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CHANGES IN SPECIES DENSITY ALONG THE SOIL pH GRADIENT – EVIDENCE FROM GERMAN PLANT COMMUNITIES

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Abstract: The relationship between small-scale species richness and soil pH in plant communities was reviewed using 40 (mainly phytosociological) studies primarily from the northern parts of Germany. Four formations were distinguished (forest, grassland, mire and sand). To examine the above relationship, two approaches were applied: (a) regression analysis using linear and quadratic models, and (b) calculation of the mean pH of the five plots with the highest species density. Despite methodological problems (lack of single plot data in some studies, varying plot sizes, different ways of measuring pH) some general patterns could be identified. In forests, the regressions in most cases indicated a linear or curved increase in species density with increasing pH, whereas maximum species density was, except in one case, found at an intermediate pH of around 5. In contrast, in grasslands and mires, most studies showed hump-backed relationships between species density and soil acidity, and, accordingly, maximum species density was found at moderately high pH between 5 and 6. For sand vegetation, the few studies available revealed an increase in species density with increasing pH. The findings imply that the predominance of calciphilous species *vs.* acidophilous species in the Central European flora does not always translate into positive relationships between plant species density and pH on a local plot scale. The hump-backed species density-pH pattern may be explained by confounding effects of other environmental factors and of productivity, but also by the large overlap of species tolerances in the middle of the acidity gradient.

Keywords: Calciphilous species, Hump-backed model, pH amplitude, Physiological tolerance, Regional species pool, Soil acidity, Species tolerance

INTRODUCTION

Species richness varies across environments. On a regional scale, the species pool – the set of all species physiologically capable of living in the environmental conditions of a certain community (ZOBEL et al. 1998) – differs considerably between vegetation types. These differ in species number also on a local scale, where factors such as competition are usually regarded as the main determinants of species diversity (GRIME 1979). In recent years, however, the species pool has also been recognized as playing an important role in regulating the plant species richness of sites (ZOBEL 1997, GRACE 1999, PÄRTEL 2002).

EWALD (2003) shows that the regional pool of vascular plants in Central Europe on base-rich and calcareous soils is much larger than the pool on more acidic soils. This appears to be true both for the flora as a whole and for broadly defined formations such as forests. PÄRTEL (2002) has shown that, in general, positive relationships between richness and pH prevail in temperate areas with evolutionary centres on high-pH soils. Supposing that the size of the regional species pool is positively correlated with the small-scale richness of plots, local communities on base-rich soils should be more diverse than those on more acidic soils. According to EWALD (2003), this prediction is supported by various studies.

It is unquestioned that there is an increase in species richness from very acidic to somewhat less acidic sites. However, across the potential range of soil acidity, the relationship between species number and pH must inevitably be unimodal as no species can survive pH values higher than about 9. The basic question is at what pH is the optimum in species richness reached, or, more specifically, is there a decrease in species number already on increasingly base-rich sites. Whereas the relationship between richness and productivity has received much attention in ecology (GRIME 1979), the effects of single factors such as pH have not been studied in much detail (but see, for example, DUPRÉ et al. 2002).

The main objective of our study was to examine the general relationship between species richness in sample plots (species density) and (soil) pH for different formations by means of linear and quadratic regression, and to compare the resulting patterns between and within these formations. For this, we gathered data across a wide array of plant communities, based on published and unpublished data mainly from Germany. We deliberately avoided using Ellenberg's indicator values for pH (reaction) to calculate site averages as surrogates for actual measurements, because there is much evidence that the relation between indicated and measured values is not linear at high-pH sites (SCHAFFERS & SÝKORA 2000).

