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RESEARCH PAPER

Plant species richness in continental southern Siberia: effects of pH and climate in the context of the species pool hypothesis

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ABSTRACT

Aim Many high-latitude floras contain more calcicole than calcifuge vascular plant species. The species pool hypothesis explains this pattern through an historical abundance of high-pH soils in the Pleistocene and an associated opportunity for the evolutionary accumulation of calcicoles. To obtain insights into the history of calcicole/calcifuge patterns, we studied species richness–pH–climate relationships across a climatic gradient, which included cool and dry landscapes resembling the Pleistocene environments of northern Eurasia.

Location Western Sayan Mountains, southern Siberia.

Methods Vegetation and environmental variables were sampled at steppe, forest and tundra sites varying in climate and soil pH, which ranged from 3.7 to 8.6. Species richness was related to pH and other variables using linear models and regression trees.

Results Species richness is higher in areas with warmer winters and at medium altitudes that are warmer than the mountains and wetter than the lowlands. In treeless vegetation, the species richness–pH relationship is unimodal. In tundra vegetation, which occurs on low-pH soils, richness increases with pH, but it decreases in steppes, which have high-pH soils. In forests, where soils are more acidic than in the open landscape, the species richness–pH relationship is monotonic positive. Most species occur on soils with a pH of 6–7.

Main conclusions Soil pH in continental southern Siberia is strongly negatively correlated with precipitation, and species richness is determined by the opposite effects of these two variables. Species richness increases with pH until the soil is very dry. In dry soils, pH is high but species richness decreases due to drought stress. Thus, the species richness–pH relationship is unimodal in treeless vegetation. Trees do not grow on the driest soils, which results in a positive species richness–pH relationship in forests. If modern species richness resulted mainly from the species pool effects, it would suggest that historically common habitats had moderate precipitation and slightly acidic to neutral soils.

Keywords

Calcicole/calcifuge, forest-steppe, plant community, Pleistocene environments, precipitation, soil acidity, tundra, vascular plants.

INTRODUCTION

The distinction between calcicole and calcifuge plant species has been recognized since the early days of plant ecology (Gigon, 1987). Many floras in the temperate and boreal zone have a higher proportion of calcicole species, i.e. those associated with high pH or calcium-rich soils, than of calcifuge species, i.e. those confined to low-pH soils (Grubb, 1987; Tyler, 1996; Ewald, 2003).

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Pärtel (2002) demonstrated that at medium and higher latitudes, species richness of vascular plant communities on a local scale (further referred to as richness) frequently increases with soil pH. He related this pattern to the species pool hypothesis (Taylor *et al.*, 1990), suggesting that the positive richness–pH relationships result from the existence of larger pools of calcicole than calcifuge species in modern floras. He hypothesized that this prevalence of calcicoles is due to the location of most evolutionary centres for the temperate and boreal zone in the areas with high-pH soils. Ewald (2003) extended Pärtel's hypothesis to consider not only species accumulation through speciation of calcicoles but also hypothetically high extinction of calcifuges in the Pleistocene, when the climate was cold and dry and high-pH soils were maintained over huge areas by decreased leaching of cations, aeolian sedimentation of fine calcium-rich particles and cryoturbation (Guthrie, 2001; Walker *et al.*, 2001). The modern disparity between the predominance of acidic soils and a considerably larger species pool of calcicole than calcifuge species in temperate Europe may be the result of the Pleistocene bottleneck effects on calcicole/calcifuge species pools (Ewald, 2003).

Even at medium and high latitudes, however, the local richness–pH relationships reported in individual studies vary considerably from negative to positive, and they are often unimodal or non-significant (Schuster & Diekmann, 2003). Interestingly, positive monotonic relationships are often found in forests, while grasslands of the same areas exhibit unimodal, non-significant or even negative relationships (Chytrý *et al.*, 2003; Palmer *et al.*, 2003; Schuster & Diekmann, 2003). Besides possible confounding effects of other environmental variables, this may partly be caused by the different width of the observation window along the pH gradient in individual studies. Plants cannot tolerate either too low pH (due to aluminium toxicity and poor availability of some nutrients) or too high pH (due to poor solubility of some essential elements; Tyler, 2003). Therefore the richness–pH relationship must be inherently unimodal, increasing at low pH and decreasing at high pH. A positive linear relationship is therefore more frequently found in studies performed on acidic to neutral soils, and a negative one is more frequently found in those performed on neutral to base-rich soils. If the entire range of pH values compatible with plant life is considered, the appropriate question is therefore not whether the richness–pH relationship is positive or negative, but whether it is left-skewed, symmetrical or right-skewed.

For a better understanding of the richness–pH relationship, it is of key importance to study it across the full range of pH values tolerated by plants and in areas with different evolutionary and biogeographical histories. So far, such studies have been rare, being based either on the meta-analyses of local case studies (Pärtel, 2002; Schuster & Diekmann, 2003) or on the richness values extracted from the large phytosociological databases combined with indicator values used as surrogates for measured pH (Chytrý *et al.*, 2003; Wohlgemuth & Gigon, 2003).

With respect to the species pool hypothesis (Pärtel, 2002; Ewald, 2003), it is of great theoretical interest to study the species–pH relationship in dry continental areas with long and cold winters, which are close modern analogies of Pleistocene environments, and on geographical transects from such areas to regions with a more oceanic climate. The modern vegetation of temperate Europe has its historical roots in the Pleistocene tundra, steppe and forest-steppe (Berglund *et al.*, 1996), which has its closest modern analogy in continental southern Siberia and northern Mongolia (Hilbig, 1995). This region's climate is locally similar to the Pleistocene climate of central Europe (Frenzel *et al.*, 1992) and its evolutionary history is also similar, as evidenced by the geographical ranges of many plant species that extend from central Europe to southern Siberia (Meusel *et al.*, 1965–1992). In addition, Last Glacial Maximum biomes reconstructed from fossil pollen data for southern Siberia and adjacent areas of Mongolia include steppe and forests, i.e. the same biomes as today (Tarasov *et al.*, 2000). Similar biomes were reconstructed from the full-glacial pollen data from eastern central Europe (Willis *et al.*, 2000; Jankovská *et al.*, 2002).

In the present study, we address the species richness–pH relationship by analysing terrestrial vegetation along a broad-scale geographical transect in continental southern Siberia, which covers a range of different climates and nearly the entire range of pH values compatible with plant life. Our questions are: (1) what is the richness–pH relationship in this landscape, which in some parts preserves conservative features of Pleistocene environments; (2) does the richness–pH relationship interact with other variables, in particular climatic ones; and (3) does this relationship differ between treeless and forest vegetation, and if so, why?

MATERIALS AND METHODS

Study area

The study area is located in southern Siberia (Russia) between the cities of Abakan and Minusinsk in the north and the Russian–Mongolian border in the south (50°43′–53°33′ N; 91°06′–93°28′ E). Its northern part includes the Minusinskaya Basin with flat or gently undulating landforms on Quaternary deposits at altitudes of 300–600 m. The largest, central part of the study area includes the Western Sayan Mountains, namely the area adjacent to the Yenisei river valley. At altitudes of 350–1700 m these mountains have a rugged topography with steep slopes on metamorphic rocks, mainly base-rich chloride slates, with igneous rocks and limestones occupying small areas. Ancient table-lands predominate at high altitudes (1700–2860 m). Similar landforms are typical of the Tannu-Ola range (2100–2930 m) in the southern part of the study area. The area between the Western Sayan and Tannu-Ola is occupied by the Central Tuvinian Basin with flat landforms at altitudes of 550–1100 m.

