Plants go with the flow

predicting spatial distribution of plant species in the boreal forest

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Abstract

The main objectives of this thesis are to study if a topographic wetness index (TWI) could be used as a tool for predicting the spatial distribution of vascular plant species richness in the boreal forest as well as to study congruence in species richness between vascular plants, liverworts, mosses and lichens. A wetness index $\ln(a/\tan\beta)$ based on topography was used to assign a specific TWI-value to every 20 x 20m grid in two 25 km^2 boreal forest landscapes (differing in average soil pH) in northern Sweden. Soil pH is known to be influenced by groundwater and to affect plant species richness in other biomes. Therefore, the relationships between plant species richness, TWI and soil pH were also studied.

The results showed that the majority of the investigated boreal forest landscapes were relatively dry and species-poor, whereas interspersed patches linked to areas with relatively high TWI had species-rich vegetation including the species of the drier parts of the landscape. There was a positive relationship between species richness of vascular plants and the TWI in both landscapes, but varied with average soil pH. TWI explained 30 % and 52 % of the variation in plant species richness in the landscape with lower and higher pH, respectively. The proportion of regionally uncommon plants also increased with TWI. Testing different calculation methods of the TWI resulted in a large variation in correlation strengths between the various TWI-values and different measured variables (species richness of vascular plants, soil pH, groundwater flow and soil moisture). The relationship between plant species richness and TWI could be further improved with some of the calculation methods.

When studying correlations in species richness using data sets from boreal forest in northern Sweden, strong positive correlations among vascular plants, mosses and liverworts were found, but no significant correlation between macrolichens and any of the other groups. This result could be explained by that the species number of each of the three related groups increases with ambient moisture, whereas the species number of macrolichens is weakly associated with moisture.

In conclusion, the TWI could become a useful tool in conservation management for identifying areas of special interest prior to field inventories. Since vascular plants can be used as an indicator taxon for species richness of mosses and liverworts, high TWI-values indicate areas of species hotspots of these taxa.

Key words: boreal forest, vascular plant, species number, species richness, wetness index, soil pH, C:N ratio, bryophyte, lichen, substrate, stand age, plot size

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SAMMANFATTNING

Syftet med avhandlingen är att dels studera om ett topografiskt fuktighetsindex skulle kunna vara användbart för att förutsäga fördelningen av kärlväxters artrikedom i boreal skog, dels att studera om den rumsliga fördelningen av artrikedom hos kärlväxter, blad- och levermossor samt lavar sammanfaller.

Ett fuktighetsindex, ln(a/tanβ), som bara är baserat på topografi användes för att beräkna ett indexvärde för varje 20 x 20 m grid i två 25 km^2 stora boreala skogslandskap (med i medeltal olika mark-pH) i norra Sverige. Det är känt att mark-pH påverkas av grundvatten och att pH i sin tur påverkar artrikedom hos kärlväxter i andra biom. Därför studerades även sambanden mellan kärlväxters artrikedom, mark pH och TWI.

Resultaten visade att större delen av det studerade boreala landskapet var relativt torrt och artfattigt, medan mindre utspridda områden med höga TWI-värden var artrika på kärlväxter och här växte även arter som återfanns i de torra delarna av skogen. Sambandet mellan artrikedom hos kärlväxter och TWI var positivt i båda landskapen, men påverkades av de olika nivåerna på mark-pH. TWI förklarade 30 % av variationen i artrikedom i området med lägre mark-pH respektive 50 % i området med högre mark-pH. Andelen kärlväxter som klassificeras som icke vanliga i respektive region ökade också med TWI. Med andra beräkningsmetoder för TWI visade det sig att styrkan på korrelationerna mellan TWI och olika uppmätta variabler (artrikedom hos kärlväxter, mark-pH, grundvattennivå och markfuktighet) varierade mycket. Sambandet mellan artrikedom hos kärlväxter och TWI kunde förbättras ytterligare med vissa beräkningsmetoder.

Då korrelationer i artrikedom studerades användes ett dataset från boreal skog i norra Sverige. Resultaten visade på starka, positiva korrelationer mellan kärlväxter, blad- och levermossor, men inga korrelationer mellan någon av dessa grupper och lavar. Detta kunde förklaras med att artrikedom hos de tre korrelerande organismgrupperna ökar med ökad fuktighet, medan artrikedom hos lavar inte är kopplat till fukt.

Huvudslutsatsen i avhandlingen är att TWI, som endast är baserad på topograpfiskt data, skulle kunna bli ett värdefullt redskap i naturvårdsplanering för att identifiera särskilt intressanta skogsområden innan man gör fältinventeringar. Eftersom studien visar att kärlväxter kan användas som en indikator grupp för artrikedom hos blad- och levermossor indikerar höga TWI-värden områden med hög artrikedom även vad gäller dessa taxa.

TABLE OF CONTENTS

LIST OF PAPERS

This thesis is a summary of the following papers, which will be referred to in the text by their Roman numerals.

I. U. Zinko, J. Seibert, M. Dynesius, and C. Nilsson. 2005. Plant species numbers predicted by a topography based groundwater-flow index. *Ecosystems* **8**, in press.

II. U. Zinko, M. Dynesius, C. Nilsson, and J. Seibert. The importance of soil moisture and pH for the spatial variation of plant species numbers in boreal forests. *Submitted manuscript.*

III. R. Sörensen, U. Zinko, J. Seibert. On the calculation of the topographic wetness index: evaluation of different methods based on field observations. *Manuscript.*

IV. M. Dynesius and U. Zinko. Correlation in species numbers among vascular plants, mosses, liverworts and lichens in boreal forests: effects of plot size, substrate affiliation, and stand age. *Manuscript.*

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INTRODUCTION

Most of the world's forest is today heavily impacted by humans in different ways. The main human impact in the boreal forest is silviculture, which today is intensive including clear-cutting of entire stands, drainage, planting, road building, and introduction of exotics. Following the reduction of the pristine forest, forest companies are exploiting new areas and the timber frontier is being moved into the last areas of more or less intact forest, especially in Canada and Russia. The decrease of the world's biodiversity, which now has been shown to be faster than any known mass extinction (Reid 1997, Ricciardi and Rasmussen 1999), has recently become highlighted within the political community and put on the agenda. One hundred sixty-eight countries have signed the UN (Rio) Convention on Biological Diversity from 1992, committing to conserve biodiversity and to use resources in a sustainable manner. The increasing awareness of the decreasing biodiversity has also put pressure on forest companies to develop ecologically sustainable silviculture. In Sweden, the Swedish Forestry Act from 1993 (Anon. 1992), states that environmental and economic considerations should receive equal importance in forest management. This is of great importance since there are only fragments left of the pristine forest in Fennoscandia.

