

The role of soil pH in linking groundwater flow and plant species density in boreal forest landscapes

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In hilly boreal landscapes topography governs groundwater flow which strongly influences soil development, and thus vegetation composition. Soil pH is known to correlate well with plant species density and composition, but in boreal forests this relationship has been little studied. Previously, we successfully used a topography-based hydrological index, the topographical wetness index (TWI), as an approximation of the variation in groundwater flow to predict local plant species density in a boreal forest landscape. Data on species indicator values demonstrated that soil pH can be an important soil variable linking groundwater flow and plant species density. In the present paper we explore this link by relating measured soil pH to species numbers of vascular plants and TWI in 200-m² plots within two boreal forest landscapes, differing in average soil pH. The two landscapes showed almost identical relationships between plant species number and soil pH, implying that this relationship is robust. The landscapes also had similar relationships between soil pH and TWI as well as between plant species number and TWI except at high TWI values, which indicate groundwater discharge areas. In these areas, soil pH and plant species numbers were higher in the high-pH landscape at any given TWI value. We conclude that for predictive mapping of the species density of vascular plants in boreal forests, soil pH is a major factor. However, TWI as a measure of groundwater flow is a practical alternative predictor.

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The spatial pattern of species density and the factors allowing coexistence of species have been discussed for a long time among ecologists. Various hypotheses have been presented to explain the observed patterns (Palmer 1994). The underlying mechanisms can roughly be divided into historical and evolutionary versus contemporary ecological factors (Grime 1979, Grubb 1987, Ricklefs 1987, Zobel 1992). However, classifications of hypotheses or mechanisms are always difficult (Palmer 1994). The correlation between a contemporary ecological factor and species density might have a historical evolutionary explanation. One such possible example is

the relationship between plant species density and soil pH in temperate Europe. Pärtel (2002) argues that the nature of the relationship between plant species density and soil pH is a function of the composition of species pools, which in turn is affected by the commonness of soils with different acidity (Taylor et al. 1990, Zobel 1992, Pärtel et al. 1996, Zobel et al. 1998). Pärtel (2002) also showed that positive relationships between plant species density and soil pH prevail in temperate areas where the evolutionary centres have been in areas with high soil pH. Ewald (2003) proposes that the contradiction of high numbers of plant species adapted to high

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pH found in temperate Europe where soils are predominantly acid can be explained by a “bottleneck” effect during glaciations. Soils were rejuvenated over large areas, thus becoming more basic and causing an extinction of relatively more acidophilous than calciphilous plant species, subspecies or populations. However, these hypotheses are not supported by findings in south-eastern USA where the regional plant species pool increases with soil pH despite the fact that this area has a long history of acid soils (Peet et al. 2003). Other studies also indicate that the relationship between plant species density and soil pH in temperate Europe cannot be fully explained by historical evolutionary factors, and that local abiotic and biotic factors, especially competition may play an important role (Schuster and Diekmann 2003, Wohlgemuth and Gigon 2003, Redei et al. 2003). This is supported by studies where the relationship between plant species density and soil pH is found to vary with vegetation type (Schuster and Diekmann 2003, Chytry et al. 2003, Palmer et al. 2003) or life-forms (Tyler 2003). A unimodal relationship between species density and soil pH has frequently been found (see Dupré et al. 2002 for a review) and Schuster and Diekmann (2003) stated that the negative relationship at high soil pH probably has more of an ecophysiological than a historical explanation. Hylander and Dynesius (2006) suggested that a mid-domain effect (Colwell and Lees 2000) may be responsible for the unimodal relationship with more overlapping pH-ranges of species at intermediate soil pH. Spatial heterogeneity in pH may also have a strong relationship with average pH (Hylander and Dynesius 2006) affecting species density.

The relationship between species richness of vascular plants and soil pH has received much attention (Benayas and Scheiner 1993, Benayas 1995, Brunet et al. 1997, Gould and Walker 1999, Gough et al. 2000, Dupré et al. 2002), but little is known about this relationship in boreal forests (Engelmark and Hytteborn 1999). In a previous study we showed that species density of vascular plants within a boreal forest landscape increased from groundwater recharge to discharge areas (Zinko et al. 2005). We used a topographically-based hydrological index, the topographical wetness index, TWI (see Methods section for further explanation), with elevation being the only input data, to describe the variation of groundwater flow across the landscape. In the same study we also found that an ecological indicator value of soil pH solely explained 75% of the variation in species density. The indicator value was based on soil pH associations of the plant species found in a plot, using data provided by the The Swedish National Inventory of Forests. These results indicate that soil pH may be a strong link relating groundwater flow to plant species density. In this hilly landscape topography is an important factor controlling the ground-

water flow, which in turn affects soil factors. Several studies have shown that on a local scale soil pH increases from recharge to discharge areas, along with an increase in total soil N, a reduction in C:N ratio (Högberg et al. 1990, Giesler et al. 1998) as well as a change in available forms of N (Nordin et al. 2001). N is generally considered to be the most limiting nutrient in boreal forests (Tamm 1964, 1991) and the C:N ratio can affect the competition for N between plants and microorganisms (Kaye and Hart 1997). This implies that groundwater flow, in this study represented by TWI, affects plant species density both directly and indirectly by affecting soil pH and nutrients. Some other variables controlling soil factors such as bedrock, the ratio between precipitation and evaporation and acid deposition do not vary much on a landscape scale, whereas variables such as litter quality and biological activity in the soil ultimately also are governed by groundwater flow.