The climate is strongly continental. However, the northern front ranges of the Western Sayan, which intercept humid north-western air masses, have a more humid climate in comparison with the rest of Siberia. At low to medium altitudes in the north, January temperature ranges from −11 to −22 °C, July temperature from +16 to +19 °C and annual precipitation from 500 to 900 mm. Winter snow cover is up to 1.5 m, which protects soil and ground vegetation from frost. The Central Tuvinian Basin and the Tannu-Ola range are in the rain shadow area and have an arid continental climate with annual precipitation of < 400 mm, of which 88–95% falls from late July to September. January temperature ranges from −27 to −34 °C, July temperature from +16 to +18 °C and winter snow cover is shallow and irregular in this region (Gidrometeoizdat, 1966–1970).

Vegetation formations include steppe on the bottoms of the Minusinskaya and Central Tuvinian Basins, forest-steppe and forest at medium altitudes, and alpine tundra above the timberline. Forests are abundant in the wetter northern part of the Western Sayan. In contrast, in the cool and dry areas adjacent to the Central Tuvinian Basin, steppe extends to higher altitudes and tundra to lower altitudes, while forest is restricted. In the forest-steppe landscapes, steppe regularly occurs on south-facing slopes, and forest occurs on north-facing slopes. Cold and dry lowland steppes are characterized by *Artemisia frigida* Willd., *Caragana pygmaea* (L.) DC. and *Stipa krylovii* Roshev., and mountain steppes in the forest-steppe zone are often dominated by *Artemisia gmelinii* Weber, *Carex pediformis* C. A. Mey. and *Spiraea media* Schmidt. Some of the mountain steppes, occurring on mesic soils, form dense tall-grass species-rich stands, called meadow steppes. Alpine tundra is mostly dominated by dwarf shrubs (*Betula rotundifolia* Spach, *Vaccinium myrtillus* L. and *V. vitis-idaea* L.) on ridges and hillsides, and tall forbs on the valley bottoms. The forests of the study area can be divided into taiga and hemiboreal forests (Ermakov *et al.*, 2000). Taiga occurs on moist to mesic soils and is mostly dominated by *Abies sibirica* Ledeb., *Picea obovata* Ledeb. and *Pinus sibirica* Du Tour. It includes *Vaccinium myrtillus*, *V. vitis-idaea* and *Bergenia crassifolia* (L.) Fritsch in the herb layer and a well-developed moss layer. Hemiboreal forests, also called sub-taiga, occupy mesic to dry soils. They contain many shade-intolerant herbs, some of which occur both in steppe and open forests. Hemiboreal forests in the driest and coolest areas are dominated by *Larix sibirica* Ledeb and are termed ultracontinental forests, while those in the wetter and warmer areas are dominated by *Pinus sylvestris* L. or *Betula pendula* Roth, the latter often occurring in post-fire successional stands.

Data sampling

Sampling sites were located on an approximately 300-km long north–south transect that followed the gradient of increasing climate continentality and ran roughly perpendicular to the Western Sayan range. The transect started in the lowlands, dominated by steppe and forest-steppe vegetation in the Minusinskaya Basin, crossed the Western Sayan mountain range, continued to the Central Tuvinian Basin and ended at the Tannu-Ola range. Along this transect, we sampled vegetation in the zones of steppe, forest-steppe, forest and alpine tundra. Sampling units were vegetation plots of 10 × 10 m, located in central parts of physiognomically and ecologically homogeneous vegetation stands. Sites affected by recent disturbances, e.g. early stages of post-fire succession or human-made habitats, were avoided. Landscape sectors with different macroclimates, sharply separated by mountain ridges, were used as the basic sampling strata. Within each stratum, we placed one plot on each of the following landforms: north-facing slope, south-facing slope, ridge summit and valley bottom. If the same landform in a given stratum contained vegetation types of contrasting physiognomy or with different dominant species (including different dominants of forest undergrowth), we placed one plot in each of these vegetation types. In total, 180 plots of treeless vegetation (39 in tundra and 141 in steppe) and 127 plots of forest vegetation (77 in taiga and 50 in hemiboreal forest) were sampled.

In each plot, we recorded all species of vascular plants and measured the following variables (Table 1). (1) *Altitude* was measured with GPS and checked in a 1:100,000 topographic map. (2) *Climatic variables* (July and January mean temperature and mean sums of summer and winter precipitation) were estimated from a climatic model prepared in the ArcGIS 8.2 geographical information system (http://www.esri.com/). The model was based on a combination of Russian climate station data and altitudes from a digitized 1:200,000 topographic map. Temperature values for different altitudes were computed based on the adiabatic lapse rate of 0.65 °C per 100 m of altitude. Precipitation was computed from precipitation–altitude charts compiled for each of the aridity–humidity sectors of the Altai-Sayan region (Polikarpov *et al.*, 1986). (3) *Potential solar radiation above the canopy* was calculated from slope aspect, inclination and latitude, and accounted for shading by the surrounding topographic features. Topographic shading was measured from digital hemispheric photographs taken in a vertical direction at the height of 1.5 m above ground at each site. Calculation was performed using Gap Light Analyser 2.0 software (http://www.rem.sfu.ca/forestry/downloads/gap_light_analyzer.htm). Radiation was estimated as the daily sum of direct and diffuse radiation for 21 June. (4) *Potential solar radiation below the canopy* was calculated for the forest plots only. It was obtained in the same way as radiation above the canopy, but it additionally accounted for shading by canopy. (5) *Slope inclination* was measured with a clinometer. (6) *Soil depth* was measured in three places in each plot and averaged. Soils deeper than 30 cm were arbitrarily given a value of 30 cm. (7) *Soil pH and conductivity of soil solution* were measured from a mixed soil sample from three places in each plot. Samples were taken from the mineral topsoil horizon at a depth of 5–10 cm or less if the soil was very shallow. Each sample was extracted in distilled water for 24 h (weight ratio of soil/water was 0.4) and measured using the digital PH114 pH-meter and CM113 conductivity meter (Snail Instruments, Beroun, Czech Republic). Conductivity caused by H^+ ions was subtracted according to Sjörs (1952).

Data analysis

All the statistical analyses were computed in the STATISTICA 7.1 program (http://www.statsoft.com). To simplify the complex pattern of correlations between environmental variables, the matrix of variables × plots was subjected to principal components analysis (PCA), computed on a correlation matrix in order to remove the effect of different measurement units. Additionally, least-square linear regressions were calculated for some univariate relationships that involved pH.

Table 1 Descriptive statistics for variables used in the analysis.

