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Evaluating a nutrient availability metric against data from Swedish conifer forests

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Abstract

There currently exists no standardized metric for comparing nutrient statuses of terrestrial ecosystems at the global scale. Possibly, a non-validated formula developed by IIASA (Laxenburg, Austria) is appropriate, but as this metric only demands data on indirect drivers of nutrient availability, it may require more explicit information on nitrogen (N) and phosphorus (P) availabilities, apart from evaluations against empirical data. We evaluated the metric against forest data for the first time, by exploring if it could describe patterns in 'normalized' (climate-independent) productivity for 1099 Norway spruce (*Picea abies* (L.) H. Karst.) and 1422 Scots pine (*Pinus sylvestris* L.) ecosystems across Sweden, where N is strongly limiting. Furthermore, we examined whether soil factors not yet included explained variation. Lastly, soils were sampled at three fertilizer experiments in northern Sweden to clarify whether i) outcomes of the national database would be valid here and ii) soil measurements not included in the database could be useful for a future metric.

The ratio of actual to attainable spruce productivity increased from northern (0.2-0.3) to southern (0.6-0.7) Sweden, indicating increasing nutrient availability in the same direction. IIASA's metric could not describe variation in nutrient availability, because the variables it includes are apparently not well implemented and important factors are missing. While the metric was unrelated to normalized productivity (R^2 = 0.000-0.008), the soil C:N ratio correlated negatively with it at the countrywide scale (R^2 = 0.021-0.131). However, N addition in the experiments had not consistently altered the C:N ratio. N availability was better reflected there by plant root simulator N supply rates, which related to productivity (R^2 = 0.177-0.730). Hence, supply rates may be included in the metric, whereas adding the C:N ratio might only allow describing large-scale patterns in nutrient availability, for it does not capture temporal dynamics like fertilizer addition responses.

Samenvatting

Momenteel bestaat er geen gestandaardiseerde uitdrukking die toelaat de nutriëntenbeschikbaarheid van landecosystemen op aarde te vergelijken, al ontwikkelde IIASA (Laxenburg, Oostenrijk) een niet gevalideerde formule die mogelijk als dusdanig dienst kan doen. Omdat hun indicator enkel indirecte invloeden bevat, moet die mogelijk verbeterd worden met expliciete informatie over stikstof (N) en fosfor (P) beschikbaarheden, naast het gegeven dat evaluatie tegen empirische data nodig is. We onderzochten of de indicator patronen in 'genormaliseerde' (klimaatonafhankelijke) productiviteit kan beschrijven voor 1099 bossen met Fijnspar (*Picea abies* (L.) H. Karst.) en 1422 met Grove den (*Pinus sylvestris* L.) in Zweden, waar N limiterend is. Bovendien controleerden we of aparte bodemfactoren ook variatie verklaren. Bodemstalen van drie bemestingsexperimenten in noord Zweden lieten verder toe te onderzoeken of i) conclusies uit de nationale database ook hier gelden en ii) bodemvariabelen die niet in de database staan nuttig blijken voor verbeteringen.

De verhouding van de huidige tot een theoretisch maximale productiviteit voor sparren stijgt van noord (0.2-0.3) naar zuid (0.6-0.7) in Zweden, wat suggereert dat de nutriëntenbeschikbaarheid toeneemt in dezelfde richting. IIASA's indicator kon geen variatie in nutriëntenbeschikbaarheid beschrijven, omdat de ingebouwde bodemvariabelen schijnbaar suboptimaal geïmplementeerd zijn en ze belangrijke factoren niet bevat. Terwijl de indicator niet gerelateerd was aan genormaliseerde productiviteit (R^2 = 0.000-0.008), was de C:N ratio er negatief mee gecorreleerd op nationale schaal (R^2 = 0.021-0.131). In de experimenten daarentegen bleek N bemesting niet steeds te leiden tot een daling in C:N, terwijl N-aanvoer, gemeten met 'plant root simulator' probes, wel goed productiviteit beschreef (R^2 = 0.177-0.730). Kortom, zulke metingen door probes zouden deel kunnen uitmaken van een toekomstige indicator, terwijl implementatie van de C:N ratio ten hoogste voldoende is voor het beschrijven van patronen op grote schaal, aangezien die niet steeds een respons vertoont op temporele dynamieken ten gevolge van bijvoorbeeld N additie.

Layman's abstract

Nutrients in the soil are among the determinants of ecosystem functioning. This not only implies that plant growth is stimulated when we add nutrients. Impacts of climate change, for example, are dependent on soil fertility. Our understanding of this last aspect is however incomplete, and research aiming at unravelling global patterns suffers from the absence of a good metric of nutrient availability. In other words, it is virtually impossible to compare the nutrient status of for instance a Swedish conifer forest and a tropical rainforest in French Guiana.

In this dissertation, we investigated whether a non-validated metric, developed by the Austrian IIASA-institute, would be able to describe patterns in productivity across more than 2000 spruce and pine forests in Sweden. Moreover, we examined whether some soil factors not yet included in the metric could be useful for future improvements. Finally, we sampled soils in some nutrient addition experiments in northern Swedish forests, to link more detailed measurements to productivity.

The indicator hardly managed to describe nutrient availability in Sweden, which clearly increases from north to south. In contrast, the soil carbon to nitrogen (C:N) ratio might prove useful: the lower the ratio, the more productivity is supported. However, the experiments unraveled that N additions do not necessarily lower C:N, thus other measures sensitive to N availability are needed there. Inorganic N supplies, measured using plant root simulator probes, were however related to productivity in these experiments. Hence, including C:N in the formula can certainly be useful for a better description of nutrient availability at large scales, but additional data such as N supplies to probes may well be part of a future metric too, especially if it has to be capable of describing patterns at nutrient addition experiments.

Samenvatting voor het brede publiek

Voedingsstoffen of nutriënten bepalen in belangrijke mate hoe een ecosysteem functioneert. Dit betekent niet enkel dat plantengroei wordt gestimuleerd wanneer we nutriënten toevoegen, maar ook bijvoorbeeld dat de impact van klimaatverandering afhangt van de vruchtbaarheid van de bodem. Van dit laatste is nog lang niet alles geweten, en onderzoek naar wereldwijde patronen wordt bemoeilijkt door gebrek aan een goede indicator of formule voor nutriëntenbeschikbaarheid. Met andere woorden, het is quasi onmogelijk om de nutriëntenstatus van pakweg een naaldbos in Zweden te vergelijken met die van een tropisch regenwoud in Frans-Guyana.

In dit project trachtten we een deeltje van deze knoop te ontwarren door na te gaan of een niet gevalideerde indicator, ontwikkeld door het Oostenrijkse IIASA-instituut, patronen in productiviteit over meer dan 2000 Zweedse sparren- en dennenbossen kan beschrijven. Ook onderzochten we of nog niet geïncorporeerde bodemfactoren van pas kunnen komen om de indicator te verbeteren. Bij enkele bemestingsexperimenten in Noord-Zweedse bossen ten slotte, verzamelden we bodemstalen om gedetailleerdere metingen te linken aan productiviteit.

De indicator blijkt nutriëntenbeschikbaarheid in Zweden (die stijgt van noord naar zuid) nauwelijks te beschrijven. De verhouding koolstof:stikstof (C:N) in de bodem daarentegen, lijkt wel nuttig: waar C:N laag is, wordt productiviteit bevorderd en omgekeerd. De experimenten maakten echter duidelijk dat toevoeging van N niet steeds gepaard gaat met een daling in C:N, zodat andere metingen daar nodig zijn om N-beschikbaarheid te bepalen. Aanvoer van N, gemeten met probes die plantenwortels simuleren, kon wel in verband worden gebracht met productiviteit in de experimenten. Invoegen van C:N in de formule kan dus zeker nuttig zijn voor een betere beschrijving van bodemvruchtbaarheid op grote schaal, maar gegevens zoals de N-aanvoer gemeten met probes maken dus ook mogelijk deel uit van een toekomstige indicator voor nutriëntenbeschikbaarheid, zeker indien die bij bemestingsexperimenten patronen moet kunnen beschrijven.

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I do neither forget the people in Sweden. I am thankful to the coordinators and principal investigators of the sites I worked in for giving us the chance to sample soils and, equally important, for sending the necessary productivity data on time. Concerning the national database, I had interesting e-mail conversations with Dr. Johan Stendahl, Prof. Michael Bergh and Prof. em. Sune Linder, whose answers all inspired me during the process of making this dissertation.

I have noticed that some of my family members and friends were sincerely interested in what I have been doing over the past few months, and they often helped me indirectly by asking questions from a different angle (or by not walking on my laptop's keyboard in case of my cat, Musti). I thank them all for this, and I hope they keep on being just as curious as I am in the future; an interesting path of research lies ahead, much is still to be discovered.

I dedicate this work to my grandmother, who passed away on 23-12-2016.

May 2017
Innsbruck, Austria
Kevin Van Sundert

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Introduction

Determinants of plant productivity

The Sun's radiant energy largely drives carbon fixation of terrestrial ecosystems (Chapin *et al.*, 2002; Smith & Smith, 2003). On a global scale, their gross (e.g. Beer *et al.*, 2010; Wang *et al.*, 2014) and net (e.g. Chapin *et al.*, 2002; Smith & Smith, 2003) primary productivities vary by more than an order of magnitude, owing to differences in environmental conditions. Up to a certain level, climate, i.e. precipitation (or water availability, e.g. Smith & Smith, 2003; Fernández-Martínez, Vicca, Janssens, Luyssaert *et al.*, 2014), temperature and their interactions (Fernández-Martínez, Vicca, Janssens, Luyssaert *et al.*, 2014), correlate positively with productivity, as do light and atmospheric carbon dioxide concentrations, *ceteris paribus* (Chapin *et al.*, 2002; Smith & Smith, 2003). However, correlations do not necessarily imply causation: certainly, temperature, water, light and CO_2 affect the photosynthetic rate at the leaf (Larcher, 2003) and canopy level, but indirect effects are of paramount importance. Climatological variables define the length of the growing season and affect the availability of soil resources (i.e. nutrients and water). In turn, these soil resources strongly influence productivity, mainly through their effect on the leaf area (LAI), thus promoting photosynthesis (Chapin *et al.*, 2002).

The role of nutrients

All organisms on Earth require nutrients to support their vital functions. Plants are no exception, and accordingly they usually gain essential mineral elements, to be found in the soil, through their root system. These elements are necessary for plant survival, growth and reproduction because they are constituents of biomolecules such as nucleotides, amino acids, cofactors, chlorophylls or phospholipids. Moreover, some are directly involved in cellular processes in their ionic form, e.g. calcium serves as a secondary messenger and potassium plays a key role in stomatal closure (Evert & Eichhorn, 2013). Given that plants need nutrients and soils vary in their ability to supply them, plants have developed different evolutionary traits. For example, where soils are fertile, competitive or ruderal species typically rapidly acquire nutrients. On poor soils, on the other hand, stress-tolerant species are – among other things – characterized by low leaf and root turnover, so as to avoid ample nutrient losses (Chapin, 1980). At the community scale, these insights can be used to explain patterns of biodiversity: for instance, species richness typically shows a unimodal (humped-back shaped) curve if it is plotted against nutrient availability, because only few species are adapted to tolerate high stress (i.e. low nutrient) levels, while at the other end, the most dominant species outcompete the others (Fraser *et al.*, 2015). Lastly, nutrients also influence patterns, processes and functioning at the ecosystem scale and beyond. As already touched upon above, soil resources correlate positively with LAI (Vose *et al.*, 1994) and therefore productivity. Furthermore, nutrient availability may regulate the biomass production efficiency of forests (Vicca *et al.*, 2012). In addition, there is emerging evidence that nutrients mediate ecosystem responses to various global change factors, such as N deposition (From *et al.*, 2016), increasing CO_2 concentrations (Norby *et al.*, 2010; Terrer *et al.*, 2016), warming (Dieleman *et al.*, 2012) and drought (Friedrich *et al.*, 2012).

Our current understanding of nutrient availability

The total content of a nutrient in the soil is ultimately dependent on atmospheric, lithospheric or hydrospheric inputs, and outputs back into these compartments. For nitrogen (N), the primary limiting element in boreal and most temperate ecosystems (Vitousek & Howarth, 1991), atmospheric inputs through fixation or deposition dominate, unless riverine import is high. Leaching into the groundwater and denitrification into the atmosphere are common outputs (Thomas *et al.*, 2015). In contrast to N, the primary reservoir for phosphorus (P) and base cations (potassium (K), calcium (Ca) and magnesium (Mg)) is not the atmosphere, but the parent material from which these nutrients are released by weathering, while leaching plays an important role in ultimately removing these nutrients from the total pool (Hynicka *et al.*, 2016; Augusto *et al.*, in press). Total soil N contents are thus more dependent on biological processes than those of P and base cations.

The availability of nutrients is not simply described by their total content in the soil. Fractions of each nutrient are distributed over the soil solution, exchange sites and unavailable soil pools (Roy *et al.*, 2006). Nutrients in the soil solution are readily available for plant uptake (Roy *et al.*, 2006). Forms of N taken up by plants are either nitrate (NO_3^-), ammonia (NH_4^+) or small organic molecules (Aerts & Chapin, 2000; Oyewole *et al.*, 2016), while most P, K, Ca and Mg are available as inorganic $H_2PO_4^-$, K^+, Ca^{2+} and Mg^{2+} (Chapin *et al.*, 2002). Furthermore, these charged elements can adsorb to oppositely charged organic matter and clay colloids, which represent the exchangeable pool, from which plants can acquire the nutrients in exchange for H^+ they excrete (Larcher, 2003; Roy *et al.*, 2006). Lastly, the unavailable pool represents the stock from which nutrients are slowly released and thus made available over longer time scales. Soil organic matter (SOM) constitutes the main pool of unavailable N to plants (Binkley & Hart, 1989), whereas for base cations, and even more for P, mineral soil resources contribute to a great extent to the unavailable pool (Chapin *et al.*, 2002). Consequently, the processes that dominate replenishment of the available soil solution and exchangeable pools from the unavailable pool differ among nutrients: for N, biological processes (e.g. decomposition, mineralization and immobilization) play a key role (Augusto *et al.*, in press), while especially for P, geochemical reactions related to release and fixation of the nutrient are more important (Chapin *et al.*, 2002; Batjes, 2011; Achat *et al.*, 2016).

Given the differential molecular characteristics (e.g. charge, solubilities) and importance of processes governing supply to the available pools, we can expect that the availability of N, P and exchangeable base cations is controlled by varying factors as well. In general, environmental factors (notably temperature and moisture - Binkley & Hart, 1989) are more important to N availability than to the availability of P and exchangeable bases, because these factors substantially regulate the rate of biological processes, on which particularly N availability relies (Augusto *et al.*, in press). Soil properties, on the other hand, affect availabilities of all nutrients, albeit not in exactly the same way. First, SOM content has a positive influence on nutrient availability by acting as a nutrient reserve (Grand & Lavkulich, 2015) and providing anion and cation exchange sites (IIASA & FAO, 2012). Moreover, the chemical composition and molecular structure of SOM has a great influence as well. Especially the soil (and SOM) C:N ratio may be a good indicator of N availability, even at the global scale, as high values indicate low N stocks plus slow decomposition and thus mineralization, and vice versa (Roy *et al.*, 2006). Another factor is soil texture: a high clay fraction corresponds to a high cation exchange capacity (CEC), i.e. the soil's potential to retain positively charged, exchangeable ions such as NH_4^+, K^+, Ca^{2+} and Mg^{2+} (Chapman, 1982; Chapin *et al.*, 2002). Finally, soil pH strongly influences availability of P and base cations. The capacity of various compounds to lock up P are pH dependent, leading to maximal P availability at intermediate pH (Chapin *et al.*, 2002), while enhanced leaching of base cations occurs in acidic soils, thus reducing the amount of total exchangeable bases (TEB = cation equivalent of summed Ca, Mg, K and Na - IIASA & FAO, 2012). In summary, environmental factors and organic matter characteristics mainly influence N availability, whereas chemical soil properties especially define P availability and TEB.