In this paper we test the hypothesis that the effect of groundwater flow (here represented by the TWI) on plant species density is mediated to a large extent by its influence on soil factors, especially soil pH, but also the C:N ratio. We also examine the relationship between plant species density and soil pH per se. We discuss the results taking historical as well as contemporary ecological factors into account. We compare two boreal forest landscapes, one with low average soil pH (LP) and the other with relatively high average soil pH (HP, data from The Swedish Forest Soil Inventory). In each landscape we examine the relationships among plant species density, soil pH and TWI and in the HP landscape we also consider the C:N-ratio. In our previous study (Zinko et al. 2005), other environmental variables such as soil type, light, basal area of various tree species and altitude were found to be poor predictors of plant species numbers, and these were therefore not included in this study.

Methods

Study area

Both study areas comprised squares of 25 km², and were located in the middle boreal zone of Sweden (Ahti et al. 1968). The LP landscape (64°33'N, 19°35'E, Västerbotten county) is identical to the one used by Zinko et al. (2005) and the HP landscape (62°59'N, 16°01'E, Jämtland county) is located 240 km to the SW (Fig. 1, Table 1). The landscapes are comparable with respect to elevation, precipitation and temperature sum (Table 1). The postglacial highest coast line, an important geomorphological border, intersects the lowest parts of both landscapes (Table 1). The bedrock is acidic in both landscapes, consisting mainly of granite. The soil is dominated by glacial till covered by an organic soil layer

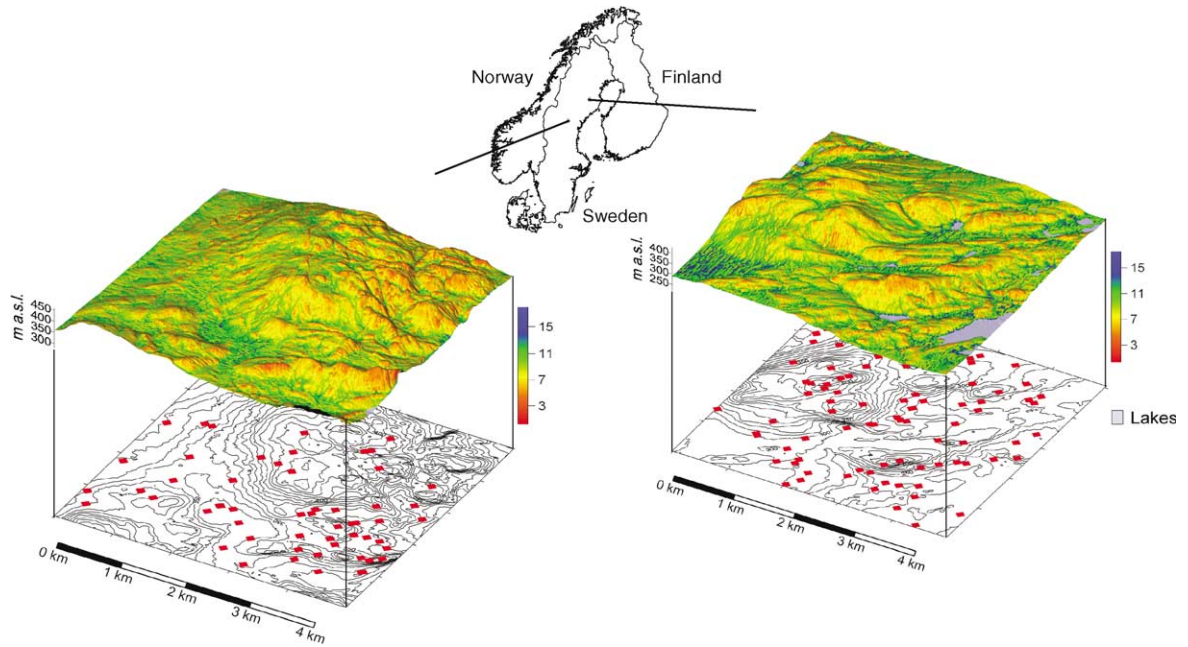


Fig. 1. Location of the study sites in boreal Sweden and maps of the topographical wetness index (TWI) calculated for all 20×20 m grids in the two landscapes [left: landscape with high average soil pH; right: landscape with low average soil pH]. The red circles on the contour maps show the location of the 200-m^2 plots sampled in each landscape. The range of TWI-values included in the study was 3–14.

of varying depth, from very thin in dry areas on hilltops to thick layers of peat in poorly drained depressions. The average soil pH of the O-horizon is ca 3.9 in the LP and ca 4.3 in the HP landscape (data from national maps produced by the Swedish Forest Soil Inventory). The difference in soil pH is probably due to differences in soil mineral composition. The areal extent of the separate TWI-classes (see below) was very similar in the two areas (Fig. 1).

