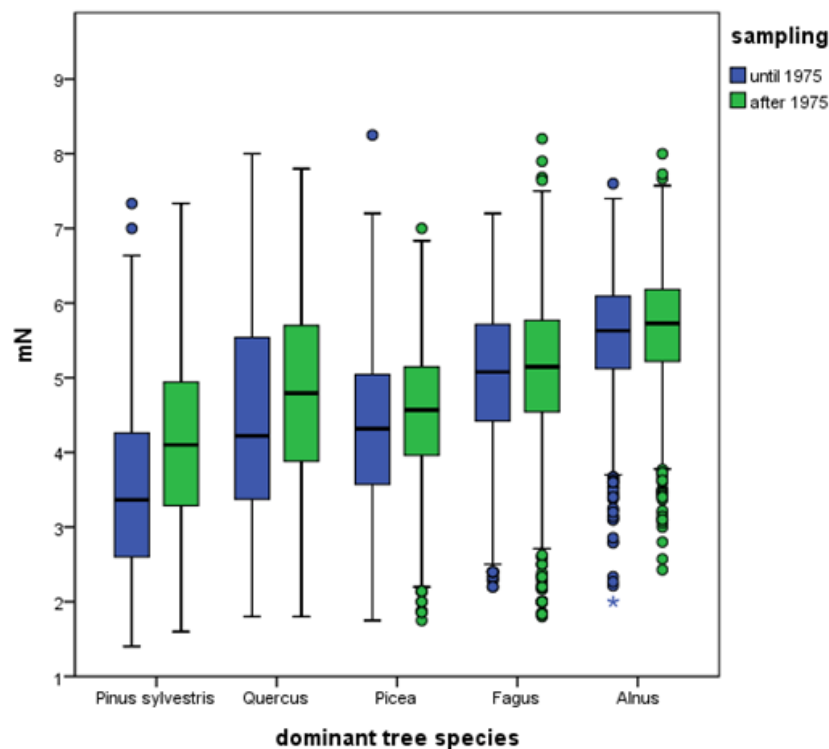


Fig. 5. Boxplots of mN for tree species dominance types and sampling periods.

Abb. 5. Boxplots von mN nach Typen der Baumartendominanz und Aufnahmezeitraum.

dered here, the Northern Alps stand out as the only large region where eutrophic and hypertrophic forests are generally rare. We hypothesize that the absence of intensive agriculture in conjunction with prevalent young and stony postglacial soils has spared alpine mountain forests from stronger eutrophication (cf. KOHLI 2011), although NO_x-deposition from long-distance transport may be considerable due to high precipitation (PRÖLL et al. 2011). In addition to high geodiversity and endemism, this peculiarity of the Alps deserves consideration by conservation policies (e.g. ARDUINO et al. 2006, CIPRA 2010).

Saxony-Anhalt is the only region outside the Alps with comparably low proportions of eutrophic and hypertrophic forest plots. Neither N-deposition nor geology offer any obvious explanations for this, but the preponderance of *Pinus* plots (Table 3, 66% of all plots from this region) in the database may cause bias towards low mN.

The remaining regions may be differentiated by the incidence of very oligotrophic forests, which is high in regions with prevalent nutrient-poor bedrock, such as granite, gneiss in northern Austria and western Czech Republic and Pleistocene sand in the Netherlands and Brandenburg. Despite being the most important refuge of oligotrophy outside the Alps, *Pinus sylvestris* forests in NE-Germany have recently suffered pronounced eutrophication (JENSSEN & HOFMANN 2005), leading to novel species combinations with unbalanced spectra of indicator plants (EWALD 2007). Interestingly, the pine forest region of Brandenburg exhibits one of the largest increases of hypertrophic conditions (Fig. 4). Incidence and relative

increase of hypertrophy is highest in Belgium, where local and regional proofs of eutrophication abound (LAMEIRE et al. 2000; GODEFROID & KOEDAM 2003, 2004; VAN DER VEKEN et al. 2004; CORNELIS et al. 2007).