Measuring nutrient availability

A large range of local methods exists to assess soil fertility, especially in an agricultural context (e.g. Roy *et al.*, 2006; Havlin *et al.*, 2013). Overall, each of these methods can be assigned to one of four categories: lab experiments, nutrient manipulations in the field, plant tissue measurements and analyses of the soil itself (Sullivan *et al.*, 2014). In the context of this dissertation, we focus on the soil measurements. Apart from soil $\delta^{15}N$ (e.g. Sullivan *et al.*, 2014; Jeffers *et al.*, 2015) and measurements of short-term fluctuations of ecosystem processes related to nutrient cycling (e.g. mineralization, (de)nitrification, NH_4^+ volatilization, … - Chapin *et al.*, 2002), most evaluations of nutrient availability based on measurements in the soil itself can be subdivided into two groups: chemical extractions on soil samples and supply rate analyses using probes. The basic principle of the extractions is as follows: a certain solution is added to a given amount of soil sample, so that the solvent will make the extractable or nearly plant available pools of the considered element go into the solution (Havlin *et al.*, 2013) through complexation, dissolution, desorption, exchange or hydrolysis (Sims, 1999). Subsequently, a colorimetric analysis on the filtered extract can be performed to determine the concentration of a certain nutrient. Hence, this represents a combination of the pool that was already in solution and the part that was passed to the solution by the solvent.

Although extractions are frequently used to assess soil fertility, they are meant to represent available nutrient pools rather than the real supply of molecules towards plant root hairs (Mobley *et al.*, 2014; Sullivan *et al.*, 2014; Oyewole *et al.*, 2016). Instead, ion exchange membranes such as plant root simulator (PRS) probes aim to mimic roots or root hairs and are indicative of the integrated nutrient supply through the soil solution during the time they were buried (Dijkstra *et al.*, 2012). They thus incorporate the effect of diffusive transport, which is known to play a prominent role in actual plant uptake of nutrients. Not surprisingly, therefore, various studies suggested that supply rates obtained by PRS probes might approximate nutrient availability more closely than snapshots of extractable pools (e.g. Qian & Schoenau, 2002; Johnson *et al.*, 2005).

Comparing nutrient availability across ecosystems

Despite the qualitative knowledge described above and a multitude of methods that allow a local (but imperfect - Cleveland *et al.*, 2011) soil fertility evaluation, a validated and standardized quantitative multifactorial metric to compare the nutrient status of different sites at a large scale (e.g. national, continental or worldwide) does not yet exist. As a result, publications on studies in which nutrient availability across sites had to be compared, describe soil fertility related approximations such as the height of 100-year old trees (Tupek *et al.*, 2016) or manually classify sites into categories (e.g. low, medium, high nutrient availability) based on existing site information (Vicca *et al.*, 2012; Fernández-Martínez, Vicca, Janssens, Sardans *et al.*, 2014). Indeed, the absence of a more nuanced expression restricts possibilities for carrying out meta-analyses and other studies in which researchers would want to elucidate the role of nutrient availability in ecosystem processes and functioning (Cleveland *et al.*, 2011) and responses hereof to global change. Such knowledge is of great importance, especially since it feeds global carbon cycle models with information on how nutrients could limit future CO_2 uptake by the terrestrial biosphere (Goll *et al.*, 2012; Thomas *et al.*, 2015; Wieder *et al.*, 2015). Hence, there is need for a standardized nutrient availability metric, which allows comparisons in nutrient status for ecosystems worldwide. It should be able to grasp large patterns of variation, without being too complex so that a limited set of field measurements suffices to evaluate the fertility of a site.

Only a few exploratory attempts to find an expression for nutrient availability at the global scale have been made. A first effort to find a globally applicable productivity index based on real soil data was made by the Food and Agriculture Organization of the United Nations (FAO, Rome, Italy) in 1970 (Riquier *et al.*, 1970): they developed a score, depending on soil moisture, drainage, depth, texture, base saturation, salt, SOM, CEC and mineral reserves. In their Global Agro-ecological Zones report of 2012 (IIASA & FAO, 2012), the International Institute for Applied Systems Analysis (IIASA, Laxenburg, Austria) and FAO provide another, less complex index. It is a worldwide applicable metric for constraints on nutrient availability, principally meant for agricultural purposes. This metric represents, for a particular crop species, the percentage of the maximum attainable productivity that could be reached given constraints imposed by environmental characteristics such as climate, rooting conditions and soil oxygen availability, but absent nutrient limitation:

$$\text{Equation 1 | Actual productivity} = \frac{\text{Metric score [\%] x Attainable productivity}}{100}$$

The species-specific score of the metric is dependent on four measurable soil variables: soil organic carbon concentration (SOC - %), texture, total exchangeable bases (TEB - $\text{cmol}_{+}\ \text{kg}^{-1}$ dw) and pH_{H2O}. Consequently, the exchangeable bases are included explicitly, whereas the availability of N and P are not. The metric is therefore considered as an indicator of constraints on nutrient availability rather than of nutrient availability as such.

Objectives

To our knowledge, the accuracy of IIASA's metric has not yet been tested against data from natural ecosystems. As sufficiently detailed and comparable soil and productivity data are not available for ecosystems worldwide, we have to evaluate the metric for separate regions where such information is already available. In the current dissertation, we therefore evaluate the metric against aboveground productivity data from Norway spruce (*Picea abies* (L.) H. Karst.) and Scots pine (*Pinus sylvestris* L.) forests across Sweden. A national dataset from Swedish forests was used in particular because of its many data points and the fact that it contains all required soil information to calculate the metric. It moreover holds additional information on soil N. As we anticipated that explicitly incorporating N (and perhaps P) could considerably enhance variation explained by the metric, compared to the default formula with only some built-in indirect drivers, we further explored if particular soil variables related to N availability could be of use for improvements of the metric in the future.

Apart from linking soil and productivity information from a Swedish national database, we collected and analyzed soil samples from fertilizer experiments in northern Sweden in order to link local, more detailed soil data to productivity in plots with varying fertilizer application treatments. Such experiments are especially useful for finding appropriate soil variables for future inclusion of N in the formula, as the treatments represent very different nutrient (nitrogen) availabilities while climate remains unaltered. Hence, the advantage of sampling at nutrient manipulation experiments is that the differences in productivity can immediately be attributed to corresponding variation in nutrient availability. Moreover, results from such experiments may shed light on whether local productivity patterns, primarily influenced by fertilizer applications, can be explained by the same soil factors as those describing large-scale patterns in the national database.

Research questions

In the current dissertation, we address the following questions and hypotheses:

Questions regarding a national database across Sweden

Question 1: how is aboveground biomass production of conifer forests in Sweden related to spatial variation in climatological variables? (Why) is this different for spruces and pines?

Question 2: can IIASA's metric of constraints on nutrient availability explain variation in normalized (i.e. climate-independent) productivity across Sweden? Are the soil variables already included in the metric (SOC, texture, TEB and pH_{H2O}) well implemented?

Question 3: which single soil variables best explain variation in normalized productivity? Which combination of soil factors best explains patterns in normalized productivity?

Questions regarding investigated nutrient manipulation experiments in northern Sweden

Question 4: can IIASA's metric of constraints on nutrient availability explain patterns in productivity among fertilization treatments?

Question 5: which single soil variables best explain variation in productivity? Which combination of soil factors best explains patterns in productivity? Is the outcome similar as for the database (*question 3*)?

Materials & Methods

Before evaluating the metric, we tested the influence of climate on forest productivity (Q1). This relationship was then used to normalize productivity for climate effects so that its association with the metric (Q2) and soil factors (Q3) could be investigated. Normalized productivity was calculated in two alternative ways, each with its own advantages and drawbacks. In brief, the first method was a residual analysis, for which residual values of the regression model of Q1 served as the normalized productivity response. For the alternative method, the same original productivities of the database were divided by a theoretical maximum under non-nutrient-limited conditions, thus adopting a similar approach as IIASA (cf. Equation 1). As this theoretical maximum, further referred to as attainable productivity, was only available for spruce, this second method could only be applied to this species. Normalized productivity was then fitted against IIASA's metric to test its performance, after which residuals were set out against the four variables of the metric to investigate whether they are well implemented (Q2). Regression analyses in addition elucidated how soil variables could explain variation in normalized productivity (Q3). Lastly, the same methods as for the previous two questions were adopted to productivity and more detailed soil data of a few nutrient addition experiments in northern Sweden (Q4 and Q5). An overview of the methodology is presented in Fig. 1.

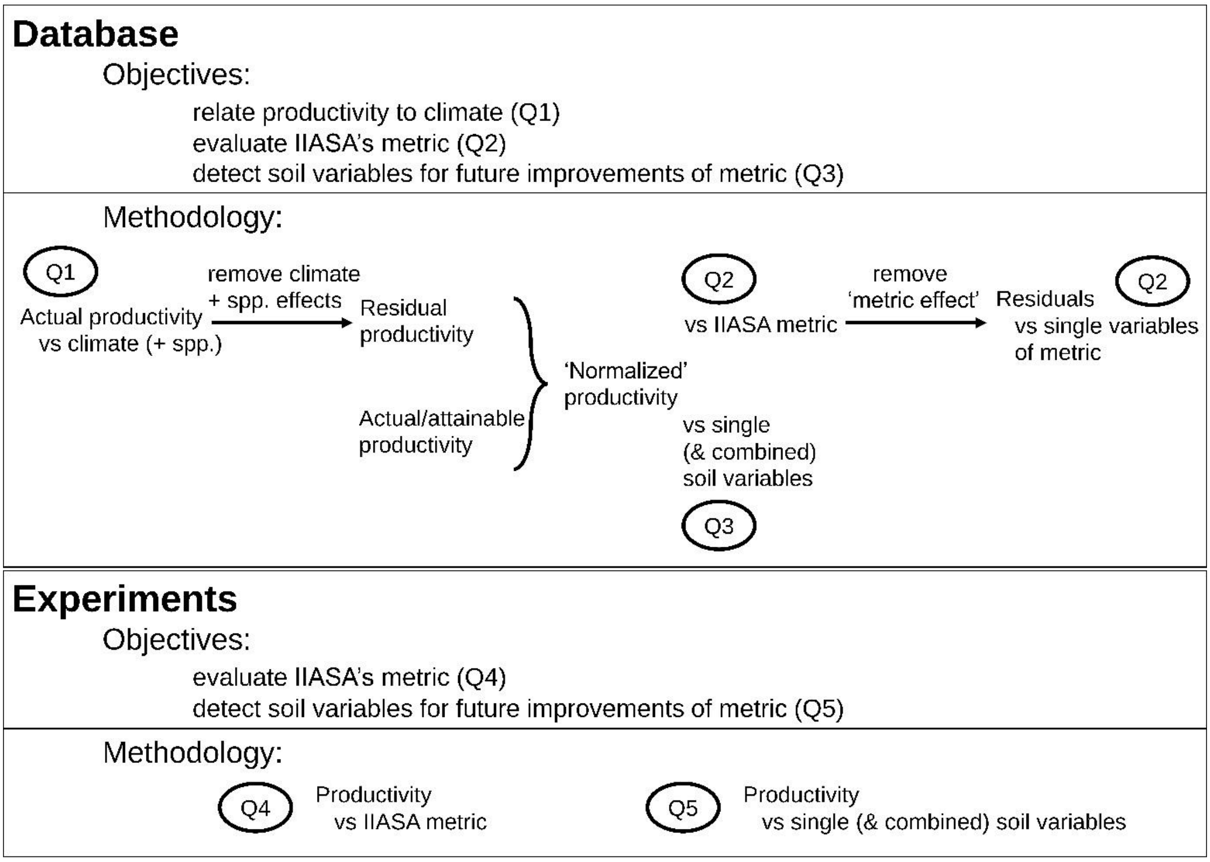


Figure 1 | Objectives and methods followed in the current dissertation, in which IIASA's metric of constraints on nutrient availability was evaluated. Abbreviations: Q = research question; spp. = species (Norway spruce or Scots pine).

The Swedish forest & soil inventories *(Questions 1-3)*

Swedish forest soil inventory & Swedish national forest inventory

We combined a Swedish forest soil (Olsson, 1999; Lundin, 2011) and forest inventory database (Lundin, 2011) with a database with soil texture and climate information across Sweden. Climatic data (air temperature and precipitation) were extracted from EC-JRC-MARS (a dataset based on ECMWF model outputs and a reanalysis of ERA-Interim; see http://spirits.jrc.ec.europa.eu/), based on the geographic location of each site. The dataset's spatial resolution is 0.25° and averages were calculated for the period 1989-2012. The resulting data collection thus incorporated information on location, climate, soil horizons and vegetation for about 2500 forested plots (n = 1099 for spruce, n = 1422 for pine), spread over Sweden (Table 1).

Table 1 | Overview of variables of the database used in the current study. Abbreviations: MAP = mean annual precipitation; TSUM = growing season temperature sum; SOC = soil organic carbon concentration; TEB = total exchangeable bases; TN = total nitrogen; C:N ratio = carbon to nitrogen ratio.

Information about	location	climate	soil	vegetation
Variables	latitude [° N] longitude [° E] elevation [m]	MAP [mm] TSUM[1] [°C days]	horizon thickness [cm] humus stock [ton ha^{-1}] humus depth [cm] SOC [%] texture [% sand, silt, clay] TEB [cmol$_+$ kg^{-1} or cmol$_+$ m^{-2}] pH$_{H2O}$, pH$_{KCl}$ TN, C:N ratio, moisture	age [yrs], tree species composition [%] productivity[2] [m³ ha^{-1} yr^{-1}]

[1] TSUM was calculated for each data point based on its latitude, longitude and elevation (see below).

[2] Productivities or mean annual volume increments (MAI) over a full rotation were estimated based on height development curves (Dr. J. Stendahl, pers. comm.). *In situ* productivities may be lower, depending on the management.

Pre-processing of the database

Many of the forest plots were not monocultures, but contained both Norway spruce (*Picea abies* (L.) H. Karst.) and Scots (or Lodgepole) pine (*Pinus sylvestris* L. or *Pinus contorta* Douglas) trees, as well as other species. In order to contrast spruce and pine forests, we classified forests with ≥ 50% spruce (pine) trees as spruce (pine). To quantify the influence of climate on productivity across Sweden (*question 1*), we first determined the annual growing season temperature sum (TSUM) following Odin *et al.* (1983) (www.kunskapdirekt.se):

Equation 2 | TSUM [°C days]

$$
\begin{aligned}
&= 4203.212488 - 40.21083 \times \text{latitude [°N]} - 2.564434 \times \text{elevation [m]} \\
&+ 0.030492 \times \text{latitude [°N]} \times \text{elevation [m]} - 0.117532 \times \text{latitude}^2\ \text{[°N]} + 0.00188 \times \text{elevation}^2\ \text{[m]} \\
&- 0.000000556 \times \text{latitude}^2\ \text{[°N]} \times \text{elevation}^2\ \text{[m]}
\end{aligned}
$$

In order to ensure compatibility with our soil sampling strategy in the experiments (see below), we converted the soil measurements (SOC, texture, TEB, pH_{H2O}, pH_{KCl}, total nitrogen and C:N ratio) taken per horizon to values representative of the upper 10 cm (i.e. the 0-10 cm layer), the 10 cm below (i.e. the 10-20 cm layer) and the upper 20 cm (i.e. 0-20 cm layer). To this end, we first calculated bulk densities as

Equation 3 | $BD_{\text{organic horizon}}$ [kg m^{-3}] = $\frac{humus\ stock\ [kg/m^2]}{humus\ depth\ [m]}$ for the organic horizons and

Equation 4 | $BD_{\text{mineral horizon}}$ [kg m^{-3}] = 1546.3 x exp(-0.3130 x $\sqrt{SOC\ [\%]}$) for the mineral soil (Nilsson & Lundin, 2006 and Dr. Johan Stendahl, pers. comm.).

Conversions of soil data ('variables') per horizon to data per depth interval (layer x-y cm) were then performed as follows (soil mass [kg m^{-2}] = BD [kg m^{-3}] x $\text{thickness}_{\text{horizon or layer}}$ [m]):

Equation 5 | $\text{Variable}_{\text{x-ycm}}$ = (soil $\text{mass}_{\text{horizon1}}$/soil $\text{mass}_{\text{x-ycm}}$) x $\text{variable}_{\text{horizon1}}$

+ (soil $\text{mass}_{\text{horizon2}}$/soil $\text{mass}_{\text{x-ycm}}$) x $\text{variable}_{\text{horizon2}}$ + …

IIASA's metric of constraints on nutrient availability incorporates four crop specific scores (estimated for SOC, texture, TEB and pH_{H2O}), which can be assigned to any soil using look-up tables (IIASA & FAO, 2012), available at http://webarchive.iiasa.ac.at/Research/LUC/GAEZv3.0/soil_evaluation.html. As we eventually aim to develop a globally applicable species-independent metric, we averaged each of the four scores for the different species. In addition, we replaced the look-up table derived step functions by continuous empirical (not necessarily meaningful) formulas, to facilitate its calculation as well as its modification (Fig. 2):

Equation 6 | SOC score [%] = 38.94 + (100 - 38.94) * (1-exp(-1.4192 * SOC [%]))
Equation 7 | Texture score [%] = max(100 + 0.4911 * (1-exp(0.0522 * SAND [%])), 35)
Equation 8 | TEB score [%] = 28.05 + (100 - 28.05) * (1-exp(-0.4508 * TEB [cmol$_+$ kg^{-1}]))
Equation 9 | pH score [%] = max(-17.228 * (pH_{H2O} - 4.04) * (pH_{H2O} - 8.84), 0)
= max(-17.228 * (pH_{H2O} - 6.44)^2 + 99.32, 0)

The total score for nutrient availability, roughly interpretable as the expected actual yield (i.e. aboveground productivity) proportional to the maximum attainable yield (i.e. without nutrient constraints), could then be calculated as follows (IIASA & FAO, 2012):

Equation 10 | Total IIASA metric score [%] = 0.5 * Lowest score + 0.5 * Average of other scores

National maps of this overall score were created for spruce and pine forests separately.