	Mean	Standard deviation	Minimum	Lower quartile	Upper quartile	Maximum
Treeless vegetation (*n* = 180)						
Altitude (m a.s.l.)	1004	480	318	592	1461	2160
July temperature (°C)	14.9	3.1	7.0	14.0	17.0	19.0
January temperature (°C)	–28.0	5.5	–36.0	–32.0	–26.5	–17.0
Summer precipitation (mm)	475	347	170	231	559	1341
Winter precipitation (mm)	87	83	28	33	117	369
Radiation (mol m^{-2} day^{-1})	38.0	4.0	26.0	37.0	40.0	42.0
Inclination (°)	19	13	0	9	29	52
Soil depth (cm)	16	10	1	6	30	30[a]
Soil pH	6.7	1.1	3.7	6.3	7.5	8.6
Soil conductivity (μS cm^{-1})	120	251	2	49	152	353[b]
Number of vascular plants	31.6	12.4	7.0	22.5	41.0	64.0
Forests (*n* = 127)						
Altitude (m a.s.l.)	968	414	346	614	1241	1948
July temperature (°C)	13.9	2.2	9.0	12.0	16.0	18.0
January temperature (°C)	–25.0	5.5	–37.0	–29.0	–20.0	–17.0
Summer precipitation (mm)	657	267	171	425	821	1283
Winter precipitation (mm)	144	78	28	76	187	371
Radiation above canopy (mol m^{-2} d^{-1})	36.1	3.5	24.7	34.7	39.0	41.0
Radiation below canopy (mol m^{-2} d^{-1})	13.3	4.3	6.0	10.0	15.7	33.0
Inclination (°)	21	12	0	10	29	46
Soil depth (cm)	20	10	1	10	30	30[a]
Soil pH	5.7	0.9	3.7	5.0	6.3	7.8
Soil conductivity (μS cm^{-1})	56	45	12	29	65	290
Number of vascular plants	29.3	12.5	6.0	19.0	38.0	69.0

[a] Soils deeper than 30 cm were arbitrarily given a value of 30 cm.

[b] In one plot an outlying conductivity value of 3350 μS cm^{-1} was measured.

In ecological data sets sampled across heterogeneous landscapes, representation of plots with different combinations of environmental variables is typically more or less unequal. This occurs in spite of the use of a stratified sampling scheme such as that applied in the current study, because some combinations may be rare or non-existent in some of the studied landscapes. In traditional statistical analyses, e.g. linear models, such an unbalanced structure of the data set can be problematic if several explanatory variables are involved. Therefore, we analysed the relationships between the response variable (species richness) and several environmental explanatory variables with regression trees (CART; Breiman *et al.*, 1984). This method is suitable for exploratory analysis of complex unbalanced data sets that involve higher-order interactions and nonlinear relationships between predictor variables. It is able to reveal ecologically meaningful relationships that would remain hidden in such data sets if standard techniques such as linear models were used. The regression tree is constructed by a hierarchical splitting of the data set into smaller groups, which minimizes within-group variation in the response variable. At each split, sampling units are divided into two groups based on a single explanatory variable.

We applied regression tree analysis separately to the data sets of treeless and forest vegetation and used the number of vascular plants as the response variable. To select the optimal tree size (optimal number of branches, also called nodes or splits), we used the 10-fold cross-validation method. This method calculates regression trees on smaller subsamples of the basic data set and provides the value of cross-validation cost for the tree of each size, i.e. the error in predicted values relative to the corresponding tree calculated with the entire data set. The tree with the lowest cross-validation error is usually accepted as the optimal tree because it maximizes the variation in the response variable and simultaneously minimizes the risk of over-learning, i.e. the danger of erroneous prediction of previously unobserved cases. For selection of the optimal tree based on the cross-validation results, we followed SE Rule = 0 (Breiman *et al.*, 1984) because SE Rule = 1 led to very simple trees. For each node of the tree, we identified not only the primary splitter variable but also surrogates, i.e. the variables that are able to allocate cases similarly as the primary splitter. To consider a variable as a surrogate, we required that the variable had associated value higher than 0.6. To assess the relative importance of each predictor variable in the optimal tree, we calculated their Importance values, which are relative to the best predictor variable, scored as 100. The importance values reflect the contribution that each explanatory variable makes in explaining the variation in the response variable, with

Table 2 Coordinates of environmental variables on axes 1–4 of the PCA calculated from a matrix of vegetation plots × environmental variables. As PCA was based on the correlation matrix, the coordinates are identical with the correlations between PCA axes and environmental variables. Coordinates ≥ |0.60| are set in bold.

PCA axis	1	2	3	4
Percentage variation explained	34.5	18.8	15.4	9.9
Altitude	−0.49	**−0.80**	0.11	−0.01
July temperature	**0.78**	0.52	−0.13	0.06
January temperature	−0.13	**0.87**	−0.39	−0.14
Summer precipitation	**−0.90**	0.18	−0.10	−0.27
Winter precipitation	**−0.88**	0.24	−0.18	−0.25
Radiation above canopy	0.30	−0.27	**−0.63**	−0.49
Radiation below canopy	0.59	−0.28	−0.01	**−0.60**
Slope inclination	−0.09	0.38	**0.77**	−0.06
Soil depth	0.13	−0.13	**−0.62**	0.52
Soil pH	**0.88**	−0.02	0.15	−0.04
Soil conductivity	0.31	0.06	0.22	−0.23

its contribution stemming both from the variable's role as a primary splitter of a node and its role as a surrogate to any of the primary splitters.

RESULTS

PCA revealed groups of related environmental variables (Table 2). The main complex environmental gradient associated with PCA axis 1 is that of decreasing precipitation and increasing soil pH. The second most important gradient (axis 2) is related to decreasing altitude and increasing winter temperature, the third gradient (axis 3) to slope steepness and associated variables such as soil depth and site insolation, and the fourth gradient (axis 4) to canopy closure and light availability above the herb layer. An important relationship revealed by PCA axis 1 is the strong negative correlation of pH with precipitation; this trend is consistent in both treeless vegetation and forests, although the mean pH is lower in the latter (Fig. 1). Another remarkable relationship revealed by PCA is that precipitation is not correlated with winter temperature. While winter temperature generally decreases with increasing altitude, precipitation in both winter and summer is to a large extent determined by the position on the windward or leeward side of the main mountain ranges, although at local scale it also tends to increase with altitude.

Univariate regressions of species richness on pH revealed a positive relationship for both treeless and forest vegetation (Table 3). In the treeless vegetation, pH explained only 2.5% of variation in species richness in linear regression, but after adding the quadratic term the variation explained increased to 17.0%, indicating unimodal richness–pH relationship with a peak at pH 6.4. In tundra vegetation, which occurred in the pH range of 3.8–6.1 (–7.4), there was a positive linear relationship between richness and pH that explained 13.0% of variation (Fig. 2a). However, in steppe vegetation, which occurred in the pH range of 5.9–8.1 (–8.6), the linear relationship was negative. In forests, variation explained by the linear regression was considerably higher than in treeless vegetation (25.8%), but it was improved only to 28.1% after adding the quadratic term (although the quadratic model improved the model significantly; $P < 0.05$). The curve of the quadratic relationship was upward convex, with an indistinct peak occurring at pH 7.2 which did not provide reliable support for the existence of the unimodal richness–pH