The fast decrease of biodiversity causes great concern since it may lead to negative ecosystem consequences. It has long been recognized that high species diversity gives rise to ecosystem stability (Odum 1953, MacArthur 1955, Elton 1958). Recent research suggests that it is not the high species number per se that creates the stability but rather that the species in a community are capable of differential responses to environmental variables, or that a community contains species that are capable of functionally replacing important species (reviewed in McCann 2000). A high species number is more likely to guarantee that a community has this capacity. It has also been shown that a high species number leads to higher productivity in plant communities as well as greater nutrient retention in ecosystems (Tilman and Downing 1994, Tilman et al. 1996, Hector et al. 1999). Not only aboveground, but also belowground diversity is important, since high diversity of arbuscular vesicular mycorrhiza has been found to increase plant production (van der Heijden et al. 1998). Another reason for maintaining high diversity is a higher resistance against invading species (Tilman 1997, Levine and D'Antonio 1999). Conservation management to maintain biodiversity is therefore important in areas such as Fennoscandia with little remaining pristine forest.

To improve conservation management, many forest companies in Sweden started in the 1990s to plan their activities on a landscape level.

Efficient planning on this level would benefit from easy identification of areas of special interest, as for example biodiversity hotspots. Today, aerial photographs and field inventories are used to find such areas. This work could become more efficient if there was a good tool for identifying areas that deserve special consideration in the office preceding field surveys. Understanding the processes creating the patterns of species distribution on a landscape level is also important for proper conservation management. One might ask which factors are important for creating hotspots of different organism groups in certain areas. Do hotspots of species richness coincide between different organism groups? If so, are the species distribution patterns for these organism groups regulated by the same environmental factors? Only by understanding these processes and knowing how human impact affects them, can we act to maintain biodiversity on a landscape level.

I have in this thesis mainly focused on vascular plants, being the organisms that provide much of the structure to the forest ecosystem, as test taxa for studying if the spatial distribution of plant species in boreal forest landscapes can be predicted by a wetness index, based only on topography. The idea is that groundwater flow is the main controlling factor for the distribution of vascular plants in a boreal forest landscape, and that variation in groundwater flow is governed by landscape topography. Groundwater flow strongly affects many abiotic variables (e.g. soil moisture, soil pH, concentrations of soil N and base cations), and biotic components (e.g. mycorrhiza type and species composition of soil fauna) important for the distribution of plant species richness in the boreal forest, and could therefore serve as a good predictor of plant species richness (Fig. 1). To study if hotspots of species richness coincide for different organism groups within the same trophic level, I also assessed species numbers of liverworts, mosses and lichens in addition to vascular plants, and whether these groups are controlled by the same ecological processes.

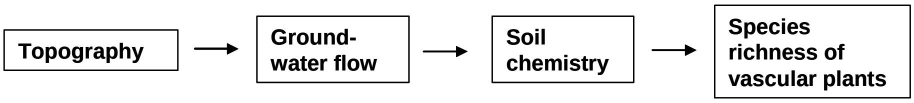

Fig. 1. *Schematic illustration of the idea behind using a Topographic Wetness Index (TWI) as a predictor of plant species richness. Topography controls groundwater flow on a landscape level in the boreal forest. Groundwater flow in turn influences many abiotic variables mainly in the soil, which affect the distribution of plant species richness.*

Brief history of vegetation type classification in the boreal forest

It is well known that certain vegetation types are linked to specific soil characteristics as well as other environmental variables such as light, temperature and precipitation. In the beginning of the 20th century several classification schemes of forest types were developed in northern Europe. The first more well-known classification was made by the Finnish botanist Cajander (1909) in 'Ueber Waldtypen' where he identified forest types classified by the vegetation of the field layer. Cajander developed these forest types to serve as units for determining site indices and thus provide a tool for forest management. This work was based on studies conducted in Germany, but some data from Finland were also reported. This classification gained much attention in Finland where it also was extensively used within forestry. During this time, important research on soil ecology was conducted where soil profiles were linked to vegetation types (Tamm 1929). This knowledge was included in the development of forest type classification schemes in Sweden (Tamm 1935, Eneroth 1936, Ronge 1936, Arnborg 1945), which were used for deciding on forestry operations and stand regenerations. Malmström (1949) made an extensive survey of the boreal forest in northern Sweden (Västerbottens län) in the mid 1930s and used his knowledge to further develop the forest type classification schemes. Based on contemporary research he also more extensively linked forest types to soil moisture, nutrient levels and pH. Malmström (1949, p. 102) observed that the most species rich and productive forest sites were linked to areas rich in lateral groundwater flow close to the ground surface ('rörligt vatten'), but he did not study this phenomenon further. In Norway, Dahl et al. (1967) published a paper in which they linked chemical characteristics of the soil to different vegetation types defined by sociological classification methods of the Zürich-Montpellier school. They associated some vegetation types to areas with laterally flowing groundwater.

Since 1923, an extensive inventory program of the forests in Sweden (the Swedish National Forest Inventory) has been carried out. The main purpose is to monitor the state of and changes in the Swedish forest resources. Data from this inventory program were used to further develop and modify the forest type classification schemes and to link forest types to site indices (Hägglund 1979, Hägglund and Lundmark 1981). In these new schemes, certain forest species of vascular plants are indicators of high nutrient content in the soil. These vascular plant species are divided into two groups, depending on their relative requirements for nutrients. Groundwater flow is also recognized by these schemes as important for site productivity. Lateral groundwater flow close to the ground surface increases productivity, giving the site a high site index. If vascular plant species of the most nutrient requiring group (tall herbs, Sw. ‘högörter’) are growing at the site, the site index increases. The forest type classification schemes demonstrate that there is a link between vegetation type and groundwater flow. However, the link between species number of vascular plants and groundwater flow, although observed (Malmström 1949) has not been explored more closely. One of the main questions in my thesis is: Can groundwater flow predict the spatial distribution of species numbers of vascular plants in the boreal forest?