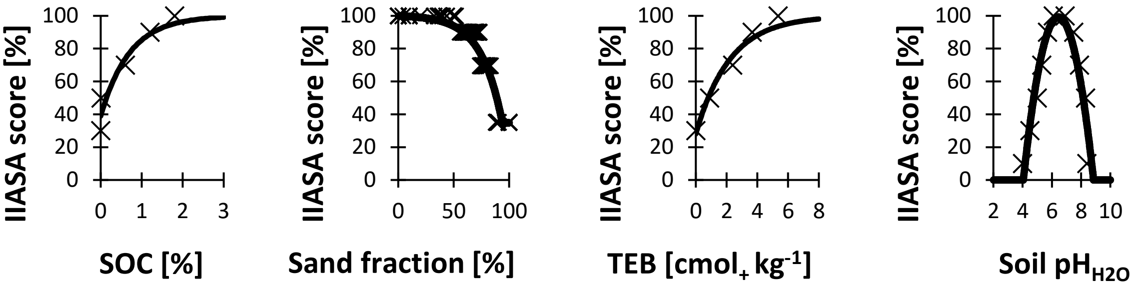


Figure 2 | Species-averaged IIASA soil scores for soil organic carbon concentration (SOC), texture, total exchangeable bases (TEB) and pH_{H2O}. The curves indicate approximate functions through the points, which represent values from a look-up table (IIASA & FAO, 2012). For texture, scores were originally assigned based on FAO texture classes (e.g. sand, loamy sand, …). Since it turned out these scores could almost exclusively be calculated based on information on sand alone, the formula for texture was designed using the data points from the database used in the present study.

Statistical analysis

Question 1 - climate versus productivity (database)

We disentangled the influence of climatological variables (TSUM and precipitation) on productivities of spruce and pine forests using ANCOVA (Analysis of Covariance). All possible combinations of single continuous variables and their interactions with species were alternatively included in data-driven regression models to finally select the one with the lowest mean squared error according to 10-fold cross-validation (package DAAG - Maindonald & Braun, 2015).

Diverging climate responses for spruce versus pine productivity may either indicate ecophysiological differences or differential soil conditions. To test whether soils differed significantly between both species, we performed a linear discriminant analysis (functions lda and MANOVA - package MASS - Venables & Ripley, 2002) and two-sample t-tests on a set of key soil characteristics (SOC, C:N ratio, clay fraction and TEB) that show clear variation in Sweden and are related to nutrient availability.

Before proceeding to *questions 2* and *3*, we specifically searched for a particular type of heteroscedasticity in the data (with the Glejser test - Glejser, 1969): variation around an average productivity may increase from north to south, where higher temperatures and light (and perhaps precipitation) increase maximum potential productivities. Consequently, a given % reduction of this maximal productivity due to nutrient limitation would be reflected in a higher yield gap and thus larger residuals where it is warmer. Hence, if the absolute values of residuals present a positive association with a climatological variable, this would create an artifact in the analyses on residuals described below if they were to be performed on data for entire Sweden at once. Therefore, instead, the database should be split up into regions for which separate analyses are carried out.

Question 2 - evaluation of IIASA's metric (database)

Two approaches were used to evaluate the accuracy of IIASA's metric, each considering a different 'normalized' response to test the metric scores against. The first approach consisted of fitting the residuals of the general linear models, discussed under *question 1*, against the calculated metric scores for soil depth 0-20 cm. The sites were classified into three groups (north (N), middle (M) and south (S)) according to their growing season temperature sum (< 900, 900-1200 and > 1200 °C days) and the evaluations were performed for each group separately to reduce heteroscedasticity effects (residuals deviated stronger from zero in the warmer south, see results). Further, ANOVAs tested for differences in residuals between spruce and pine, in order to decide whether data for the two species could be combined. The alternative approach involved a similar analysis, but in this case, actual rotation productivities for spruce were divided by hypothetical attainable productivities (based on ecophysiological principles and experiments in Sweden) obtained from Bergh *et al.* (2005). Consequently, the ratio actual/attainable productivity was employed as a response instead of residuals. Lastly, national maps displaying i) residual, climate-independent productivity and ii) actual/attainable productivity were made in ArcGIS (ESRI, 2011).

Irrespective of the method applied, a well-functioning nutrient availability metric would be recognized by a clear, positive trend with the productivity related response it aims to predict. Therefore, linear models were used to find the shape, significance and R^2 value of the normalized productivity-metric associations. Additionally, the residuals of the normalized productivity versus metric relationship should not be correlated with the variables already included in the metric (SOC, texture, TEB and pH_{H2O}), as this would mean they are not well implemented. Hence, the shape, significance and variation explained by these associations were investigated as well.

Question 3 - how nutrient availability related variables influence productivity (database)

The correlation structure of some potential key soil variables (SOC, C:N ratio, clay fraction, TEB and pH_{KCl}) was investigated to determine the overlap in the information they shared and thus to conclude if some variables would be redundant for the following steps. This set of five soil variables was chosen because i) SOC, texture, TEB and pH are included in IIASA's metric (yet clay was used instead of sand here as it was considered as a proxy for CEC (IIASA & FAO, 2012), and pH_{KCl} shows less seasonal variation than pH_{H2O} (Soil Survey Staff, 2014), thus it would perhaps be more appropriate for inclusion in a metric) and ii) the C:N ratio is theoretically related to N availability (Roy *et al.*, 2006), rather than total N. We performed a principal component analysis (princomp function, package MASS - Venables & Ripley, 2002) for a visualization and constructed a correlation matrix with Pearson's r as correlation coefficients for each variable pair.

Since soil moisture may act as a confounding factor for associations between productivity and the nutrient availability related soil variables presented above (e.g. by inhibiting decomposition (Olsson *et al.*, 2009), leading to reduced productivity and accumulating SOM at wet sites), it should be included in the analyses to allow correct interpretations. Therefore, we searched for differences in soil variables among soil moisture classes in the database (dry, fresh, fresh-moist and moist) with a two-way ANOVA (soil moisture and tree species as factors).

Quantitative associations between single soil variables (SOC, C:N ratio, clay fraction, TEB, pH_{KCl}, soil moisture) and normalized productivity were studied to elucidate which factors might have an important effect on productivity. Simple regression analyses were thus carried out for normalized productivity vs continuous explanatory variables, while ANOVAs tested for effects of soil moisture.

In a last step, using multiple regression models, we tested which combination of continuous soil variables (SOC, C:N ratio, clay fraction, TEB, pH_{KCl}) best explained variation in normalized productivity across Sweden. Starting from the full model, non-significant variables were removed one by one, the order based on significance, after which the mean squared error (mse), based on cross-validation (package DAAG - Maindonald & Braun, 2015) each time indicated whether the variable in question could be removed definitively. Interaction effects up to the first order were added if suggested by regression trees (package tree - Ripley, 2015). For the approach adopting residual productivity as a response, first-order interactions of continuous variables with region as a factor (levels: N, M, S) were included in the selection procedure, i.e. an ANCOVA was used for this approach.

Experiments *(Questions 4-5)*

Site descriptions, experimental design & sampling

In July and August 2016, we collected soil samples at three nutrient manipulation experiments in forests near Vindeln, northern Sweden (Table 2), where the climate is characterized by a mean annual temperature of 1-2°C and an annual precipitation of around 600 mm (Lim *et al.*, 2015; From *et al.*, 2016; Oyewole *et al.*, 2016). Productivity data, to be linked to the soil nutrient status, were provided by the principal investigators of each site. These consisted of both absolute growth rates (AGR - i.e. basal area increment [m^2 ha^{-1} yr^{-1}]) and relative growth rates (RGR - i.e. basal area increment relative to the current basal area), averaged over the last five years for which data were available (i.e. 2010-2014 for Åheden and Svartberget; 2012-2016 for Flakaliden).

In each of the plots, we installed four plant root simulator (PRS) probe pairs (cathode + anode - Western Ag Innovations, Saskatoon, Canada, USA) for exactly seven days to assess the supply rate of inorganic substances (NH_4^+, NO_3^-, PO_4^{3-}, K^+, Ca^{2+}, Mg^{2+}, BO_3^{3-}, Fe^{2+}, Al^{3+}, …) to plant roots at a depth of roughly 3-9 cm. In addition, we collected soil (organic F- and H- and mineral layers) at 0-10 cm and 10-20 cm depth for analyses of key soil characteristics and nutrients (see below). Finally, we took another soil sample with known volume at the same depths for analyses of bulk density and soil moisture (except for the 10-20 cm depth at Svartberget, where these characteristics had already been determined by Maaroufi *et al.* (2015)). At the Åheden site, typified by a soil low in gravel content, we employed a 100 ml core sampler for this task. At the gravel rich Flakaliden and Svartberget sites, on the other hand, the core method (Blake & Hartge, 1986) was unfeasible. Instead, we excavated soil using a knife and subsequently estimated the removed soil volume by placing a sufficiently large piece of plastic in the excavation and tracking the volume of water needed to fill it up to the soil surface (Blake & Hartge, 1986). Alternatively, the volume was calculated based on its dimensions if the shape of the excavation made this more practical (Blake & Hartge, 1986). After the daily sampling session, we brought the collected soil (stored in zip-locked plastic bags and kept cool) to the Svartberget Field Station, where they were stored at 4°C.

Table 2 | (A)biotic characteristics and treatment details of the four nutrient manipulation experiments selected for soil sampling. Numbers refer to literature: [1] = Gundale *et al.*, 2011; [2] = From *et al.*, 2016; [3] = Olsson *et al.*, 2005; [4] = Ryan, 2013; [5] = Maaroufi *et al.*, 2015; [6] = Nordin *et al.*, 2009; [7] = Bergh *et al.*, 1999; [8] = Metcalfe *et al.*, 2013.

Site	Åheden	Flakaliden	Svartberget
Soil	Silt + sand Cambic podzol [1];[2]	Silty-sandy tills Haplic podzol [3]	Coarse-grained podzol till [2]
Forest age & origin	140 yr Naturally regenerated [2]	55 yr Plantation [4]	120 yr Naturally regenerated [2];[5]
Dominant tree species	*Pinus sylvestris* L. [1];[2]	*Picea abies* (L.) H. Karst. [4]	*Picea abies* (L.) H. Karst. [2];[6]
Understory vegetation & forest floor	*Vaccinium vitis-idaea* L. *Calluna vulgaris* (L.) Hull *Pleurozium schreberi* (Brid.) Mitt. *Cladonia* P. Browne [1];[2]	*Vaccinium myrtillus* L. *Pteridium aquilinum* (L.) Kuhn Mosses (personal observation)	*Vaccinium myrtillus* L. *Vaccinium vitis-idaea* L. *Linnaea borealis* L. *Deschampsia flexuosa* (L.) Trin. *Pleurozium schreberi* (Brid.) Mitt. *Hylocomium splendens* (Hedw.) Schimp. [6]
Start of experiments	2005 [2]	1986 [4]	1996 [5];[8];[28]
Treatments	Control (C - *n* = 6) + 3.0 kg N ha^{-1} yr^{-1} (Nmin - *n* = 6) + 6.25 kg N ha^{-1} yr^{-1} (Nmed - *n* = 6) + 12.5 kg N ha^{-1} yr^{-1} (N1 - *n* = 6) + 50 kg N ha^{-1} yr^{-1} (N2 - *n* = 6) [2]	Control (C - *n* = 4) Optimal nutrition (IL - *n* = 4) New plots with optimal nutrition since 2007 (nIL - *n* = 4) [7]	Control (C - *n* = 6) + 12.5 kg N ha^{-1} yr^{-1} (N1 - *n* = 6) + 50 kg N ha^{-1} yr^{-1} (N2 - *n* = 6) [5];[6];[8] (organized in 6 blocks)

Laboratory analysis

We measured pH_{H2O} and pH_{KCl} on the fresh soil samples. The remains of the soil samples were sieved (mesh size = 2 mm) and air-dried at 30°C, at the Svartberget Field Station. For determining pH, 10 ± 0.5 g of fresh soil was weighed into a plastic tube and subsequently, 25 ml H_2O, resp. 1 M KCl was added. Then, the solutions were shaken and rested for an hour before measuring the pH with a direct soil pH meter (no. 99121 Hanna Instruments, Temse, Belgium).

In August, September and October 2016, we further investigated the air-dried soil samples for various nutrient availability related features at the Centre of Excellence PLECO at the University of Antwerp, Wilrijk, Belgium. Firstly, total carbon and total nitrogen were determined on ground samples, using an Elemental Analyzer (Flash 2000 CN Soil Analyser, Interscience, Louvain-la-Neuve, Belgium), while we followed the standard Loss-On-Ignition protocol (Heiri *et al.*, 2001) for determination of organic matter content. Brown's procedures (1943) were used for CEC and TEB, for which 1 M NH_4Ac at pH = 7 served as the extractant. Extractable phosphorus was measured as well, following both the Olsen (1982) and Bray (Dickman & Bray, 1940; Bray & Kurtz, 1945) methods, respectively requiring 0.5 M

NaHCO3 at pH = 8.5 and 0.03 N NH4F + 0.025 N HCl solutions. Extracts were evaluated with either an iCAP6300 Duo ICP-OES (for CEC and TEB - Thermo Fisher Scientific, Waltham, USA) or a San++ Automated Wet Chemistry Analyzer (for available P - Skalar Analytical, Breda, Netherlands). Lastly, we determined the soil texture (percentages of sand, silt and clay) with the hydrometer method (Gee & Bauder, 1986) after removing most of the organic matter by regularly adding dilute H_2O_2 until the chemical reactions stopped.

At the University of Antwerp, all samples collected for bulk density and soil moisture were freshly weighed and weighed again after oven-drying at 105°C (Blake & Hartge, 1986). The dry bulk density [kg m^{-3}] was then calculated as $\frac{oven\ dry\ weight}{in\ situ\ soil\ volume}$ (Blake & Hartge, 1986) and the soil water content (SWC) as $\frac{fresh\ weight - oven\ dry\ weight}{fresh\ weight}$ [g g^{-1}] or $\frac{fresh\ weight - oven\ dry\ weight}{in\ situ\ soil\ volume}$ [g ml^{-1}] (Gardner, 1986).

Data processing

Soils were sampled in the upper 10 cm (i.e. the 0-10 cm layer) and the 10 cm below (i.e. the 10-20 cm layer). As we wanted to perform most of the analyses on data for the upper 20 cm (i.e. the 0-20 cm layer, covering the main rooting zone), we averaged the results for both depths in the same fashion as for the database. In order to test whether IIASA's metric could explain the fertilization effect (*question 4*), we calculated single (for SOC, texture, TEB and pH_{H2O}) and combined IIASA scores on nutrient availability constraints with the aforementioned formulas (Equations 6-10).

Statistical analysis

Question 4 - evaluation of IIASA's metric (experiments)

The accuracy of IIASA's metric of constraints on nutrient availability was assessed in the same way as for the database. Simple linear regressions were used to fit productivity (AGR, and RGR to check robustness) against IIASA's metric. Analyses were performed for each of the sites separately, because the starting year of the experiments, forest age, treatments and dominant species differed, which could induce artifacts if sites were to be considered together. Similarly, nIL and IL plots at the Flakaliden experimental site could not be taken together in one analysis as they represent the same treatment, but initiated in different years (Table 2).

Question 5 - how nutrient availability related variables influence productivity (experiments)

For each site, treatment effects on productivity and soil conditions were analyzed using ANOVA (including block as a factor for Svartberget). General linear models were used to determine the single best predictor of productivity for each site.