The mid-boreal vegetation in Sweden is dominated by coniferous forest, composed of *Pinus sylvestris* and *Picea abies*. The forestry practice has developed from selective cuttings of large trees from the 18th up to the mid 20th centuries, to clear-cutting of entire stands often followed by planting (including introduction of the exotic tree *Pinus contorta*). Today, a fragmented forest with clear-cut areas, young managed stands and older semi-natural forest patches covers the landscapes. Only

Table 1. Environmental properties and species numbers in the landscapes with low (LP) and high (HP) average soil pH. Range and mean value (\bar{X}) are given where appropriate. Study plots were 200 m^2 . TWI values are topographical wetness index values calculated for 400-m^2 pixels.

	LP area		HP area	
	Range	\bar{X}	Range	\bar{X}
Elevation of entire area (m)	221–427	293	282–461	365
Highest postglacial coast line (m a.s.l.) [#]	240		285	
Temperature sum ($^{\circ}\text{C}$) ^{* #}		900		900
Yearly precipitation (mm) [#]		600		600
Number of study plots	84		55	
Total number of plant species	113		141	
Number of species per plot	8–48	22.8	7–60	27.7
Proportion of uncommon species per plot (%)	0–15	4.9	0–33	11.0
TWI values of study plots	3.9–13.5	8.5	3.4–14.2	8.5
TWI values in entire landscape	2.7–22.8	8.4	2.2–18.7	7.8
pH values of study plots	4.0–5.2	4.5	3.9–6.3	4.9
C:N ratio of study plots			17.6–48.8	31.9

*The sum of the daily mean temperature $>5^{\circ}\text{C}$ during the growing season.

[#]Data from Raab and Vedin (1995).

one of the 159 plant species found in the study was absent in the floristic province where the LP landscape is situated, whereas all species occurred in the floristic province where the HP landscape is situated (Krok and Almquist 2001).

Topographical wetness index

Topography is a suitable surrogate for the spatial variations of hydrological processes and conditions across the landscape (Moore et al. 1991). A simple way to capture the control of topography on hydrology is to use topographical indices. In this study a topographical wetness index (TWI) was calculated from a digital elevation model with a grid resolution of 20 m. The TWI, also called TOPMODEL index (Beven and Kirkby 1979), is one of the most frequently used indices to estimate spatial wetness distributions. It is computed as $\ln(a/\tan\beta)$ with "a" being the upslope area per unit contour length (a [m]), which indicates the amount of the water flowing towards a certain location, and the local slope ($\tan\beta$ [-]), calculated as $\Delta h/\Delta x$ where Δh is the elevation difference and Δx the horizontal difference. While high values of TWI indicate high groundwater levels, these do not necessarily coincide with locations of high groundwater flow. The upslope area, a, would be a better proxy for the flow amount, but at locations with steep slopes even a large flow amount might not correspond to near-surface groundwater, which is crucial for vascular plants. In general, the TWI variations were controlled more by the variations of a than those of $\tan\beta$. Therefore, we decided to use TWI as a measure of near-surface groundwater flow.

The TWI can be calculated from gridded elevation data using various algorithms, which differ mainly in the way the upslope area is computed (Wolock and McCabe 1995, Quinn et al. 1995, Tarboton 1997, Sørensen et al. 2006). We used a combination of the multiple-flow-direction algorithm proposed by Quinn et al. (1991, 1995) and the approach by Tarboton (1997), which removes the limitation that the steepest gradient from a certain cell has to be one of the eight cardinal and diagonal directions (Zinko et al. 2005 give a more detailed description). We considered the stream network in the calculations by assuming that streams start when the accumulated area exceeds a certain threshold area (set to 50 000 m²). The accumulated area of a "stream cell" was routed downslope as "stream area" and not considered in the calculation of the upslope area, because the basic assumptions, which underlie the derivation of the TWI (Beven and Kirkby 1979), do not hold when there is a stream. Furthermore, we replaced the local gradient, $\tan\beta$, by a downslope index, $\tan\beta_d$ (Hjerdt et al. 2004). This index is calculated as d/L_d where L_d is the distance to the nearest cell having

a height $\geq d$ length units (here set to 5 m) below the cell in question. By taking downslope topography into account, the gradient of the groundwater table and, thus, the drainage from a certain location will be better estimated (Hjerdt et al. 2004). The calculated TWI in this study differs slightly from the one used by Zinko et al. (2005) where we used lower values for both d and the stream initiation threshold area. These changes caused a slightly stronger correlation of TWI with observed groundwater levels (Zinko et al. unpubl.).