MATERIAL AND METHODS

Compilation of data

For the compilation of data, phytosociological and other plant ecological literature was screened for information on plot species density (mostly vascular plants, but often also including cryptogams) linked with measurements of pH. A total of 40 studies are represented in the data set (Appendix 1). Study regions included various parts of Germany with an emphasis on the north of the country, as well as two surrounding countries (France and Austria). We preferably used data where information was given for single plots. Many of the studies, however, contained floristic and environmental information only for clusters including several plots, i.e., mean values of species density and pH for certain community types. Cluster data are less reliable than single plot data, because species density values usually were the mean of all plots in a cluster, whereas pH was measured only in a few selected plots that are not necessarily representative of the whole cluster.

There were two further methodological problems that we had to cope with. The first arose from the fact that almost all plots were established as relevés according to the Braun-Blanquet approach, meaning that plot sizes usually differed considerably. Non-standardized plot sizes may distort the analysis if there is a systematic relationship between pH and plot size chosen, as species density increases with increasing plot size. The relations between plot size, pH and species density will be dealt with in more detail below. The second problem concerns the pH measurements that were made with different methods. Most studies relied on pH (H_2O) data, while in several cases pH (KCl or $CaCl_2$) was measured, resulting in considerably lower values (cf. TYLER 1997). When both pH values were given in a study, however, the two ways of measuring soil acidity resulted in very similar correlations with species density, and only pH (H_2O) was used for further analysis. To be able to include data of both types in comparative analyses, we calculated the mean difference between pH (KCl or $CaCl_2$) and pH (H_2O) across all studies (0.62 units) and added this mean to all values of pH (KCl or $CaCl_2$) to arrive at corrected values.

To examine if the relation between species density and pH differed between formations, we distinguished four broadly defined vegetation types (see Appendix 1):

Forest: deciduous and coniferous woodland on fresh and wet soils (classes *Alnetea glutinosae*, *Querco-Fagetea*, *Vaccinio-Piceetea* and *Vaccinietea uliginosae*);
Grassland: intensively and extensively managed, open communities dominated by graminoids (*Molinio-Arrhenatheretea*, *Nardo-Callunetea* [*Nardetalia*] and *Festuco-Brometea*);
Mire: bog, poor mire and fen communities (*Oxycocco-Sphagnetea* and *Scheuchzerio-Caricetea*);
Sand: vegetation of open sandy heaths and dunes (*Sedo-Scleranthetea* [*Corynephoretalia canescentis* and *Thero-Airetalia*] and *Nardo-Callunetea* [*Calluno-Ulicetalia*]).

Statistical data analysis

The relationship between species density and pH was first analyzed separately for each study by means of regression. We only used linear and quadratic models, because other model types, though possible or even realistic, did not serve the purpose of our study aiming at discriminating between linear or hump-shaped relationships. The model with the higher adjusted R^2 (R^2_{adj}) was regarded as the one fitting the data best. The regression lines for studies belonging to the same formation were displayed in one figure by overlaying the graphs, using the pH (H_2O) values and corrected pH (KCl or $CaCl_2$) values. Differences in species density between studies of the same formation were not analyzed and are mainly an effect of different plot sizes.

Differences in the relationship between species density and pH between formations were analyzed by calculating the slope of the fitted regression lines (either linear or quadratic) at pH 5 for all studies. The slopes were then compared between formations by means of unpaired *t*-tests.

The regression analysis describes the general relationship between species density and pH, but does not tell us where along the acidity gradient species density is at its maximum. Also a flat hump-backed curve may still rise at high pH. In addition, differences in the variation in species density along the acidity gradient may imply that the peak of the optimum curve does not fully correspond to the pH of maximum species density. Therefore, we calculated the mean pH of the five most species-rich plots, cut the pH range into 3 equal sections of low (2.00–3.99) , middle (4.00–5.99) and high (6.00–8.00) pH and then checked in which section the above mean value was situated. The results were basically the same when we used the mean pH of a larger or smaller number of the most species-rich plots. This analysis could only be conducted on studies with single plot data.