In the same way as for the database, a PCA and correlation matrix were used to investigate the correlation structure of some important soil variables (0-10 cm soil C:N ratio and plant root simulator

(PRS) measured supply rates for inorganic nitrogen, phosphorus and exchangeable base cations). For these descriptive statistics, all treatments and sites were combined in one analysis. This step indicated whether some variables covaried strongly or not. Moreover, a PCA biplot gives – in combination with the ANOVA outputs explained earlier – an easily interpretable overview of how soil conditions varied among treatments and experimental sites.

For the Åheden experimental site, where sufficient data points were available, stepwise cross-validation selected regression models with optimal combinations of soil variables, explaining variation in productivity. Since the number of data points was limited ($n = 30$), all combinations with up to three parameters were inspected. Regression trees from the tree package (Ripley, 2015) indicated possible interactions among explanatory variables.

Software and assumptions

All statistical analyses were performed in R version 3.2.2 (R Core Team, 2015). We examined the validity of the linear models' assumptions (linearity, normality of residuals, no influential outliers, homoscedasticity) with standard functions built-in in the program (including diagnostic plots) and additional tests from packages. For all regressions, potential non-linearities were detected with histograms of all variables' distributions and generalized additive models from the mgcv package (Wood, 2006). Data were accordingly log-transformed if their distribution was right-skewed, while polynomial (e.g. quadratic) functions were included in the model selection procedure where the general additive models suggested non-linear patterns. If assumptions of influential cases or normality (based on Shapiro's test) were not met, robust regressions (package MASS - Venables & Ripley, 2002) or non-parametric permutation tests (package lmPerm - Wheeler, 2010) were used for parameter and significance estimations, respectively. The variance inflation factor (package car - Fox & Weisberg, 2011) assessed possible multicollinearity. Lastly, Kruskal-Wallis tests were employed as a non-parametric alternative to ANOVAs where assumptions for the latter were not met. Whenever confidence intervals are given, they represent standard errors of the mean. For all analyses, $\alpha = 0.05$ was taken as significance level, whereas P-values between 0.05 and 0.10 were considered as borderline significant.

Results

The Swedish forest & soil inventories

Question 1 - climate versus productivity (database)

Across the country, spruce and pine productivity averaged 6.3 ± 0.1 (n = 1099) and 4.00 ± 0.04 m^3 ha^{-1} $year^{-1}$ (n = 1422), respectively. However, this difference between both species was temperature dependent (Table 3 and Fig. 3a). We acquired the following empirical equation (mse of candidate models is shown in Table S1, while parameter estimates and statistics for each species can be found in Table 3):

Equation 11 | MAI [m^3 ha^{-1} $year^{-1}$] = a x $TSUM^2$ [°C days] + b x TSUM [°C days] + c x MAP [mm] + d

Table 3 | Species specific estimates, statistics (*t* and partial *R^2*) and significance (*P* values) for the parameters in Equation 11 and *F* statistics and significance for species differences in these estimates. (Partial) R^2 values were approximated based on comparing fitted values with actual productivities.

Parameter	Species difference	Spruce			Pine		
		Estimate	Statistics		Estimate	Statistics	
a	$F_{1,2475}$ = 175.3 $P < 0.01$	(9.0 ± 0.6) x 10^{-6}	t_{1071} = 14.15 $P < 0.01$	$R^2 \approx 0.854$	(-3.0 ± 0.6) x 10^{-6}	t_{1403} = -4.64 $P < 0.01$	$R^2 \approx 0.480$
b	$F_{1,2475}$ = 1112.2 $P < 0.01$	-0.008 ± 0.001	t_{1071} = -5.76 $P < 0.01$		0.011 ± 0.001	t_{1403} = 7.80 $P < 0.01$	
c	N/A[a]	(0.3 ± 0.3) x 10^{-3}	t_{1071} = 0.97 $P = 0.33$	$R^2 \approx 0.001$	(0.3 ± 0.3) x 10^{-3}	t_{1403} = 0.97 $P = 0.33$	$R^2 \approx 0$
d	$F_{1,2475}$ = 1731.1 $P < 0.01$	3.5 ± 0.8	t_{1071} = 4.59 $P < 0.01$		-4.1 ± 0.7	t_{1403} = -5.24 $P < 0.01$	
Total				$R^2 \approx 0.856$			$R^2 \approx 0.480$
					$R^2 = 0.805$		

[a] A regression model without MAP x species interaction was selected by the cross-validation procedure (Table 4).

Forests of spruce and pine differed in soil characteristics (MANOVA: $F_{5,1698}$ = 75.03, $P < 0.01$ - Fig. 3c). Spruce forests had a significantly lower 0-10 cm C:N ratio compared to pine sites (24.8 ± 0.2 vs 29.3 ± 0.2, t_{2381} = 14.09, $P < 0.01$), whereas (log) SOC (6.0 ± 0.2% vs 4.0 ± 0.1%, t_{2313} = 8.44, $P < 0.01$), (log) TEB stock (59 ± 2 $cmol_+$ m^{-2} vs 39.0 ± 0.8 $cmol_+$ m^{-2}, t_{2312} = 12.49, $P < 0.01$) and mineral soil clay fraction (5.8 ± 0.2% vs 4.2 ± 0.2%, t_{2519} = 6.59, $P < 0.01$) were significantly higher in spruce than in pine forests and pH_{KCl} (3.55 ± 0.01 vs 3.54 ± 0.01, t_{2310} = 0.56; $P = 0.58$) did not significantly differ.

The Glejser test for the climate-productivity regression model (Equation 11, Table 3 and Fig. 3a) unveiled a significant positive trend of the absolute residuals versus temperature relationship (Fig. 3b). In order to reduce heteroscedasticity-induced artifacts, the database was split into northern, middle and southern sites (i.e. 'region' was considered as a fixed factor) for the subsequent residual analyses. Within regions, residuals did not differ between both species (north - $F_{1,570} = 0.27$, $P = 0.60$; middle - $\chi_1^2 = 1.65$, $P = 0.20$; south - $F_{1,1059} = 0.05$, $P = 0.82$), so that both species could be considered together for the 'residuals approach' in research *questions 2* and *3*.

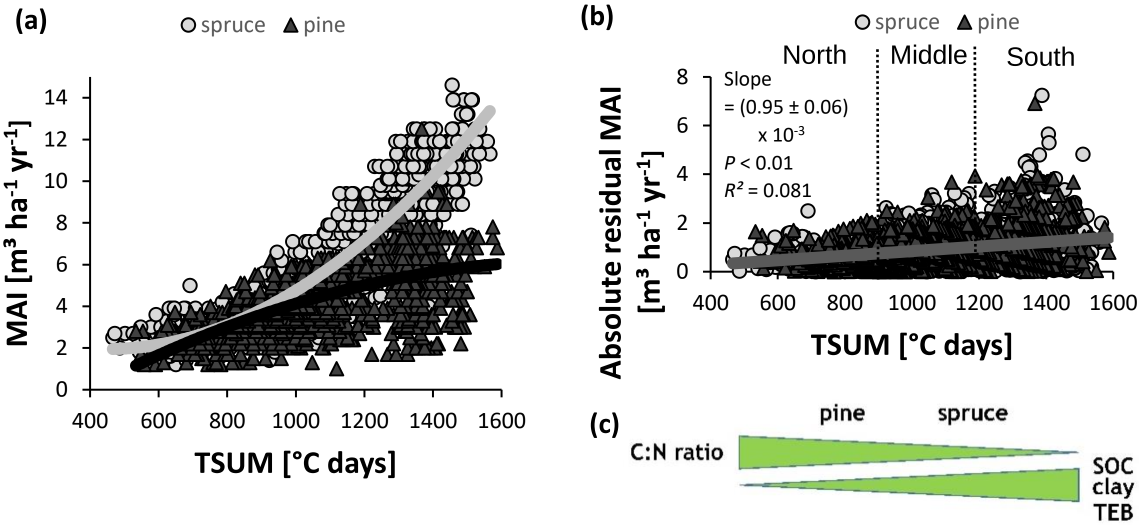


Figure 3 | (a) Productivity (mean annual increment - MAI) of spruce and pine in relation to the growing season temperature (TSUM) in Sweden. Curves were drawn based on fitted values of the quadratic regression model in Equation 11 and Table 3. Statistics for subplot a can be found in Table 3. **(b) Relationship between absolute values of residuals of panel a and TSUM to test for heteroscedasticity.** Because of this heteroscedasticity, the subsequent residual analyses in *questions 2* and *3* were performed separately for the northern (TSUM < 900°C days), middle (TSUM 900-1200°C days) and southern (TSUM > 1200°C days) region**.** **(c) Schematic representation of the (significant) differences in soil factors between spruce and pine forests.** Abbreviations: C:N ratio = 0-10 cm soil carbon to nitrogen ratio; SOC = 0-20 cm soil organic carbon concentration [%], clay = mineral soil clay fraction [%], TEB = 0-20 cm total exchangeable bases [$\text{cmol}_+ \text{m}^{-2}$].

Question 2 - evaluation of IIASA's metric (database)

IIASA's metric could only poorly elucidate patterns in nutrient availability, as there existed no clear, strong, positive correlation between normalized productivity and the metric (Figs. 4 and 5). The ratio $\frac{actual\ MAI}{attainable\ MAI}$ tended to increase from north to south (Fig. 4c), while the IIASA scores and residual productivities did not show straightforward geographical patterns (Fig. 4a,b,d,e), except for the aforementioned increasing deviations from the mean (heteroscedasticity) in the south.

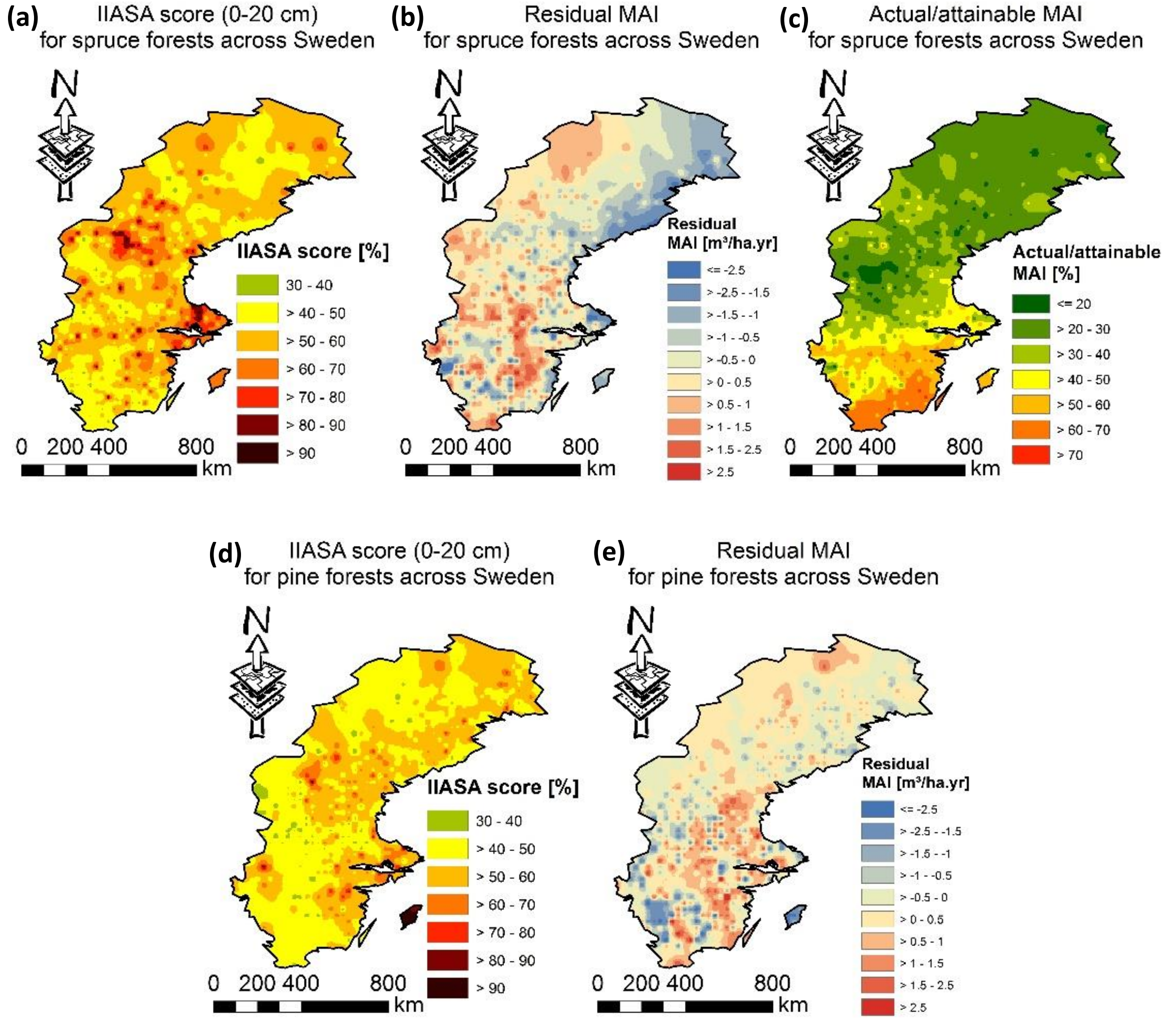


Figure 4 | Maps of calculated IIASA metric scores (a,d), residuals of the productivity-climate regression model (b,e) and actual/attainable productivity (mean annual increment - MAI) (c) for spruce (upper row) and pine (lower row) across Sweden. Note that maps a and d have the same color scale as map c.

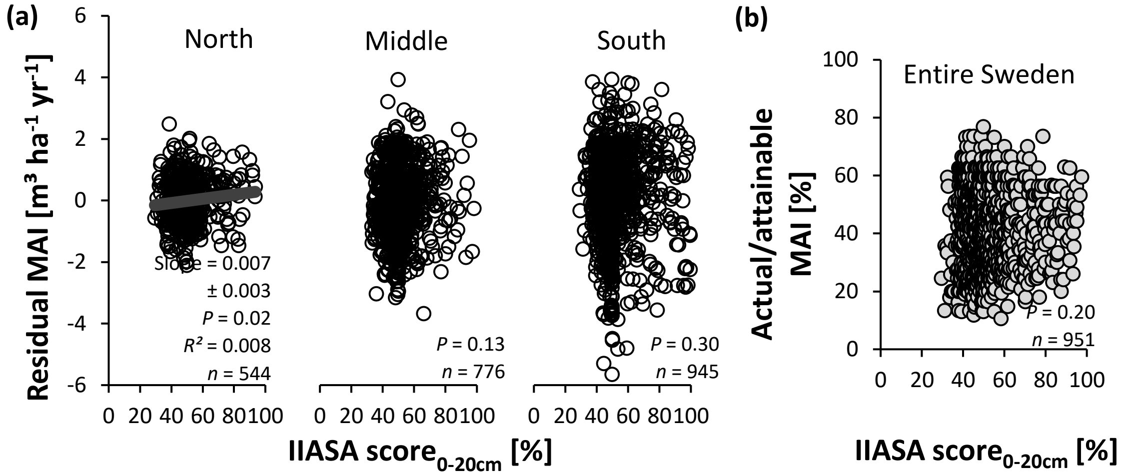


Figure 5 | Evaluation of IIASA's metric of constraints on nutrient availability for Swedish conifer forests. (a) Association with residual mean annual increments (MAI) of the productivity-climate regression model (Equation 11, Table 3 and Fig. 3a), distinguishing northern, middle and southern Sweden. (b) Association with actual/attainable MAI (Fig. 4c) for the entire Swedish land area. Full line = significant slope ($P < 0.05$).

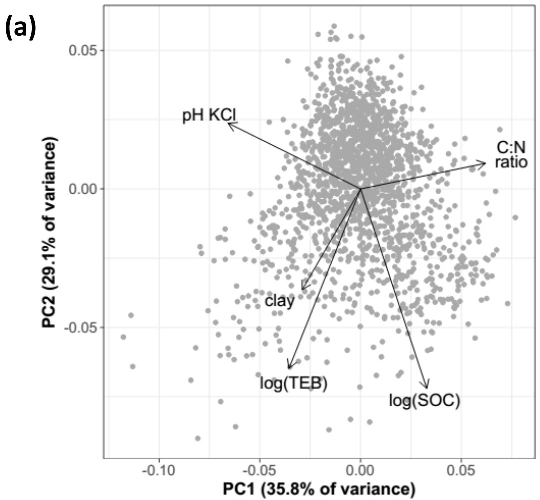
Residual values of the relationship between residual productivity and IIASA score (Fig. 5a) were significantly associated with all four input variables of the metric (SOC, texture, TEB and pH_{H2O} - Table 4). High levels of SOC and TEB correlated negatively with the residuals, while sand was significantly positively related to these same residuals, and productivities at low pH_{H2O} were overestimated (the quadratic functions were concave; not shown in Table 4). Residuals of the alternative response – actual/attainable productivity (Fig. 5b) – confirmed the negative trend with SOC and with TEB, albeit not significantly. A relationship of the residuals versus texture and pH_{H2O} did not appear in this case (Table 4). Overall, the fact that residual productivities were still correlated with the variables in the metric suggested the input variables were not optimally implemented in the formula.