Sampling of sites

The landscapes included wide ranges of TWI values (Fig. 1, Table 1). We restricted the study to areas with TWI values <15 (Table 1), because higher TWI mostly represented treeless marshlands, streams and lakes, which are commonly interspersed in the boreal forest. For the sampling procedure, TWI values were classified by rounding to the closest integer (i.e. TWI class 3 corresponds to values between 2.5 and 3.5). In 1999, square plots of 200 m² were located in the centre of eighty-four 20 × 20-m cells of the digital elevation data in the LP landscape. The selection of these cells was random but stratified according to TWI-values so that the study plots were evenly distributed along the TWI gradient. The plots were identified in the field using a differential global positioning system receiver (DGPS). Assuming similar variation in species density along the TWI gradient as in the LP landscape, we used power analysis in PASS 6.0 (Hintze 1996) to determine the number of plots needed to get significant results in regression analysis for the study in the HP landscape. Based on this and because the variation in species number was higher at high compared to low TWI-values in the LP landscape, we randomly sampled 55 plots in the HP landscape in 2002, stratified so that there were more plots in high than in low TWI-classes.

Field sampling

We recorded the presence of all vascular plant species in the 200-m² plots during July in 1999 and 2002 for the LP and HP landscapes, respectively. We also determined the number of uncommon species per plot, defining uncommon as those not classified as common by Krok and Almquist (2001) in the floristic province of each study landscape. To determine soil pH, we sampled the O-horizon in each plot in the HP (in 2002) and in the LP (in 2003) landscapes. If the plot was covered by peat, the whole cores (up to 30 cm) were used. The soil cores were taken from eight evenly spaced locations in each plot, ca 2 m from the plot centres. For each plot, the eight soil samples were mixed to one gross sample. The samples

from the LP landscape were left to air-dry for 2 months at ca 20°C and then sealed in polyethylene bags. The samples from the HP landscape were air-dried at the same temperature for a month before further drying at 30°C for 3 d in a drying chamber and then sealed in polyethylene bags. Prior to analysis, the dry samples were sieved through a 2 mm sieve to remove the coarse fragments, and then homogenised. In 2003, pH (H₂O, 1:25, soil:solution mass ratio) of all soil samples were analysed with a glass-calomel electrode. In the HP landscape, also total C and N of the O-horizon were analysed by dry combustion, using LECO CNS-2000. We calculated the C:N ratio using the total amounts of C and N.

Data analysis

All correlations were statistically evaluated with Pearson's correlation coefficient. We used linear least squares regression analysis to quantify how well each of the predictor variables (soil pH, TWI, C:N ratio) per se explained the variation in plant species density within a landscape. To explore the nature of the relationships among species number, TWI and soil pH more closely, we performed locally weighted regression scatterplot smoothing, or LOWESS regressions (Trexler and Travis 1993), using 50% of the total number of points to calculate each LOWESS regression point in SigmaPlot ver. 7.101 (SPSS, Chicago, IL, USA). We tested for differences in both the intercepts and the slopes (the interaction between TWI and landscape) of the plant species number – TWI relationship between the two landscapes, using a univariate analysis of covariance (ANCOVA) of plant species numbers with landscapes as fixed factor and TWI as covariate. In the same way, we tested if the species numbers of vascular plant–soil pH and soil pH–TWI relationships differed in intercept and slope between the two landscapes, with soil pH and TWI, respectively, as covariates.

We used path analysis (Sokal and Rohlf 1995) to test whether the direct or indirect (through soil pH and C:N-ratio) effect of groundwater flow (TWI) has greater influence on plant species density. In path analysis, explicit assumptions are made about the causal relationships among variables by specifying causal linkages between them. Mathematically, it is equivalent to a series of linear regressions. The technique allows decomposition of the overall correlation between two variables into direct effects of one on the other, indirect effects mediated by other variables and non-causal variables resulting from common causes. Path analysis assumes that all important variables are identified, that effects are linear, additive and unidirectional, and that residuals are uncorrelated. We propose that TWI affects plant species density both directly and indirectly by influencing soil

pH and the C:N ratio. It is still unknown in what way soil pH and nitrogen interact and therefore this relationship could not be considered in the path analysis. Multiple linear regression models were also tested for these relationships.

All calculations except for LOWESS regressions were performed with the software package SPSS ver. 11.0 (SPSS, Chicago, IL, USA).