Table 1. Relationship between plot size and pH and relationship between species density and plot size, given for studies with varying plot size. R^2_{adj} values are given; significant positive correlations are indicated by plus signs, significant negative ones by minus signs (+/- – $P < 0.05$; ++/-- – $P < 0.01$; +++/--- – $P < 0.001$).

	No. of study	Relationship between plot size and pH	 species density and plot size
Forest	6	0.0	0.0
Grassland	16	13.8 -	0.0
	22	0.1	2.7 ++
	28	2.8 ++	2.1 ++
Mire	1	0.0	1.0
	7	0.0	24.0 +++
	17	0.0	0.0
	38	0.0	0.0
Sand	13	1.4	0.2
	20	1.8	11.4 +++

RESULTS

Plot size varies in all but a few studies, but detailed information for single plots was available only in 14 studies. In two cases, plot size was significantly correlated with pH (Table 1), and in only one of the two (no. 28) species density was also correlated with plot size. It therefore, in general, appears unlikely that varying plot size had a distorting effect on the analysis between species density and pH. In more than half of the studies there was no significant positive relationship between species density and plot size.

In forests, there was a significant relationship between species density and pH in 9 out of 11 studies (Table 2). All regression lines showed a rather steep rise at low pH, while the curves differed in their slopes at higher pH (Fig. 1). Those with maximum values around or lower than 6 were largely linear, whereas those exceeding pH 6 were quadratic, exhibiting a reduced slope or even tapering off (no. 18).

The majority of studies in grasslands (9 out of 14) also gave significant fits for the relationship between species density and pH (Table 2). Again, there was a steep increase in species number from low to moderately high pH (Fig. 1). The hump-backed pattern was more pronounced than in forests, with five studies having clear optimum curves (no. 4, 8, 16, 22, 24). One of the studies including pH values > 7 (no. 14) was found to have a positive linear regression line.

Five of the ten studies of mires resulted in significant relationships between the two variables (Table 2). The two studies with pH maximum values around 6 resulted in linear, positively sloping regression lines, and those with higher top values had hump-backed curves, two of which exhibited a clear optimum (Fig. 1).

For the sand formation the number of studies was lower (Table 2). Three regression lines were found to be significant, two of which exhibited a linear, and the third a quadratic, but concave shape (Fig. 1). There was, however, a clear increase in species density with pH on increasingly neutral soils.

The slopes of the regression curves at pH 5 in forests were significantly higher than in mires ($t = 2.32$, $P = 0.033$, df = 19), and they tended to be higher than in grasslands ($t = 1.02$, $P = 0.319$, df = 22) and in sand vegetation ($t = 1.02$, $P = 0.332$, df = 13). The grassland slopes were not different from those of mires ($t = 0.89$, $P = 0.384$, df = 21) nor did they differ from those of sandy vegetation ($t = -0.16$, $P = 0.872$, df = 15). Finally, also mires and sandy vegetation did not significantly differ from each other ($t = -0.132$, $P = 0.227$, df = 12).

Table 2. Basic data analysis of the 40 studies: pH (minimum, maximum and mean values), species number (minimum, maximum and mean values), regression statistics of the relationship between species density and pH (R^2_{adj} are given for both linear and quadratic models; significant fits are marked with an asterisk: * – $P < 0.05$; ** – $P < 0.01$; *** – $P < 0.001$. (u) – **EXPLAIN !!!)**, and pH of maximum species density (mean pH of the five sites with the highest species number).

