

THE CALCAREOUS RIDDLE: WHY ARE THERE SO MANY CALCIPHILIOUS SPECIES IN THE CENTRAL EUROPEAN FLORA?

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Abstract: The pool of the Central European flora consists of a majority of vascular plant taxa that are restricted to very base rich and calcareous soils. Ellenberg indicator values for Germany indicate that this floristic pattern is one of the potentially most powerful determinants of the richness of modern temperate plant communities. Considering the example of the forest flora, which, as the putative natural core of the species pool, exhibits the same skew, it is shown that neither the frequency of suitable soil types nor other correlated ecological factors can explain this striking pattern. Also, the ramification of higher taxa offers no indication of higher evolution speeds in calciphilous plants. As an alternative, it is hypothesized that Pleistocene range contractions have caused the extinction of more acidophilous than calciphilous species, because acid soils were much rarer when refugial areas were at their minimum. If this is correct, one of the most significant ecological patterns in the contemporary distribution of plant diversity must be regarded as a result of ecological drift imposed by a historical bottleneck.

Keywords: Biodiversity, Indicator plants, Soil acidity, Species pool, Species richness

Nomenclature: ELLENBERG et al. (1991).

INTRODUCTION

The dichotomy of calciphilous versus acidophilous plant species has long been recognized as a striking feature of European vegetation (KERNER VON MARILAUN 1896, SCHIMPER 1903). Although its ecophysiological background is not entirely understood (KINZEL 1982, LARCHER 1994), the importance of pH and the concentrations of “base” (Ca, Mg, K, Na) versus “acid” cations (H, Al, Fe, Mn) in soil solutions for the composition of plant communities is undoubted (e. g. GÖNNERT 1989, HAKES 1994, FALKENGREN-GRERUP et al. 1995, ELLENBERG 1996, TYLER 1999). It is also a widespread notion that temperate and arctic plant communities of neutral soils tend to possess higher species densities than those of acid soils (GRIME 1979, GRUBB 1987, PEET & CHRISTENSEN 1988, GOUGH et al. 2000). This may be ultimately due to a reservoir (GRIME 1979) or species pool effect (ZOBEL et al. 1998), i.e., to a disparity in the number of calciphilous versus acidophilous species on the broad geographic scale of temperate floras (PÄRTEL 2002). A query of the list of indicator plants for soil reaction compiled by ELLENBERG et al. (1991) demonstrates that markedly basiphilous and calciphilous plants constitute more than 50% of the German vascular flora (Fig. 1).

Uneven distribution of broad-scale richness along a particular environmental gradient and among the corresponding habitat types (γ -diversity *sensu* WHITTAKER 1960) can be explained in several ways:

(1) The species richness of a habitat type increases with its areal extent (ROSENZWEIG 1995). If the species-area relationship causes the calciphyte-acidophyte disparity, neutral and alkaline soils should be more widespread than acid soils.

(2) Species richness is a result of speciation and extinction (RICKLEFS 1987). If base-rich environments have higher evolution rates (IVERSEN 1958, GRIME 1979), calciphilous plants should be part of more ramified evolutionary lineages, i.e., they should tend to be found in the more species-rich genera and families.

(3) Finally, the increase in richness with pH could be confounded with other environmental gradients. If the disparity results from such hidden drivers, calciphilous plants should also be members of other particularly diverse indicator groups, e.g. for low nitrogen and high light availability (Fig. 1).

This paper presents the calciphyte/acidophyte disparity in the Central European flora in quantitative detail, assesses available evidence for the validity of explanations and attempts to draw the attention of contemporary biodiversity research to a fascinating and, as I believe, largely unresolved phenomenon.

MATERIAL AND METHODS

Ellenberg's list contains 2726 Central European plant taxa (mostly species, in a few cases species groups) and lists indicator values of soil reaction (R-values) derived on the basis of a large body of phytosociological field data and pH measurements (ELLENBERG et al. 1991). Species optima are expressed by ordinal numbers between 1 and 9 (x for indifferent species). Each R-value corresponds to a certain amplitude on the pH gradient, as shown in Fig. 2. For simplicity's sake species will be juxtaposed as "acidophilous" (R = 1–6) and "calciphilous" (R = 7–9) throughout this paper. ELLENBERG et al. (1991) describe species with R-value 7 as "indicators of moderately acid to moderately basic conditions, entirely absent from strongly acid soils", those of R-value 9 as "indicators of bases and lime, exclusively on calcareous soils" and indicators 8 as "intermediate between 7 and 9, i.e., mostly indicating the presence of lime". Calciphilous plants in the sense used here should therefore rarely find suitable habitats on soils with pH < 5 (see Fig. 2).