Topography, hillslope hydrogeochemistry and vegetation types

Topography and groundwater flow

In most parts of Sweden groundwater flow closely follows the surface topography. The reason for this is the relatively low hydraulic conductivity of the till layer and especially its decrease with depth. Due to the low conductivity, almost the entire soil layer is needed to transport water. At some meter(s) depth in the compact till, the water flows slowly creating a cushion of water. Above this cushion the water flows laterally through a more permeable layer close to the surface, following the topography of the landscape. At hilltops, in groundwater recharge areas, where groundwater mainly derives from precipitation, there is a vertical downward component in the groundwater flow (Fig. 2). Further downslope, groundwater comes not only from precipitation but also from upslope groundwater. At the end of a longer slope, in groundwater discharge areas, so much water is gathering that the groundwater surface is forced up onto or close to the ground surface. In tracts where there are thick layers of sediment or many bedrock fractures, the groundwater flow cannot be expected to follow topography to the same extent.

Topography, soil chemistry and vegetation types

Soil chemistry changes along a hill slope. In boreal forests soil pH as well as base saturation of the mor layer has been found to increase from groundwater recharge to discharge areas. The high pH-values in groundwater discharge areas are caused by a high base saturation (Skyllberg 1996, Giesler et al. 1998). This in turn is probably caused by a transport of leached base cations with the groundwater from further upslope. In addition to soil pH and concentration of base cation variations, the N content of the soil solution increases from groundwater recharge to discharge area (Giesler et al. 1998, Nordin et al. 2001). Changes in chemical properties of the soil are reflected in vegetation types and productivity. At hilltops, in groundwater recharge areas where the soil is dry and the soil pH, N and base cation content of the soil are all low, the understory is dominated by dwarf-

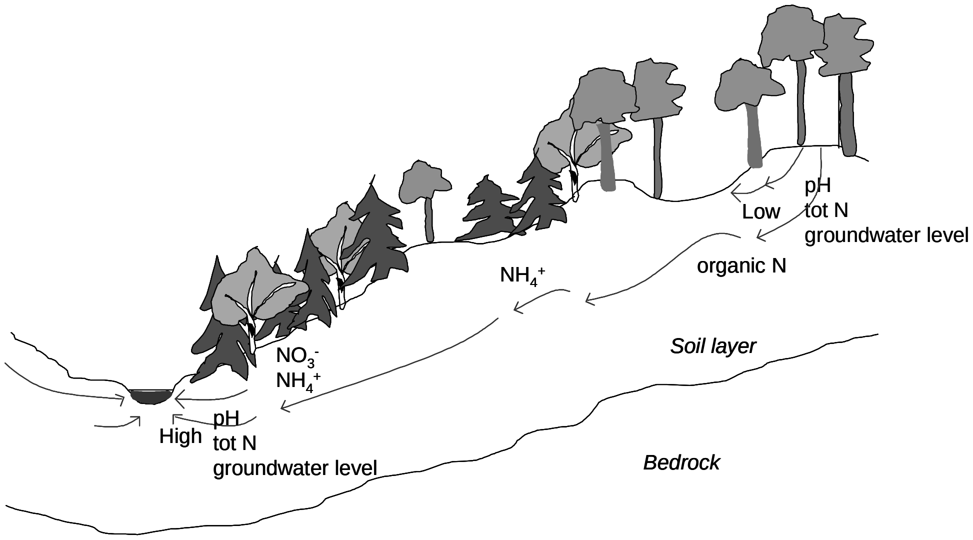

Fig. 2. *Abiotic and biotic variables change along a hillslope from groundwater recharge to discharge area. In recharge areas there is a vertical downward component in the groundwater flow, whereas in discharge areas the groundwater table can be forced up onto or close to the ground surface. Soil pH, groundwater level and total nitrogen concentration increase from groundwater recharge to discharge area.*

shrubs and the tree layer by Scots pine (*Pinus sylvestris*, Fig. 2). The shrub layer is often scarce. Further down the slope, where the forest ground is mesic with higher soil pH, N and base cation contents, the dwarf-shrub vegetation is mixed with grasses and low herbs. The tree layer is a mixture of Scots pine, Norway spruce (*Picea abies*), and birch (*Betula pubescens*). Other deciduous trees and shrubs such as rowan (*Sorbus aucuparia*) and different *Salix* species are increasing in number. Tall herbs can be found in the understory of the moist to wet groundwater discharge areas at the base of hills with highest soil pH, N and base cation contents, and can often dominate the field vegetation. The tree layer consists mainly of Norway spruce, often mixed with birch (Fig. 2).

Vegetation types and nitrogen uptake

Nordin et al. (2001) found that the availability of different forms of N in the soil water, as well as plant uptake of different forms of N, change from groundwater recharge to discharge areas. In recharge areas with dwarf-shrub vegetation the plants used mainly organic N (amino acid glycine) and NH_4^+. The water-extractable N pool of the soil solution in the groundwater recharge area was dominated by glycine, whereas NH_4^+ only made up a very small part. Therefore, organic forms of N seem to be important as an N source even if the plants are capable of extracting NH_4^+. Further down the slope, plants in the low-herb forest mainly took up NH_4^+, which was the major part of the soil N pool in this forest type, but the plants also used organic N and NO_3^-. Plants in the tall-herb forest of the groundwater discharge area used equal amounts of the two inorganic forms, and this uptake exceeded several-fold that of glycine. This uptake coincided with the inorganic forms dominating the N soil pool in the groundwater discharge area.

Mycorrhizas play a vital role for nutrient uptake. In the relatively acid mor layer in groundwater recharge areas where ericaceous plants often dominate, ericoid mycorrhizas are predominant (Read 1991). This mycorrhiza type is able to break down lignin and polyphenols which are found in high concentrations in ericaceous litter and together with lipids create high C:N ratios in the mor layer. The ability of the ericoid myccorhizas to break down these organic compounds provides the fungi with N which otherwise would be inaccessible. This is crucial in the overall nitrogen poor soil, which is the growth limiting nutrient in the main part of the boreal forest (Tamm 1991). In the low-herb forest there are also ericaceous species with ericoid mycorrhiza, as well as tree species associated with ectomycorrhiza and herb species which can be associated with arbuscular mycorrhiza. Nordin et al. (2001) found that plant species associated with ectomycorrhiza or arbuscular mycorrhiza also took up organic N. This is important since the litter produced in this low-herb forest type can have a relatively high C:N ratio (even if it is lower than in the dwarf-shrub forest), leading to shortage of inorganic N. In the tall-herb forest where soil pH is relatively high, nitrification is enhanced and NO_3^- becomes more available. Phosphorus may in these areas replace nitrogen as the major growth-limiting nutrient (Giesler et al. 2002). The plant species in the tall-herb forest are mainly associated with arbuscular mycorrhiza (Nordin et al. 2001), which enhances the ability to capture phosphate ions.