Table 4 | Associations between residuals of normalized productivities in Fig. 5 and soil variables in IIASA's metric of constraints on nutrient availability. For (near) significant variables (i.e. $P < 0.10$), parameter estimates ± s.e.m. and the proportion of variation explained (R^2) are given. Abbreviations: N = north; M = middle; S = south; SOC = soil organic carbon concentration, TEB = total exchangeable bases. Note that TEB is expressed here per kg dry weight as defined for IIASA's metric, whereas elsewhere in this dissertation, TEB is often referred to as a stock, i.e. an amount per m², thus better representing the actual number of base cations available to plants.

Residuals of	**Region**	**$SOC_{0\text{-}20cm}$ [%]**	**$Sand_{0\text{-}20cm}$ [%]**	**$TEB_{0\text{-}20cm}$ [$cmol_+ \ kg^{-1}$]**	**$pH_{H2O,0\text{-}20cm}$**
Residual MAI	N	slope = -0.016 ± 0.002 $P < 0.01$ $R^2 = 0.065$	slope = 0.005 ± 0.001 $P < 0.01$ $R^2 = 0.025$	slope = -0.021 ± 0.006 $P < 0.01$ $R^2 = 0.020$	$P < 0.01$ $R^2 = 0.019$
	M	slope = -0.029 ± 0.003 $P < 0.01$ $R^2 = 0.135$	slope = 0.012 ± 0.002 $P < 0.01$ $R^2 = 0.065$	slope = -0.039 ± 0.006 $P < 0.01$ $R^2 = 0.051$	$P < 0.01$ $R^2 = 0.055$
	S	slope = -0.041 ± 0.003 $P < 0.01$ $R^2 = 0.171$	slope = 0.015 ± 0.002 $P < 0.01$ $R^2 = 0.076$	slope = -0.019 ± 0.004 $P < 0.01$ $R^2 = 0.020$	$P < 0.01$ $R^2 = 0.166$
Actual/attainable MAI	entire Sweden	slope = -0.12 ± 0.03 $P < 0.01$ $R^2 = 0.013$	$P = 0.33$	slope = -0.06 ± 0.04 $P = 0.10$ $R^2 = 0.002$	$P = 0.94$

Question 3 - how nutrient availability related variables influence productivity (database)

We used single and combined relationships of SOC, C:N ratio, mineral soil clay fraction, TEB and pH_{KCl} with residual or actual/attainable productivities to elucidate how they might affect nutrient availabilities across Sweden. In this database, no soil variable pairs showed high correlations (|Pearson's *r*| < 0.50; Fig. 6). Consequently, none of them was redundant for the following analyses.

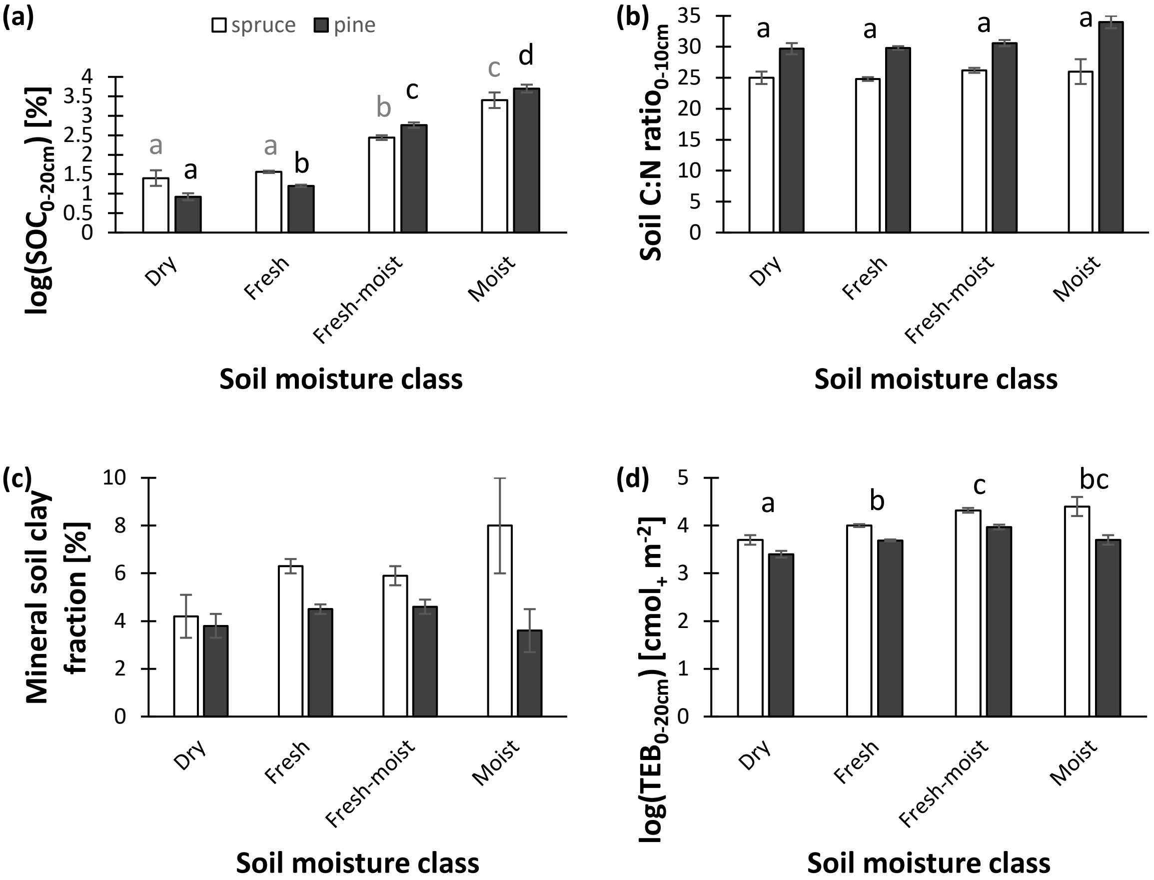


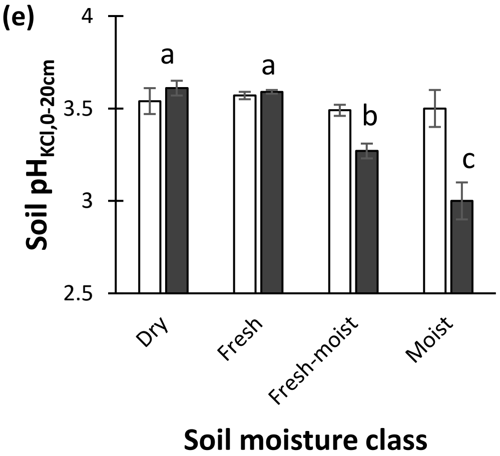
(b)

soil variable	C:N ratio	clay	log(TEB)	pH_{KCl}
log(SOC)	0.15	0.05	0.33	-0.45
C:N ratio		-0.17	-0.30	-0.43
clay			0.21	0.10
log(TEB)				0.22

Figure 6 | Correlation structure of a set of five potential key soil variables for a soil depth of 0-20 cm (0-10 cm for C:N ratio). (a) = PCA biplot (sd for PC1 = 1.34, sd for PC2 = 1.21). (b) = correlation matrix, showing Pearson's *r* for the variable pairs. Abbreviations: SOC = soil organic carbon concentration [%]; C:N ratio = soil carbon to nitrogen ratio; clay = % clay in the mineral soil; log(TEB) = log-transformed total exchangeable bases [cmol_+ m^{-2}].

Soil moisture may influence nutrient availability of ecosystems by – among other things – affecting the rate of decomposition, and might also change other soil parameters through this effect. In the database, each forest was originally assigned to a soil moisture category. Using these categories, we found that the wetter a site is, the higher is its SOC and C:N ratio. A similar trend was observed for TEB, while pH_{KCl} decreased from dry to moist. For clay, no significant differences among soil moisture classes occurred (Fig. 7). Hence, the wetness of a site could confound observed patterns in productivity associated with the five soil variables and should thus be considered for interpretations.





(f)

	spp.*m	m spruce	m pine	m	spp.
a	$F_{4,2305}$ = 15.16 $P < 0.01$	$F_{4,993}$ = 58.52 $P < 0.01$	$F_{4,1312}$ = 188.03 $P < 0.01$		
b				$F_{4,2377}$ = 3.02 $P = 0.02$	$F_{1,2377}$ = 231.48 $P < 0.01$
c				$F_{4,2515}$ = 1.77 $P = 0.13$	$F_{1,2515}$ = 39.87 $P < 0.01$
d				$F_{4,2304}$ = 29.84 $P < 0.01$	$F_{1,2304}$ = 96.84 $P < 0.01$
e	$F_{4,2302}$ = 10.51 $P < 0.01$	$F_{4,992}$ = 1.94 $P = 0.10$	$F_{4,1310}$ = 36.17 $P < 0.01$		

Figure 7 | Soil conditions in spruce and pine forests with varying soil moisture. Panel f summarizes statistics for panels a-e, based on ANOVA tables of models selected by cross-validation. Note that although the overall effect was significant for panel b, no significant two-by-two differences were detected. Abbreviations: SOC = soil organic carbon concentration; TEB = total exchangeable bases; spp. = species; m = moisture. * indicates an interaction, while letters indicate statistical differences among moisture classes, either within spruce and pine forests (if spp. x m was significant) or for spruce and pine forests combined (if spp. x m was not significant). Error bars represent the s.e.m.

We found significant associations between most single soil variables and normalized productivity (Table 5). Residual productivities were significantly negatively correlated with the soil C:N ratio (Fig. 8b), for which the effect became more pronounced towards the south ($F_{2,2274} = 34.23$; $P < 0.01$). Residual productivities exhibited quadratic relationships with both SOC (Fig. 8a) and $\mathrm{pH_{KCl}}$, while the association with clay was weak yet significantly positive. Residual productivity and TEB did not significantly correlate, but the trend was weakly positive, too. Lastly, residual productivity was highest in the 'fresh' soil moisture class and lowest for the most wet forests (Fig. 8c). Again, these patterns were clearest in southern Sweden (north – $F_{3,568} = 22.43$, $P < 0.01$; middle – $F_{4,844} = 39.47$, $P < 0.01$; south – $F_{4,1056} = 35.23$, $P < 0.01$; moisture x region – $F_{7,2468} = 3.77$, $P < 0.01$). Overall, the strongest relationships were found for residual productivity versus SOC, $\mathrm{pH_{KCl}}$, and soil C:N ratio (and moisture). Accordingly, these soil variables were among the selected data for the model with multiple covariates (Table 6).

Results of the alternative approach, taking actual/attainable productivities for spruce forests as a response variable (Fig. 4c and Table 5), were qualitatively similar to those of the other approach for SOC (Fig. 9a), C:N ratio (Fig. 9b), clay fraction, TEB and soil moisture ($F_{4,1054} = 24.90$, $P < 0.01$; Fig. 9c), although the curve for actual/attainable productivity decreased logarithmically rather than linearly with increasing C:N ratio in this case. However, the function for $\mathrm{pH_{KCl}}$ was not quadratic, but linear with a significantly positive slope. In short, SOC and the soil C:N ratio were the only soil factors that consistently described a distinct, clear effect on normalized productivity (i.e. R^2 of at least a few percent), and were correspondingly among the selected soil variables in the multiple regression models of both residual productivity and actual/attainable productivity (Table 6).

Table 5 | Associations between single soil variables and normalized productivity for Swedish conifer forests. Significance (*P*-values) of single soil variable effects on residual productivity (mean annual increment - MAI [m^3 ha^{-1} yr^{-1}]) and actual/attainable MAI (for spruce only) across Sweden are given. For (near) significant variables (i.e. $P < 0.10$), parameter estimates ± s.e.m. and the proportion of variation explained (R^2) are shown as well. Abbreviations: SOC = soil organic carbon content; C:N = soil carbon to nitrogen ratio; TEB = total exchangeable bases; quad = parameter estimate for quadratic term; lin = parameter estimate for linear term of a quadratic function. For residual MAI, the 0-20 cm soil C:N ratio was used instead of 0-10 cm soil C:N because of a lower cross-validation overall mean square (ms = 1.34 vs 1.36). For actual/attainable MAI, the model including 0-10 cm soil C:N performed best (ms = 173 vs 159). Elsewhere in this dissertation, the 0-10 cm C:N ratio was used. Data for residual MAI are for both spruce and pine, whereas actual/attainable MAI was only available for spruce.

Normalized productivity response	**Region**	**log SOC** 0-20cm **[%]**	**C:N** 0-20cm	**log C:N** 0-10 cm	**Mineral soil clay [%]**	**log TEB** 0-20cm **[$cmol_+$ m^{-2}]**	**pH_{KCl}** 0-20cm
Residual MAI	N	quad = -0.16 ± 0.02 $P < 0.01$ lin = 0.49 ± 0.08 $P < 0.01$ intercept = -0.19 ± 0.08 $P = 0.03$ $R^2_{tot} = 0.145$	slope = -0.014 ± 0.004 $P < 0.01$ intercept = 0.3 ± 0.1 $P < 0.01$ $R^2 = 0.021$	N/A	slope = 0.009 ± 0.004 $P = 0.02$ intercept = -0.05 ± 0.03 $P = 0.14$ ns $R^2_{tot} = 0.002$	$P = 0.11$	quad = -0.71 ± 0.06 $P < 0.01$ lin = 5.3 ± 0.4 $P < 0.01$ intercept = -9.7 ± 0.9 $P < 0.01$ $R^2_{tot} = 0.099$
	M	quad = -0.16 ± 0.02 $P < 0.01$ lin = 0.35 ± 0.08 $P < 0.01$ intercept = -0.03 ± 0.08 $P = 0.71$ $R^2_{tot} = 0.145$	slope = -0.027 ± 0.005 $P < 0.01$ intercept = 0.7 ± 0.2 $P < 0.01$ $R^2 = 0.029$	N/A	slope = 0.009 ± 0.004 $P = 0.02$ intercept = -0.05 ± 0.03 $P = 0.14$ ns $R^2_{tot} = 0.002$	$P = 0.11$	quad = -0.71 ± 0.06 $P < 0.01$ lin = 5.6 ± 0.4 $P < 0.01$ intercept = -10.8 ± 0.8 $P < 0.01$ $R^2_{tot} = 0.099$
	S	quad = -0.16 ± 0.02 $P < 0.01$ lin = 0.19 ± 0.09 $P = 0.03$ intercept = 0.5 ± 0.1 $P < 0.01$ $R^2_{tot} = 0.145$	slope = -0.082 ± 0.007 $P < 0.01$ intercept = 2.0 ± 0.2 $P < 0.01$ $R^2 = 0.112$	N/A	slope = 0.009 ± 0.004 $P = 0.02$ intercept = -0.05 ± 0.03 $P = 0.14$ ns $R^2_{tot} = 0.002$	$P = 0.11$	quad = -0.71 ± 0.06 $P < 0.01$ lin = 5.9 ± 0.4 $P < 0.01$ intercept = -11.5 ± 0.8 $P < 0.01$ $R^2_{tot} = 0.099$
Actual/attainable MAI	entire Sweden	quad = -2.6 ± 0.4 $P < 0.01$ lin = 11 ± 2 $P < 0.01$ intercept = 32 ± 2 $P < 0.01$; $R^2 = 0.048$	N/A	slope = -19 ± 5 $P < 0.01$ intercept = 100 ± 5 $P < 0.01$ $R^2 = 0.131$	slope = 0.18 ± 0.06 $P < 0.01$ intercept = 39.2 ± 0.6 $P < 0.01$ $R^2 = 0.008$	slope = 2.0 ± 0.5 $P < 0.01$ intercept = 32 ± 2 $P < 0.01$ $R^2 = 0.014$	slope = 3 ± 1 $P < 0.01$ intercept = 29 ± 4 $P < 0.01$ $R^2 = 0.009$

Table 6 | Estimates ± s.e.m. for parameters of the selected multiple regression equations linking soil variables to normalized productivity for Swedish conifer forests. Significance of the pattern (P values) and proportion of variation explained (R^2) are given as well. Interactions were added if suggested by a regression tree (not shown). Abbreviations: MAI = mean annual increment [$m^3\ ha^{-1}\ yr^{-1}$]; N = north; M = middle; S = south; SOC = soil organic carbon concentration; C:N = soil carbon to nitrogen ratio; TEB = total exchangeable bases. Output of the model selection procedures for residual MAI and actual/attainable MAI is shown in Tables S2 and S3. Data for residual MAI are for both spruce and pine, whereas actual/attainable MAI was only available for spruce.