I screened the data base of ELLENBERG et al. (1991) for the numbers of species assigned to reaction values 1 to 9. Separate assessments were done for each of 8 plant formations distinguished by ELLENBERG et al. (1991). The forest formation (not including deciduous scrub communities) was further subdivided into phytosociological classes, of which the character species were assessed for their preference on the soil reaction gradient.

The areal extent of forest soils of different acidity in Germany was estimated from the frequency of measured pH values in federal forest soil monitoring (ANONYMOUS 1997). The distribution of habitats suitable for natural vegetation types was assessed by analyzing the spatial extent of units in the map of potential natural vegetation in Germany (BOHN et al. 2003; author's interpretations with respect to soil acidity in mapping units are available on request).

Based on the Ellenberg list I calculated the number of species per genus and per family as indices of taxonomic ramification. Differences in the values of these indices taken by

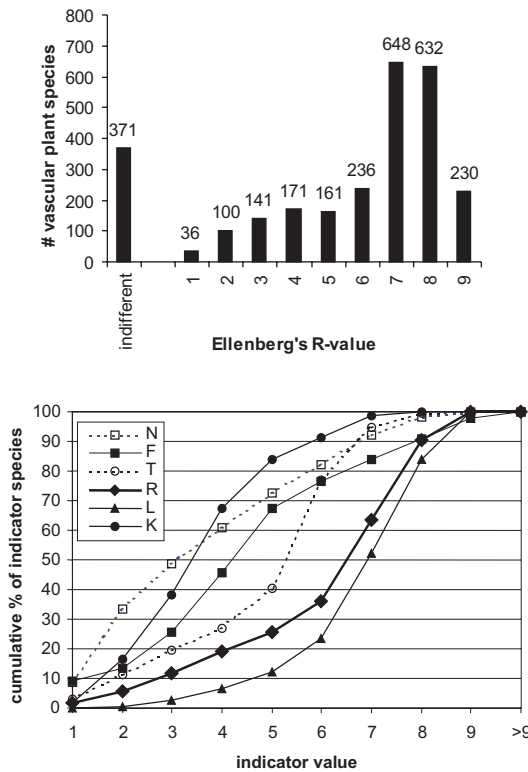


Fig. 1. Richness of indicator groups in the German flora; above: histogramme of indicators for soil reaction; below: cumulative curves summarizing the γ -diversity in indicator groups for nitrogen (N), moisture (F), temperature (T), reaction (R), light (L) and continentality (K).

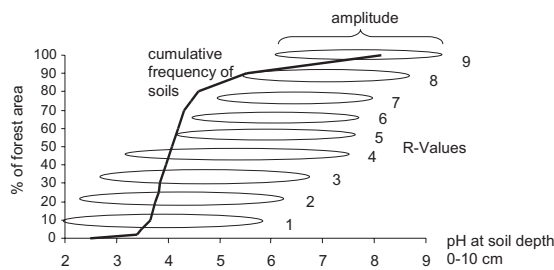


Fig. 2. Amplitudes of reaction indicator species on the pH gradient as verbally defined by ELLENBERG et al. (1991); cumulative frequency of pH in forest soil monitoring (mineral soil, ANONYMOUS 1997).

acidophilous and calciphilous species were assessed by non-parametric Mann-Whitney *U*-tests.

Systematic differences between acidophilous and calciphilous plant species regarding other indicator values were detected by comparing both groups by Mann-Whitney *U*-tests.

RESULTS

pH-dependence of species richness across formations

Of the 2726 vascular plant species listed in ELLENBERG et al. (1991) 86% are regarded as indicators of the acidity status of soils. Species richness is distributed highly unevenly among reaction indicator groups (Fig. 1): R-values 7 and 8 contribute far more species than any other class. Consequently 55% of all species in the German vascular flora – or 64% of all reaction indicators – prefer to grow on calcareous or at least very base-rich soil.