No. of study	pH			No. of species			Regression - R^2_{adj}		pH of highest species density
	Min.	Max.	Mean	Min.	Max.	Mean	Linear	Quadratic	
1	3.7	6.4	4.7	7	39	19.1	5.3 *	8.8 *	4.8
2	4.0	7.3	5.5	6	36	21.4	60.3 ***	60.7 **	6.3
3	4.9	6.3	5.6	18	41	32.6	22.5	27.4	5.3
4	3.9	7.2	5.9	27	61	49.2	0.0	16.8 *	5.5
5	2.6	4.1	3.3	5	9	4.8	25.3	15.9	2.8
6	2.9	6.3	4.8	12	65	37.3	58.5 ***	59.7 ***	5.4
7	4.8	7.7	6.8	5	45	18.1	0.0	0.0	6.0
8	3.6	7.6	5.5	7	71	33.8	15.3 ***	18.1 ***	5.9
9	4.4	7.0	5.6	14	59	37.0	4.9	14.7 *	5.8
10	3.8	4.9	4.4	13	29	20.0	4.7	12.8 *	4.4
11	3.3	5.7	4.6	14	59	22.0	37.6 ***	36.2 ***	5.1
12	3.5	6.1	5.0	15	36	24.4	62.7 *	55.7	5.4
13	3.4	6.5	5.0	1	44	22.8	36.6 ***	35.8 ***	5.4
14	4.0	8.0	6.0	18	61	35.6	10.9 ***	10.9 ***	6.5
15	3.1	5.7	3.8	3	39	15.1	35.2 ***	39.0 ***	4.7
16	3.5	5.4	4.3	18	50	34.7	23.8 **	28.2 **	4.5
17	4.0	7.0	5.0	13	42	27.9	0.0	2.2	5.2
18	2.7	7.1	4.3	22	55	33.9	35.0 **	50.9 **	5.6
19	4.0	7.2	5.3	4	29	16.3	37.0 **	33.9 **	6.0
20	6.2	7.6	7.1	11	66	35.9	2.9	6.6 (u)	7.0
21	4.0	7.7	5.8	5	25	13.8	0.0	0.8	6.0
22	3.4	8.0	7.3	10	71	37.7	3.4 ***	7.7 ***	7.0
23	4.9	8.0	6.3	20	61	40.1	6.7 **	5.9 *	6.5
24	3.7	8.1	5.9	5	49	22.5	1.7	13.4 ***	5.2
25	3.3	5.2	4.6	12	28	18.1	3.2	2.9	4.7
26	4.3	7.1	5.0	31	55	44.0	0.9	0.0	5.0
27	6.0	8.1	7.0	1	29	11.5	0.0	0.0	7.2
28	3.0	5.7	4.5	7	72	31.4	41.3 ***	41.8 ***	4.8
29	3.4	7.2	4.6	2	59	25.1	13.1 ***	13.8 ***	5.8
30	3.9	4.5	4.1	5	16	10.7	16.5	0.0	4.1
31	4.3	5.6	4.8	14	44	24.7	0.0	12.2	4.9
32	4.0	6.1	5.0	16	56	30.8	33.4 ***	32.3 ***	5.4
33	2.5	3.4	2.9	11	47	21.6	40.9 ***	40.2 (u) ***	3.2
34	3.8	5.7	4.7	3	29	14.1	35.4 ***	61.6 ***	5.3
35	4.6	7.3	6.0	12	21	16.9	9.1	7.5	5.9
36	3.0	5.4	4.0	13	46	23.0	75.2 ***	74.1 ***	5.0
37	2.9	6.7	4.8	8	44	20.8	2.7	0.0	5.3
38	2.1	5.6	3.8	5	34	13.8	29.9 ***	29.4 ***	4.6
39	2.8	6.1	4.0	3	57	32.4	72.8 ***	75.9 ***	5.5
40	4.8	5.8	5.3	25	42	34.5	60.1	40.7	5.0

