# COARSE-SCALE SUBSTRATE MAPPING USING PLANT FUNCTIONAL RESPONSE TYPES

With 12 figures, 1 table and 2 appendices

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*Zusammenfassung:* Substratkartierung auf der Grundlage von funktionellen Reaktionstypen in der Flora Deutschlands Aufgrund von Substratunterschieden auf niedrigstem Skalenniveau muss räumliche Information über Böden generalisiert werden bevor sie Eingang in Karten oder GIS-Layer findet. Die räumliche Aggregation der Muster orientiert sich üblicherweise an landschaftlichen Steuerfaktoren der Bodenmosaike, insbesondere an Relief, Gestein und Klima. Die vorliegende Studie zeigt eine Möglichkeit auf, die Generalisierung auf tatsächlichen feinskaligen Substratmustern aufzubauen. Das Vorgehen beruht auf dem Effekt von Substratvorkommen auf das Vorkommen oder Nicht-Vorkommen bestimmter funktioneller Pflanzengruppen. Deren relative Häufigkeiten wurden dafür genutzt, Typen von Bodenlandschaften abzuleiten.

Das Untersuchungsgebiet ist Deutschland. Die funktionellen Pflanzengruppen wurden anhand von Ellenbergs Indikatorskalen für Nährstoffverfügbarkeit, Wasserversorgung und Bodenreaktion zusammengestellt. Diese Indikatorskalen ordnen Pflanzensippen nach ihren realisierten Optima entlang von Umweltgradienten. Die Analyse fußt auf relativen Anteilen von Indikatoren in Messtischblättern anstatt auf den in früheren Arbeiten verwendeten absoluten Häufigkeiten. Anhand einer Hauptkomponenten-Transformation wurden nicht-generalisierbare Merkmale aus der Datenmatrix entfernt. Die Hauptkomponentenwerte der Messtischblätter wurden einer Klassifikation von Bodenlandschaften zugrunde gelegt, die im Nachhinein durch Salz-Indikatoren verfeinert wurde.

Die geografische Gliederung spiegelt erwartungsgemäß eine räumlich wechselnde Dominanz verschiedener landschaftlicher Hauptmerkmale wieder (Gestein, Klima, Relief). Im Unterschied zu anderen geografischen Landschaftsgliederungen und -ordnungen auf hoher Skalenebene sind das jeweilige Gewicht dieser Steuerfaktoren und die räumlichen Muster induktive Ergebnisse der Analyse. Die Ergebnisse können unter anderem bei der Auswahl unabhängiger Variablen in Bodenlandschaftsmodellen Verwendung finden.

*Summary:* Due to the fine-scale variation of substrates, spatial information about soils must be generalized for mapping. The process of generalization is conventionally based on landscape controls of soil mosaics (like terrain and climate), and not on the real fine-scale patterns. In order to base generalization on real patterns, the present study aims to implement an indirect method for the spatial aggregation of substrate types. It relies on the effects of substrate occurrences on frequency spectra of plant functional response types. These spectra have been used to derive types of soil-landscapes.

The area of investigation is Germany. Plants have been affiliated to response types using indicator values for nutrient supply, water supply and soil *pH*. These values rank species according to their realised optima on environmental gradients. The analysis was based on proportions of indicator groups in grid-cells of the German floristic survey. It was not based on absolute frequencies as in earlier studies. Features of the frequency spectra that could not be related to generalizable trends in the data have been omitted by a Principal Component Analysis (PCA). The PCA-scores have been used for a classification of soil-landscapes that could be enhanced afterwards by salinity indicators.

The geographical breakdown resembles a spatially alternating dominance of various controls (rocks, climate, terrain) on substrate patterns. Unlike other coarse-scale geographical landscape classifications, both the varying weights of differentiating controls and coarse-scale spatial patterns are inductive outcomes of the analyses. These outcomes have the potential to help in the selection of controls used for predictive models of soil-landscapes.

# *1 Introduction*

Soils are among the most important landscape attributes to be considered for spatial landscape-ecological analyses, environmental modelling and landscape management. Due to the fine-scale variation of substrates, spatial information about soils must be generalized for mapping. The process of generalization is conventionally based on landscape controls of soil mosaics (like terrain and climate), and not on the real, unknown fine-scale patterns (HOLE a. CAMPBELL 1985). In order to base generalization on real patterns, the present study aims to implement an *indirect* method for the spatial aggregation of substrate types that relies on the effects of substrate occurrences on frequency spectra of plant functional response types. These spectra have been used to derive types of soil-landscapes.

Plant functional response types describe groups of plants with common response to certain environmental influences (LAVOREL a. GARNIER 2002). In the present study, "indicator plants" for soil *pH*, water supply, nutrient supply and soil salinity as defined by ELLENBERG et al. (1991) have been used for a soil-landscape classification of Germany. The starting point for the development of the method was an earlier investigation in the German Alps (SCHMIDTLEIN a. EWALD 2003).

## *2 Data and area of investigation*

The study is based on data about distributions of vascular plants in Germany and on data about their affiliation to functional response types. The distribution data has been taken from the 'Florkart' database (BUN-DESAMT FÜR NATURSCHUTZ 2002) that contains the results of the German floristic survey of vascular plants. It consists of a cumulative collection of plant records for grid-cells extending 3' in latitude and 5' in longitude. Because of missing data, survey grid-cells have been aggregated to a coarser resolution. Aggregated grid cells equate to map sheets of the German topographic maps 1: 25,000 (6' in latitude and 10' in longitude; approximately  $119 \text{ km}^2$  in the northern parts and 139 km2 in the south). All records of indigenous or es-tablished vascular plants from 1950 onwards have been considered.

Plants have been affiliated to plant functional response types using Ellenberg indicator values for soil nutrient supply (N), water supply (F), soil *pH* /carbonate content  $(R)$  and salinity  $(S)$  (App. 1, ELLENBERG et al. 1991). These values rank species according to their realised optima on environmental gradients. Substraterelated indicator values of plant species lists proved to be well correlated to measured substrate attributes (ELLENBERG et al. 1991; SEIDLING a. ROHNER 1993; THOMPSON et al. 1993; HILL a. CAREY 1997; ERTSEN et al. 1998; SCHAFFERS a. SYKORA 2000; WAMELINK et al. 2002; DIEKMANN 2003) but are less sensible to shorttime temporal fluctuations and micro-scale heterogeneity of soils; essentially they depict the part of variation in soil conditions that matters to plants. Indicator values have a limited validity in space. This brought about different lists for various parts of the world (LANDOLT 1977; KLINKA et al. 1989; ELLENBERG et al. 1991; BORHIDI 1995; KOJIĆ et al. 1997; HILL et al. 1999).