ELLENBERG et al. (1991) assign 2503 or 92% of the species to one of 8 broad vegetation formations, among which overall species diversity is unevenly distributed. The most diverse formations are anthropogenic heaths and meadows (23%) and ruderal vegetation (22%), followed by alpine talus and meadows (13%), deciduous forest and scrub (12%) and freshwater and bogs (12%). Only small fractions of the vascular flora prefer natural tall herb communities (6%), coniferous forests (3%) or saline habitats (3%). Calciphytic richness (Fig. 3, left) is basically proportional to the overall γ -diversity of formations. The floras of halophytic,

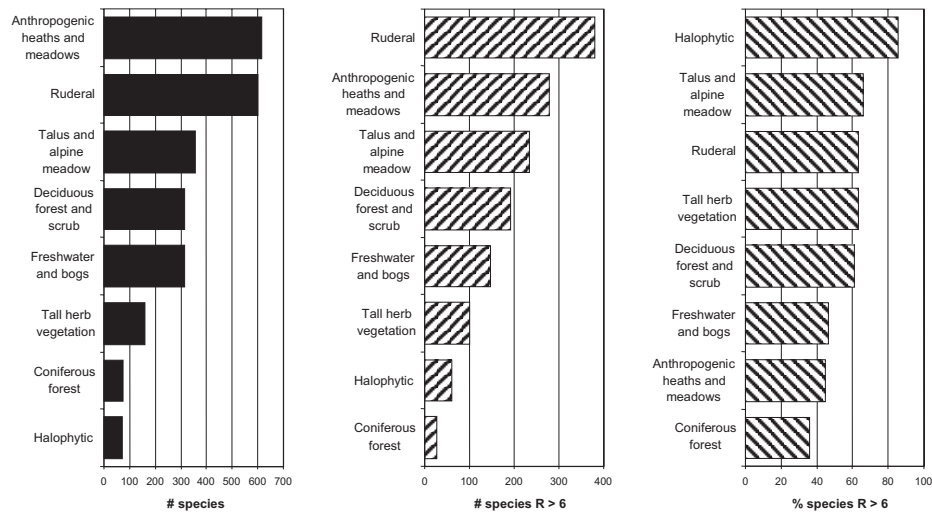


Fig. 3. Distribution of overall and calciphilous richness (species with R indicator values > 6) across broadly defined vegetation formations; left – absolute numbers of species; centre – absolute numbers of calciphilous species; right – proportion of calciphilous species

Table 1. Species richness of the Central European forest flora and its distribution across indicator values. x – species indifferent towards R, S – # species total, F – % of forest flora, C – % calciphilous.

	x	R-value									S	F	C
		1	2	3	4	5	6	7	8	9			
Tree species	11			1	1	5	10	8	1		37	10	24
Understorey species													
<i>Erico-Pinetea</i>	3							3	10	8	24	6	88
<i>Pulsatillo-Pinetea</i>						1	2		2	1	6	2	50
<i>Vaccinio-Piceetea</i>	5	4	14	8	3	3	1	1			39	10	3
Coniferous forest	8	4	14	8	3	4	3	4	12	9	69	18	36
<i>Salicetea</i>							1	2	5		8	2	88
<i>Alnetea</i>	1			1	5	6	3	1			17	4	6
<i>Quercetea</i>			4	4	5	2					15	4	0
<i>Querc-Fagetea</i>	8			3	5	17	34	73	46	2	188	49	64
<i>Quercetea, Querc-Fagetea</i>	8		4	7	10	19	34	73	46	2	203	52	60
Deciduous forest	9		4	8	15	25	38	76	51	2	228	59	57
Other sciophytes	18		3	7	5	2	3	7	8		53	14	28
Understorey total	35	4	21	23	23	31	44	87	71	11	350	90	48
Forest total	46	4	21	24	24	36	54	95	72	11	387	100	46