Normalized productivity response	**Region**	**log SOC** 0-20cm **[%]**	**C:N** 0-20cm	**log C:N** 0-10 cm	**log TEB** 0-20cm **[$cmol_+\ m^{-2}$]**	**pH_{KCl}** 0-20cm	**intercept**	**P and R^2**
Residual MAI	N	quad = -0.15 ± 0.02 $P < 0.01$ lin = 0.44 ± 0.09 $P < 0.01$	lin = -0.009 ± 0.007 $P = 0.21$	N/A	lin = 0.13 ± 0.04 $P < 0.01$	quad = 0.0 ± 0.3 $P = 0.92$ lin = 0 ± 2 $P = 0.94$	0 ± 3 $P = 0.93$	$P < 0.01$ $R^2_{tot} = 0.182$
	M	quad = -0.15 ± 0.02 $P < 0.01$ lin = 0.29 ± 0.09 $P < 0.01$	lin = -0.013 ± 0.006 $P = 0.04$	N/A	lin = 0.13 ± 0.04 $P < 0.01$	quad = 0.0 ± 0.1 $P = 0.94$ lin = 0.1 ± 0.9 $P = 0.93$	0 ± 2 $P = 0.90$	
	S	quad = -0.15 ± 0.02 $P < 0.01$ lin = 0.23 ± 0.09 $P = 0.02$	lin = -0.050 ± 0.008 $P < 0.01$	N/A	lin = 0.13 ± 0.04 $P < 0.01$	quad = -0.35 ± 0.08 $P < 0.01$ lin = 2.2 ± 0.6 $P < 0.01$	-2 ± 1 $P = 0.09$	
Actual/attainable MAI	entire Sweden	quad = -3.2 ± 0.3 $P < 0.01$ lin = 14 ± 2 $P < 0.01$	N/A	lin = -22 ± 2 $P < 0.01$	not selected	lin = 3 ± 1 $P < 0.01$	111 ± 8 $P < 0.01$	$P < 0.01$ $R^2 = 0.199$

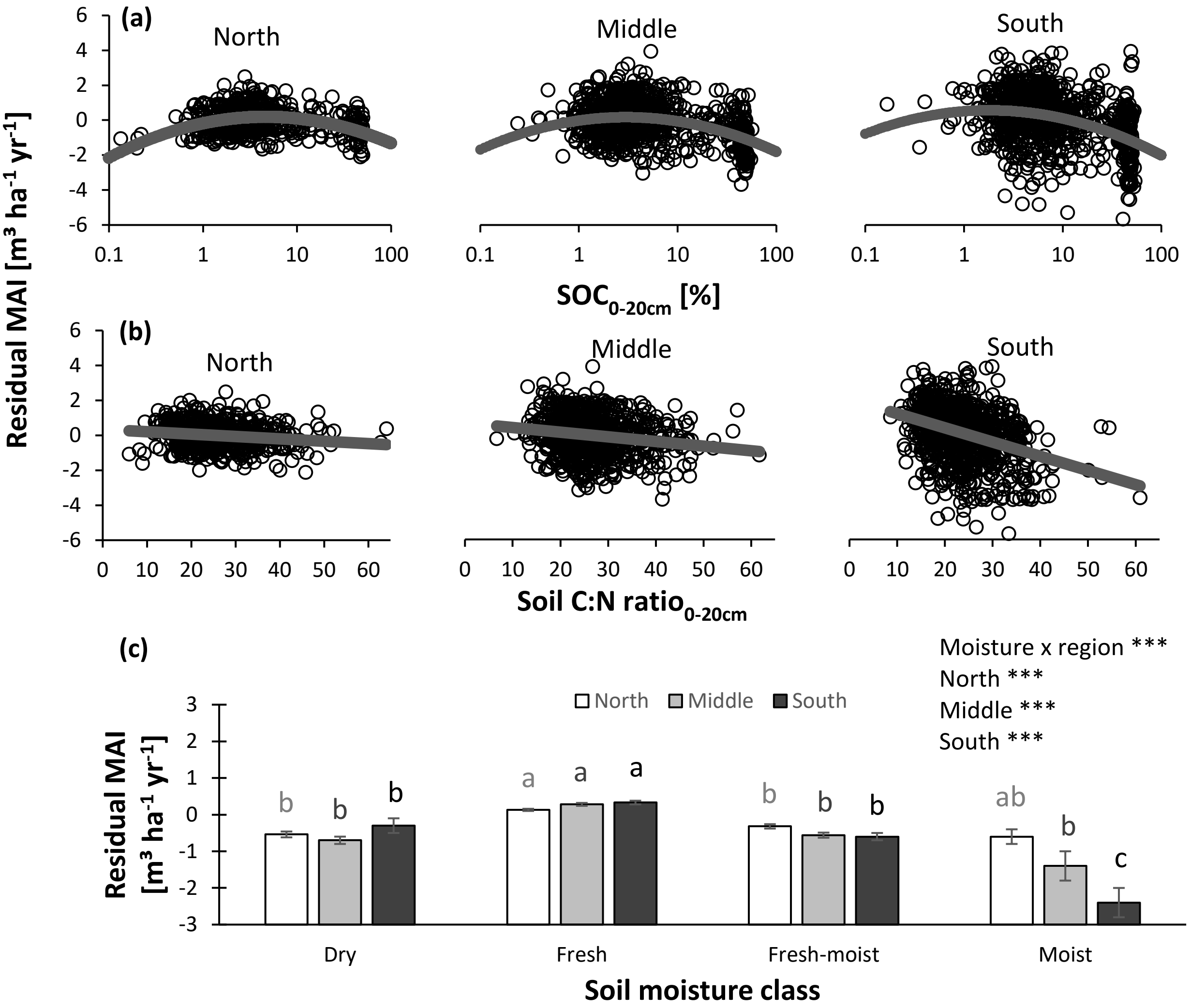


Figure 8 | Relationship between residual productivity (mean annual increment - MAI) and, (a) log-transformed soil organic carbon (SOC) concentration, (b) soil carbon to nitrogen (C:N) ratio at depth 0-20 cm and (c) soil moisture class. Separate analyses were performed for northern, middle and southern Sweden, as the SOC, C:N and moisture effects differed among regions. Statistics corresponding to panels a and b are presented in Table 5. *** indicates significant differences at the *P* < 0.01 level. Error bars represent standard errors of the mean (s.e.m.).

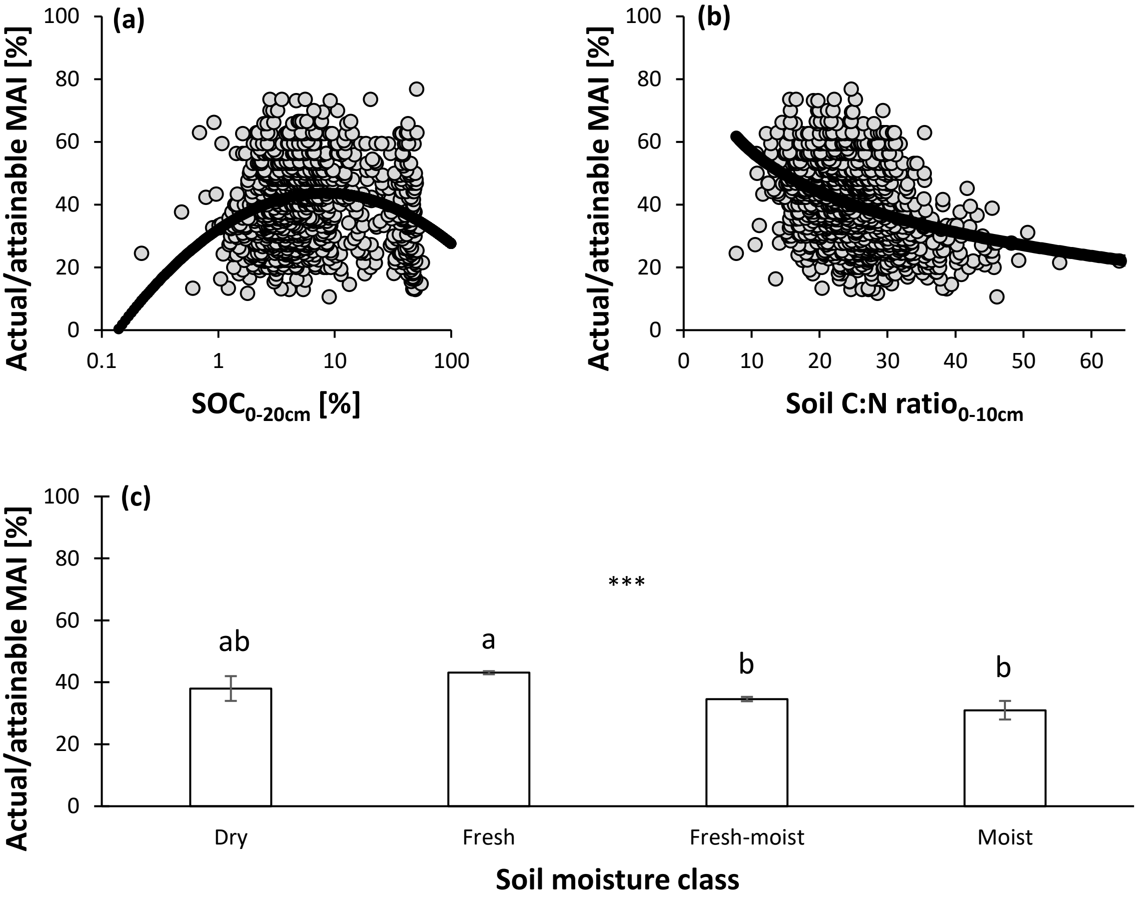


Figure 9 | Relationship between actual/attainable spruce productivity (mean annual increment - MAI) and, (a) log-transformed soil organic carbon (SOC) concentration, (b) soil carbon to nitrogen (C:N) ratio and (c) soil moisture class. Statistics corresponding to panels a and b are presented in Table 5. *** indicates significant differences at the *P* < 0.01 level. Error bars represent standard errors of the mean (s.e.m.). Note that the C:N ratio of the upper 10 cm was used instead of the upper 20 cm here, owing to a better description of variation in the response variable. Even though the C:N ratio roughly decreases southwards (not shown), it was only weakly correlated with the growing season temperature sum (*r* = -0.13 for $C:N_{0\text{-}20cm}$ and *r* = -0.28 for $C:N_{0\text{-}10cm}$).

Experiments

Question 4 - evaluation of IIASA's metric (experiments)

IIASA's metric of constraints on nutrient availability did not show a significant association with productivity at any of the experimental sites (Tables 7 and S4). Therefore, the association between the residuals of the productivity-metric relationship and the metric's soil factors was not considered. The relationship between productivity and different soil factors was investigated for *question 5*.

Table 7 | Summary of statistics linking IIASA's metric of constraints on nutrient availability (for soil depth 0-20 cm) with absolute growth rate (AGR) at a few nutrient manipulation experiments in northern Sweden. IL and nIL treatments were included in separate analyses because they were initiated at different moments, which is known to affect the current productivity response.

Site/Productivity response	AGR [$m^2\ ha^{-1}\ yr^{-1}$]
Åheden	$t_{28} = -0.55$; $P = 0.58$
Flakaliden C & IL treatments	$t_6 = 0.48$; $P = 0.65$
Flakaliden C & nIL treatments	$t_6 = -0.11$; $P = 0.92$
Svartberget	$t_{13} = -0.37$; $P = 0.72$

Question 5 - how nutrient availability related variables influence productivity (experiments)

At all sites, absolute growth rates (AGR - i.e. basal area increment [$m^2\ ha^{-1}\ yr^{-1}$]) were significantly higher for plots with the maximal nutrient treatment as compared to control plots (Figs. S1-3a). However, in case productivity was expressed as a relative growth rate (RGR), differences between C and IL treated plots in Flakaliden disappeared (Fig. S2b). For the other forests, RGR remained significantly lower in control plots than in fertilized plots (Figs. S1,3b). Both current AGR and RGR differed strongly among the sites, and this was also the case for the IL and nIL treatments in Flakaliden (Fig. S2 a vs b), which were initiated in 1987 and 2007, respectively (Table 2).

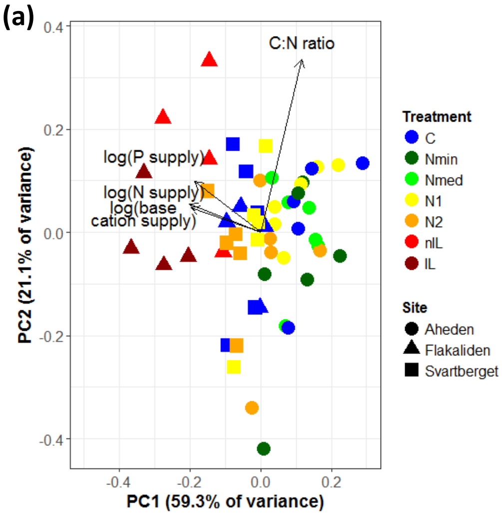
The variables that could potentially be appropriate for inclusion in a new or updated nutrient availability metric according to the analysis of the national database (i.e. SOC, C:N ratio, and to a lesser extent clay fraction, TEB and pH_{KCl}, cf. above) did only to a limited extent suggest the same patterns with productivity in the experiments (Tables 8 and S5). SOC was significantly positively correlated with AGR (and RGR if the C and nIL treatments were considered) for Flakaliden, whereas no significant effects were found for the Åheden and Svartberget experimental forests. Results for CEC were similar as for SOC, as both variables were strongly related ($r = 0.74$ at Åheden, $r = 0.84$ at Flakaliden and $r = 0.83$ at Svartberget). The soil C:N ratio (0-10 cm depth) did not significantly correlate with productivity, although one borderline significantly negative association between C:N and AGR could be observed. The clay fraction did not exhibit a significant association with productivity for any of the sites, nor did TEB if expressed as a stock. Lastly, associations of productivity vs pH_{KCl} were mostly convex or non-significant.

Inorganic ion supply rates measured by plant root simulator (PRS) probes showed strong, positive logarithmic associations with productivity (Tables 8 and S5): at all three sites, inorganic nitrogen (N) supply rates explained a considerable fraction of the variation in AGR ($0.177 < R^2 < 0.703$). For the pine forest in Åheden and the spruce forest in Flakaliden (C and nIL treatments), effects of N supply on RGR were also (borderline) significant and positive. Moreover, inorganic phosphorus (P) supply had a significantly positive effect on AGR in all sites but Svartberget, while its influence on RGR was only significant in Åheden and the C vs nIL plots in Flakaliden. Finally, fluxes of base cations ($Ca^{2+} + K^{+} + Mg^{2+}$) displayed significantly positive trends with productivity in Flakaliden, except for the relationship with RGR if the C and IL plots were considered.

Table 8 | Associations between single soil variables and absolute growth rate [$m^2\ ha^{-1}\ yr^{-1}$] at the experimental sites mentioned in Table 2. For (near) significant variables (i.e. $P < 0.10$), parameter estimates ± s.e.m. and the proportion of variation explained (R^2) are given. Abbreviations: n = number of plots; SOC = soil organic carbon content; TEB = total exchangeable bases; TN = total nitrogen; C:N = carbon to nitrogen ratio; CEC = cation exchange capacity; PRS iN flux = inorganic nitrogen ($NH_4^+ + NO_3^-$) supply rate measured with PRS probes; PRS iP flux = inorganic phosphorus supply rate measured with PRS probes; PRS base cation flux = base cation ($Ca^{2+} + K^+ + Mg^{2+}$) supply measured with PRS probes.