The minimum number of N-, F- or R-indicators per map-sheet has been fixed at 100; map-sheets with a lower number of indicators for one of these three factors have been excluded from the analysis. 2,392 out of 2,726 taxa mentioned by ELLENBERG et al. (1991) were present in the remaining 2,971 map-sheets. 2,072 taxa are considered indicators for soil *pH* and carbonate content, 2,213 are considered indicators for nutrient

supply and 2,310 are considered indicators for water supply. The remaining taxa do not fit into the categories defined by ELLENBERG et al. (1991). All taxa are considered salinity indicators (S), most of them indicating no salt; only 37 taxa indicated the presence of salt  $(S > 5)$ . Many indicators of water and nutrient pointed to moderate conditions (Fig. 1), while more thoroughgoing indicators were less frequent. This was not true for indicators of soil *pH* and carbonate content where the frequency distribution was more biased towards high soil  $pH$  ( $R > 7$ ). This bias accords with other reports from the arctic (GOUGH et al. 2000), boreal (TYLER 1999), and temperate zones (PÄRTEL 2002; EWALD 2003a).

Several other landscape attributes of map-sheets have been considered for a better causal understanding of the substrate patterns: proportions of elevation belts, proportions of areas with certain ranges of mean temperatures in January and July, proportions of areas with certain ranges of annual precipitation, proportions of 35 broad land-cover types from the Corine land-cover classification (STATISTISCHES BUNDESAMT 1997), proportions of 72 aggregated soil types from the soil map 1:1,000,000 of Germany (HARTWICH et al. 1995) and proportions of 243 geological types from the geological map of Germany 1:1,000,000 (BUNDES-ANSTALT FÜR GEOWISSENSCHAFTEN UND ROH-STOFFE 1993). An overall number of 398 variables has been considered.

# *3 Methods*

The classification method presented for soil-landscapes relies on spectra of indicator plants. In order to avoid many zeros and outlier cases in the data matrix and auto-correlations between adjacent indicator classes, the original indicator scales of F, R and N have been down-sampled to a coarser resolution with three instead of  $9$  ( $R$  and  $N$ ) or 12 ( $F$ ) indicator groups (App. 1). All nine indicator groups of F, R, and N were present in all map-sheets and have been used for the numerical derivation of soil-landscape patterns in Germany. Plants indicating salt (S) were mostly restricted to few areas and could not add much spatial information to this analysis. They have been used for an after-the fact indication of saline sites within the geographical breakdown derived from F, R and N values.

The analysis was based on proportions of indicator groups in map-sheets instead on absolute frequencies of indicator groups (step 4 in Fig. 2). Proportions were expected to be less affected by sampling biases, sampling intensity and phyto-diversity (SCHMIDTLEIN a. EWALD 2003). In the present study, Mantel tests of the strength of relationship between indicator matrices and known coarse-scale environmental patterns illustrated the difference in quality between absolute and proportional data (tests based on Euclidean distances; MANTEL 1967; SOKAL 1979). 364 of the above-mentioned environmental attributes have been considered in this test (rock types, soils, temperatures, precipitation, elevation), while land-use types have been excluded for sake of circular reasoning.

Since typifying was the goal of this study, the spectral information was reduced to generalizable features. Thus, only features repeated on a regular base have been used for computation. This has been achieved using a Principal Component Analysis (PCA) of the indicator proportions (step 5 in Fig. 2). The first four principal components provided a noise-whitened picture of the most prominent structures. Another Mantel test with the environmental variables and PCA-scores served as a test if the strength of the relationship to known environmental variation was affected by this procedure.

The classification has been performed using a *k*-means cluster analysis of the PCA-scores (step 6 in



*Fig. 1:* Proportions of indicator groups in the map sheets of the whole area (2,971 map sheets). Box-plots show median and percentiles (10%, 25%, 75%, 90%). The proportions of indicator groups of each factor (F, R, or N) sum up to 1. For a definition of indicator groups see Appendix 1

Anteile von Indikatorgruppen in den Messtischblättern (2.971 Blätter). Die Box-plots zeigen Mediane und Prozentsätze (10%, 25%, 75%, 90%). Die Anteile der Indikatorengruppen jedes Faktors (F, R oder N) ergeben zusammen den Wert 1. Eine Definition der Indikatorengruppen bietet Appendix 1

Fig. 2). The *k*-means algorithm, originally described by MACQUEEN (1967) is suited for divisions into an *a priori* defined number (*k*) of groups that are as distinct as possible. It uses an iterative relocation procedure that starts with *k* groups and moves cases in order to minimize variability within clusters and maximize variability between clusters. There is no such thing as a single "right" number of clusters because clumping of values occurs on multiple scale levels and the proportions of indicator groups are changing in more or less continuous manners that allow the insertion of more or less transitional classes. Accordingly, the number of clusters has been chosen in order to achieve a compromise between appropriate resolution and necessary generalization at a given scale of 1:1,000,000. The starting cluster centres have been placed maximizing the initial cluster distances in the 4-dimensional PCA ordination space. It has been mentioned before that the proportions of indicator values for salinity (S) have been used for an after-the-fact indication of saline sites. This has been realized by marking map-sheets with a proportion of salt indicators  $(S > 5)$  that exceeded standard deviation.



*Fig. 2:* Flowchart of the most important steps in the analysis Flussdiagramm der wichtigsten Analyseschritte

An *ex post* characterization of soil landscapes has been achieved using the average proportions of indicator groups within the 18 classes (step 9 in Fig. 2).

Classification is simplification, but 18 classes and the underlying differences between the frequency spectra of nine indicator groups still comprise a lot of information and difficult to describe. Thus, for descriptive purposes, classes have been affiliated to higher-order groups. This agglomeration (step 10 in Fig. 2) has been achieved with another *k*-means cluster analysis based on the above-mentioned average proportions of indicator groups within the 18 classes. The selected number of 6 higher-order clusters was the smallest number that did not separate single classes.