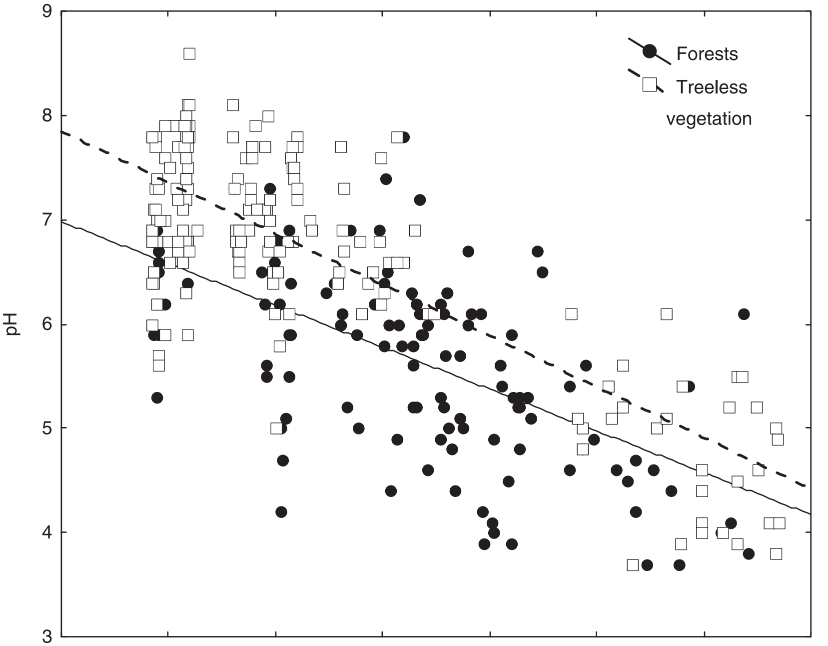

Figure 1 The relationship between pH and summer precipitation in the study area. Precipitation values were predicted by the climatic model and soil pH(H_20) was measured in vegetation plots. Treeless vegetation: $R^2_{adj} = 0.633$; forests: $R^2_{adj} = 0.325$. The slopes of the two regression lines are significant ($P < 0.001$), but do not differ significantly from each other at $P < 0.05$. The difference in intercept between them is significant ($P < 0.001$). Values of pH also decrease significantly with winter precipitation at $P < 0.001$ (not shown; treeless vegetation: $R^2_{adj} = 0.594$, forests: $R^2_{adj} = 0.332$).

Table 3 Standardized regression coefficients (beta), variation explained (R^2_{adj}) and significances (P) of the linear and quadratic regression models of the relationship between species richness and pH for different subsets of vegetation plots. Quadratic regressions were not considered for tundra, steppe, taiga and hemiboreal forests.

	beta-pH	beta-(pH)^2	R^2_{adj}	P
Treeless vegetation:				
both types, linear regression	0.17	—	0.025	0.025
both types, quadratic regression	3.94	−3.80	0.170	< 0.001
tundra	0.36	—	0.130	0.022
steppe	−0.31	—	0.091	< 0.001
Forests:				
both types, linear regression	0.52	—	0.258	< 0.001
both types, quadratic regression	2.36	−1.85	0.281	< 0.001
taiga	0.44	—	0.170	< 0.001
hemiboreal forests	0.09	—	0.0	0.525

relationship in forests. After splitting the forest data set into taiga and hemiboreal forests (Fig. 2b), a positive relationship only remained in the more acidic taiga (pH 3.7–6.9) while no relationship was detected in the base-rich hemiboreal forests (pH 5.2–7.8).

Regression trees were constructed separately for treeless and forest vegetation. In both of them, January temperature, altitude and pH were the most important predictors of species richness (Table 4). For treeless vegetation, the optimal regression tree with the lowest cross-validation cost had seven terminal nodes (Fig. 3). This tree explained 56.1% of variation in species richness. In the first node the tree split based on mean January temperature, predicting lower species numbers in areas with January means below −21 °C and at altitudes above 532 m. In low-altitude areas with warmer winters, species richness increased with altitude, i.e. with precipitation. The highest richness was found at altitudes slightly above 500 m and summer precipitation above 479 mm:

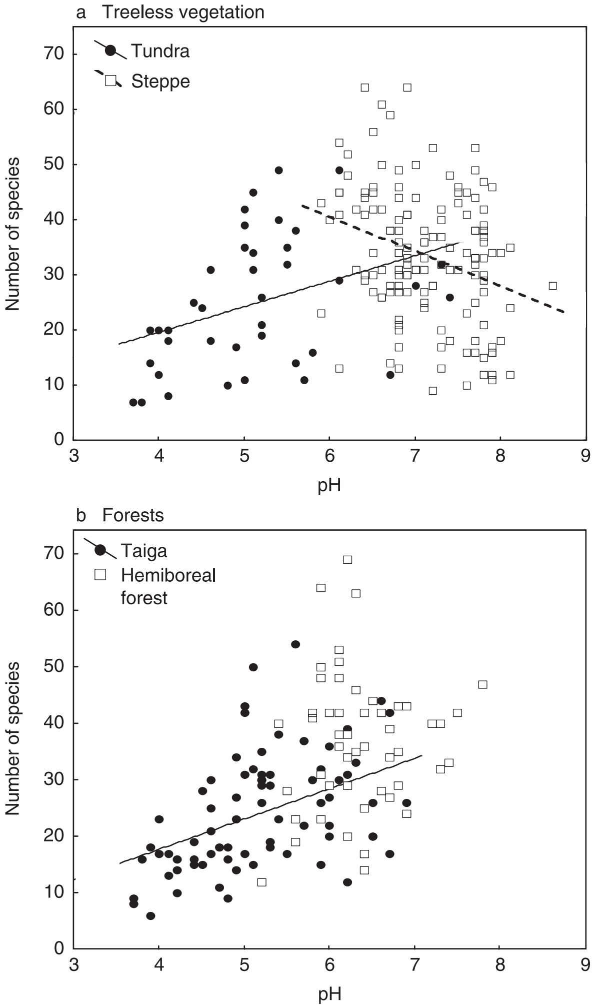

Figure 2 Relationships between number of vascular plant species per 100 m^2 and pH. See Table 3 for regression coefficients. The slope of the regression line was not significant for hemiboreal forests, therefore the line was not fitted.

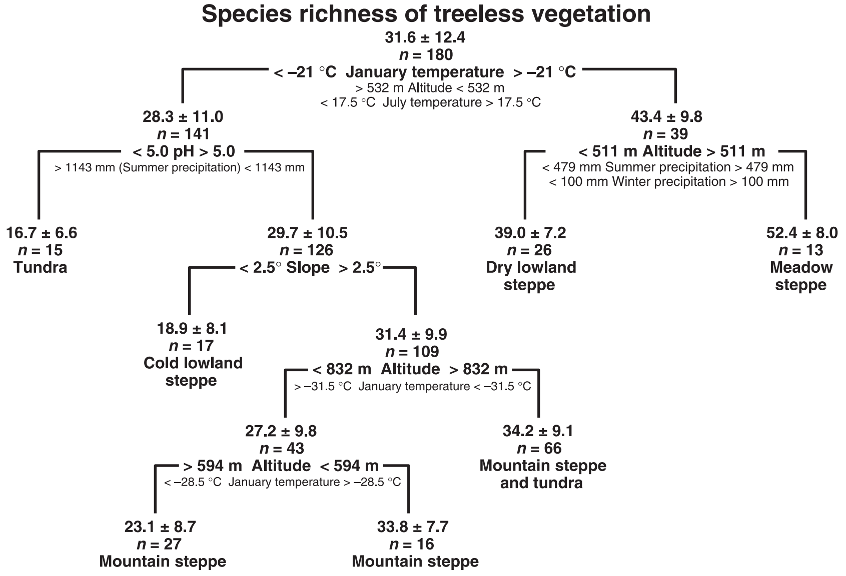

Figure 3 Regression tree for species richness of treeless vegetation. Numbers at each node indicate the mean number of vascular plant species per 100 m^2 ± standard deviation and number of plots assigned to that node. The primary splitter variable and its split value at each node is given in bold. Surrogates, i.e. variables that allocate most cases to the identical group as the primary splitter, are given in smaller letters below the primary splitter.