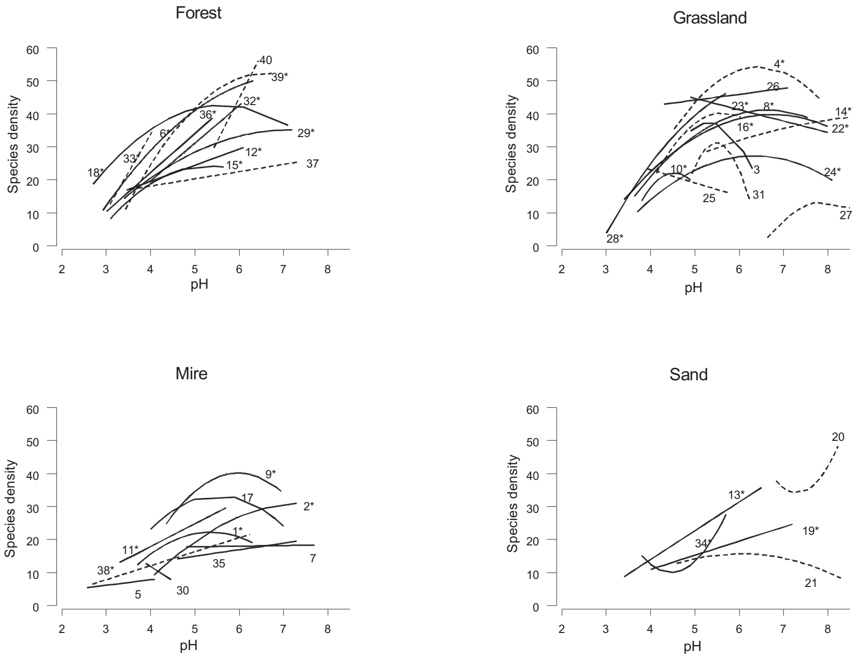

Fig. 1. Relationship between species density and soil pH as assessed by regression analysis, shown separately for the four formations: forest, grassland, mire and sand. Each regression line denotes one study, referred to by its number (see Appendix 1). For regression statistics, see Table 1. Significant fits are marked with an asterisk added to the study no. In most cases, pH (H_2O) was measured; studies based on pH (KCl or $CaCl_2$) that were moved 0.62 pH units to the right to be comparable with pH (H_2O) measurements are indicated by dashed lines (see Material and Methods).

When calculating the mean soil pH of the five plots with the highest species number, the emerging pattern was consistent (Table 2; Fig. 2): For forests, grasslands, mires and sand, the maximum species density was found in the middle section (pH 4.00–5.99), i.e., on sites with moderately high pH, followed by the high pH section (pH 6.00–8.00). In only a few cases was species number at its maximum on low-pH sites. Across all 40 studies, maximum species density was on average reached at pH 5.4, and of 26 studies with maximum pH values exceeding 6, only 9 had values of maximum species richness at pH ≥ 6.

DISCUSSION

Effects of varying plot size

Plot size was positively correlated with species density in less than half of the studies (Table 1). This supports the observation made by CHYTRÝ (2001) who assumed that researchers, especially those with a strong interest in phytosociology, tend to use larger plots in species-poor vegetation to include more taxa of interest or potential value as diagnostic species. However, there appeared to be no systematic bias as to the relationship between the