An "Indicator Species Analysis" (ISA) after DUFRENE a. LEGENDRE (1997; step 8 in Fig. 2) has been used for an analysis of the strength of the spatial relationship between soil-landscapes and various landscape attributes. The final scores are calculated as a combination of a) the average abundances of the attributes in soil-landscape classes over the average abundance in all classes expressed as a percentage and b) the percentage of map-sheets in a given class where an attribute is present. Values a) and b) are combined by multiplying them. Significance testing determines the proportion of 999 randomized trials with final scores equal to or exceeding the observed maximum score. The analyses have been performed using PC-ORD 4 software. Landscape attributes with  $p \leq 0.001$  and with a maximum percentage of perfect indication of  $\geq 10\%$  are given in the Appendix 2.

### *4 Results*

The proportions of indicator values in map-sheets (Fig. 3) gave interesting insights into the distribution of indicated landscape qualities across Germany and showed a stronger relationship to coarse-scale environmental patterns than absolute frequencies of indicator values published before (e.g., KORSCH 1999; SCHEUE-RER a. SCHÖNFELDER 2000). The standardized Mantel statistic of the relationship between crude indicator frequencies and coarse-scale environmental patterns took a value of  $r = 0.113$  with 364 environmental variables (and  $r = 0.089$  with 72 soil types), while proportional values took  $r = 0.256$  with 364 variables (and  $r = 0.208$  with only soil types; *p* for all analyses = 0.001).

The four principal components in this data as depicted by PCA (Fig. 4) explained 94.1% of the total variation in indicator proportions (45.3%, 28.4%, 13.7%, 6.7%). The loss of non-generalizable information did not reduce the strength of the relationship to known environmental attributes. The use of the four principal components rather added another small amount of strength to the relationship; the respective Mantel tests resulted in  $r = 0.263$  or  $r = 0.216$  for only soil types ( $\phi$  for all = 0.001). The largest part of the variance (depicted by factor 1) is determined by indicators for soil *pH* and water supply. The second component is mainly an expression of more or less nutrient supply; the third component is a matter of occurring wetland plants or more moderate species. The fourth component depicts coincidences of high *pH* and wet places versus map sheets with low *pH* and dry places.

The classification of PCA scores resulted in 18 units with characteristic indicator frequency spectra. The number of map-sheets per cluster varied between 16 and 345 (Tab. 1). The averaged Euclidean within-cluster distances from cluster centres ranged from 0.37 to 0.7 meanwhile the distances between cluster-centres took values between 0.58 and 4.12.

The resulting patterns (Fig. 5) frequently reflect zonations (or dissected continua) of consecutive soillandscapes with similar spectra. Zonations can be observed in the northern, coastal planes (B1-B2-X7), in the Hercynian hills (A1-A2-X1), or in southern Bavaria (C1-C2-X5). Some types with similar spectra are spatially aggregated in a more patchy way (D1-D2), yet others have a rather unattached distribution (D3). The geographical breakdown resembles a spatially alternating dominance of various controls (geological substrate types, climate and terrain) on soil-landscape patterns. A visual examination suggests a dominance of geological substrate types (very emergent in the limestone-area of D3), climate (e.g., D1 that occurs mainly in low-precipitation areas) and terrain. The elevation-gradient is depicted quite well (albeit crabwise by means of lower soil *pH*, fewer wet-lands and reduced nutrient supply). Appendix 2 provides a numerical overview of the strength of the spatial relationship between single soillandscapes and environmental attributes. When interpreting the affiliation of single map-sheets to soil-landscapes, consider the distance from the respective class means (Fig. 6, see the discussion section of this paper).

The following section introduces the 18 soil-landscape types and their characterization by indicator spectra; the 18 types are ordered by their affiliation to 6 higher-order groups (A to X).

# **A** *Acidic types with few wetland-plants*

This group of soil-landscapes is characterized by a high proportion of acidophytes and few indicators of high soil *pH*. The types are somewhat similar to group B but they are lacking wetland-plants or indicators of dry places.



500 km

*Fig. 3:* Relative proportions of indicator groups across Germany. Grid-cells equal map-sheets of the German topographic map 1: 25,000. In white grid-cells, indicator groups reach the maximum occurring proportion with respect to the other indicators of the same factor (F, R, N or S); black grid-cells indicate minimum proportions near zero.  $F =$  indicators of low to high water supply,  $R =$  indicators of low to high soil  $pH$ , N = indicators of low to high nutrient supply,  $S =$  indicators of low to high salinity; for a definition of indicator groups see Appendix 1. Circles are major cities (see Fig. 5)

Regionale Anteile der Indikatorengruppen in Deutschland. Die Rasterzellen entsprechen Messtischblättern (Topografische Karte 1: 25 000). In weißen Rasterzellen erreichen die jeweiligen Indikatorengruppen ihren maximalen Anteil an allen Indikatoren derselben Skala (F, R, N oder S); schwarze Rasterzellen zeigen einen minimalen Anteil nahe Null. F = Indikatoren von niedriger bis hoher Wasserverfügbarkeit, R = Indikatoren von niedriger bis hoher Bodenreaktion, N = Indikatoren von niedriger bis hoher Nährstoffverfügbarkeit, S = Indikatoren von niedriger bis hoher Salinität. Die Kreise sind größere Städte (s. Abb. 5)

 $\mathbf{A1}$  ( $n = 77$  map-sheets). The indicator characteristics of type A are much more accentuated in this type than in type A2: there are more acidophytes, fewer wetlandplants, more indicators of poor nutrient supply (Fig. 7). Map-sheets with affiliation to this type are located in the higher Hercynian hills and are characterized by high annual precipitation and low average temperatures and siliceous rocks. Characteristic soils are dystric or spodic cambisols. Coniferous forests are more frequent than usual (App. 2).

**A2** ( $n = 213$ ). This soil-landscape type is less "extreme" than the latter and indicators of poor nutrient supply are less frequent (Fig. 7). The type is common in the lower parts of the above-mentioned Hercynian hills but there are also some map-sheets in sandy areas of the northern planes. The discriminating landscape attributes resemble the latter type but elevations and precipitation are lower while summer temperatures are higher (App. 2).

## **B** *Acidic types with many wetland plants*

Like the last group (A), this one is characterized by high proportions of acidophytes but it includes many wetland-plants (Fig. 8).