Site	Åheden (n = 30)	Flakaliden C & IL treatments (n = 8)	Flakaliden C & nIL treatments (n = 8)	Svartberget (n = 18)
log SOC$_{0\text{-}20cm}$ [%]	$P = 0.48$	slope = 0.6 ± 0.2; $P = 0.04$ intercept = 0.3 ± 0.3; $P = 0.38$ $R^2 = 0.446$	slope = 0.5 ± 0.2; $P = 0.05$ intercept = 0.5 ± 0.3; $P = 0.17$ $R^2 = 0.429$	$P = 0.29$
Clay$_{10\text{-}20cm}$ [%]	$P = 0.59$	$P = 0.77$	$P = 0.88$	$P = 0.86$
log TEB$_{0\text{-}20cm}$ [cmol$_+$ kg^{-1}]	$P = 0.40$	slope = 0.3 ± 0.2; $P = 0.10$ intercept = 0.9 ± 0.1; $P < 0.01$ $R^2 = 0.288$	$P = 0.19$	slope = -0.15 ± 0.07; $P = 0.05$ intercept = 0.44 ± 0.03; $P < 0.01$ $R^2 = 0.210$
pH$_{KCl,0\text{-}20cm}$	$P = 0.21$	$P = 0.53$	$P = 0.25$	quad = 0.8 ± 0.4; $P = 0.05$ lin = -5 ± 2; $P = 0.05$ intercept = 8 ± 4; $P = 0.04$ $R^2 = 0.163$
log TN$_{0\text{-}20cm}$ [%]	$P = 0.32$	slope = 0.5 ± 0.2; $P = 0.03$ intercept = 2.0 ± 0.4; $P < 0.01$ $R^2 = 0.518$	slope = 0.4 ± 0.2; $P = 0.08$ intercept = 2.1 ± 0.5; $P < 0.01$ $R^2 = 0.331$	$P = 0.14$
C:N$_{0\text{-}10cm}$	$P = 0.64$	slope = -0.04 ± 0.02; $P = 0.07$ intercept = 2.2 ± 0.5; $P < 0.01$ $R^2 = 0.355$	$P = 0.25$	$P = 0.67$
log CEC$_{0\text{-}20cm}$ [cmol$_+$ kg^{-1}]	$P = 0.18$	slope = 0.5 ± 0.2; $t_6 = 2.22$ intercept = 0.2 ± 0.4; $t_6 = 0.4$ $R^2 \approx 0.482$	slope = 0.6 ± 0.2; $P = 0.01$ intercept = 0.1 ± 0.3; $P = 0.80$ $R^2 = 0.650$	$P = 0.20$
log TEB$_{0\text{-}20cm}$ [cmol$_+$ m^{-2}]	$P = 0.55$	$P = 0.27$	$P = 0.55$	$P = 0.32$
log P$_{Bray,0\text{-}20cm}$ [mg kg^{-1}]	$P = 0.21$	$P = 0.12$	slope = 0.3 ± 0.2; $P = 0.07$ intercept = 0.4 ± 0.4; $P = 0.33$ $R^2 = 0.348$	$P = 0.63$
log PRS iN flux [µg 10cm^{-2} week^{-1}]	slope = 0.03 ± 0.01^1; $P < 0.01$ intercept = 0.10 ± 0.02; $P < 0.01$ $R^2 = 0.265$	slope = 0.22 ± 0.05; $P = 0.02$ intercept = 0.2 ± 0.2; $P = 0.23$ $R^2 = 0.730$	slope = 0.4 ± 0.1; $P = 0.02$ intercept = -0.1 ± 0.4; $P = 0.85$ $R^2 = 0.558$	slope = 0.05 ± 0.02; $P = 0.05$ intercept = 0.27 ± 0.07; $P < 0.01$ $R^2 = 0.177$
log PRS iP flux [µg 10cm^{-2} week^{-1}]	slope = 0.05 ± 0.02^1; $P = 0.04$ intercept = 0.17 ± 0.01; $P < 0.01$ $R^2 = 0.123$	slope = 0.25 ± 0.07; $P = 0.02$ intercept = 0.7 ± 0.1; $P < 0.01$ $R^2 = 0.597$	slope = 0.4 ± 0.1; $P = 0.03$ intercept = 0.7 ± 0.2; $P = 0.01$ $R^2 = 0.514$	$P = 0.71$
log PRS base cation flux [µg 10cm^{-2} week^{-1}]	$P = 0.46^1$	slope = 0.4 ± 0.2; $P = 0.03$ intercept = -1.5 ± 0.9; $P = 0.16$ $R^2 = 0.486$	slope = 1.2 ± 0.3; $P < 0.01$ intercept = -6 ± 2; $P = 0.01$ $R^2 = 0.724$	$P = 0.74$

Soil C:N ratio was only weakly related to PRS N, P and base cation fluxes (Fig. 10). Where nutrients were added, supply rates of the respective elements were (almost) significantly higher (i.e. shifted to the left in Fig. 10a; Figs. S1-3 d-f), whereas shifts in the soil C:N ratio were only observed for Flakaliden (Figs. 10a and S1-3c).



(b)

Soil variable	log(PRS iN flux)	log(PRS iP flux)	log(PRS base cation flux)
C:N ratio	-0.29	-0.22	-0.30
log(PRS iN flux)		0.55	0.67
log(PRS iP flux)			0.60

Figure 10 | Correlation structure of four potential key soil variables across treatments in the experiments from Table 2. (a) = PCA biplot (sd for PC1 = 1.54, sd for PC2 = 0.92), (b) = correlation matrix, showing Pearson's *r* for variable pairs. Abbreviations: C:N ratio = soil carbon to nitrogen ratio; N supply = iN PRS flux = inorganic nitrogen (NH_4^+ + NO_3^-) supply rate measured with PRS probes [µg 10 cm^{-2} week^{-1}]; P supply = iP PRS flux = inorganic phosphorus supply rate measured with PRS probes [µg 10 cm^{-2} week^{-1}]; PRS base cation flux = base cation (Ca^{2+} + K^+ + Mg^{2+}) supply measured with PRS probes [µg 10 cm^{-2} week^{-1}].

PRS measured fluxes were among the selected variables in the multiple regressions that explained variation in AGR (Table 9) and RGR (Table S7) at the Åheden experimental site. The soil C:N ratio was not among the selected explanatory variables.

Table 9 | Estimates ± s.e.m. for parameters of the selected multiple regression equations linking soil variables to absolute growth rate (AGR - m² ha^{-1} yr^{-1}) at the Åheden experimental site. Degrees of freedom (*df*), significance of the pattern (*P* values) and proportion of variation explained (R^2) are given as well. Interactions were added if suggested by a regression tree (not shown). Multiple regression was not performed for Flakaliden and Svartberget owing to an insufficient number of data points. Output of the model selection procedure is shown in Table S6. Abbreviations: PRS iN flux = inorganic nitrogen (NH_4^+ + NO_3^-) supply rate measured with PRS probes; PRS iP flux = inorganic phosphorus supply rate measured with PRS probes.

Site	**Response**	**log PRS iN flux [µg N 10^{-1} cm^{-2} week^{-1}]**	**log PRS iP flux [µg P 10^{-1} cm^{-2} week^{-1}]**	**log PRS iN flux x log PRS iP flux**	**intercept**	***P* and R^2**
Åheden (*df* = 25)	AGR	0.04 ± 0.01	-0.04 ± 0.04	0.05 ± 0.02	0.10 ± 0.02	$P < 0.01$ $R^2 = 0.384$

Discussion

The Swedish forest & soil inventories

Question 1 - climate versus productivity (database)

For both conifer species considered in this project, productivity clearly increased southwards in Sweden. The most important (indirect) environmental driver behind this pattern is definitely temperature (Fries *et al.*, 1998; Stendahl *et al.*, 2010; Xenakis & Mencuccini, 2012; Lim *et al.*, 2015 - Fig. 3a): the warmer climate in the south allows a longer growing season length, so that more radiation can be intercepted throughout the year to promote photosynthetic activity (Bergh *et al.*, 1999, 2005). Apart from its effect on the growing season length and direct influence on the photosynthetic rate (Larcher, 2003), temperature may also augment biomass production through its influence on nitrogen availability (Rustad *et al.*, 2001; Chapin *et al.*, 2002): in the temperature range observed in Sweden, rates of organic matter decomposition and mineralization do indeed correlate positively with temperature (Chapin *et al.*, 2002; Larcher, 2003), thus likely leading to higher N availability in the south than in the north.

Differences in productivities between the two conifer species were especially explicit in the warmest regions (Fig. 3a). One reason could be that soils are nutrient poor in the north and tend to increase in nutrient availability towards the south (see below). Pine trees perform better than spruces where nutrients are strongly limiting (which is the reason why pine trees are often the preferred species for forestry in northern Sweden), whereas spruces have a competitive advantage and higher biomass production when nutrients are more readily available (Nilsson *et al.*, 2012). Nutrient manipulation experiments have indeed shown that spruces are more responsive to nutrient applications than pines (e.g. Tamm *et al.*, 1999; Ladanai *et al.*, 2007), mainly because they have a higher potential to increase their leaf area (Tamm *et al.*, 1999) and have a higher leaf longevity (Prof. Johan Bergh, pers. comm.). Differences in soil C:N ratio, SOC, clay fraction and exchangeable base cations (Fig. 3c) further confirm that spruce forests in Sweden grow more often on the more fertile soils (i.e. lower C:N ratio and higher SOC, clay fraction and TEB).

Besides the average of productivity, its variation also increased towards the south, as is shown by the heteroscedasticity in Fig. 3b. This likely reflects the fact that potential production under hypothetical non-nutrient limited conditions is lowest in the north (Bergh *et al.*, 2005), so that variation in nutrient availability may have a similar *relative* effect on tree productivity across Sweden (e.g. Paine *et al.*, 2012), while in *absolute* terms, differential nutrient availabilities among sites may result in the most pronounced variation in productivity in the south (i.e. a residual value of +1 likely represents a much larger increase in nutrient availability in the north than in the south). Additionally, soil conditions are more homogeneous in the northern half of the country, while more variation occurs in the south (e.g. Troedsson & Wiberg, 1986). In other words, the heteroscedastic nature of the data complicates disentangling the role of nutrients in explaining variation in productivity across Sweden as residuals in the north cannot directly be compared to their counterparts in the south. Therefore, this problem was avoided by distinguishing three climatic regions across Sweden: a northern, middle and southern region.

Question 2 - evaluation of IIASA's metric (database)

Based on Fig. 4 a,d vs b,c,e, IIASA's metric of constraints on nutrient availability, originally designed for evaluating soil fertility of arable lands, does not clarify much variation in normalized productivity among Swedish forests. Regression analyses largely confirmed this: only in the north, the metric was significantly positively associated with residual productivity, yet it only explained a small proportion of the variation (R^2 = 0.008). In middle and southern Sweden, and for actual/attainable productivity across the country, IIASA's metric was not significantly correlated with the response (Fig. 5).

Although IIASA's metric was not or only weakly related to normalized productivity, the variables included in the metric did exhibit significant relationships with residual productivity. The factors governing nutrient availability are apparently not well implemented. For example, in the national database, SOC and TEB appeared to have negative instead of positive associations with productivity (Table 4). In this case, the high organic matter contents are very likely not the direct reason for the suppressed productivity. Instead, organic matter probably accumulated in places where decomposition rates are low (Minderma, 1968). This slow decomposition, in turn, presumably arises from high soil moisture contents (Olsson *et al.*, 2009 - see *question 3* for evidence) and/or low temperatures (Larcher, 2003). Similarly, the organic matter typically retains exchangeable base cations (IIASA & FAO, 2012), explaining the association of TEB with residual productivity. At low pH, biomass production is reduced (not shown). This can again be explained based on the results for SOC: where organic matter accumulates, a thick humus layer, typically marked by a low pH compared to mineral soil (Sposito, 2008), makes that the 0-20 cm soil profile considered is acidic. Although SOC, soil texture, TEB and pH_{H2O} are clearly related to nutrient availability, these factors alone will not be sufficient to accurately describe its variation (Fig. 11). Additional or alternative soil data, more closely related to actual availability of nutrients like N and P (e.g. C:N ratio or PRS derived supply rates, see below) are definitely needed to successfully fulfill the task of developing a nutrient availability metric.

Question 3 - how nutrient availability related variables influence productivity (database)

Soil C:N ratio had the most straightforward effect on normalized productivity across both methods, as it had a significantly negative and likely direct influence on both residual and actual/attainable productivity (Figs. 8b and 9b). Part of this influence could perhaps not be distinguished from other confounding effects along the latitudinal gradient in Sweden: the C:N ratio roughly decreases towards lower latitudes (not shown), while N deposition (Akselsson *et al.*, 2010) and temperature show the opposite trend. Nevertheless, the C:N ratio and temperature sum were not strongly correlated and the ratio was able to significantly describe variation for all three regions in the ‘residuals approach’ (within which climate related effects were small). We can thus carefully state that most of the variation in productivity explained by the C:N ratio cannot be ascribed to underlying climatic factors.

Increased productivities with decreasing C:N ratio do make sense because this soil characteristic influences rates of litter decomposition and mineralization, and therefore affects nutrient availability: when the ratio in organic matter is high, microbes more strongly immobilize N so as to adjust their internal C to N stoichiometry. As a consequence, N is not easily being released and made available for plant uptake. A low C:N ratio, on the other hand, facilitates N mineralization (Roy *et al.*, 2006) and thus enhances N availability (Wilkinson *et al.*, 1999). As a last point concerning C:N ratios, we would like to emphasize the rationale behind a possibly logarithmic association with actual/attainable productivity: in the lower range of ratios, close to the internal C:N stoichiometry microbes pursue (i.e. 5-17:1 - Cleveland & Liptzin, 2007), a small shift in C:N can be expected to have a large effect on mineralization rates and subsequent N supply to sustain plant biomass production. Where the ratio is high, in contrast, microbial nutrient release is in any case low, so that a shift in C:N would be of little importance. In other words, intuitively, we can hypothesize that a shift in the C:N ratio from, for instance, 25:1 to 20:1 will arguably make a larger difference to the equilibrium between mineralization and immobilization as compared to a change from 60:1 to 55:1.

An important determinant of soil characteristics like SOC is soil moisture, which varies from dry to very wet across Sweden. Therefore, considering moisture may help explaining some patterns observed between soil factors and normalized productivity. Especially the quadratic association between log SOC and normalized productivity (Figs. 8a and 9a) illustrates the influence of soil moisture: at high water contents, the wetness of the soil inhibits decomposition (cf. Olsson *et al.*, 2009), thus leading to organic matter accumulation and a high SOC (Fig. 7a), and moreover a reduced supply of newly available nutrients (Gorham, 1991), which in the end suppresses productivity (Figs. 8c and 9c). For intermediate soil moisture levels, on the other hand, SOC is lower while productivity is promoted. Only for even drier soils with minimal SOC, productivity is lower again because of limiting water availability (Bergh *et al.*, 1999), lower nutrient inputs through groundwater and less frequent periods with easily available nutrients in the soil solution (Qian & Schoenau, 2002) and lower retention (Larcher, 2003; Roy *et al.*, 2006) and supply (Binkley & Hart, 1989) of nutrients by organic matter. Together, these results suggest that the empirical relationship between SOC and nutrient availability might have an optimum (cf. a parabolic curve), under which soil fertility is reduced due to a lack of sufficient organic matter itself, among other things, whereas a high SOC indicates organic matter accumulation and therefore a lowered decomposition and supply of nutrients. The first aspect is thus included in IIASA's metric (Fig. 2), while the decreasing part of the curve should be included in SOC's empirical relationship with nutrient availability if the effect of reduced decomposition is not captured by another soil variable in an updated metric.

Soil factors other than the soil C:N ratio and SOC either exhibited only a marginal influence on normalized productivity or their effect depended on the approach (Table 5). Mineral soil clay fractions had a weak but significantly positive effect on normalized productivity. Even though clay particles can protect SOM from decomposition (Xu *et al.*, 2016), clay soils in the Swedish database in all likelihood positively alter nutrient availability by means of their negative charges that serve as cation exchange sites (i.e. for NH_4^+, K^+, Ca^{2+} and Mg^{2+} - IIASA & FAO, 2012). Effects of TEB and pH were dependent on the productivity response considered (i.e. residual or actual/attainable productivity), possibly reflecting differences between regional ('residual approach') and national ('actual/attainable approach') variation in nutrient availability. All equations resulting from multiple regression analysis combining different soil variables contained the soil C:N ratio and SOC (Table 6), suggesting these are key determinants of nutrient availability in Sweden. Qualitatively considered, associations of C:N ratio (-), SOC (concave quadratic after log-transformation) and clay fraction (+) with normalized productivity were consistent for both approaches (Table 5). Consequently, the latter three have most potential for inclusion in an improved nutrient availability metric.

Experiments

Question 4 - evaluation of IIASA's metric (experiments)

IIASA's metric of constraints on nutrient availability could not describe variation in productivity (absolute or relative growth rates of basal area increment - resp. AGR and RGR) for any of the sampled nutrient manipulation experiments (Table 7). In other words, this result is consistent with the outcome for the national database, where only one minor positive correlation was found. This again suggests that the metric does not adequately describe nutrient availability of (nutrient manipulated) boreal forests, owing to suboptimal implementations of SOC, soil texture, TEB and pH_{H2O} and/or a lack of built-in variables that are more closely related to N availability (Fig. 11).