Table 4 Ranked values of the relative importance of explanatory variables of the optimal regression trees for treeless and forest vegetation. The values reflect the contribution each explanatory variable makes in explaining the variation in species richness, with its contribution stemming both from the primary splitter of a node, and its role as a surrogate to any of the primary splitters. The variable with the highest relative importance is scored as 100 in each regression tree.

Treeless vegetation		Forests	
Variable	Relative importance	Variable	Relative importance
January temperature	100	Altitude	100
Altitude	82.1	January temperature	97.6
Soil pH	72.3	Soil pH	94.9
Winter precipitation	61.8	July temperature	77.7
Slope inclination	59.3	Soil conductivity	77.1
Summer precipitation	56.9	Summer precipitation	61.7
Soil conductivity	48.8	Winter precipitation	46.2
July temperature	44.7	Soil depth	19.6
Soil depth	29.7	Slope inclination	17.0
Radiation	16.0	Radiation above canopy	15.5
		Radiation below canopy	14.2

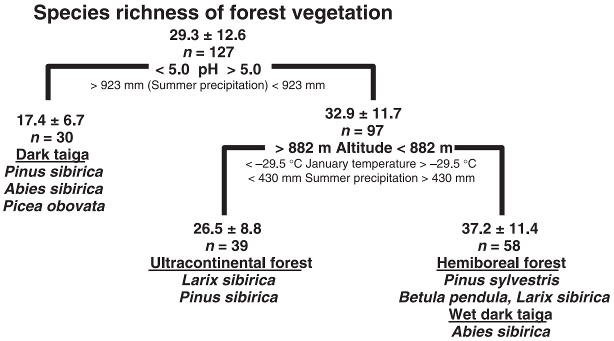

Figure 4 Regression tree for species richness of forests. See Fig. 3 for a detailed explanation. At the first node, the best surrogate, summer precipitation, had only 30% similarity to the primary splitter.

grassland vegetation occurring there included mostly tall-grass meadow steppes, containing on average over 50 species per 100 m^2. In the branch of the tree with low January temperatures, the most important predictor of species richness was pH. It discriminated between very poor tundra vegetation on soils with pH < 5.0 and richer vegetation of both tundra and steppe on more base-rich soils. In the latter, the poorest vegetation was the cold short-grass steppe on the flat bottoms of large basins, while mountain steppe and tundra vegetation was richer. The latter types of mountain grasslands were poorer at medium altitudes (594–832 m) where forest forms the landscape matrix and treeless vegetation mostly occurs in smaller patches surrounded by forest.

The optimal regression tree for forest vegetation had only three terminal nodes (Fig. 4). First it separated species-poor dark taiga forests on acidic soils with pH < 5.0 from richer forests on more base-rich soils. Low pH was weakly related to higher summer precipitation. The group of species-richer forests on high-pH soils was further divided into two subgroups. The poorer subgroup at altitudes above 882 m, with low winter temperatures and low summer precipitation, contained ultracontinental forests of *L. sibirica* and *P. sibirica*. The richer subgroup at lower altitudes with warmer winters and higher summer rainfall included hemiboreal forests and wet *Abies sibirica* taiga; this subgroup included the richest forests of the Western Sayan, containing on average 37 species per 100 m^2. This regression tree explained 41.2% of variation in species richness. For comparison, we fitted a multiple least-square regression model with the two predictors used as primary splitters in this tree: pH and altitude. This model explained only 38.0% of variation.

Higher mean local species richness in steppe and hemiboreal forests than in tundra and taiga, revealed by the regression trees, corresponded to the relative size of species pools for these formations. The relative size of the species pools was estimated as the total number of all species occurring in 39 plots selected randomly from each of these formations. These relative estimations yielded 305 species for steppe, 223 for tundra, 303 for hemiboreal forests and 212 for taiga (means of 10 random selections).

DISCUSSION

The relationship between pH, precipitation and species richness

The study area contains bedrocks of varying base status and soils of different type and depth. Yet, soil pH was shown to depend predominantly on precipitation: summer precipitation explained 63.3% of variation in soil pH in sites with treeless vegetation (Fig. 1). Such an amount of variation explicable by a single predictor variable is surprisingly large, given that the precipitation model used included inaccuracies due to a sparse network of climate stations. In addition, the moisture status of particular sites depends not only on precipitation but also on the topographic position on the valley bottom or the ridge, slope aspect, inclination and soil properties. The strong pH–precipitation relationship suggests that on the transition between arid continental and more humid landscapes, the intensity of leaching of basic cations from soils is crucial for maintaining high or low pH.

In forests, mean pH was significantly lower than in treeless vegetation (Fig. 1). This partly reflects the fact that in forest-steppe landscapes, forest grows in moister places with a higher intensity of leaching than steppe vegetation. However, as forest soils are more acidic than non-forest soils in the precipitation-rich areas as well, more intensive acidification processes probably occur in forest soils. These may result from: (1) higher moisture status and more intensive soil leaching under the forest canopy, which decreases evaporation; (2) larger uptake of bases and their replacement by H^+ cations in the more productive forest vegetation; (3) higher abundance of mosses contributing to acidification (Vitt, 2000); or (4) inputs of organic acids from conifer litter (Ovington, 1953; Finzi *et al.*, 1998). A much lower variation in pH explained by summer precipitation for forest sites (33.2%) than for treeless sites (63.3%) is another indication of a stronger effect of vegetation on soil pH in forests than in open landscape.

In both treeless and forest vegetation, the best correlates of species richness were January temperature, pH and altitude (Figs 3 and 4, Table 4). Climatic variables such as summer temperatures and precipitation were correlated with them (Table 2). Other measured variables were either correlated with these variables or weakly related to the species richness pattern (Tables 2 & 4). This corresponds to the alpine vegetation of the Alps, where species richness is mainly determined by the joint effects of temperature and pH, while other variables are less important (Vonlanthen *et al.*, 2006). In the continental climate of the study area with its very cold winters, frost can be an important ecological factor limiting plant life, especially in combination with low winter precipitation and shallow or discontinuous snow cover. Actually, areas with the strongest winter frosts had the species-poorest vegetation. Both treeless and forest vegetation were consistently poorer on soils with $pH < 5.0$, which corresponds to the value where toxic Al^{3+} cations start to solubilize (Tyler, 1996). The relationship between richness and altitude was more complex in the study area, reflecting interactions between climatic variables. At high altitudes, richness was lower due to low winter temperatures, irrespective of the amount of precipitation, whereas at lower altitudes, richness increased with precipitation.