In conclusion, visual interpretation of the regional patterns supports the idea that mN can be explained by a combination of natural soil fertility, (historical) land-use and anthropogenic deposition regime. The broad temporal trend of mN supports the notion that the second half of the 20th century has been a period of broad-scale eutrophication. We chose 1975 as a limit for our comparison because it marks the turning point in the perception of nitrogen in terrestrial ecosystems (KREUTZER 1989). The split brings out the structure of the data particularly well, but we could not detect a concurrent abrupt vegetation change (Fig. 3), so that we interpret this date as a political rather than an ecological turning point.

The temporal trend of mN is visible under all major dominant tree species. The maximum of mN in *Alnus* forests is a well-known pattern, which can be explained by biological N-fixation and litter quality. With respect to past and present levels as well as to the magnitude of increase in mN, the other tree species are ordered by shade tolerance and their role in succession. Low mN levels and strong trends in *Pinus* and *Quercus* forests can be related to the degree of historical degradation, e.g. by litter raking, and the abandonment of such traditional land-use practices during the 20th century. A negative relationship between initial mN level and eutrophication strength was also found in the metanalysis of resurvey studies by VERHEYEN et al. (2012). The preference of *Picea* for acid soils, partly resulting from bedrock, partly from anthropogenic degradation, offers an explanation for lower mN levels than in *Fagus* forests. The stronger increase in mN under *Picea* can be explained by higher deposition (ROTHER & MELLERT 2004), as well as by the higher intensity of disturbance (short rotations, insect outbreaks) as compared to *Fagus* forests.

The following alternative hypotheses must be considered as explanations for the observed increase in mN across the 20th century: (1) The preference of phytosociological sampling may have systematically shifted from oligotrophic to eutrophic and hypertrophic conditions. (2) N availability has increased due to relief from nutrient deficiency at the low and eutrophication at the high end of the trophic gradient.

As to the first hypothesis, the differentiation by dominant tree species confirms this covariable as a potential source of bias. In fact, mN is systematically lower under conifers, and increases from *Quercus* to *Fagus* to *Alnus* stands. However, the hypothesis that temporal changes in mN are due to changes in sampling preference for certain stand types must be rejected because mN has increased in all stand types. Based on our knowledge of the underlying datasets the first hypothesis can be rejected. In fact, we know of regional sampling biases in both directions. For example, in the Bavarian Alps pre-1975 plots were concentrated in the flysch zone with its fertile clay soils, which were studied because of landslide hazards at the time, whereas the bulk of plots the post-1975 was recorded in the context of National Park establishment and forest decline research (EWALD 1995) on nutrient-poor limestones. In the Austrian lowlands post-1975 data contain many plots from a single, extremely oligotrophic peat bog. On the other hand in the Bavarian forest reserve system, which was established after 1975, nutrient-rich *Tilio-Acerion* communities are over-represented and degraded *Pinus sylvestris* forests under-represented (ABS et al. 2008). While such local biases may level each other out, we are not aware of any supra-regionally consistent shift of sampling preference from oligotrophic to eutrophic forest types.

The second hypothesis is in accordance with a wide variety of local studies on permanent and quasi-permanent plots. Increased nutrient availability in forests may be a function of recovering nutrient cycles following historical degradation (GLATZEL 1991), of purposeful amelioration by liming, fertilisation or draining (REHFUESS 1990, EVERS 1991) and of anthropogenic deposition from agriculture and combustion. Often these factors act in concert and are difficult to separate (BERNHARDT-RÖRMANN & EWALD 2006, VERHEYEN et al. 2012).

Our synthesis shows that combining ecological indicator values with large phytosociological databases offers a powerful framework for detecting the eutrophication signal on broad scales. For the time being, we have restricted ourselves to compiling average nutrient values, obtained by simple queries in the contributing phytosociological databases. In a next step, the approach should be extended to more complex operations in a network of databases, which could ultimately result in a European vegetation information system (SCHAMINÉE & HENNEKENS 2006, EUROPEAN VEGETATION SURVEY 2012). At the same time, our database might allow drawing a much more differentiated picture (see WOHLGEMUTH et al. 1999 for a regional example), provided plots are stratified according to other relevant attributes, such as elevation, bedrock and other indicator values. Careful sub-sampling of the database (ROLEČEK et al. 2007, HAVEMAN & JANSSEN 2008, JANDT et al. 2011) and analysis of residuals after accounting for covariables (SEIDLING & FISCHER 2008) would not yield direct proofs of causal pathways, but it would allow testing the plausibility of alternative hypotheses.