Results

There were positive relationships between plant species density and soil pH in both landscapes (Fig. 2A). Neither elevation nor slope of the curves differed ($p > 0.05$, univariate ANCOVA). According to LOWESS regressions the relationships had similar monotonous increases in both landscapes along their common pH gradient (soil pH 4.0–5.2, Fig. 2A). In the HP landscape the species number started to level off at a pH-value of ca 5.4. Soil pH explained a larger proportion of the variation in plant species numbers in the HP ($R^2 = 0.74$, $p < 0.001$, $n = 55$, linear least square regression) than in the LP landscape ($R^2 = 0.40$, $p < 0.001$, $n = 84$). This difference persisted also when we restricted the analysis to the soil pH range common to both landscapes (HP landscape: $R^2 = 0.67$, $p < 0.001$, $n = 43$).

Soil pH increased with TWI in both landscapes (Fig. 2B) but both the rate of increase (slope) and the elevation of the curves were significantly higher in the HP than in the LP landscape (for both: $p < 0.001$, univariate ANCOVA). However, the LOWESS curves revealed that at lower TWI-values the rates of increase were rather similar in both landscapes, but above TWI ca 10 the rate of increase in soil pH was higher in the HP than in the LP area and curves diverged. TWI explained 53% of the variation in soil pH in the HP landscape (linear least square regression: $R^2 = 0.53$, $p < 0.001$, $n = 55$), but only 23% in the LP landscape ($R^2 = 0.23$, $p < 0.001$, $n = 84$).

Plant species numbers also increased with TWI in both landscapes (Fig. 2C, D) and the rate of increase was higher in the HP than in the LP landscape ($p = 0.025$, univariate ANCOVA). There was no significant difference in the elevation of the curves between landscapes ($p > 0.05$). The LOWESS curves were similar to the ones describing the relationship between soil pH and TWI (Fig. 2B, C). TWI explained more of the variation in vascular-plant species density in the HP ($R^2 = 0.52$, $p < 0.001$, $n = 55$) than in the LP landscape ($R^2 = 0.30$, $p < 0.001$, $n = 84$), (Fig. 2D).

Decomposing the relationship between plant species density and TWI using path analysis revealed that the indirect effect of TWI as a measure of groundwater flow through soil pH was stronger than the direct effect in the HP but not in the LP landscape (Fig. 3, Table 2). The