The most species-rich treeless vegetation corresponded to tall-grass meadow steppe, occurring at altitudes slightly above 500 m, which still have comparatively warm winters but higher precipitation than dry lowlands. The poorest treeless vegetation was tundra occurring in areas with pronounced winter frosts and high precipitation, which causes soil leaching and acidification. The richest forest vegetation occurred in areas where precipitation was not too high to cause pronounced soil leaching and not too low to exclude mesic forest species. Such habitats supported either *Pinus sylvestris* hemiboreal forest or *Abies sibirica* wet taiga on footslopes and valley bottoms. The poorest forest was dark taiga with *Pinus sibirica, Abies sibirica* or *Picea obovata*, occurring on low-pH soils in precipitation-rich areas.

Unimodal pH–richness relationship in treeless vegetation

A positive richness–pH relationship has been more frequently reported from the temperate, boreal and arctic zones than has a negative one (Pärtel, 2002). In more detail, the sign and shape of this relationship depends on vegetation types (Chytrý *et al.*, 2003; Schuster & Diekmann, 2003). The relationship tends to be positive in vegetation types that grow predominantly on acidic to neutral soils, e.g. in forests and tundra. In contrast, treeless vegetation on neutral to base-rich soils tends to have a non-significant or negative richness–pH relationship.

Our study provides a finer and more complete picture than most others because it covers nearly the whole range of soil pH compatible with plant life. The existence of upper and lower physiological limits to plant growth on the pH gradient implies that the relationship is inherently unimodal. This is reported by some studies covering broad ranges of pH values, especially in grasslands (e.g. Tyler, 2000; Löbel *et al.*, 2006) and mires (e.g. Glaser *et al.*, 1990). We found a pronounced unimodal richness–pH relationship in treeless vegetation but not in forests.

Within treeless vegetation, tundra occurred on low-pH soils in precipitation-rich areas, and steppe on high-pH soils in precipitation-poor areas. After splitting these two vegetation types, the former showed a positive linear relationship to soil pH and the latter showed a negative linear relationship. The positive relationship in the southern Siberian alpine tundra is consistent with a number of earlier studies from the arctic tundra, where increasing pH was identified as one of the major factors enhancing species richness (Gough *et al.*, 2000; Walker *et al.*, 2001; van der Welle *et al.*, 2003). In contrast, steppe vegetation, which occurred on soils with pH 5.9–8.6, exhibited a weak yet significant negative linear relationship between richness and pH. This relationship appears to be consistent with earlier studies from North American prairies (Palmer *et al.*, 2003). Our data suggest that the decreasing species richness of steppe vegetation on high-pH soils could be caused by climatic stress instead of or in addition to the physiological effect of high pH. The highest pH values are found in the driest soils with strongly limited or no cation leaching (Fig. 1). However, these habitats experience not only pronounced summer droughts but also strong winter frosts without protective snow cover. As most species of the study area are not adapted to such harsh conditions, the negative richness–pH correlation appears. The richest vegetation occurs where soil is not too dry and not too acidic at the same time. Our data suggest that for the treeless vegetation of the study area it is at pH 6–7.

The putative role of drought stress in limiting species richness on high-pH soils is supported by the comparison with richness–pH relationships reported for wetlands and mires. In these habitats, high pH is usually due to cation saturation from mineral springs and it is not associated with drought stress. In such environments, species richness often increases up to pH 7 or even beyond (Glaser *et al.*, 1990; Hájková & Hájek, 2003; Güsewell *et al.*, 2005). However, no base-rich wetlands or mires were included in the current study because they are very rare in the study area.

Positive pH–richness relationship in forests

Unlike in treeless vegetation, the richness–pH relationship in forests is mostly reported as monotonic positive (Dupré *et al.*, 2002; Schuster & Diekmann, 2003), while unimodal relationships are rare and negative relationships are exceptional. The latter are usually attributed to the confounding effects of factors other than pH (Dupré *et al.*, 2002). Species richness in forests usually increases steeply in acidic soils, but the curve becomes less steep above pH 5.5 and often levels off at a pH value close to 7.0. A positive relationship is documented both from deciduous forests of Europe (e.g. Brunet *et al.*, 1997; Dumortier *et al.*, 2002; Chytrý *et al.*, 2003; Wohlgemuth & Gigon, 2003; Coudun & Gégout, 2005; Schuster & Diekmann, 2005) and North America (e.g. Peet & Christensen, 1980; Brosofske *et al.*, 2001; Peet *et al.*, 2003) and from coniferous forests in both continents (Rey Benayas, 1995; Brosofske *et al.*, 2001; Zinko *et al.*, 2006). Palmer *et al.* (2003) pointed to the contrasting pH–richness relationships in Oklahoma forests and prairies, positive in the former and negative in the latter. The same pattern, based on entirely different species pools, was found in forests and steppes in our study area (Fig. 2).

We hypothesize that the predominance of the positive richness–pH relationship in forests mainly results from the truncated pH gradient at its base-rich end (Fig. 5). There are two reasons for this truncation. First, forest cannot grow at extremely dry sites that only support grassland, but these sites tend to have the highest pH, at least in the semi-arid areas such as forest-steppe. Second, productive vegetation with trees tends to decrease soil pH (Fig. 1; Tyler, 2003). Truncation of the pH gradient in forests is also apparent in the meta-analysis of German case studies (Schuster & Diekmann 2003), where grasslands were often recorded on soils with pH 7–8, but very few studies reported forests on soils with pH > 7. Because the truncation removes habitats where species pool sizes have already started to decrease due to drought stress, most richness–pH relationships reported in the literature from forests are monotonic positive. Besides this main explanation, we suggest two other mechanisms that can explain why the richness–pH curve of forest vegetation does not usually decrease at high-pH conditions (Fig. 5). First, the species richness of forests on soils with pH values of about 7 can be partly increased by the mass effect at the forest-steppe ecotone. Forests on such soils, which are usually rather dry, contain several species typical of adjacent dry grasslands. These light-demanding species find a suitable habitat under the open canopy formed by pine or larch. In contrast, no such mass effect can enhance the species richness of grasslands at pH 7.5–8.5 because there are no sufficiently large species pools of other vegetation types available for this pH range in the study area. Second, in dry areas such as the forest-steppe zone, the forest canopy maintains higher air humidity in the understorey than in treeless habitats (Moore *et al.*, 2000). Therefore, forest richness may not be so much limited by drought stress as is steppe richness on soils with pH values of about 7.0–7.5.