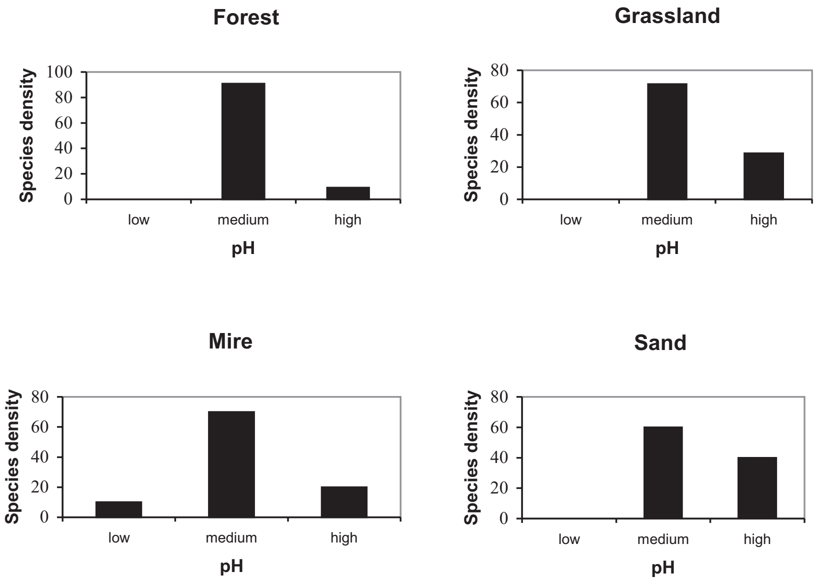

Fig. 2. pH of maximum species density in relation to the pH gradient length. For each study, the mean pH of the five sites with the highest species number was calculated. After dividing the whole pH range into equally long sections of low (2.00–3.99), middle (4.00–5.99) and high (6.00–8.00), the section comprising the mean pH was determined. The proportion of studies assigned to the three sections in each formation is given on the *y* axis.

plot size chosen and pH, which justifies the use of phytosociological relevés for our purpose, in absence of more standardized data.

Relationship between species density and pH

In all formations we found a distinct and sometimes steep increase in species number from low to moderately high pH. This is in accordance with the literature (e.g. DUPRÉ et al. 2002) and reflects the poor diversity of the most acidic and, at the same time, infertile sites. On soils of higher pH, however, the formations differed from each other in their relationship between species density and pH.

For forests, the two ways of examining this relationship gave slightly different results. Whereas the regression analysis showed that species density generally continues to increase even on sites with weakly acid or neutral pH of 6 to 7, the analysis of maximum species density indicated that the top values are found on moderately acidic soils of around pH 5–6. We believe that the latter pattern would have been even stronger if data had been available from the most base-rich forest sites that are absent from or clearly under-represented in our survey, namely beech and mixed deciduous forests on dry calcareous slopes (*Cephalanthero--Fagion*) and mixed deciduous forests with *Acer*, *Fraxinus*, *Tilia* and *Ulmus* on highly fertile slopes and glens (*Tilio-Acerion*). The first type has especially been associated with high floristic diversity (ELLENBERG 1996, and DIEKMANN, unpubl. data). This result of our survey is also in contrast to the findings of DUPRÉ et al. (2002), who, based on forest data mainly from Scandinavia, reported a predominance of unimodal relationships between species density and pH. More reliable data from forests are needed to understand if the relationship between species richness and pH varies consistently between different forest subtypes, or if there simply is no consistent pattern. The slopes of the regression lines found in forests were or tended to be higher than in the other three formations, indicating that the highest species richness in forests is reached at comparatively high pH.

In accordance, the regression lines in grasslands in most cases had their optima at a moderately high pH of 5–6, a result that was supported also by the analysis of pH of maximum species number. This was somewhat unexpected, as the survey included dry calcareous grasslands of the class *Festuco-Brometea* occurring on high-pH soils that are well-known for their high species number. Mires also tended to have their highest species density at intermediate pH, although the patterns were less clear and the changes in diversity along the acidity gradient generally less pronounced than in grasslands. Because species density included both vascular plants and cryptogams, mainly bryophytes, and because the latter are of particularly great importance in mires with respect to cover and species number, we assumed that the numbers of bryophytes and vascular plants were reciprocal to each other. However, this was not the case: in those studies that allowed us to test this assumption, species densities of the two groups were significantly positively correlated.

The species density-pH relationship in the sand formation was difficult to assess and interpret, partly due to the small number of studies included. In the following, the discussion will therefore focus on forests, grasslands and mires.