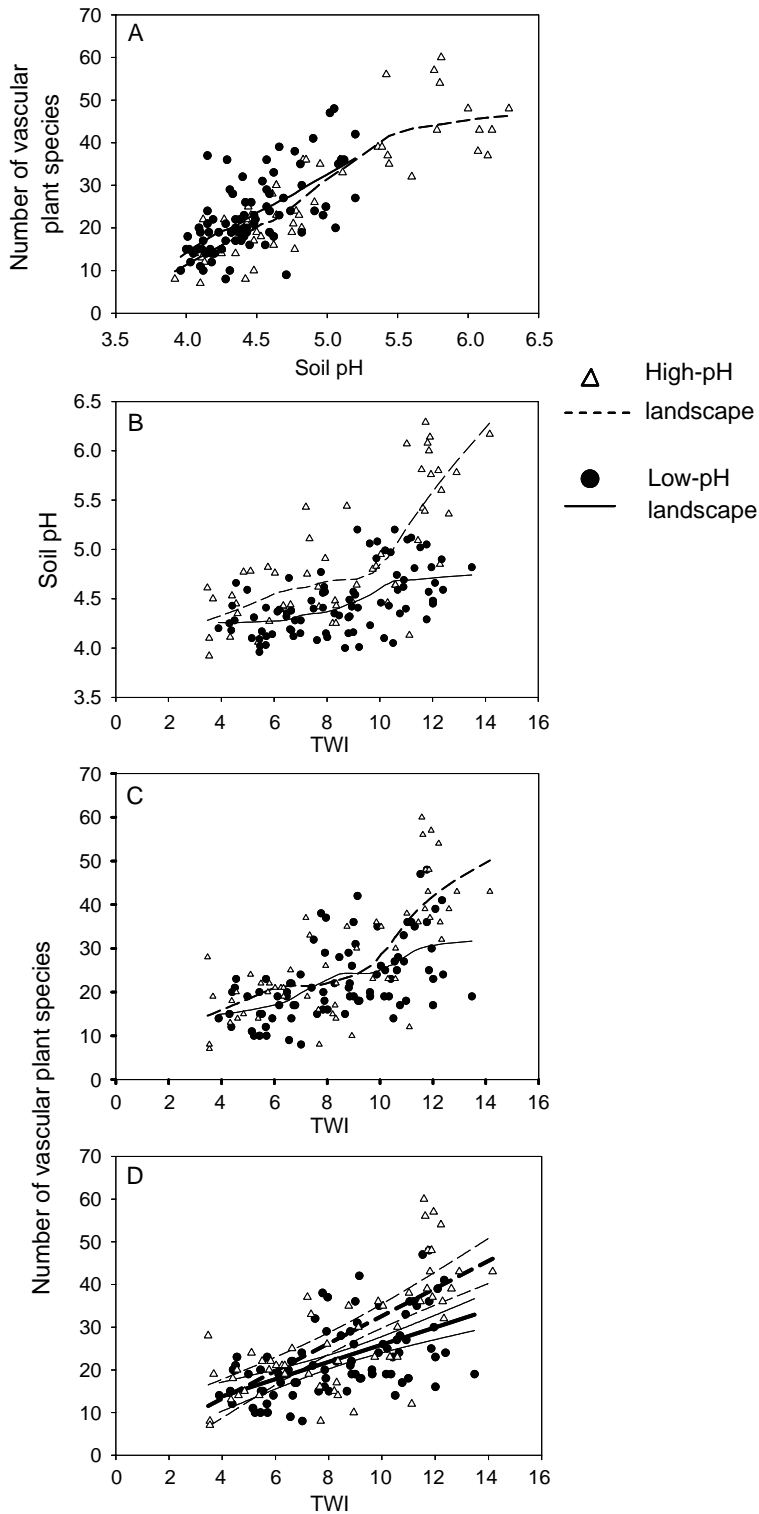


Fig. 2. (A) The number of vascular plant species plotted against soil pH in the landscapes with low (LP) and high (HP) average soil pH. (B) Soil pH plotted against TWI for the HP and LP landscapes. (C) The relationship between number of vascular plant species and TWI for the HP and LP landscapes. The curves in graph A–C were constructed using LOWESS regression. (D) Same as (C), but the curves are linear least squares regressions with 95%-confidence bands. Plot size = 200 m².

inclusion of the C:N-ratio in the path analysis did not change the relationship between direct and indirect effects (Table 2). As stated above the causal relationship

between soil pH and the C:N ratio is not clear, but an assumption of that the causal pathway is unidirectional from soil pH to C:N ratio (not shown in Fig. 3) would

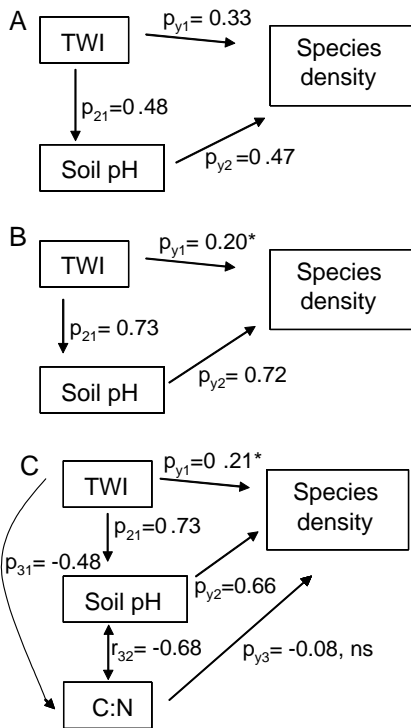


Fig. 3. Path analysis of the relationships between TWI, soil pH and species density in the landscape with (A) low and (B) high average soil pH. (C) depicts a path analysis of the relationships between TWI, soil pH, C:N ratio and species density in the high pH landscape. Any box receiving an arrow was a dependent variable and all boxes that are sources of arrows are independent variables. The correlations between species density and TWI were assumed to be either direct or indirect by influencing soil pH only (A–B) or both soil pH and nitrogen (C). The relationships are assumed to be unidirectional causal (single-headed arrows) except for soil pH vs C:N-ratio (double-headed arrow). The values associated with the single-headed arrows are the standardized partial regression coefficients from multiple linear regressions. The value associated with the double-headed arrow is the Pearson's correlation coefficient. If not indicated otherwise $p < 0.001$, * $0.001 < p < 0.05$, ns = not significant.

only change the overall path equation negligibly since the product of this path coefficient with p_{y3} would be very small (Fig. 3C). There were negative correlations between the C:N ratio and plant species numbers, TWI and soil pH in the HP landscape (Fig. 4). The C:N ratio per se explained less than TWI and soil pH of the variation in plant species numbers in the HP landscape ($R^2 = 0.40$, $p < 0.001$, $n = 53$, linear least square regression analysis). The coefficient of determination did not change significantly when adding the C:N ratio as a third predictor together with TWI and soil pH in a multiple regression with plant species density as the dependent variable (Table 2).

The proportion of uncommon species in each plot increased with both TWI and soil pH in the HP (linear least square regression; TWI: $R^2 = 0.38$; soil pH: $R^2 = 0.57$; for both: $p < 0.001$, $n = 55$) as well as in the LP landscape (TWI: $R^2 = 0.08$, $p = 0.009$; soil pH: $R^2 = 0.14$, $p < 0.001$; for both: $n = 84$), although the coefficient of determination was low for the latter.