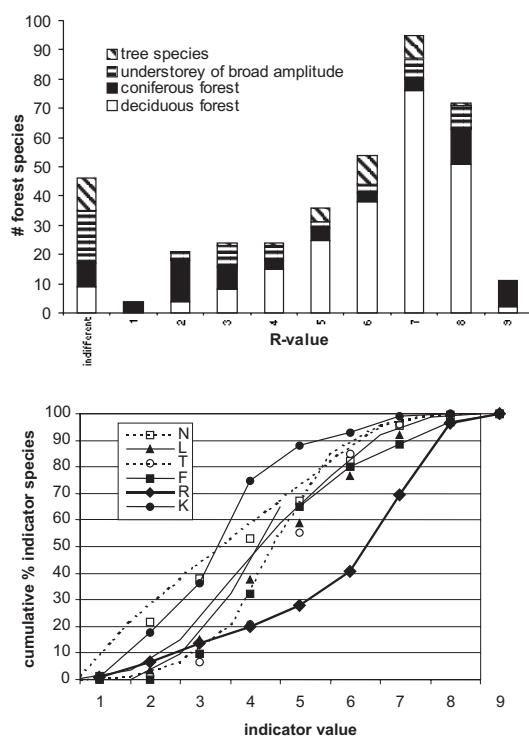


Fig. 4. Richness of indicator groups in the character species of German forests; above: histogramme of indicators for soil reaction; below: cumulative curves summarizing the γ -diversity in indicator groups.

Calciphilous species make up 60% of their character species. Acidophytic spruce (*Vaccinio-Piceetea*) and oak forests (*Quercetea robori-petraeae*) are the only forest types that contain a majority of understorey species with low R-values. Character species of alder swamps (*Alnetea glutinosae*) have mostly intermediate R-values.

Frequency of acid versus calcareous forest sites

The results of federal forest soil monitoring in Germany (ANONYMOUS 1997) reveal that the present-day areal extent of habitat conditions does not coincide with the distribution of species richness across the acidity gradient. In a systematic grid of 1650 points 75% of the forest sites had pH-values of less than 4.46 in the uppermost 10 cm of mineral soil, in 90% pH-values of less than 5.52 were measured. If we assume the amplitudes in Fig. 1 are correct, 46% of the German forest flora depends on 25% of the forest habitats. It is at a soil depth of 60–90 cm ($n = 1194$) that the proportion of sites favourable to calciphilous species approximately matches the contribution of this group to the forest flora (50% of sites with pH 4.66 or above) – a zone that is hardly reached by roots of the vast majority of species

alpine, ruderal, tall herb and deciduous forest communities consist of a majority of calciphilous species (Fig. 3, right). The deciduous forest formation is in this respect (61% calciphilous species) more or less representative of the total flora, while coniferous forest species are largely acidophytes.

pH-dependence of species richness in forests

Tree species, that make up only 10% of the forest flora (Tab. 1), were most often judged as indifferent towards soil reaction or as moderately basiphytic by ELLENBERG et al. (1991). By far the most listed forest species are understorey species (Fig. 4) characteristic of the classes *Quercetea robori-petraeae* and *Querceto-Fagetetea* (52%), which according to OBERDORFER (1992) comprise the temperate forests of *Fagus*, *Quercus*, *Acer*, *Fraxinus*, *Carpinus*, *Ulmus* and *Tilia*, that form the potential natural vegetation of large parts of Central Europe (BOHN et al. 2003).

Table 2. Comparison of reaction indicator species groups with regard to other attributes by Mann-Whitney *U*-test. L – light, T – temperature, K – continentality, F – moisture, N – nitrogen, *n* – # species, *U*, *z* – test statistics, *P* – significance level.

	acidophilous		calciphilous		Mann-Whitney test		
	mean	<i>n</i>	mean	<i>n</i>	<i>U</i>	<i>z</i>	<i>P</i>
All species							
Species per family	114	845	116	1510	631778	0.392	0.695
Species per genus	18	845	13	1510	570832	-4.242	0.000
L	7.1	835	7.3	1502	594572	2.080	0.032
T	4.8	750	5.5	1389	390500	9.565	0.000
K	3.7	768	4.2	1378	412980	8.443	0.000
F	5.4	822	4.9	1481	510160	-6.445	0.000
N	3.2	802	4.3	1418	410499	10.899	0.000
Forest species							
Species per family	90	158	77	230	17426	-0.686	0.492
Species per genus	17	158	11	230	16077	-1.929	0.053
L	4.9	154	5.3	230	15558	2.019	0.040
T	5.0	121	5.6	207	9025	4.222	0.000
K	3.7	144	4.0	226	13948	2.317	0.016
F	5.7	150	5.0	222	13135	-3.455	0.000
N	3.8	149	4.8	215	10796	5.290	0.000

(POLOMSKI & KUHN 1998). In good accordance with the findings of soil monitoring the map of potential natural vegetation by BOHN & NEUHÄUSL (2000) designates 53% of Germany as habitat of acidophytic, 30% as habitat of basiphytic and only 7% of calciphytic community types. Thus in Germany, the richness of reaction indicator plants runs counter to the frequency of suitable habitats (Fig. 5).