**B1** (n = 277). The soil-landscapes pertaining to this type host many wetland-plants. The corresponding map-sheets are mainly restricted to the coastal northwestern plains with oceanic climate, Pleistocene sediments and peat substrates. Outposts exist in exceptionally acid and wet areas, e.g. on sand in the Upper Palatinate or in extensive peat-bog areas near Lake Chiemsee in Upper Bavaria. Characteristic soils are podzols, spodic luvisols, dystric regosols and dystric histosols.

**B2** ( $n = 204$ ). Differing from the latter type (B1), these landscapes do host fewer wetland-plants (but still more than type A). The type replaces the latter one in areas distant from coast, e.g. on old moraines from the Lüneburg Heath to the Lausitz area, on acid igneous and metamorphic rocks in the Upper Palatinate and on quartzitic sandstone in the Palatinate (App. 2).

### **C** *Infertile types with extremes in soil pH*

The group is characterized by high proportions of plants indicating poor nutrient supply and by a lack of nitrophytes (Fig. 9). These landscapes are extreme with respect to soil acidity indicators (many indicators of high and low soil *pH*). The extremes in soil *pH* are likely to be caused by fine-scale diversity in substrates, e.g. by acid histosols on limestone in the Alps or in coastal dune areas.

**C1** ( $n = 19$ ). This type is more "extreme" than C2



*Fig. 4:* Results of a Principal Component Analysis (PCA) of the proportions of indicator groups in all map-sheets. The largest part of the variance (depicted by factor 1) is determined by indicators for soil *pH* and water supply. The second component is mainly an expression of more or less nutrient supply; the third component is a matter of occurring wetland plants or more moderate species. The fourth component depicts coincidences of high *pH* and wet places versus map sheets with low *pH* and dry places.

Ergebnisse einer Hauptkomponentenanalyse der Anteile von Indikatorengruppen in allen Messtischblättern. Der größte Teil der Varianz (durch Faktor 1 abgebildet) ist von Indikatoren für Boden-*pH* und Wasserverfügbarkeit bestimmt. Die zweite Hauptkomponente ist vor allem Ausdruck von mehr oder weniger Nährstoffverfügbarkeit; die dritte beruht auf Unterschieden im Auftreten von Feuchtgebiets-Pflanzen auf der einen und gemäßigten Feuchtezeigern auf der anderen Seite. Die vierte Komponente ist zwischen Orten mit Zeigern hohen Boden-*pHs* und nassen Verhältnissen und Orten mit Zeigern niedrigen *pHs* und trockenen Verhältnissen aufgespannt.

with respect to indicator proportions; it hosts the highest proportion of plants indicating poor nutrient supply. The type is limited to the extreme south with the highest mountain ranges. Characteristic elevations start at 900 m a.s.l. and reach altitudes above 2,700 m; temperatures are correspondingly low and annual precipitation exceeds 2,000 mm (App. 2).

 $C2$  ( $n = 50$ ). The type hosts much higher proportions of wetland plants than C1. Map-sheets of this type are found in the alpine forelands and sometimes in dune areas at the North Sea coast that provide similar conditions with respect to extremes in soil acidity spectra and nutrient supply. Elevations are lower than in C1 and so is the annual precipitation (App. 2).



*Fig. 5:* Soil-landscapes in Germany, based on a classification of the PCA scores. The grid-cells equal map-sheets of the German topographic survey 1:25,000. B = Berlin, D = Düsseldorf, DD = Dresden, DO = Dortmund, DU = Duisburg,  $F =$  Frankfurt,  $H =$  Hanover,  $HB =$  Bremen,  $HH =$  Hamburg,  $K =$  Cologne,  $L =$  Leipzig,  $M =$  Munich,  $N =$  Nuremberg Bodenlandschaften in Deutschland als Ergebnis einer Clusteranalyse der Achsenwerte aus der Hauptkomponentenanalyse



*Fig. 6:* Euclidean distances from cluster means. Higher dis-tances indicate borderline cases in the classification Euklidische Distanzen der Messtischblätter von den jeweiligen Cluster-Mittelwerten. Hohe Distanzen bezeichnen Grenzfälle der Klassifikation

#### **D** *Dry carbonate and loess types*

These types have high proportions of plants indicating dry places, many indicators of high soil *pH* and few acidophytes (Fig. 10).

**D1** ( $n = 196$ ). Soil-landscapes of this type are characterized by a lower proportion of plants indicating poor nutrient supply as compared to types D2 and D3. The type is common in the loess areas of Central and Southern Germany but it is also present in other carbonate-rich regions with high nutrient supply, e.g. in the urban areas of Cologne and Munich. The most characteristic soils are chernozems, phaeozems and luvisols derived from loess, others are derived from lime and marlstone (App. 2).

**D2** ( $n = 184$ ). Map-sheets of this type have similar features like D1, but they are extreme with respect to indicators of dry places and less favourable to nitrophytes. Their distribution points to low precipitation areas with loess and Triassic lime or marlstone (rendzic leptosols over triassic limestones are characteristic at-tributes). A characteristic land cover type is viticulture, but it does not meet the significance criteria of the ISA analysis.

**D3** ( $n = 193$ ). This type is the least favourable to nitrophytes. The area is mostly limited to the distribution of limestone, marlstone, dolomite and other carbonate rocks from the Jurassic era (Swabia, Franconia, Thuringia, Eifel) with some outposts, e.g. on glacio-fluvial calcareous gravel of the Upper Bavarian plane.

## **E** *Fertile wetland types*

The group joins map-sheets with high proportions of wetland-plants and many indicators of high soil *pH* (Fig. 11).