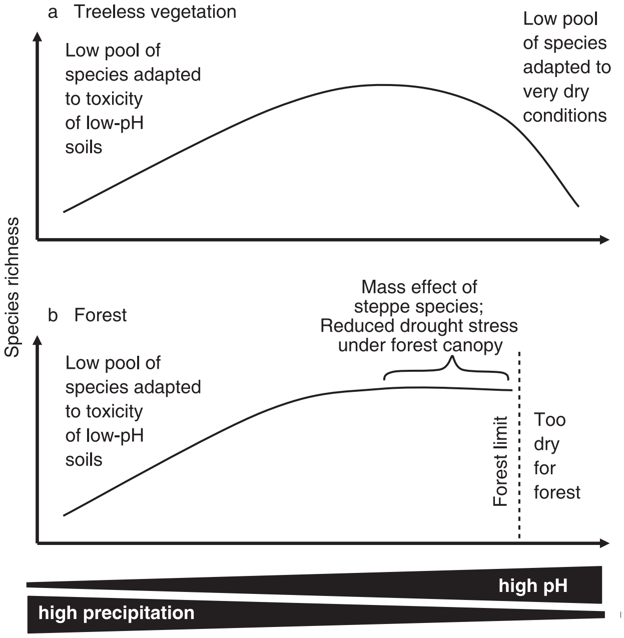

Figure 5 Conceptual model of species richness in treeless vegetation and forests across the combined gradient of decreasing precipitation and increasing pH. On low-pH soils in precipitation-rich areas, pools of species adapted to toxic effects of Al^{3+} and H^+ ions are limited and species richness is low. With decreasing precipitation and increasing pH, richness first increases but subsequently decreases, because of a limited pool of species adapted to very dry conditions. In contrast, forest richness does not decrease or decreases only slightly in precipitation-poor areas for the following reasons: (1) forests do not occur in the driest areas, so the extreme end of the precipitation–pH gradient is truncated; (2) forests occurring on their ecological limit have an open canopy and their herb layer is saturated by steppe species pools; and (3) the protective effect of forest canopy maintains higher air humidity and reduces drought stress.

Species pools and the Pleistocene bottleneck

The species pool hypothesis predicts that the species richness of particular habitats is correlated with the historical habitat commonness and associated opportunities for species accumulation over evolutionary time (i.e. speciation minus extinction; Aarssen & Schamp, 2002). Over most of today's temperate zone of Eurasia, the Pleistocene climate was not only cool but was also dry (Frenzel *et al.*, 1992). Such a climate supported the development of dry calcium-rich soils over vast areas of cold steppe, the habitat of large Pleistocene herbivores (Guthrie, 2001; Walker *et al.,* 2001). Patches of coniferous forests also occurred in some areas, mainly in the mountains and wet lowland sites; they have been reconstructed from the full-glacial fossil data both from the Russian–Mongolian border area (Tarasov *et al.*, 2000) and from central Europe (Willis *et al.*, 2000; Jankovská *et al.*, 2002). Tundra was confined to places with higher precipitation or lower evapotranspiration, e.g. in the mountains or at non-glaciated higher latitudes, often in the close vicinity of steppe (Tarasov *et al.*, 2000).

The present-day landscape in some parts of southern Siberia and Mongolia is probably the closest modern analogy to the Pleistocene environments that existed in the non-glaciated part of northern Eurasia. It has to be pointed out that modern analogies are never perfect. Predictions based on analogies must not be taken too seriously until there is independent and reliable fossil evidence. However, if modern analogies exist, they may provide valuable insights and enhance our understanding of ecological patterns and processes in the past environments.

The current study included vegetation types with the same leading species as reconstructed from the full-glacial central Europe (Willis *et al.*, 2000; Jankovská *et al.*, 2002), and parts of the study area had a climate corresponding to the cool periods of the Pleistocene (Frenzel *et al.*, 1992). In southern Siberia, the richest vegetation is found on soils with a pH of 6–7 (Fig. 2), which are associated with moderate precipitation (Fig. 1). If the modern species richness of different habitats resulted from speciation and extinction in the historically prevailing environments (species pool effects; Aarssen & Schamp, 2002; Pärtel, 2002; Ewald, 2003), this pattern would suggest that such slightly acidic to neutral soils were common in the pre-Holocene environments of temperate Eurasia. In contrast, very dry calcium-rich steppe or wet acidic tundra probably never supported species-rich vegetation.

Increasing precipitation in the Holocene, especially in areas with an oceanic climate, caused large-scale soil acidification (Roberts, 1998). The species-pool hypothesis predicts that today's acidic soils, although prevailing in large areas, are poor in species because of the lack of calcifuge species, which may have become largely extinct during the Pleistocene (Ewald, 2003). Such acidified habitats are represented in the wetter parts of the study area by taiga forests (in warmer climate) or by tundra (in cooler climate). Both of these habitats are generally species poor, but exhibit positive richness–pH relationships, for which the species pool hypothesis provides a plausible explanation.

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REFERENCES

Aarssen, L.W. & Schamp, B.S. (2002) Predicting distributions of species richness and species sizes in regional floras: applying the species pool hypothesis to the habitat templet model. *Perspectives in Plant Ecology, Evolution and Systematics*, **5**, 3–12.

Berglund, B.E., Birks, H.J.B., Ralska-Jasiewiczowa, M. & Wright, H.E. (1996) *Palaeoecological events during the last 15,000 years.* John Wiley & Sons, Chichester.

Breiman, L., Friedman, J.H., Olshen, R.A. & Stone, C.G. (1984) *Classification and regression trees.* Wadsworth International Group, Belmont, CA.

Brosofske, K.D., Chen, J. & Crow, T.R. (2001) Understory vegetation and site factors: implications for a managed Wisconsin landscape. *Forest Ecology and Management*, **146**, 75–87.

Brunet, J., Falkengren-Grerup, U., Rühling, A. & Tyler, G. (1997) Regional differences in floristic change in South Swedish oak forests as related to soil chemistry and land use. *Journal of Vegetation Science*, **8**, 329–336.

Chytrý, M., Tichý, L. & Roleček, J. (2003) Local and regional patterns of species richness in Central European vegetation types along the pH/calcium gradient. *Folia Geobotanica*, **38**, 429–442.

Coudun, C. & Gégout, J.-C. (2005) Ecological behaviour of herbaceous forest species along a pH gradient: a comparison between oceanic and semicontinental regions in northern France. *Global Ecology and Biogeography*, **14**, 263–270.

Dumortier, M., Butaye, J., Jacquemyn, H., Van Camp, N., Lust, N. & Hermy, M. (2002) Predicting vascular plant species richness of fragmented forests in agricultural landscapes in central Belgium. *Forest Ecology and Management*, **158**, 85–102.

Dupré, C., Wessberg, C. & Diekmann, M. (2002) Species richness in deciduous forests: Effects of species pools and environmental variables. *Journal of Vegetation Science*, **13**, 505–516.

Ermakov, N., Dring, J. & Rodwell, J. (2000) Classification of continental hemiboreal forests of North Asia. *Braun-Blanquetia*, **28**, 1–131.

Ewald, J. (2003) The calcareous riddle: why are there so many calciphilous species in the Central European flora? *Folia Geobotanica*, **38**, 357–366.

Finzi, A.C., Canham, C.D. & van Breemen, N. (1998) Canopy tree–soil interactions within temperate forests: species effects on pH and cations. *Ecological Applications*, **8**, 447–454.

Frenzel, B., Pécsi, M. & Velichko, A.A. (eds) (1992) *Atlas of paleoclimates and paleoenvironments of the Northern Hemisphere*. Geographical Research Institute, Budapest & Gustav Fischer Verlag, Stuttgart.