Modeling soil moisture

Soil moisture is controlled by numerous factors like precipitation, evapotranspiration, topography, lateral flow, soil types and vegetation (Moore et al. 1991, Wilson et al. 2004). Within limited areas precipitation and evaporation can be assumed to be spatially uniform and thus these factors can be neglected. While there can be huge differences in precipitation for single events, the assumption of homogeneous precipitation and evaporation is reasonable for the landscape scale when one looks at longer time scales. As mentioned above, in regions with relatively thick till layer (with few bedrock edges where water could follow alternative routes) groundwater flow is to a large extent dependent on topography (which is the case in the areas presented in this thesis). Topography has a major influence on hydrologic processes and the spatial distribution of soil moisture. However, the importance of soil type (Famiglietti et al. 1998, Houser et al. 1998, Famiglietti et al. 1999) and vegetation (Hupet and Vanclooster 2002) has also been pointed out. Soil type can heavily affect soil moisture since coarse texture leads to good vertical drainage whereas fine texture can hold more water. On a landscape level the surface geology is often quite homogenous and this factor can be neglected (O'Loughlin 1986, Western et al. 1999). In the study areas used in this thesis, the soil types are fairly homogeneous. They consist mainly of sandy-silty till mixed with boulders, whereas peat often was found in depressions. The vegetation influences soil moisture by the degree of canopy conductance, root distribution and plant cover density (Hillel 1998). However, vegetation and soil moisture are tightly interlinked since soil moisture also affects vegetation as mentioned above.

The availability of digital elevation models has led to topographic-hydrologic indices being one of the most common predictors used to estimate spatial soil moisture distribution (Moore et al. 1991). The most commonly used topographic index is the wetness index $\ln(a/\tan\beta)$ developed by Beven and Kirkby (1979). It was first used for predicting spatial distribution of soil moisture (Burt and Butcher 1985, Moore and Thompson 1996, Bardossy and Lehmann 1998) but has also been used to predict for example groundwater level (Thompson and Moore 1996). This topographic index has been implemented in various hydrologic models such as TOPMODEL (Beven and Kirkby 1979). In this rainfall-runoff model the topographic index represents the extension of saturated areas and the spatial variation of soil moisture and groundwater levels. TOPMODEL in turn has been used for studying several hydrologic processes such as flood frequency (Beven 1987), flow paths (Beven and Wood 1983, Quinn et al. 1991) and water quality (Wolock et al. 1989, 1990) but also to represent the hydrologic variable in models to study photosynthesis and annual net primary production (White and Running 1994), carbon budgets (Band 1993) and vegetation patterns (Moore et al. 1993). I have in this thesis used this index (hereafter called Topographic Wetness Index, TWI) in a modified form to study the spatial distribution of species numbers of vascular plants.

Congruence in species richness

The global biodiversity crisis evokes an urgency to identify which geographic areas to protect to sustain most of the biological diversity. ‘Biodiversity hotspot’ has become a frequently used term when setting up conservation strategies. It was first applied to regions threatened by habitat loss that contained large numbers of endemic species in a relatively small area (Myers 1988, 1990). This term has since been used for a geographic area that contains high numbers of species, endemic species, rare species or which is threatened to lose much of its habitat (Reid 1998).

The resolution of scale affects patterns in congruence (Gaston 1996, Flather et al. 1997, Reid 1998). The well known pattern of increasing species richness with decreasing latitude applies to most taxa. This implies congruence in species richness among different taxa on a global or continental scale. It has been shown that the number of endemic species varies with latitude (Jansson 2003), implying that there also is a global pattern of endemism across taxonomic groups corresponding to the one in species richness. Carroll and Pearson (1998) found congruence in species richness for butterflies and tiger beetles across North America, using a 275 x 275 km grid size. In contrast, Prendergast et al. (1993) found poor overlap of species richness hotspots among butterflies, dragonflies, breeding birds, liverworts and aquatic plants covering Britain using 10 x 10 km grid size. Some of these taxa showed congruence in species richness in some, but not in other areas of Britain, but there was no consistent pattern. Poor overlap of hotspots in species richness among taxa at this and smaller scales of resolution is also supported by other studies (Lombard 1995, Flather et al. 1997). The underlying processes creating overlap or lack of overlap in hotspots among different taxa are poorly understood, but it is obvious that the taxa chosen are of importance (Lombard 1995, Jonsson and Jonsell 1999, Saetersdal et al. 2003). For example, it is not very surprising that hotspots in species richness of breeding birds, liverworts and aquatic plants do not coincide (Prendergast 1997).

Conservation planning is often made on landscape or regional scales. On these scales, a more efficient method for choosing priority areas for maximizing the number of protected species is to use complementary areas (Reid 1998). The species content of existing reserves is identified and new areas are then selected that add the greatest number of new species (Pressey et al. 1993, Williams et al. 1996, Csuti et al. 1997). Even if this method would be the optimal, in reality it is most often not feasible because of restricted finances. Often, only a small number of sites are possible to protect. In this case, approaches based on species richness work well to capture a large proportion of overall diversity when identifying priority areas (Csuti et al. 1997). Since it is virtually impossible to make complete inventories of all organism groups in an area, a common approach for identifying areas of high species richness or rarity is to use indicator species. Another approach is to use well-known organism groups which are easy to get reliable data on to predict other less known groups (e.g. Kremen 1992, 1994, Lombard 1995, Dobson et al. 1997, Virolainen et al. 2000). For indicator taxa to be useful in setting priorities, they have to be chosen carefully depending on both scale and taxonomic resolution of interest. It is unlikely that one organism group would constitute a good indicator group for all other taxa in one area. The target taxa of interest need to be decided before choosing an indicator taxon. An indicator taxon which has high overlap in species richness with a wide range of other taxa would be very valuable when seeking hotspots for species richness in general.