**E1** ( $n = 76$ ). Proportions of wetland-plants and indicators for soil *pH* and nutrient supply are less pronounced in this type than in E2. It is frequent along the





Die sauren Typen mit wenigen Feuchtgebiets-Pflanzen und ihre Kennzeichnung durch Anteile von Indikatorengruppen (% des mittleren Anteils)



*Fig. 8:* The acidic types with many wetland-plants and their characterization by proportions of indicator groups as percentage of mean proportion

Die sauren Typen mit vielen Feuchtgebiets-Pflanzen und ihre Kennzeichnung durch Anteile von Indikatorengruppen (% des mittleren Anteils)



*Fig. 9:* Infertile types with extremes in soil *pH* and their characterization by proportions of indicator groups as percentage of mean proportion

Die nährstoffarmen Typen mit extremer Bodenreaktion und ihre Kennzeichnung durch Anteile von Indikatorengruppen (% des mittleren Anteils)



*Fig. 10:* The dry carbonate and loess types and their characterization by proportions of indicator groups as percentage of mean proportion

Die trockenen Karbonat- und Löss-Typen und ihre Kennzeichnung durch Anteile von Indikatorengruppen (% des mittleren Anteils)



*Fig. 11:* The fertile wetland types and their characterization by proportions of indicator groups as percentage of mean proportion

Die nährstoffreichen Feuchtgebiets-Typen und ihre Kennzeichnung durch Anteile von Indikatorengruppen (% des mittleren Anteils)

*Table 1:* Basic statistics of the classification. A1 to X7 = soil-landscapes; n = number of map-sheets; d = average Euclidean distances from cluster-centres;  $N7-9$  to  $F1-4 =$  indicator groups; proportions of indicator groups as percent of mean proportion.

Einige Kenngrößen der Klassifikation. A1 bis X7 = Bodenlandschaften; n = Anzahl der Messtischblätter; d = mittlere Euklidische Distanz vom Cluster-Zentrum; N7–9 bis F1–4 = Indikatorengruppen; Anteile der Indikatorengruppen als Prozent vom Mittelwert.

	A1	A <sub>2</sub>	B1	B <sub>2</sub>	C1	C <sub>2</sub>	D1	D <sub>2</sub>	D <sub>3</sub>	Εl	E <sub>2</sub>	Χl	X <sub>2</sub>	X3	X4	X5	X6	- X7
n	77	213	277	204	19	50	196	184	193	76	16	207	274	217	126	144	153	345
d	0.52	0.44	0.46	0.46	0.66	0.60	0.46	0.43	0.42	0.64	0.70	0.42	0.41	0.42	0.50	0.53	0.39	0.37
$N7-9$	90	99	102	96	57	74	104	91	89	123	144	104	96	113	110	94	96	105
$N4-6$	100	101	100	99	71	84	102	94	96	107	109	105	99	106	106	97	95	101
$N1-3$	110	100	98	106	184	148	94	117	116	68	44	89	105	79	81	109	111	93
$R7-9$	72	88	81	84	113	110	19	118	115	111	124	101	102	101	107	110	96	97
$R4-6$	125	113	l 14	116	72	82	83	81	84	92	76	103	99	103	97	89	104	103
$R1-3$	170	125	158	140	108	98	52	61	68	68	42	89	94	89	73	78	112	106
$F9-12$	76	80	158	119	45	94	73	63	66	138	146	72	75	110	85	107	133	126
$F5-8$	122	113	100	96	122	109	94	86	97	100	109	107	98	101	111	103	88	95
$F1-4$	71	85	72	98	87	87	124	143	122	82	61	101	115	93	87	91	107	96

coasts of both North Sea and Baltic Sea and has some more scattered occurrences, e.g. along the rivers Oder and Rhine.

**E2** ( $n = 16$ ). Here, the properties of group E are taken to their extremes. Apart from two exceptions the corresponding map-sheets are limited to the coasts of the North Sea including the offshore island Helgoland.

# **X** *Near-average types*

**X1** ( $n = 207$ ) A relative lack of wetland-plants and slightly diminished proportions of plants indicating poor and acid conditions are features of this type. X1 is scattered throughout the area with some concentration on the foothills of the Hercynian mountains, frequently adjoining to A2.

**X2** ( $n = 274$ ). Like in X1, wetland-plants are unusually rare here; instead, plants of dryer places are more frequent than in the other intermediate types. These soil-landscapes are often accompanying the dry carbonate and loess types (D).

**X3** ( $n = 217$ ) The type is characterised by many wetland-plants and indicators of good nutrient status, thus pointing to the fertile wetland-type E1. Map-sheets of this category are common in the loess areas of the Lower Rhine basin and Westphalia. Further occurrences are scattered across Mecklenburg-West Pomerania and along the coasts of the Baltic Sea.

**X4** ( $n = 126$ ) Few plants of acid or poor sites, indicators of moderate water supply and a tendency to nitrophytes are features of this kind of soil-landscape, which is, like the latter, common in the loess areas of the Lower Rhine basin and in Westphalia, but also in the loess areas of the alpine forelands.

 **(** $n = 144$ **) Areas that are affiliated to this category** are concentrated in the alpine foreland adjoining to the infertile type C2. Indeed, indicators of infertile sites are more frequent than usual but, unlike in C2, extremity in soil *pH* is reduced to a slightly elevated proportion of high soil *pH*. Acidophytes are less frequent than usual. Like C2, the type has a secondary focal area along the coasts. Most of the East Frisian Islands belong here.

**X6** ( $n = 153$ ). As in X5, an elevated proportion of plants indicating poor nutrient supply is a feature of this soil-landscape type. In addition, the spectra of both humidity indicators and soil *pH* indicators are reversed with respect to normal conditions: plants that point to high soil *pH* and moderate water supply are less frequent than usual. Map-sheets of this type are generally found in the most eastern parts of Germany with fen deposits, Pleistocene sand and gravel substrates and low annual precipitation (App. 2). Some outposts of the type can be localized in other sand and swamp areas.

**X7** (n= 345). This soil-landscape type resembles the latter in many respects without being as extreme; indicators of poor nutrient supply are rarer than usual. The type is frequent in the northern planes and replaces the last type (X6) to the west, often adjoining B2 on more fertile and less acid sites rich in wet-land.

# **S** *Map-sheets with many salt indicators*

The 181 map-sheets with exceptional frequencies of salt indicators are mostly limited to the coast. Outposts are concentrated in Saxony-Anhalt and are caused by local inland salt marshes, salt meadows or salt deposits.

# *5 Discussion*

The aim of the present study was to implement an indirect method for the spatial aggregation of substrate types that takes account of the full variation, including the fine-scale variation of substrates. The spectra of indicator proportions in map-sheets could be typified and used for the desired aggregation.

A numerical evaluation of the proportion of variation shown by indicator spectra is not possible because the real substrate variation is unknown. However, all substrate modulations that are relevant to plant growth have an equal chance to enter the classification. Examples for fine-scale modulations affecting the classification are spectra of indicators for soil *pH* in high calcareous mountain areas (type C1) that combine occurrences of many extreme basiphytes and acidophytes, the latter growing on organic humus layers (SCHMIDT-LEIN a. EWALD 2003).