Gidrometeoizdat (1966–1970) *Spravochnik po klimatu SSSR* [Reference books on the climate of the USSR]. Gidrometeoizdat, Leningrad.

Gigon, A. (1987) A hierarchic approach in causal ecosystem analysis: the calcifuge-calcicole problem in alpine grasslands. *Ecological Studies*, **61**, 228–244.

Glaser, P.H., Janssens, J.A. & Siegel, D.I. (1990) The response of vegetation to chemical and hydrological gradients in the Lost River peatland, northern Minnesota. *Journal of Ecology*, **78**, 1021–1048.

Gough, L., Shaver, G.R., Carroll, J., Royer, D.L. & Laundre, J.A. (2000) Vascular plant species richness in Alaskan arctic tundra: the importance of soil pH. *Journal of Ecology*, **88**, 54–66.

Grubb, P.J. (1987) Global trends in species-richness in terrestrial vegetation: a view from the northern hemisphere. *Organization of communities: past and present* (ed. by J.H.R. Gee and P.S. Giller), pp. 99–118. Blackwell Science, Oxford.

Güsewell, S., Bailey, K.M., Roem, W.J. & Bedford, B.L. (2005) Nutrient limitation and botanical diversity in wetlands: can fertilisation raise species richness? *Oikos*, **109**, 71–80.

Guthrie, R.D. (2001) Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. *Quaternary Science Reviews*, **20**, 549–574.

Hájková, P. & Hájek, M. (2003) Species richness and above-ground biomass of poor and calcareous spring fens in the flysch West Carpathians, and their relationships to water and soil chemistry. *Preslia*, **75**, 271–287.

Hilbig, W. (1995) *The vegetation of Mongolia*. SPB Academic Publishing, Amsterdam.

Jankovská, V., Chromý, P. & Nižnianská, M. (2002) Šafárka — first palaeobotanical data of the character of Last Glacial vegetation and landscape in the West Carpathians (Slovakia). *Acta Palaeobotanica*, **42**, 39–50.

Löbel, S., Dengler, J. & Hobohm, C. (2006) Species richness of vascular plants, bryophytes and lichens in dry grasslands: the effects of environment, landscape structure and competition. *Folia Geobotanica*, **41**, 377–393.

Meusel, H., Jäger, E.J., Weinert, E. & Rauschert, S. (1965–1992) *Vergleichende Chorologie der zentraleuropäischen Flora I–III*. Gustav Fischer Verlag, Jena.

Moore, K.E., Fitzjarrald, D.R., Sakai, R.K. & Freedman, J.M. (2000) Growing season water balance at a boreal jack pine forest. *Water Resources Research*, **36**, 483–493.

Ovington, J.D. (1953) Studies of the development of woodland conditions under different trees. I. Soil pH. *Journal of Ecology*, **41**,13–52.

Palmer, M.W., Arévalo, J.R., del Carmen Cobo, M. & Earls, P.G. (2003) Species richness and soil reaction in a northeastern Oklahoma landscape. *Folia Geobotanica*, **38**, 381–389.

Pärtel, M. (2002) Local plant diversity patterns and evolutionary history at the regional scale. *Ecology*, **83**, 2361–2366.

Peet, R.K. & Christensen, N.L. (1980) Hardwood forest vegetation of the North Carolina piedmont. *Veröffentlichungen des Geobotanischen Institutes ETH, Stiftung Rübel, Zürich*, **69**, 14–39.

Peet, R.K., Fridley, J.D. & Gramling, J.M. (2003) Variation in species richness and species pool size across a pH gradient in forests of the southern Blue Ridge Mountains. *Folia Geobotanica*, **38**, 391–401.

Polikarpov, N.P., Chebakova, N.M. & Nazimova, D.I. (1986) *Klimat i gornye lesa Sibiri* [Climate and mountain forests of Siberia]. Nauka, Novosibirsk.

Rey Benayas, J.M. (1995) Patterns of diversity in the strata of boreal montane forest in British Columbia. *Journal of Vegetation Science*, **6**, 95–98.

Roberts, N. (1998) *The Holocene: an environmental history*, 2nd edn. Blackwell Science, Oxford.

Schuster, B. & Diekmann, M. (2003) Changes in species density along the soil pH gradient — evidence from German plant communities. *Folia Geobotanica*, **38**, 367–379.

Schuster, B. & Diekmann, M. (2005) Species richness and environmental correlates in deciduous forests of Northwest Germany. *Forest Ecology and Management*, **206**, 197–205.

Sjörs, H. (1952) On the relation between vegetation and electrolytes in north Swedish mire waters. *Oikos*, **2**, 241–258.

Tarasov, P.E., Volkova, V.S., Webb, T., III, Guiot, J., Andreev, A.A., Bezusko, L.G., Bezusko, T.V., Bykova, G.V., Dorofeyuk, N.I., Kvavadze, E.V., Osipova, I.M., Panova, N.K. & Sevastyanov, D.V. (2000) Last glacial maximum biomes reconstructed from pollen and plant macrofossil data from northern Eurasia. *Journal of Biogeography*, **27**, 609–620.

Taylor, D.R., Aarssen, L.W. & Loehle, C. (1990) On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos*, **58**, 239–250.

Tyler, G. (1996) Soil chemistry and plant distributions in rock habitats of southern Sweden. *Nordic Journal of Botany*, **16**, 609–635.

Tyler, G. (2000) Integrated analysis of conditions accounting for intersite distribution of grassland plants. *Nordic Journal of Botany*, **20**, 485–500.

Tyler, G. (2003) Some ecophysiological and historical approaches to species richness and calcicole/calcifuge behaviour — contribution to a debate. *Folia Geobotanica*, **38**, 419–428.

van der Welle, M.E.W., Vermeulen, P.J. Shaver, G.R. & Berendse, F. (2003) Factors determining plant species richness in Alaskan arctic tundra. *Journal of Vegetation Science*, **14**, 711–720.

Vitt, D.H. (2000) Peatlands: ecosystems dominated by bryophytes. *Bryophyte biology* (ed. by A.J. Shaw and B. Goffinet), pp. 312–343. Cambridge University Press, Cambridge.

Vonlanthen, C.M., Kammer, P.M., Eugster, W., Bühler, A. & Veit, H. (2006) Alpine vascular plant species richness: the importance of daily maximum temperature and pH. *Plant Ecology*, **184**, 13–25.

Walker, D.A., Bockheim, J.G., Chapin, F.S., III, Eugster, W., Nelson, F.E. & Ping, C.L. (2001) Calcium-rich tundra, wildlife, and the 'Mammoth Steppe'. *Quaternary Science Reviews*, **20**, 149–163.

Willis, K.J., Rudner, E. & Sümegi, P. (2000) The full-glacial forests of central and southeastern Europe. *Quaternary Research*, **53**, 203–213.

Wohlgemuth, T. & Gigon, A. (2003) Calcicole plant diversity in Switzerland may reflect a variety of habitat templets. *Folia Geobotanica*, **38**, 443–452.

Zinko, U., Dynesius, M., Nilsson, C. & Seibert, J. (2006) The role of soil pH in linking groundwater flow and plant species density in boreal forest landscapes. *Ecography*, **29**, 515–524.

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