In boreal forests mixed results with both negative and positive correlations have been reported regarding species richness of vascular plants, mosses and liverworts (Jonsson and Jonsell 1999, Berglund and Jonsson 2001). One possible explanation for poor congruence in species richness could be the narrow range in soil moisture and vegetation type used in these studies. Positive correlations for species numbers of vascular plants and bryophytes were found in the boreo-nemoral forests of Norway (r = 0.69, 0.25 ha plot size, Saetersdal et al. 2003) and Estonia (r = 0.25 – 0. 65, 1 ha plot size, Ingerpuu et al. 2001). Sætersdal et al. (2003) also reported positive correlations between macrolichens and each of vascular plants and bryophytes. In this thesis I discuss further the correlation between the four dominating groups of primary producers (vascular plants, mosses, liverworts and macrolichens) in the boreal forests (paper **IV**), using a wider range of vegetation type and soil moisture than in the previous studies conducted in the boreal forest.

I have also studied which processes could cause the correlations in species richness or the lack thereof (**IV**). *Substrate affiliation* could be important for the mosses, liverworts and lichens since they grow on a wide range of substrates. Species groups growing on the same substrate should correlate better than total species richness provided there is a considerable variation in amount and/or quality of the substrate in question. However, dividing species into subgroups may decrease correlations by making the range in species number among plots narrower. The sampled *plot size* should also be important since more individuals and more different habitats are included when sample grid size increases. If species numbers in these four different taxa respond differently to disturbance and succession, the congruence in species richness could be influenced by *stand age*.

OBJECTIVES

The main objectives of this thesis are to investigate if spatial distribution of vascular plant species richness could be predicted by using a wetness index based only on topography, and to increase the understanding of the processes causing the spatial distribution of the four main autotrophic organism groups in the boreal landscape.

Specific objectives were:

- To study if the spatial distribution of vascular plant species numbers can be predicted by a topographic wetness index in the boreal forest (papers **I, II**)
- To evaluate if hotspots - areas of high numbers of vascular plant species - can be identified by using a topographic wetness index in the boreal forest (papers **I, II**)
- To quantify how well soil pH can explain the distribution in plant species number in the boreal forest (paper **II**)
- To test different variants of the topographic wetness index with the aim of improving the prediction of vascular plant richness, soil pH and soil moisture (paper **III**)
- To assess whether vascular plant species richness correlates with species richness of other less known groups of primary producers in the boreal forest (paper **IV**)

STUDY AREA

The field studies in this thesis have mainly been conducted in two landscape sections, each comprising 25 km^2, in the middle boreal zone of Sweden (Ahti et al. 1968). One landscape section is situated 15 km east of Åmsele (64º33'N, 19º35'E, midpoint of the area), Västerbotten county and the other one is located 240 km to the SW, just west of Kälarne, Jämtland (62º59'N, 16º01'E, midpoint of the area). Both landscape sections are fairly similar with elevations ranging 220 – 440 m a.s.l. in Västerbotten and 300 – 440 m a.s.l. in Jämtland. The soil type is mainly till in both areas with peat covering many of the depressions. In both landscapes, the bedrock is acidic consisting mainly of granite. Also climatologically the two areas are quite similar. The yearly precipitation is ~600 mm in both areas. The mean temperature in January is –13°C and –10°C for the landscapes in Västerbotten and Jämtland, respectively, and in July +14°C for both landscape sections (Raab and Vedin 1995). The areas were chosen to mainly differ in soil pH of the O-horizon. The soil pH ranges from 4.0 to 5.2 in the landscape situated in Västerbotten and from 3.9 to 6.3 in the landscape situated in Jämtland. The vegetation in both areas is dominated by boreal conifer forest, composed mainly of *Pinus sylvestris* and *Picea abies*. The forestry has developed from selective cuttings of large trees from the 19th century to intensive silviculture starting in the mid 20th century. In both landscapes square study plots of 200 m^2 were randomly distributed but constrained in order to provide a certain range of wetness values (see below). High wetness values were not included since they represented tree-less mires, streams or lakes. Subplots of 0.01, 0.25, and 1 m^2 were set up in the 200 m^2 plots.

To study congruence in species richness among four taxa (**IV**), I used data from the short pH-gradient landscape and a regional dataset. The regional study area comprised much of the northern half of Sweden between 62º11' and 66º25', situated within the Middle and North Boreal Zone (Ahti et al. 1968). In this region we selected 18 main study sites each consisting of four plots, one plot in old and one in young small-stream forest, and one plot in old and one in young non-riparian forest. Old forest sites were located within unmanaged, old-growth forest, whereas young sites were located within managed forests that had been completely clear-cut 30–50 years prior to observation. Pairs of old and young forest sites within each main site were selected to be as similar as possible in terms of physical and ecological characteristics, apart from forest management history. Each plot covered 20 x 50 m with one 10 x 20 m subplot located in the center. The data set of young forests included another six main study sites with each one plot in small-stream forest and one in non-riparian forest (in total 12 additional plots).

TOPOGRAPHIC WETNESS INDEX

In this thesis, I have used the well known Topographic Wetness Index (TWI, $\ln(a/\tan\beta)$) for producing a spatially distributed representation of groundwater flow. TWI is based mainly on contributing upslope area and slope. The upslope area is the local catchment area draining water through a certain location. In the TWI a is calculated as the upslope area per unit contour length. The upslope area can be calculated in several different ways by using calculations for the *flow distribution***,** which determine how much catchment area contributes to the groundwater flow in a specific point. In papers **I** and **II** we used a triangularly calculated flow (Tarboton 1997), which was modified so that the flow could be directed to non-restricted multiple directions. In another well known multidirectional flow distribution method developed by Quinn (1991), the flow is limited to eight possible directions of the surrounding cells. In paper **III**, we tested which of these two flow distributions performed best in correlations between TWI-values and each of for measured variables (species number of vascular plants, soil pH, groundwater level and soil moisture).

The flow distribution among down slope directions calculated according to Tarboton (1997) or Quinn (1991) can be modified by an exponent, h, according to $\tan\beta_i^h/\Sigma\tan\beta_i^h$, where $0 \leq h \leq \infty$, so that the steeper slopes receive a higher proportion of the area distributed. We tested 8 different values of the h for each of the flow distribution calculation methods (**III**).