# *Species pool effects*

An unresolved problem is the influence of regional species pools on indicator spectra. E.g., an isolated limestone area is likely to be less populated by calciphytes than large coherent limestone areas (MACARTHUR a. WILSON 1969); the vicinities of large siliceous areas may be prone to a bias that favours acidophytes. Instead, species pool effects at high scale levels, like the general lack of acidophytes (EWALD 2003a), are neutralized by the algorithm: e.g., since acidophytes are generally rare, an increase of acidophytes causes a higher proportional increase than an equal increase of basiphytes. Thus, smaller modulations of acidophytes are able to cause larger differences in the classification, a property of the algorithm that may be seen as an advantage (because it compensates coarse-scale speciespool effects) or as a drawback (because indicators are not given the same weight). Anyway, the use of proportions instead of absolute values enhanced the results, at least with respect to the strength of the relationship to known coarse-scale environmental patterns. The reasons have been mentioned before: proportional patterns are much less affected by sampling intensity and absolute species richness.

In this paper, indicator spectra are treated as a summarizing expression of the quantity and quality of opportunities for the occurrence of certain plant functional response types in a given area. Both quality and quantity of biotopes may influence the spectra. Single, species-rich stands may determine parts of the shape of a spectrum, causing a shift in classification from one landscape-type to another. This may frequently happen in border-line cases of the classification but the spatially coherent pattern of soil-landscapes suggests that it rarely happens in other cases. Spatial outliers seem to have substantial reasons for being in their class. Examples are the urban areas of Cologne and Munich with numerous species-rich, dry, nutrient-rich and carbonate-rich sites that cause a shift to type D1.





Die durchschnittsnahen Typen und ihre Kennzeichnung durch Anteile von Indikatorengruppen (% des mittleren Anteils). Die Skalierung der Y-Achse weicht hier von jener der Abbildungen 6 bis 10 ab

# *Scale effects and modifiable areal unit problems*

The indicator method provides a summarizing ('bottom-up') measure of sub-scale variation in substrates relevant for plant growth. The indicator spectra of map-sheets may be seen as the sum of numerous spectra that belong to sub-scale landscapes and single stands. Similarities of spectra in adjacent map-sheets can be an expression of real gradual transitions from one map-sheet to another. But, since sampling was schematic, similarities between spectral features can also be caused by mixed sampling of originally well separated sub-scale landscapes. In many cases both may be true.

#### *Problems due to the clustering approach*

The results from the *k*-means clustering are far from being the "only right" classification. There are two major reasons. The first reason is the number of clusters selected: it has been mentioned before that the data is "clumped" at multiple scale levels and these levels change from place to place. Thus, the selection of the number of clusters followed only criteria that did not lie in the data structure but in the needs of finding a good compromise between enough generalization and enough detail at a given scale. The second major reason is that the results of the classification vary with the initial seed of cluster means. There may be other solutions that are equally justified. Due to the gradual transitions in the PCA ordination space, map-sheets tend to "jump" between clusters if parameters of the algorithms get changed. It can be assumed that fuzzy *k*-means algorithms (*c*-means, BEZDEK 1987) would gather more stable results because they take account of the transitions. The selection of *k*-means instead of *c*-means followed practical reasoning: the sense of this landscape classification was to provide stratification and to reduce complexity instead of depicting the original complexity. Anyway, affiliations of single mapsheets have to be interpreted with care and in any case the distances to cluster means (Fig. 6) should be considered. The algorithm produces clusters even if no obvious groups are present. In these cases clustering can be considered a tool for finding the best divisions rather than for revealing groups.

## *General drawbacks of Ellenberg indicator values*

Lists of indicator plants have been proved to be a reliable mirror of substrate conditions (review in DIEK-MANN 2003) that is quite insensitive to incomplete sampling (EWALD 2003c). Nevertheless there are a couple of well known limitations and drawbacks that are discussed at length in the literature (DURWEN 1982; BÖCKER et al. 1983; KOWARIK a. SEIDLING 1989; DIERSCHKE 1994; ENGLISCH a. KARRER 2001; WAME-LINK et al. 2002). The present study may be affected by these problems, such as changing ecological behaviour of species in different places or under environmental change, and incorrect judgements on individual species responses. But, since the numbers of indicators per map-sheet are large, the sensitivity to these effects is expected to be small. One major pitfall of the Ellenberg indicator values is bypassed in the present study: it takes full account of the ordinal nature of the scales by leaving spectra intact instead of using mean indicator values or weighted averages (JONGMAN et al. 1995).

### *Relations to soil maps and spatial soil models*

The most recent coarse-scale soil map of the investigated area (the soil map 1:1,000,000 of Germany, HARTWICH et al. 1995) differentiates 72 non-numerically aggregated soil-landscape units that are characterized rather than typified by combinations of soil types. The geographical breakdown reflects rock types and major landforms, essentially like the numerically derived, typifying indicator-map. The increasing availability of spatial data and enhanced process technology facilitates a numerical derivation of maps of substrate types and soil-landscapes from controls like terrain, rock-types and climate (GESSLER et al. 1995; ZHU et al. 2001; SCHOLTEN a. BEHRENS 2002). Predictive models of soil-landscapes are based on complex rules regarding the soil-environment relationship. These rules can be constructed linking field observations of soils with continuous spatial information about landscape controls (SCHOLTEN a. BEHRENS 2002). Crucial for the quality of those empirical models are an appropriate field sampling and the selection of relevant landscape controls (like geological substrate types, climate and terrain). The indicator approach has the potential to help in the selection of considered landscape controls: the spatial distribution of indicator plants can be used for computing the spatially alternating dominance of various controls on soil-landscape patterns.

### *Relations to geographical landscape classifications*

Traditional, geographical coarse-scale landscape classifications of Germany aimed to find a 'natural system' of landscape ecosystems (MEYNEN a. SCHMIT-HÜSEN 1953–1962; RENNERS 1991). These landscape ecosystems were thought to be composed of "all natural components of the landscape and their interac-

tions" (KLINK 1966, 229). The task turned out to be difficult because there are infinite possible landscape classifications depending on thresholds and importance given to single components, processes and controls. In practice, traditional coarse-scale landscape classification relied on intuitively pre-defined units with delimitations defined by subjectively set thresholds of landscape controls (like landforms, rock types, soils, climate; LESER 1991). A 'bottom up' approach that was based on the aggregation of areas according to site-scale patterns (NEEF 1967; HAASE 1967) seemed to provide a more objective solution, but the result was impossible at high-scale levels (NEEF 1975; LESER 1991).