Ramification of families and genera

Among the 158 plant families listed in ELLENBERG et al. (1991) the most species rich are the *Asteraceae* (340 species, 103 acidophytes/237 calciphytes), *Poaceae* (225, 72/151) and *Cyperaceae* (146, 60/84). Despite the overrepresentation of calciphytes in the two largest families, calciphilous and acidophilous species do not differ significantly in their tendency to occur in more species-rich families according to the Mann-Whitney *U*-test (Tab. 2). Of the 733 genera *Carex* (103, 47/55), *Hieracium* (54, 28/26) and *Alchemilla* (40, 16/19) are the most ramified and do not contain remarkably high numbers of calciphytes. The *U*-test detects a significant tendency for calciphilous species to occur in smaller genera (Tab. 2). The same tendencies are found for acidophilous and calciphilous forest species.

Relationships between R and other indicator values

When considering the whole flora, the two groups of reaction indicators differ significantly with respect to all other indicator values (Tab. 2): Calciphilous species tend to have their optima in habitats enjoying more nitrogen and light, but less moisture. Climatically, they have a slight preference for warmer sites and their distributions extend further into the continent. Again, the same trends are found, when reaction indicators occurring in forests are compared.

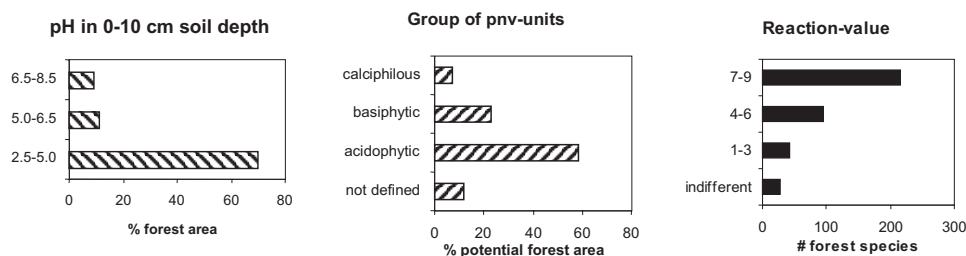


Fig. 5. Frequency of topsoil pH (after federal forest soil monitoring), areal extent of units of potential natural vegetation (after BOHN & NEUHÄUSL 2000) and richness of reaction indicator groups in forests (after ELLENBERG et al. 1991).

DISCUSSION

More than half of the German vascular flora belongs to ecological groups favouring calcareous or very base-rich soils, while a markedly smaller number of species appear to be adapted to acid conditions. The same skew is found in the vascular floras of Austria, where KARRER (unpubl.) assigns 54% out of 3228 taxa to R-classes 7–9, of Hungary, where BORHIDI (1995) put 63% out of 2174 taxa in R-classes 7–9, and of Switzerland, where LANDOLT (1977) places 64% of 3363 taxa in classes 4 and 5 on his 5-point reaction scale. With minor exceptions, the disproportion between calciphytes and acidophytes exists across the major vegetation formations, which makes it unlikely that the proportions are generally biased by the large number of synanthropic species of mediterranean and Irano-Turanian origin. I analyzed the forest flora as the putative core of the natural flora in particular detail.

Plant ecologists familiar with the temperate flora will be far from surprised by this pattern of species richness, and some may even find it uninteresting. In an elegant metaanalysis PÄRTEL (2002) has shown how far from self-evident it is: Acidophytic communities of the south of the temperate zone are usually richer in species because the acidophytic species pools are larger.

The vast majority of contemporary German forest soils are acid and unsuitable habitats for calciphytes, which is also mirrored in maps of potential natural vegetation. The species-area relationship can therefore not explain the large pool of calciphilous forest species. Instead, the majority of forest species appear to depend on quite rare habitats. This raises the question if species pools are in equilibrium with the environment. In fact, industrial immissions have recently enforced the acidification of forest soils beyond its natural level (ULRICH & MEYER 1987), but there is yet little evidence for a corresponding shift in floristic composition (FISCHER 1999).