Species pools and local species richness

As there are physiological pH limits to the survival of plants, species densities beyond these limits must be zero (PÄRTEL 2002). This implies that, close to the upper pH limit of about 9, species density-pH relationships are expected to be negative. This may be relevant in grasslands, where pH exceeded 8 in several studies and where, except in one case, richness decreased between pH 7 and 8. On such alkaline soils, species suffer from the low availability of iron, manganese and phosphate and their incapacity to render these soluble for uptake (TYLER 1999). However, species density in grasslands in most cases was at maximum at pH 5 to 6.5, i.e., at somewhat or considerably higher acidity, and this also applies to mires where pH values often exceeded 7. Thus, it is unlikely that the predominance of hump-backed curves found in grasslands and mires is solely explained by the physiological tolerances of species. In contrast, the often sharp decrease in species density on increasingly acidic soils found in most formations may be primarily explained by the small pool of species physiologically capable of surviving the high hydrogen ion concentration and overcoming the Al^{3+} toxicity of these soils (cf. TYLER 1999).

Our results contradict the general statement by EWALD (2003) that there is a “positive relationship between pH and plant species density throughout the temperate zone”. Even though this survey shows that the relationship is more positive than negative (when only linear regression is applied, the large majority of studies had positive slopes), at high pH it is in fact no longer positive. The results of the analysis of pH of maximum species density also give evidence for the hump-backed pattern. Thus, the large pool of calciphilous species present in the flora of Central Europe may explain the higher floristic diversity of the most base-rich sites compared to the most acidic sites, but it cannot explain the high species density found in sites with intermediate pH. Here, we attempt to offer some possible explanations that are not mutually exclusive:

(a) The term species pool was actually coined for communities affected by many environmental variables at the same time, not by a single one such as pH. There may be confounding effects of other factors that are correlated with pH across different environments. If high pH were associated with a certain value of another variable, for example low light availability in forests for which the species pool is low, then species density on such sites would be low despite the large pool of calciphilous species. The importance of analyzing and interpreting such habitat-specific species pools was emphasised by DUPRÉ et al. (2002). However, the problem remains of how to identify or calculate the species pools of communities in a statistically sound way (ERIKSSON 1993, PÄRTEL et al. 1996, DUPRÉ 2000, GRACE 2001).

(b) This explanation is somewhat related to the one presented under (a). Productivity increases with decreasing soil acidity from low to intermediate pH, whereas the pattern becomes more complicated at higher pH. For example, base-rich forest sites can both be highly productive (*Tilio-Acerion* communities) and relatively unproductive (*Cephalanthero-Fagion*, cf. ELLENBERG 1996). In some formations such as grasslands, high pH sites are probably often more productive than soils with intermediate pH, although we do not know of any systematic study of the relationship between the two variables across different formations. If this holds true, the relationship between species density and pH may interfere with the hump-backed relationship between species density and productivity (GRIME 1979).

(c) The overlap of pH amplitudes of species with different indicator values, hypothetically shown by EWALD (2003) in Fig. 2, implies another explanation: as the indicator values for reaction denote the supposed species optima relative to pH, the high number of species with scores between 7 and 9 does not necessarily result in high species densities on high-pH sites, because species density is first of all dependent on the number of species tolerant of these conditions. At pH of about 5 to 6, both acidophilous and calciphilous species may be able to (co-)exist, while at lower or higher pH the numbers of tolerant species decline. In other words, intermediate pH conditions exclude only few species from growing there, and therefore we may argue that the species pool in such conditions is large. The explanation relates to the mid-domain effect described by COLWELL & LEES (2000).

It may be concluded that the large pool of calciphilous species in Central Europe certainly affects the small-scale richness of many plant communities on high-pH soils, but that it cannot fully account for the patterns of hump-backed species density-pH relationships found in this study, especially in grasslands and mires. We believe that the decline in species richness on increasingly base-rich soils partly results from the correlation of pH with other environmental factors across the landscape. To get a clearer view of the issues raised by EWALD (2003) we need to collect more measurement data of pH and other variables accompanied by species richness data. The collection of these data should be made with more or less standardized sampling methods to avoid the drawbacks of the phytosociological approach in this context.