New approaches intend to construct a 'natural system' of landscapes by means of numerical methods. SCHRÖDER and SCHMIDT (2001) and SCHMIDT (2002) transform the traditional approach, replacing the intuitive knowledge of landscape delimitations by the observed distribution of natural vegetation units. They still define limits of coarse-scale landscape units by thresholds of controls, but these thresholds are found numerically using a regression tree analysis. The latter is basically an iterative search for the best fit between limits defined by landscape controls on the one hand and spatial vegetation patterns on the other hand. The results contain valuable information about the rules of various controls for the differentiation of natural vegetation that is thought to reflect the 'ecological potential' of landscapes (SCHRÖDER a. SCHMIDT 2001).

The present study does not aim at a holistic geographical landscape classification because it is based exclusively on soil-related parameters. But the method has the potential for being used in this kind of analysis. The difference to the approaches described before is that there is no need for any pre-defined spatial units, similar to the above-mentioned 'bottom-up' method proposed by NEEF (1967) and HAASE (1967). This could be an advantage, because even the spatial vegetation patterns used by SCHRÖDER and SCHMIDT (2001) are subjected to individual decisions during the generalization of vegetation patterns, to changing definitions of vegetation types, and to further problems with the concept of the natural potential vegetation discussed in literature (KOWARIK 1988).

## *Data availability*

The 'bottom-up' indicator approach is currently limited to soil-related landscape classifications. Non soilrelated indicator values (for temperature and continentality, ELLENBERG et al. 1991) are available but they would introduce a 'top-down' element: these values are derived from coarse-scale distribution data. E.g., continentality values according to ELLENBERG et al. (1991) are based on the limitation of plants to more or less oceanic regions. Basing a coarse-scale landscape classification on these values means partly reproducing Ellenberg's ideas regarding large-scale patterns of continentality. Thus, it would be more straightforward to use climate data.

The most serious problem for the transferability of the approach is a frequent lack of floristic data with the necessary quality and spatial resolution. Sometimes the collection of local floristic and vegetation data has been seen as natural history rather than science (EWALD 2003b). The present paper may help to overcome this fallacy.

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## **Appendix 1**

Indicator groups: Definitions according to ELLENBERG et al. (1991); translation partly adapted from HILL (1999).

### **F – Water supply**

- F1 Indicator of extreme dryness, restricted to soils that often dry out for some time
- F2 Between F1 and F3
- F3 Dry-site indicator, more often found on dry ground than in moist places
- F4 Between F3 and F5
- F5 Moist-site indicator, mainly on fresh soils of average dampness
- F6 Between F5 and F6
- F7 Dampness indicator, mainly on constantly moist or damp, but not on wet soils
- F8 Between F7 and F9
- F9 Wet-site indicator, often on water-saturated, badly aerated soils
- F10 Indicator of shallow-water sites that may lack standing water for extensive periods
- F11 Plant rooting under water, but at least for a time exposed above, or plant floating on the surface
- F12 Submerged plant, permanently or almost constantly under water

# **R – Soil** *pH***, or water** *pH*

- R1 Indicator of extreme acidity, never found on weakly acid or basic soils
- R2 Between R1 and R3
- R3 Acidity indicator, mainly on acid soils, but exceptionally also on nearly neutral ones
- R4 Between R3 and R5
- R5 Indicator of moderately acid soils, only occasionally found on very acid or on neutral to basic soils
- R6 Between R5 and R7
- R7 Indicator of weakly acid to weakly basic conditions; never found on very acid soils
- R8 Between R7 and R9
- R9 Indicator of basic reaction, always found on calcareous or other high-*pH* soils

# **N – Soil fertility**

- N1 Indicator of extremely infertile sites
- N2 Between N1 and N3
- N3 Indicator of more or less infertile sites
- N4 Between N3 and N5
- N5 Indicator of sites of intermediate fertility
- N6 Between N5 and N7
- N7 Plants often found in richly fertile places
- N8 Between N7 and N9
- N9 Indicator of extremely rich situations, such as cattle resting places or near polluted rivers

## **S Salinity**

- S0–1 No tolerance with respect to salt or rarely bearing low chloride content
- S2–5 Indifferent plants (ELLENBERG et al. 1991, p. 19), but not on strongly saline soils
- S6 Plants on soils with moderate to high chloride content (0.9–1.2% Cl)
- S7 Plants on soils with high chloride content (1.2–1.6% Cl)
- S8 Plants on soils with very high chloride content (1.6–2.3% Cl)
- S9 Plants indicating extreme chloride content in drought periods (> 2.3% Cl)

## **Appendix 2**

Landscape attributes and their spatial relation to the 18 landscape types. The scores are percentages of perfect indication according to DUFRENE and LEGENDRE (1997); perfect indication means that an attribute points to a particular soil landscape type without error. The values result from a) the average abundances of the attributes in landscape classes over the average abundance in all classes expressed as a percentage and b) the percentage of map-sheets of a given class where an attribute is present. The maxima are printed in bold face. All shown maxima passed a Monte Carlo significance test with *p* ≤ 0.001. Attributes with maxima that did not pass the significance test or with a maximum percentage of perfect indication of  $\leq 10\%$ have been omitted.