Also the *slope* can be calculated in different ways. We have mainly used the downslope index (Hjerdt et al. 2004) rather than the local slope (**I, II**). The downslope index is calculated as L_d/d, where L_d is the distance to the nearest cell having a height $\geq d$ length units below the cell. The local slope $\tan\beta$ is calculated as the slope of every unit cell. In paper **III** we tested $\tan\beta$ as well as five different values of d. The distance to this point can be computed as beeline distance or distance along the flow path (i.e., always following the steepest downslope directions along the ground surface). We also tested which of these two alternatives *(slope distances)* yielded best results in correlations with the measured variables (**III**). The resolution of the digital elevation model (DEM) is important especially for the calculated slope (Wolock and Price 1994). Small scale topographic irregularities disappear as the grid size increases, leading to a smaller slope and hence to a larger wetness index than what would have otherwise been appropriate. It is important to note that the spatial resolution of the digital elevation model used for the calculations must be in accordance with the spatial resolution of the landscape properties determining the groundwater level. We used 20 x 20 m grids, since the standard 50 m grid of Swedish topographic maps was considered too coarse (Quinn et al. 1995, Rodhe and Seibert 1999). The improved DEM was produced by METRIA based on aerial photogrammetry.

The basic assumptions, which underlie the TWI, do not hold when there is a creek and, thus, creeks need to be considered. We assumed creeks to start when the accumulated area exceeded a certain *creek initiation threshold area (cta).* Eight *cta*-values were tested (**III**). When a creek is formed either all the accumulated area can be treated as creek cell soil water or the area up to the creek threshold area is considered soil water and only the area exceeding the threshold area is treated as creek water. We tested which of these two alternatives *(cta-down)* yielded the best results in correlations between the calculation parameters and the measured variables.

In total we tested 6 different calculation parameters in terms of correlating the calculated TWI-values with four different measured variables as well as one calculated wetness degree (based on the relationship between measured groundwater level and soil moisture, **III**). We used data from the two landscapes described above. In addition to testing which calculation method performed best for each of the single measured variables, we also tested which calculation method performed best when pooling different variables into groups.

RESULTS AND DISCUSSION

Relationship between plant species number and TWI

The majority of the investigated boreal forest landscape was relatively dry and species-poor, whereas interspersed patches linked to areas with relatively high TWI had species rich vegetation. There was a positive relationship between species richness of vascular plants and TWI **(I, II)**. The fact that I found this relationship in two different areas with different average soil pH-levels indicates that this is a general pattern in the boreal forest of Sweden **(II)**. Depending on calculation method of the TWI the relationship between plant species number and TWI differed somewhat, but the overall trend of a positive relationship persisted. It seems to be a robust pattern since it remained consistent regardless of plot size. Species richness of vascular plants still increased with TWI in all plot sizes, from 0.01 to 200 m^2, although the relationship became weaker with decreasing plot size **(I)**. TWI explained 30 % of the variation in plant species richness in the landscape with low average soil Ph (LP) and 52 % in the landscape with high average soil pH **(**HP**, II)**. When changing the parameter values used for calculating the TWI, the relationship between species numbers and TWI became even stronger (**III**). When using calculation methods of the TWI that performed best for the pooled group of species richness and soil pH for both study sites, TWI explained 58 % of the variation in species numbers in the (HP) landscape and 38 % in the (LP) landscape **(**Fig. 3**)**. These results support the idea that TWI can be used to predict plant species richness with reasonable accuracy, taking into consideration that the only input data into TWI is topography, i.e. meters above sea level.

Number of plant species not classified as regionally common (here called uncommon) in the two landscapes, respectively, increased with TWI

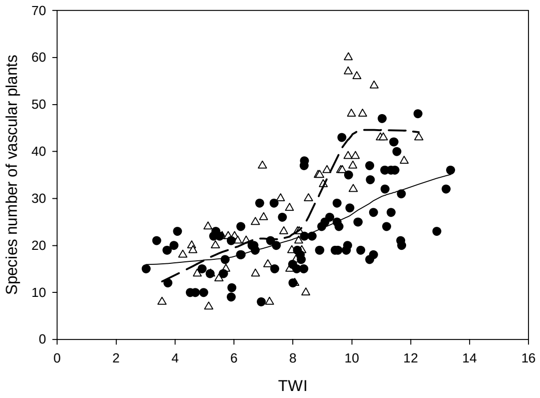

Fig. 3. *The number of vascular plant species in the HP and LP landscapes, respectively, plotted against TWI. The calculation method used to yield the TWI-values was the one performing best when pooling species richness and soil pH from both landscapes together. Linear least squares regressions (HP: $R^2 = 0.58$, $P < 0.001$, $n = 55$; LP: $R^2 = 0.38$, $P < 0.001$, $n = 80$). The curves were constructed using LOWESS regression (for each point 50 % of the total number of points were used).*

as well as for soil pH in both landscapes (**I, II**). The same results were found for the proportion of the uncommon plant species, implying that soil pH and TWI were even more important for the distribution of species classified as uncommon, than for the total species richness. The most probable reason for this is that forested areas with high TWI and pH values are scarce in boreal landscapes and plant species found mainly in such areas will therefore be classified as regionally uncommon. Plant species richness showed a nested pattern along the TWI-gradient, which explains why the highest proportion of uncommon plant species coincided with the highest total plant species numbers along the TWI gradient in both landscapes. The uncommon plant species are needed to create an unusually species rich area in the landscape.

Relationships between plant species number, soil pH and TWI

There were positive relationships between plant species number and soil pH as well as soil pH and TWI in both landscapes (**II**). The relationship between plant species number and soil pH did not differ between the two landscapes, whereas the relationship between plant species number and TWI as well as soil pH and TWI did. At low TWI-values the latter two relationships were similar in the two different landscapes, but diverged at high TWI-levels. Soil pH explained more of the variation in plant species richness than TWI. In the LP landscape soil pH explained 40 % and in the HP landscape it explained 74 % of the variation in plant species numbers

(**II**). The higher soil pH-values in areas with high TWI-values in the HP landscape compared to the LP landscape create a wider range of species numbers in the HP landscape. This wider range explains why soil pH and TWI explain more of the variation in plant species numbers in the HP landscape than in the LP landscape.