Discussion

Our hypothesis that the effect of groundwater flow (TWI) on plant species density to a large extent is mediated by its effect on soil pH was supported by the results of the path analysis. Furthermore, in both landscapes soil pH explained more of the variation in plant species number than TWI. This may, however, be due to differences in the precision of the variables. TWI is calculated from a digital elevation model with a grid size coarser than the study plots, whereas soil pH is measured within each study plot and in the rooting zone of the plants. The similarity between the plant species density–soil pH relationships and the soil pH–TWI relationships (Fig. 2B, C), also illustrates that soil pH is an important proximate factor controlling plant species density.

Table 2. Calculated path equations of the effect of TWI on plant species density and proportion of variation explained in multiple regression models (R^2).

	r_{y1}		direct		indirect		R^2	
			P_{y1}		$P_{21}P_{y2}$	$P_{31}P_{y3}$		
LP, pH	0.56	=	0.33	+	0.23		0.46	
HP, pH	0.73	=	0.20	+	0.53		0.75	
HP, C:N	0.65	=	0.21	+	0.48	–	0.04	0.75

LP, pH represents the effect of TWI on plant species density in the LP landscape; HP, pH same as A but in the HP landscape; HP, C:N represents the effect of TWI on plant species density in the HP landscape taking not only soil pH but also the C:N ratio into consideration. The decomposition of the overall correlation between plant species density and TWI in A and B is $r_{y1} = p_{y1} + p_{21}p_{y2}$, where p_{y1} represents the direct effect of TWI on plant species density, and $p_{21}p_{y2}$ represents the indirect effect via soil pH. The equivalent path equation in C is $r_{y1} = p_{y1} + p_{21}p_{y2} + p_{31}p_{y3}$, where $p_{31}p_{y3}$ represents the indirect effect via the C:N ratio. The path between soil pH and C:N ratio is not included since the causality between these two variables is unclear. All multiple regression models: $p < 0.001$, (LP): $n = 84$, (HP): $n = 55$.

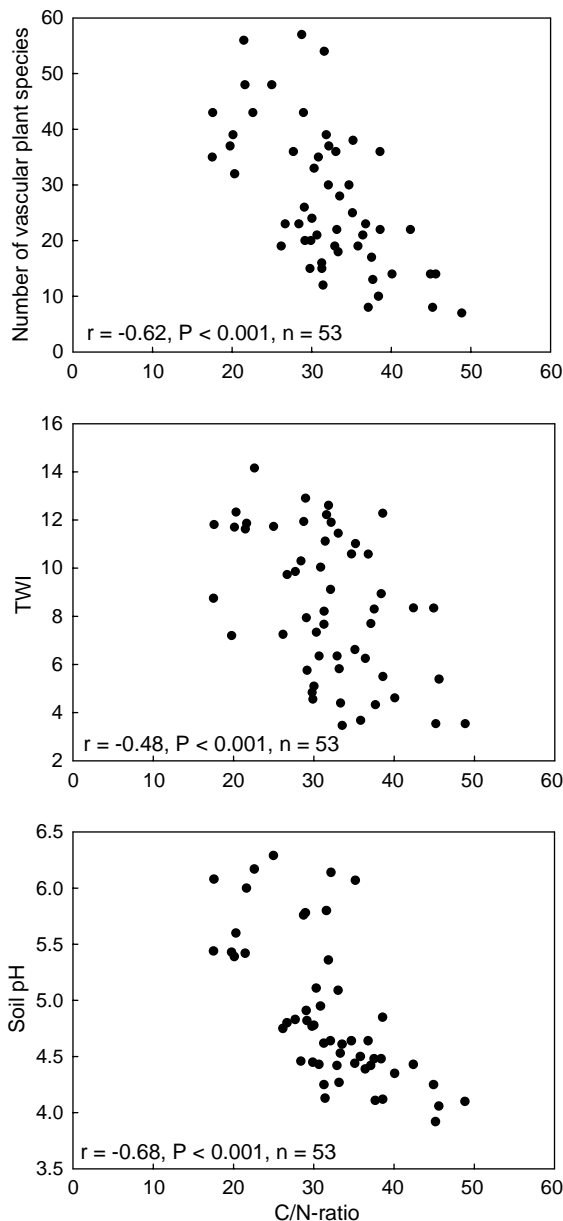


Fig. 4. Number of vascular plants, TWI, and soil pH plotted against C:N ratio in the landscape with high average soil pH. Pearson's correlation coefficients are given for each relationship. Plot size = 200 m².