GL 237 – – – – – – – – 1 – – – – – 8 **14** – –



**Geological units** – **GL 6** = Marine fine sand (holocene); **GL 9** = Marine medium sand (holocene); **GL 12** = Marine grit, gravel (holocene); **GL 17** = Tidal flat (recent, holocene); **GL 33** = Fen deposits (holocene); **GL 35** = Sphagnum peat (holocene); **GL 40** = Marine clay, silt, sand (holocene); **GL 65** = Eolian sand (holocene); **GL 85** = Fluvial sand and gravel (pleistocene: weichsel/wuerm); **GL 94** = Loess and loess loam (pleistocene: weichsel/wuerm); **GL 97** = End moraine (pleistocene: weichsel); **GL 98** = Glacial and glacio-fluvial sand and gravel (pleistocene: wuerm); **GL 102 =** Glacial silt (pleistocene: weichsel); **GL 106 =** Glacio-fluvial sand and gravel (pleistocene: weichsel); **GL 112 =** Glacio-fluvial and fluvial sand (pleistocene: weichsel); **GL 113** = Glacio-fluvial and fluvial gravel and sand (pleistocene: wuerm); **GL 222** = End moraine (pleistocene: saale); **GL 223** = Glacial and glacio-fluvial sand and gravel (pleistocene: riss); **GL 227** = Glacial silt (pleistocene: saale); **GL 230** = Glacio-fluvial sand and gravel (pleistocene: saale); **GL 237** = Glacio-fluvial and fluvial gravel and sand (pleistocene: riss); **GL 317** = Glacio-fluvial and fluvial gravel and sand (early pleistocene to mindel); **GL 321** = Glacio-limnic clay, silt and fine sand (pleistocene: elster); **GL 514** = Limno-fluvial gravel, sand, clay, marl (tertiary); **GL 516** = Limno-fluvial sandstone, marl, clay (tertiary); **GL 517** = Sandstone, clayey marlstone, (tertiary); **GL 540** = Limestone, marlstone (tertiary); **GL 541** = Flysch (cretaceous to palaeogene); **GL 547** = Cretaceous rocks (not differentiated); **GL 564** = Lime, calcareous marl, marlstone, sandstone, conglomerate (cretaceous); **GL 569** = Flysch: limestone, quartzite (cretaceous); **GL 571** = Limestone, marlstone, sandstone, conglomerate (cretaceous to eocene); **GL 579** = Marlstone, limestone, dolomite, calcarenite (jurassic); **GL 582** = Jurassic sedimentite (not differentiated); **GL 583** = Clay, clayey marlstone, calcarenite, marl, oolitic lime (jurassic); **GL 588** = Limestone, marlstone, siliceous rocks (jurassic); **GL 598** = Mudstone, marlstone (triassic); **GL 603** = Limestone and marlstone, dolomite, mudstone, sandstone (triassic); **GL 624** = Limestone, dolomite, marlstone (triassic); **GL 625** = Limestone, dolomite (triassic); **GL 626** = Conglomerate, quartzite, sandstone, mudstone, limestone, halite, plaster stone (skyth); **GL 639** = Clay schist, graywacke, dolomite, limestone, siliceous schist, phyllite (paleozoic); **GL 647** = Marlstone, mudstone, sandstone, conglomerate, lava (jurassic to cretaceous); **GL 752** = Paragneiss (proterozoic to early paleozoic); **GL 760** = Mica schists (paleozoic); **GL 761** = Paragneiss (upper proterozoic); **GL 833** = Granite, granodiorite (carboniferous); **GL 834** = Granite (devon, carboniferous);

**Land cover types** – **LC 312** = Coniferous forests; **LC 321** = Natural grasslands; **LC 322** = Heathlands; **LC 324** = Forest – Scrubland mosaic; **LC 332** = Rocks without vegetation; **LC 333** = Rocks with scarse vegetation; **LC 335** = Glacier and firn; **LC 412** = Raised bogs; **LC 421** = Salt marshes; **LC 423** = Tidal flat; **LC 522** = Estuary

**Soil units** – **SL 2** = Salo-thionic gleysols in tidal areas; **SL 3** = Calcaric and eutric gleysols from marine sediments (tidal marsh); **SL 4** = Gleyo-eutric fluvisols from brackish sediments (tidal marsh); **SL 6** = Eutric histosols; **SL 7** = Dystric histosols; **SL 11** = fluvisols / gleysols from rapidly alternating sandy to clayey fluvial sediments; **SL 12** = gleysols from sandy sediments of the ice-marginal valleys and lowlands; **SL 14** = haplic luvisols from silty to loamy periglacial sediments overlying glacial gravels; **SL 17** = Haplic podzols / cambic podzols / gleyic podzols from sandy fluviatile sediments; **SL 21** = Eutric cambisols / haplic luvisols /calcaric regosols from calcareous loamy to sandy till; **SL 25** = Spodic luvisols / spodic podzoluvisols from sandy sediments overlying boulder clay; **SL 26** = dystric podzoluvisols / luvic arenosols / dystric cambisols from sandy sediments overlying boulder clay; **SL 27** = calcaric and umbric regosols / luvic arenosols from sandy to loamy end moraine deposits; **SL 28** = Spodo-stagnic cambisols / stagnic podzoluvisols from loamy to sandy deposits overlying boulder clay; **SL 30** = Eutric cambisols / stagnic gleysols from calcareous loamy sandy to gravelly moraine deposits mixed with loess; **SL 31** = Cambic podzols / spodic arenosols from dry dystrophic sand deposits; **SL 32** = Eutric cambisols / luvic arenosols from dry dystrophic sand deposits; **SL 33** = Haplic podzols / dystric regosols from dry dystrophic sand deposits; **SL 36** = Haplic chernozems from loess; **SL 40** = Phaeozemic luvisols / luvic phaeozems from loess or loessic loam; **SL 42** = Haplic luvisols / eutric podzoluvisols / stagnic gleysols from loess or loessic loam overlying various rocks; **SL 49** = Rendzic leptosols from slope deposits over limestone, marlstone, and dolomite alternating with chromic cambisols / chromic luvisols from silty and clayey material derived from limestone weathering; **SL 50** = Eutric and chromic cambisols from redeposited material derived from limestone, marlstone and dolomite weathering and rendzic leptosols from limestone; **SL 51** = Vertic cambisols / stagnic gleyosols from marlstone and claystone weathering; **SL 52** = Eutric cambisols from marlstone and calcareous gravels; **SL 55** = Dystric cambisols from acid igneous and metamorphic rocks; **SL 57** = Spodic cambisols from acid igneous and metamorphic rocks; **SL 59** = Spodic cambisols from hard argillaceous and silty slates with greywacke, sanstone, quartzite, and phyllite; **SL 60** = Spodic cambisols from hard argillaceous and silty slates, greywacke, and phyllite; **SL 68** = Rendzic leptosols / calcaric cambisols or umbric leptosols / spodic cambisols / stagnic gleysols in varying elevation belts of the high mountain ranges; **SL 69** = Lithic leptosols of the Alps