There could be several explanations for the observed pattern of increasing species number with TWI and soil pH. The postglacial history of the boreal forest in northern Sweden could be one explanation. Many of the species found today in the boreal forest of Fennoscandia have immigrated from refugial areas on the Iberian Peninsula and in South-eastern Europe, as well as from Asia (Bennett 1997, Hewitt 2000, Willis and Whittaker 2000). The Fennoscandian boreal species pool therefore better reflects the conditions in their regions of origin with higher soil pH (Pärtel 2002) than the present-day conditions in northern and central Fennoscandia. After the latest glaciation the juvenile till was more base-rich and plant species favored by high soil pH could easily spread northwards (Grubb 1987). Where the till does not consist of base-rich minerals, the leaching process has left small base-rich areas that serve as refuges for plant species that cannot survive in the otherwise relatively acidic boreal forest soils. The groundwater discharge areas that are scattered throughout the boreal landscape constitute such an example.

Another explanation for the spatial distribution pattern of vascular plant species could be an increasing soil N availability along the TWI-gradient. This was supported by the negative correlations between the C:N ratio and TWI as well as between C:N ratio and soil pH found in the HP landscape (**II**). Other studies have shown that total soil N increased with soil pH from groundwater recharge to discharge areas in boreal forests (Högberg et al. 1990, Giesler et al. 1998). Thus, the high species numbers in groundwater discharge areas could be caused by a release from competition for N, since N is the limiting nutrient in the majority of these forests (Tamm 1964, 1991). It could also be an effect of the differentiation of the soil N pool taken up by different plants along the soil moisture gradient from groundwater recharge to discharge areas (Nordin et al. 2001), which also is related to changes in type of mycorrhizas associated with plants along such a moisture gradient (Read 1991). This is discussed further in paper **II**.

A third explanation could be increasing habitat heterogeneity within plots with higher TWI-values (**I**). In areas with low TWI values, most often the entire ground is dry and acidic, whereas in areas with high TWI and soil pH values, there are often patches of drier and more acidic conditions, for example on boulders, logs and hummocks. This is supported by the nested pattern in plant species occurrences along the TWI-gradient in both landscapes (**I, II**). None of the plant species occurred exclusively in the lower end of the TWI gradient. Species were added to the overall species list along the TWI-gradient so that species growing on plots with low TWI and soil pH values also could be found in plots with high TWI-values.

Evaluation of different calculation methods of TWI

The correlations between TWI-values and the measured variables varied much depending on the calculation methods of TWI. There was not one single calculation method, which was optimal for all measured variables and study sites. However ‘compromise’ methods, which performed well for groups of measured variables could be identified. When looking for common patterns among the measured variables we found two groups with plant species richness and soil pH in one and groundwater level, soil moisture and wetness degree in the other. Within each of these groups the calculation methods performing best overlapped quite well. The correlation coefficients decreased with the generality of the calculation method. The best overall calculation method when grouping all measured variables in both study sites together did not yield as strong correlations as the best calculation methods for each single measured variable.

In general, Quinn’s flow distribution performed better than Tarboton’s and a low value of h yielded the best results. The downslope index, *DI*, was found in most cases to be superior to the use of the usual local slope tan*ß*. A higher d and the beeline distance were best for soil pH and species richness, whereas a lower d and flow path distance was best for the hydrologic variables.

There are some known problems with Quinn’s flow distribution method with overestimation of flow dispersion in near-stream areas (Kim and Lee 2004). The reason Quinn’s flow distribution method was still superior to the modification of Tarboton’s distribution method could be that most plots in our study sites were not located in stream-cells. Low values of h, which performed best, show that a multiple flow directional algorithm is better than a single directional flow algorithm. These results are supported by Pan et al. (2004) who found that the multiple flow direction is geometrically more accurate than the single flow direction. The outcome of h could depend on the slope steepness in the study sites. Güntner et al. (2004) found h values of 8-10 to be most suitable in a mountainous catchment, whereas in our study area with gentler slopes, lower values of h yielded the best results.

The difference in which value of d performed best when calculating the DI for the two groups of measured variables indicates that downslope drainage conditions are more important for the plant species richness and soil pH than for groundwater level, soil moisture and wetness degree. This could be explained by that local slope can reflect the hydrologic variables quite well, whereas larger geomorphic features are more important for species richness of vascular plants and soil pH. For example, a site on a plateau with relatively small upstream area and a low slope can be quite moist but have low soil pH and plant species richness. A higher value of *d* gives information on the downslope conditions, which can indicate where along a slope the site is situated. A larger value of *d* can also better reflect the slope of the groundwater table, which affects groundwater flow, which in turn affects plant species richness and soil pH. Everything else being equal higher groundwater flow yields higher plant species richness and soil pH than more stagnant water.

Congruence in species richness between vascular plants, mosses, liverworts and macrolichens in the boreal forest

Species richness of vascular plants correlated well with total species richness of mosses and liverworts. These results were consistent for three datasets: (1) 200 and 1,000 m^2 plots in young (30-50 years after clear-cutting) forest on a regional level; (2) 200 and 1,000 m^2 plots in old unmanaged forest on a regional level, and (3) 0.01-200 m^2 plots in a forest dominated landscape of 25 km^2 (**IV**). The congruence in species richness among these three taxa seems to be robust since it was found irrespectively of plot size, which differed from 0.01 m^2 to 1,000 m^2. Total species richness of macrolichens (fruticose and foliose growth forms) did not correlate significantly with the other three organism groups. The reason for this could be that species numbers of vascular plants, mosses, and liverworts increase with ambient moisture, maintaining strong positive correlations despite large differences in life form distribution of their species. In contrast, for macrolichens moisture seems not to be the most important factor. Epilithic and epiphytic species contributed most to the overall variability in species numbers of lichens, suggesting amount or quality of these substrates as the major factor. Light might also be a contributing factor, explaining the lack of correlation in species richness between macrolichens and liverworts/mosses despite their large overlap in life forms. It is known that lichen ground cover is better developed in light habitats and bryophyte cover is better developed in darker habitats (Pharo and Vitt 2000, Sulyma and Coxson 2001).

Dividing the species into subgroups based on substrate affiliation resulted in still positive, but weaker correlations between vascular plants, liverworts and mosses. Otherwise, the most striking result was between mosses and lichens. Ground-living species became more negatively correlated compared to all species, whereas not ground-living became more positively correlated, which is discussed further in paper **IV**. In general, increasing plot size resulted in stronger positive correlations among vascular plants, mosses, and liverworts. Stand age did not influence the correlations much, except that ground-living mosses and liverworts correlated stronger in young, managed compared to old, unmanaged forests.