The higher soil pH at high TWI-values in the HP compared to in the LP landscape could be caused by a difference between the landscapes in soil mineral composition. In groundwater recharge areas the groundwater flow is directed downwards and dissolves cations on its way through the soil. In areas with higher TWI, where the groundwater flow at least intermittently is directed upwards, the dissolved cations raise soil pH. If the soils in the HP landscape contain more cation-rich minerals than in the LP landscape, the HP discharge areas but not

necessarily the HP recharge areas would have a higher soil pH. This explanation is reasonable since the glacial ice in this area moved towards the southeast and can have brought minerals from the more basic Precambrian bedrock of the Swedish mountain range, northwest of the HP landscape (Lundqvist 1969).

The observed plant density pattern in our study could be explained by evolutionary and geological factors (Grubb 1987, Pärtel 2002). After the glacial period plant species have immigrated from refugial areas on the Iberian Peninsula and from south-eastern Europe, as well as from Asia to the boreal forest of Fennoscandia (Bennett 1997, Hewitt 2000). The Fennoscandian pool of boreal plant species may therefore better reflect the conditions in the regions of origin than the present-day conditions in northern and central Fennoscandia. During the course of several glaciations, most soils in northern Europe have been rejuvenated with additions of base-rich mineral particles (Watts 1988). Plant species growing in soils with relatively high pH in non-glaciated areas of southern and south-eastern Europe could colonise the rejuvenated landscapes of Northern Europe after the last glaciation (Grubb 1987, see also Ewald 2003). With time, leaching reduced soil pH again, leaving only small base-rich areas. The discharge areas that are scattered throughout the boreal landscape constitute such relatively base-rich areas. This could explain the positive relationship between plant species density and TWI. The relative small percentage of discharge areas in the boreal forest implies that plant species restricted to this environment also are relatively rare. This is in accordance with the increase in proportion of uncommon plant species with both soil pH and TWI.

The path analysis indicated that the direct effect of nitrogen (C:N ratio) on species density is insignificant. However, the C:N-ratio is only a relatively coarse proxy for availability of different forms of nitrogen and nitrogen may therefore still be an important factor for plant species density. The negative correlations between the C:N ratio and plant species number, soil pH and TWI conform with the results of Giesler et al. (1998) and Nordin et al. (2001) of increasing soil N availability along hillslopes. The high species numbers in discharge areas could be caused by a relaxation of the competition (among plants and with microorganisms; Kaye and Hart 1997) for N. It could also be an effect of the differentiation of the soil N taken up by different plants along the gradient from recharge to discharge areas, which is also related to changes in the type of mycorrhizae associated with plants along such a gradient (Read 1991, Nordin et al. 2001, Nilsson et al. 2005). The results of Nordin et al. (2001) showed that amino acid N dominates the soil N pool in the recharge area, whereas NH₄⁺ makes up most of the soil N pool over the season further down the slope. In the discharge area NH₄⁺ and NO₃⁻ are the dominating forms of N in the soil, although amino

acid was still available along the whole gradient. The plant uptake of N changed correspondingly along the gradient, although all three different forms of N were taken up by plants along the whole gradient. In recharge areas plants to a large degree used amino acid N and NH_4^+ , whereas plants further downslope, in mesic to moist forests, mainly took up NH_4^+ . In discharge areas, NH_4^+ and NO_3^- dominate the N taken up by plants. This could lead to an addition of plant species that are favoured by availability of NH_4^+ or have the capability to take up NO_3^- along this gradient, rather than a species turnover. In accordance with this we found species occurrences to be significantly nested in both the LP (Zinko et al. 2005) and the HP (analysis not shown) landscapes, implying that plant species are rather added to the overall species list than replaced along the gradient.

The explanations given above for the positive relationship between plant species numbers and TWI are not mutually exclusive, but a combination of them seems rather likely. Habitat heterogeneity could be another explanation for the increase in species number with TWI. In areas with high TWI-values, small-scale topography may cause a larger variation in soil moisture, pH and N availability within 200-m² plots than in areas with low TWI-values where the soil is relatively dry and acid also in depressions. This may also explain the nested pattern of species occurrences.

Conclusions

The results show that soil pH is strongly correlated with plant species density in the boreal forest. The relationship between species number of vascular plants and TWI may differ among landscapes at relatively high TWI-values, which indicate groundwater discharge areas. Although our results suggest that soil pH is more accurate than TWI in predicting plant species richness, it requires extensive field surveys for its quantification. Such resources could preferably be used directly for plant surveys. TWI has the great advantage of being simple to obtain, requiring only topographical data and no fieldwork. In practice, therefore, TWI remains a useful predictor of local plant species density in hilly landscapes. However, to understand more of the processes regulating the flora of boreal forests, the hydrological-chemical interactions should be further explored. This can be done by analysing the partial effects of accurately measured soil water saturation and soil pH or by long term experiments where pH or nitrogen availability is manipulated along the TWI gradient.

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