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APPENDIX 1

Survey of references from which data were compiled. The studies were ordered alphabetically and referred to in the text by their numbers. The vegetation data were assigned to four broadly defined types (see text) and consist either of plots or groups of plots (Clusters). Plot size differed between studies and partly also within studies (then, range and mean are given; means are in parentheses); in some cases, no information on plot size was available. pH was measured either in water (H_2O) or in $CaCl_2$/KCl solution.

No. of study	Reference	Vegetation	Data type clusters	No. of plots/ (m^2)	Plot size	Type of pH data
1	Baumann (1996)	Mire	Plots	66	4–16 (15)	H_2O
2	Baumann (2000)	Mire	Clusters	14	4	H_2O
3	Beer (1995)	Grassland	Plots	8	no data	H_2O
4	Bohner et al. (2001)	Grassland	Plots	29	no data	$CaCl_2$
5	Borchert (1990)	Mire	Clusters	9	no data	H_2O
6	Brand (2000)	Forest	Plots	167	200–400 (100)	H_2O
7	Braun (1968)	Mire	Plots	126	0.5–100 (13)	H_2O
8	Bruelheide (1995)	Grassland	Plots	127	10	H_2O
9	Bruelheide (1995)	Mire	Plots	44	10	H_2O
10	Bruelheide & Flintrop (1994)	Grassland	Plots	36	no data	H_2O
11	Bruelheide & Flintrop (1994)	Mire	Plots	42	no data	H_2O
12	Döring-Mederake (1991)	Forest	Clusters	8	100–400	H_2O
13	Fischer (1998)	Sand	Plots	58	2–12 (5)	H_2O
14	Goebel (1995)	Grassland	Plots	168	15–70	KCl
15	Gönnert (1989)	Forest	Plots	36	100–500	H_2O
16	Hachmöller (2000)	Grassland	Plots	30	16–25	KCl
17	Harm (1990)	Mire	Plots	15	5–15 (10)	H_2O
18	Härdtle (1995)	Forest	Clusters	17	100	H_2O
19	Heinken (1990)	Sand	Plots	22	8–53 (18)	H_2O
20	Hemp (2001)	Sand	Plots	52	4–75 (17)	$CaCl_2$
21	Isermann (1997)	Sand	Clusters	17	1–25	KCl
22	Jandt (1999)	Grassland	Plots	274	3–16	H_2O
23	Klesczewski (2000)	Grassland	Plots	101	no data	H_2O
24	Kratzert & Dengler (1999)	Grassland	Plots	84	10	H_2O
25	Lienkamp (1993)	Grassland	Clusters	13	no data	$CaCl_2$
26	Lisbach & Peppler- -Lisbach (1996)	Grassland	Plots	99	15–20	H_2O
27	Mehrtens (1995)	Grassland	Plots	14	no data	$CaCl_2$
28	Peppler (1992)	Grassland	Plots	231	4–40 (18)	H_2O
29	Pflume (1999)	Forest	Plots	387	100–400	H_2O
30	Pietsch (1986)	Mire	Clusters	6	0.4–60	H_2O
31	Rosenthal (1991)	Grassland	Clusters	14	25	$CaCl_2$
32	Schönert (1994)	Forest	Plots	47	80–100	H_2O
33	Storm (1996)	Forest	Plots	77	300	$CaCl_2$
34	Täuber (1994)	Sand	Clusters	16	9–22 (16)	H_2O
35	Täuber (2002)	Mire	Clusters	20	1–2	H_2O
36	Taux (1981)	Forest	Clusters	13	no data	H_2O
37	Wiebe (1989)	Forest	Clusters	20	no data	KCl
38	Wittig (1999)	Mire	Plots	95	1–30 (18)	$CaCl_2$
39	Wulf (1985)	Forest	Plots	20	100–400	$CaCl_2$
40	Wulf (1992)	Forest	Clusters	5	100–200	$CaCl_2$