The distribution of calciphytes among genera and families does not indicate particularly high rates of evolution as compared to acidophytes. This result may be compromised by the fact that I analyzed only the German flora, which may not be representative of the larger continental arena of evolution. Furthermore, the evolution of calciphytes may have occurred quite recently and equally across taxonomic lineages, as suggested by IVERSEN (1958). He

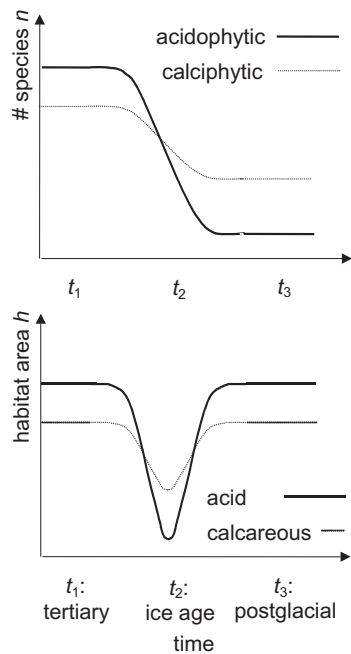


Fig. 6. Palaeoecological model of habitat area and species richness of acidophytes and calciphytes. Habitat areas go through the bottleneck of glacial refugia and recover to pre-glaciation levels, whereas species richness is lost by extinction. The contemporary calciphytic to acidophytic richness ratio corresponds to the calcareous to acid habitat area ratio in refugia:

$$\frac{h_c(t_2)}{h_a(t_2)} = \frac{n_c(t_3)}{n_a(t_3)}$$

extinctions are stochastic, their severity is negatively proportional to the size of the surviving metacommunity (sum of all individuals of all species) during the bottleneck.

Preferences of plant species for calcareous soils are not independent of responses to other environmental gradients. Looking at the total flora, this could raise the suspicion that calciphytic richness really reflects a preference of many species for dry habitats with ample light supply. However, this can be precluded in forests, where calciphytes predominate over acidophytes, although which tend to have higher indicator values for nitrogen and continentality.

In conclusion, this analysis shows that across formation types the Central European species pool for calcareous habitats is larger than that for the much more widespread acid soils. My

believed that the warming phases following continental glaciations with their open woodland communities thriving on unleached calcareous soil favoured the immigration and *in situ* evolution of calciphytes. GRUBB (1987), however, thought that calcareous habitats had been more “apparent” throughout the history of temperate floras, i.e., that the ratio between calcareous and acid habitats was reversed for much of the past.

I propose to combine Iversen’s and Grubb’s arguments with species-area theory and look at the disparity as an inherited species-area relationship (Fig. 6). The exact pre-Pleistocene calciphyte/acidophyte ratio is not crucial for this hypothesis. Nevertheless, it is not unreasonable to assume that highly leached acid soils prevailed for long time periods and favoured the evolution of a predominantly acidophytic flora (t_1), i.e., long-term adaptation proportional to habitat area (ROSENZWEIG 1995). Glaciation (t_2) sharply reduced the total habitat for the European flora causing substantial regional extinctions (WATTS 1988). Soil paleoecology suggests that periglacial processes of denudation, solifluction and loess sedimentation created young calcareous soils at the expense of mature soils (FIEDLER & HUNGER 1970), thus causing a disproportionate decline of acid habitats and their flora. As a result, the postglacial flora (t_3) is selectively impoverished, causing an ecological disparity, that cannot be explained by the contemporary environment. Note that the hypothesis rests on the asymmetry between speciation and extinction: The result of adaptive radiation is rapidly reversed by extinction, while the opposite process requires long time periods. HUBBELL (2001) has recently introduced the term “ecological drift” for such processes: Although species

hypothesis that the disparity reflects a species-area relationship of the past, and thus an example of ecological drift, requires testing by paleoecologists and biogeographers. Modern tools of systematics, biogeography and plant ecology should also be used to search for alternative explanations. Species pool size puts an upper bound on the richness, that can be encountered in individual stands of vegetation (GRIME 1979) and could provide an explanation for the positive relationship between pH and plant species density throughout the temperate zone (ERIKSSON 1993, PÄRTEL et al. 1996). Calciphytic α - and γ -diversity as one of the most consistent gradients of biological richness in the temperate biome (PÄRTEL 2002) deserves much more attention from contemporary students of biodiversity.

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