Erweiterte deutsche Zusammenfassung

Einleitung – In den vergangenen 30 Jahren hat sich die Wahrnehmung des Stickstoffs in mitteleuropäischen Wäldern grundlegend gewandelt (BERNHARDT-RÖRMANN & EWALD 2006). Einst Minimumfaktor, wurde N zu einem der wichtigsten Umweltprobleme. Angesichts der Schwierigkeit, das gesteigerte Nährstoffangebot bodenchemisch nachzuweisen, ist die Bioindikation an Hand von Vegetationsdaten unverzichtbar für den Nachweis von Eutrophierung. Die überregionale Verknüpfung von großen Vegetationsdatenbanken stellt einen wichtigen Ansatz zum Nachweis von zeitlichen Trends und räumlichen Mustern der Artenzusammensetzung dar (JANDT et al. 2011).

Material und Methoden – Auf Basis einer Datensammlung mit mehr als 100.000 Vegetationsaufnahmen aus Deutschland und angrenzenden Gebieten (Niederlande, Belgien, östliches Frankreich, Schweiz, Österreich, Tschechien) wurden ungewichtete mittlere Ellenberg-Zeigerwerte für Nährstoffe (mN) als Surrogat für pflanzenverfügbare Makronährstoffe berechnet (ELLENBERG et al. 2001). Fünf Trophie-Klassen wurden auf Grundlage der Quantile von mN in einer nach Regionen stratifizierten Stichprobe berechnet, um die Vergleichbarkeit der dimensionslosen Werte zu ermöglichen. Die Verteilung von mN in Wäldern des Untersuchungsraums wurde räumlich (17 Regionen) und zeitlich (1899–1975 und 1976–2006) differenziert dargestellt. Um statistische Verzerrungen zu vermeiden, wurden die Vegetationsaufnahmen nach dominierenden Baumarten (Waldkiefer, Eiche, Fichte, Buche, Erle), Region und Periode stratifiziert.

Ergebnisse – Nach 1975 waren eutrophe ($mN > 5,67$) und hypertrophe ($mN > 6,28$) Zustände in allen Regionen mit Ausnahme der Alpen und Sachsen-Anhalts verbreitet anzutreffen. Stark oligotrophe Zustände ($mN < 3,44$) waren in Regionen mit armen Ausgangsteinen immer noch weit verbreitet. Vor 1975 war mN mit Ausnahme der südöstlichen Regionen geringer. Zwischen den Perioden erhöhte sich der Anteil hypertropher Aufnahmen von 5,7 auf 11,8 %, während derjenige stark oligotropher Aufnahmen sich von 14,6 auf 8,3 % verringerte.

Für die bis einschließlich 1975 erhobene Vegetationsaufnahmen fanden wir die tiefsten Mediane von mN in Beständen von *Pinus sylvestris*, gefolgt von *Quercus* spp., *Picea abies*, *Fagus sylvatica* und *Alnus* spp. In den Aufnahmen nach 1975 zeigten die Mittelwerte bei den nährstoffreichsten Waldgesellschaften den geringsten und bei den oligotrophen Gesellschaften den größten Zuwachs.

Diskussion – Die Studie bestätigt Eutrophierung als Megatrend des Vegetationswandels (VERHEYEN et al. 2012) und streicht das hohe Forschungspotenzial heraus, das in der Verknüpfung von Vegetationsdatenbanken über Ländergrenzen hinweg liegt (DENGLER et al. 2011). Die weit verbreitete Zunahme von mN ist in erster Linie durch die markante Veränderung in *Quercus*- und *Pinus*-Beständen bedingt, was auf die Bedeutung des Nutzungswandels und die Erholung der Nährstoffkreisläufe nach Jahrhunderten der Niederwald-, Waldweide- und Streunutzung verweist (GLATZEL 1991).

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