CONCLUDING REMARKS AND FUTURE PROSPECTS

The main conclusions of this thesis are:

- Most boreal forest land in Sweden is relatively poor in vascular plant species. Only relatively small interspersed patches linked to groundwater flow close the ground surface are species-rich.
- The topographic wetness index can be used as a tool for identifying areas of high probability of having high species number and rarity of vascular plants.
- Total number of vascular plant species as well as number of regionally uncommon vascular plant species generally increase with the topographic wetness index and soil pH within the studied ranges of these variables.
- The proportion of uncommon plant species increases with TWI and soil pH.
- Different TWI calculation methods perform best for different measured variables and groups of these. In general, Quinn's flow distribution performs better than Tarboton's and a low value of h yielded the best results. The downslope index, *DI*, is found in most cases to be superior to the use of the usual local slope $\tan ß$. A higher d and the beeline distance are best for soil pH and species richness, whereas a lower d and flow path distance is best for the hydrologic variables.
- There is high congruence in species numbers among vascular plants, liverworts and mosses. However, lichen diversity does not correlate with these three groups of land plants.
- Moisture seems to be a main factor controlling the patterns in overlap of species rich areas among vascular plants, mosses and liverworts.

To ensure maintenance of boreal biodiversity, a better understanding is needed of the processes creating the spatial distribution of species richness. The TWI could be used both for research and as a predictive tool within conservation management. Below I outline some research which I think should follow from the results published in this thesis:

Prediction ability of the TWI

- This thesis has demonstrated a strong positive relationship between plant species richness and TWI in the boreal forest. It would be intriguing to test the generality of this relationship by studying other parts of the boreal forest, such as in Russia or Canada as well as in temperate areas. Different calculation methods of the TWI should be tested also in these areas to further investigate if it is possible to find a more general calculation method for different areas and measured variables.
- The most species-rich areas in my studies coincided with areas having the highest proportion of regionally uncommon species. This implies that the TWI could be used to identify hotspot areas regarding uncommon plants in the boreal forest. It would be interesting to identify areas in the field rich in uncommon plant species and obtain TWI-values for these areas. If these hotspots all have a TWI-value within a reasonably narrow range it would be possible to predict the location of such areas using TWI.
- This thesis provides support for congruence in species richness among vascular plants, liverworts and mosses in the boreal forest. It should be possible to construct predictive statistical models based on the relationship between vascular plant numbers and TWI to predict variability in species numbers of mosses and liverworts. This could become very useful since it is easier to collect data on vascular plants than on the other two organism groups. It would then be interesting to investigate if other taxa, which to a large extent are influenced by moisture, such as terrestrial gastropods (Hylander et al. 2004), also coincide with the land plants in species richness and whether they could be predicted using the TWI.
- In this thesis the usefulness of one specific topographic index, the topographic wetness index, calculated in different ways has been tested. Other indices such as upslope area and slope separately could also be tested by using different calculation methods. The results indicate that the downslope index could help in distinguishing between stagnant and non-stagnant groundwater conditions, which

the index failed to do in the first two studies in this thesis. These two types of area have very different soil conditions as well as species numbers and composition. To make TWI more efficient in conservation planning these two kinds of area must be discerned by the index, which is a further development of the TWI.

- Instead of using point-to-point data as in this thesis, variables could be measured more densely over the study area, which would allow more detailed analyzes of the studied relationships. In this case the study area has to be more restricted than the areas included in this thesis.

Change in species composition

- So far, my studies have focused on species richness. However, changes in species composition along the TWI-gradient are also of interest. I found a nested species richness pattern in the studied areas as well as a proportional increase in uncommon vascular plant species along the TWI-gradient. It would be interesting to study if the change in species composition along the wetness gradient in these two landscapes is similar both in terms of which species and which species characteristics such as life forms are involved.

Underlying processes creating the spatial distribution of species richness

- The processes creating the spatial distribution of species richness in the boreal forest deserve further study. The influence of amount and quality of different substrates for species richness of mosses, liverworts, lichens etc. needs to be elucidated. It would also be interesting to unveil which primary soil factors influence the distribution of vascular plant species. For example, from my results the effect of nitrogen concentration and form of nitrogen cannot be distinguished from pH.

IMPLICATIONS FOR NATURE CONSERVATION

The results presented in this thesis can potentially become very useful for conservation management of the forest landscape. Field inventories are often both time and labor consuming. To make the work more efficient, the TWI could be used for identifying areas of special interest, e.g. hotspots of species diversity. The results in my thesis show that one such habitat could be groundwater discharge areas. In these areas, the soil is characterized by high levels of groundwater, soil pH and nitrogen, especially in the form of NO_3^-, which otherwise are scarce in the boreal forest. TWI can provide data on the spatial distribution of such conditions, information that can not be extracted from topographic maps or aerial photographs. Results in this thesis show that discharge areas both have high total species numbers of vascular plants as well as high proportions of regionally uncommon vascular plant species. Since there are strong correlations in species richness between vascular plants and mosses as well as liverworts, all three taxa also have high species numbers in moist forest areas.

In Fennoscandia, the tree layer in mature natural forests of groundwater discharge areas is dominated by *Picea abies*, often together with several deciduous tree species such as *Betula* spp., *Populus tremula* and *Salix caprea*. Whereas *Pinus* dominated forests in their natural state are characterized by frequent fire disturbance, *Picea* forests are more formed by small-scale gap formations due to autogenic disturbance (Kuuluvainen et al. 1998). Single or groups of trees are killed by strong local winds, insects etc. creating multi-aged and multi-sized stands providing important microhabitats. Leaving discharge areas intact when logging the forest would lead to an accumulation of dead and dying wood in moist to wet forests. This would favor many epixylic liverwort species (Söderström 1988, Dynesius 2001) and epixylic moss species (Dynesius 2001) which are more frequent in moister than in drier sites. Moist discharge areas would also be a suitable habitat for not ground-living moss and liverwort species in general which were found in this thesis to correlate positively with number of vascular plant species.

One disadvantage of the TWI is that the digital elevation model needed to get a good index has to be of finer resolution than the 50 x 50 m grid size readily available in Sweden. The information can be obtained by aerial photogrammetric analysis, but is quite costly. However, in the future digital elevation models based on laser technique which will increase both the resolution and accuracy of the TWI method will be available, probably to a lower cost.

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