Question 5 - how nutrient availability related variables influence productivity (experiments)

Contrary to the results of the national database, the soil C:N ratio did not consistently exhibit a negative correlation with productivity (Tables 8 and S5; Fig. 11). Only for the C vs IL treatments at Flakaliden, a non-significant negative trend was found. These results unambiguously indicate that variation in soil C:N alone cannot sufficiently describe patterns in productivity related to varying N availability. This is to some extent related to the absence of a C:N response to N addition treatments: when N fertilizer is applied, increasing N availabilities can easily be measured with for example PRS probes (see below), while an expected drop in the soil C:N ratio (e.g. Gundersen *et al.*, 1998; Mulder *et al.*, 2015 - but see Tamm *et al.*, 1999; Cools *et al.*, 2014) does not necessarily occur (Figs. S1,2,3c). Indeed, the C:N ratio was not significantly affected by the nutrient addition treatments in this study, except at the Flakaliden experimental forest, and there, its response was not straightforward: soil C:N ratio was lowest for the oldest IL treatment, intermediate for the control and highest for the new nIL treatment. We presume that nutrient (nitrogen) additions indirectly raised C:N through stimulation of aboveground productivity and litterfall. The carbon rich additional organic matter (Tamm *et al.*, 1999; Cools *et al.*, 2014) might then increase the soil C:N ratio. When even more N is added or accumulated, this indirect effect may become smaller in size than the influence of additional soil N itself, resulting in a reduction of the C:N ratio as was the case for the IL treatment in Flakaliden. These results thus suggest that although the soil C:N ratio can describe patterns of nutrient availability at the countrywide scale, it rarely captures variation in N availability following fertilization, even after decades of N addition. For that reason, additional variables related to the status of N should be included in a metric to make it sufficiently accurate.

The apparent effect of SOC on productivity in the experiments also differed from the one found in the database, as its association with biomass production was absent or positive instead of quadratic/negative at high concentrations. This discrepancy can be explained as follows: for the database, high SOC concentrations were probably associated with low decomposition rates (cf. its link with high soil moisture), while at the experimental sites, they are likely a consequence of nutrient availability induced increases in productivity and therefore enhanced litterfall. Very similar results were found for CEC, as its logarithm was strongly correlated with log SOC. Increased soil organic matter contents do indeed raise the CEC as negative functional groups act as cation exchange sites (IIASA & FAO, 2012). In brief, positive correlations between SOC/CEC and productivity in the experiments are very likely a consequence of productivity raising SOC, not the other way around. Different behavior of SOC in the experiments compared to what was found for the national data, suggests that including this variable in a metric will be challenging if the metric were to describe variation in nutrient availability at both large spatial scales and experiments.

Bio-available phosphorus, extracted with the P_{Bray} method, did not show significant associations with AGR or RGR, whereas for extracted exchangeable bases (TEB per unit soil dry weight), positive effects were found for Flakaliden (C & IL, AGR) and negative effects for the Svartberget experimental forest. The positive association at Flakaliden is most likely due to the presence of base cations in the fertilizer, while in Svartberget, productivity was likely suppressed at the most wet (and base cation rich) blocks along the hydrological gradient. To conclude, extractions did not provide unambiguous results that would make it possible to include them in a nutrient availability metric (Fig. 11).

In contrast to all variables mentioned hitherto (and particularly soil C:N), inorganic N supply rates, measured with PRS probes, showed a clear positive response to N addition at all experimental sites (Figs. S1,2,3d), so that they could well explain variation in productivity everywhere (Tables 8 and S5). In a similar way, growth rates in Flakaliden were also related to P supply rates, which could be expected as P addition is part of the treatment at this experimental site (Table 2) and accordingly, PRS measurements for P responded positively to this nutrient manipulation (Fig. S2e). Surprisingly, part of the variation in productivity in the Åheden pine forest could be ascribed to P supply rates as well, while P was not added at the site. Possibly, this response to phosphorus reflects background natural variation in P supply (despite an experimental design with randomization), rather than elevated P availability at N treated plots through stimulated mineralization via boosted phosphatase production (e.g. Marklein *et al.*, 2012), because P supply did not significantly differ among treatments (Fig. S1e). Lastly, biomass production was also significantly positively related to PRS measured supplies for base cations (i.e. $Ca^{2+} + K^{+} + Mg^{2+}$) in the Flakaliden spruce forest, where addition of these elements was again part of the treatment (Table 2). In summary, nutrient supply rates explained considerable variation in productivity following nutrient addition (Fig. 11), making them candidate variables for including in a nutrient availability metric, particularly if such metric is expected to capture variation in the nutrient status following fertilizer addition.

Just as for the national database, soil variables were combined to explore which combination best explains variation in productivity at the Åheden experiment, for which sufficient data points were available. Ion supply rates (especially of inorganic N) were included in both selected models (for AGR and RGR), emphasizing their predictive power. In sharp contrast to the national data, the soil C:N ratio and SOC were not included in these final regression models. Consequently, C:N and SOC might be appropriate variables for inclusion in a metric only describing large-scale patterns, while for nutrient additions, PRS based supply rates need to be included.

Future directions

The national database and experiments have shown the advantages and drawbacks of different soil variables with respect to their potential to be included in a future nutrient availability metric. SOC, for instance, is theoretically known to have a positive influence on nutrient availability, but in the database, this positive effect was only apparent for low concentrations, whereas at high SOC, its effect was masked by other environmental factors (soil moisture and temperature), affecting both SOC and productivity through their role in regulating organic matter formation and decomposition rates. The soil C:N ratio, on the other hand, behaved as expected for the national data, yet stimulated litter production in treated plots of the nutrient addition experiments presumably blurred the theorized negative association between C:N and productivity. Such difficulties thus indicate the limits of using these variables in a future metric, ideally applicable to explain both variation at a large scale and at a local scale, including in fertilized sites. Moreover, if the metric lacks a variable that reliably responds to N availability under all circumstances, this may also imply that temporal changes in nutrient availability induced by N deposition are not detected.

This dissertation is part of a larger project of which the aim is to ultimately develop a globally applicable, standardized metric of nutrient availability. Future research should therefore in the first place answer whether our findings with respect to SOC, the soil C:N ratio, PRS derived supply rates and to a lesser extent clay fraction are also valid for other places on Earth, using additional local (experimental and gradient-based), regional and global datasets. Moreover, other nutrient status related data not assessed in the present dissertation, such as stable N isotope signatures (e.g. Craine *et al.*, 2009, 2015) could be of use too. Finally, in part based on results of this dissertation, Fig. 11 sums up the main (dis)advantages of various techniques to assess nutrient availability, regarding their potential to be included in a future metric.

Potential nutrient availability related **soil characteristics to include in a new metric**

	Advantages	Disadvantages
extractions of bio-available pools (N, P, TEB)	+ possible to assess amino acids (e.g. uptake of **organic N**) + simple, low-cost	- **experiments**: no good link with AGR, RGR - **pool ≠ supply** and availability - especially **for N inaccurate** due to many N cycle transformations
nutrient supply rates (**PRS probes**)	+ **experiments**: good link with AGR, RGR + diffusional **transport** more closely related to availability than pools	- ≠ **real root**: has more uptake mechanisms - **organic N** not measured - at low nutrient availability: supply may be close to **detection limits** or **blanks** - strongly dependent on **soil moisture** → current soil moisture representative? - rather for **relative differences**
soil and leaf **δ^{15}N**	+ related to **N availability**	- also dependent on **N sources** → correction necessary (does not exist yet) - can differ between **species** (e.g. N fixers and mycorrhiza type) - N only
leaf **nutrient concentrations and stoichiometry**	+ can be determined for **all nutrients** + reflects **plant perspective**	- (optima) **species** and **age** dependent
C:nutrient ratios	+ affects **mineralization** rate + most important variable in Swedish **database**	- **experiments**: no good link with AGR, RGR - only one of the factors governing decomposition rate
ecosystem process rates (mineralization, (de)nitrification, …)	+ detailed information + related to **modelling** approach	- short **time scale** variations >< general status - would require many measurements → **too complex** for this purpose
other soil characteristics (pH, SOC, CEC, texture)	+ **help explain** how nutrient availability **is regulated** + simple, low-cost	- dataset and experiments: **additional soil characteristics** are needed

Figure 11 | Overview of soil fertility related variables, that could be included in a future nutrient availability metric. + = advantage; - = limitation.

Conclusions

Both the results of the national database and the experiments indicate that IIASA's metric is incapable of explaining variation in nutrient availability for the nitrogen limited spruce and pine forests in Sweden. As expected, the four soil variables included in this metric (SOC, texture, TEB and pH_{H2O}) alone will not be sufficient to develop a worldwide applicable expression for nutrient availability. The national forest inventory data revealed that the empirical relationship between SOC and normalized productivity shows an optimum. Therefore, this pattern should be represented in a future nutrient availability metric if it does not include another soil variable that captures the effect of inhibited decomposition at high SOC. Furthermore, the soil carbon to nitrogen ratio can in part describe large-scale patterns in productivity, making it a good candidate to be included in a future metric. The nutrient addition experiments, however, demonstrated that an increase in nitrogen availability following fertilizer addition is not necessarily accompanied by a decreasing C:N ratio. As a result, this ratio could not significantly explain variation in productivity for any of the investigated experiments, in contrast to nutrient (nitrogen) supply rates measured with plant root simulator probes. Hence, such supply rates may well be needed in a globally applicable metric of nutrient availability.

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Supplementary information

Text-files of the national database and experiments are available at https://www.dropbox.com/sh/spxv6vqahiacmvm/AABLdtY2d23vxmHQiDIESJC9a?dl=0.

Table S1 | Overall mean squared error (mse) after 10-fold cross-validation for the most relevant (i.e. TSUM and spp clearly had to be included) candidate model structures that explain variation in productivity (mean annual increment - MAI - $m^3\ ha^{-1}\ yr^{-1}$) by climate (TSUM and PRECIP) and species across Swedish spruce and pine forests. The selected model is marked in gray. Abbreviations: TSUM = growing season temperature sum [°C days]; MAP = mean annual precipitation [mm]; spp = species.

Variables in model	Overall ms	Variables in model	Overall ms
TSUM^2:spp, TSUM:spp, TSUM^2, TSUM, MAP, spp	*1.48*	TSUM:spp, MAP, TSUM, spp	1.63
TSUM^2:spp, TSUM:spp, MAP:spp, TSUM^2, TSUM, MAP, spp	1.48	TSUM:spp, TSUM, spp	1.64
TSUM^2:spp, TSUM:spp, TSUM, spp	1.49	TSUM^2, TSUM, MAP, spp	2.23
TSUM^2, TSUM:spp, MAP:spp, TSUM, MAP, spp	1.58	TSUM^2, TSUM, spp	2.24
TSUM:spp, TSUM^2, TSUM, MAP, spp	1.59	MAP:spp, TSUM, MAP, spp	2.24
TSUM:spp, TSUM^2, TSUM, spp	1.60	TSUM, MAP, spp	2.27
TSUM:spp, MAP:spp, TSUM, MAP, spp	1.61	TSUM, spp	2.28

Table S2 | Overall mean squared error (mse) after 10-fold cross-validation for the most relevant candidate model structures that explain variation in residual mean annual increments (MAI) by soil variables for Swedish spruce and pine forests. The selected model is marked in gray. Abbreviations: C:N = carbon to nitrogen ratio, pH = pH_{KCl}; SOC = soil organic carbon concentration; $CLAY_{min.soil}$ = clay fraction in the mineral soil; TEB = total exchangeable bases. REGION is a factor with north, middle and south as levels (cf. Fig. 3).

Variables in model	Overall ms	Variables in model	Overall ms
LOG^2(SOC$_{0\text{-}20cm}$), LOG(SOC$_{0\text{-}20cm}$), C:N$_{0\text{-}20cm}$, CLAY$_{min.soil}$, LOG(TEB$_{0\text{-}20cm}$), pH^2, pH, REGION, all interactions with REGION	1.24	*LOG^2(SOC$_{0\text{-}20cm}$), LOG(SOC$_{0\text{-}20cm}$), C:N$_{0\text{-}20cm}$, LOG(TEB$_{0\text{-}20cm}$), pH^2, pH, REGION, all interactions with REGION except LOG^2(SOC$_{0\text{-}20cm}$):REGION, LOG(TEB$_{0\text{-}20cm}$):REGION*	*1.23*
LOG^2(SOC$_{0\text{-}20cm}$), LOG(SOC$_{0\text{-}20cm}$), C:N$_{0\text{-}20cm}$, CLAY$_{min.soil}$, LOG(TEB$_{0\text{-}20cm}$), pH^2, pH, REGION, all interactions with REGION except LOG^2(SOC$_{0\text{-}20cm}$):REGION	1.24	LOG^2(SOC$_{0\text{-}20cm}$), LOG(SOC$_{0\text{-}20cm}$), C:N$_{0\text{-}20cm}$, LOG(TEB$_{0\text{-}20cm}$), pH^2, pH, REGION, all interactions with REGION except LOG^2(SOC$_{0\text{-}20cm}$):REGION, LOG(TEB$_{0\text{-}20cm}$):REGION, pH^2:REGION	1.24
LOG^2(SOC$_{0\text{-}20cm}$), LOG(SOC$_{0\text{-}20cm}$), C:N$_{0\text{-}20cm}$, CLAY$_{min.soil}$, LOG(TEB$_{0\text{-}20cm}$), pH^2, pH, REGION, all interactions with REGION except LOG^2(SOC$_{0\text{-}20cm}$):REGION, LOG(TEB$_{0\text{-}20cm}$): REGION	1.24	LOG^2(SOC$_{0\text{-}20cm}$), LOG(SOC$_{0\text{-}20cm}$), C:N$_{0\text{-}20cm}$, pH^2, pH, REGION, all interactions with REGION except LOG^2(SOC$_{0\text{-}20cm}$):REGION, pH^2:REGION	1.24
LOG^2(SOC$_{0\text{-}20cm}$), LOG(SOC$_{0\text{-}20cm}$), C:N$_{0\text{-}20cm}$, CLAY$_{min.soil}$, LOG(TEB$_{0\text{-}20cm}$), pH^2, pH, REGION, all interactions with REGION except LOG^2(SOC$_{0\text{-}20cm}$):REGION, LOG(TEB$_{0\text{-}20cm}$):REGION, CLAY$_{min.soil}$:REGION	1.24		

Table S3 | Overall mean squared error (mse) after 10-fold cross-validation for the most relevant candidate model structures that explain variation in actual/attainable mean annual increments (MAI) by soil variables for Swedish spruce forests. The selected model is marked in gray. Abbreviations: C:N = carbon to nitrogen ratio; TEB = total exchangeable bases; pH = pH$_{KCl}$; CLAY$_{min.soil}$ = clay fraction in the mineral soil; SOC = soil organic carbon concentration.

Variables in model	Overall ms
LOG^2(SOC$_{0\text{-}20cm}$), LOG(SOC$_{0\text{-}20cm}$), LOG(C:N$_{0\text{-}10cm}$), CLAY$_{min.soil}$, LOG(TEB$_{0\text{-}20cm}$), pH	141
LOG^2(SOC$_{0\text{-}20cm}$), LOG(SOC$_{0\text{-}20cm}$), LOG(C:N$_{0\text{-}10cm}$), CLAY$_{min.soil}$, pH	141
LOG^2(SOC$_{0\text{-}20cm}$), LOG(SOC$_{0\text{-}20cm}$), LOG(C:N$_{0\text{-}10cm}$), pH	*140*
LOG^2(SOC$_{0\text{-}20cm}$), LOG(SOC$_{0\text{-}20cm}$), LOG(C:N$_{0\text{-}10cm}$)	145

Table S4 | Summary of statistics linking IIASA's metric of constraints on nutrient availability (for soil depth 0-20 cm) with relative growth rate (RGR) at a few nutrient manipulation experiments in northern Sweden. IL and nIL treatments were included in separate analyses because they were initiated at different moments, which is known to affect the current productivity response.

Site/Productivity response	RGR
Åheden	$t_{28} = -0.58$; $P = 0.57$
Flakaliden C & IL treatments	$t_6 = 0.86$; $P = 0.42$
Flakaliden C & nIL treatments	$t_6 = 0.19$; $P = 0.85$
Svartberget	$t_{13} = -0.75$; $P = 0.47$

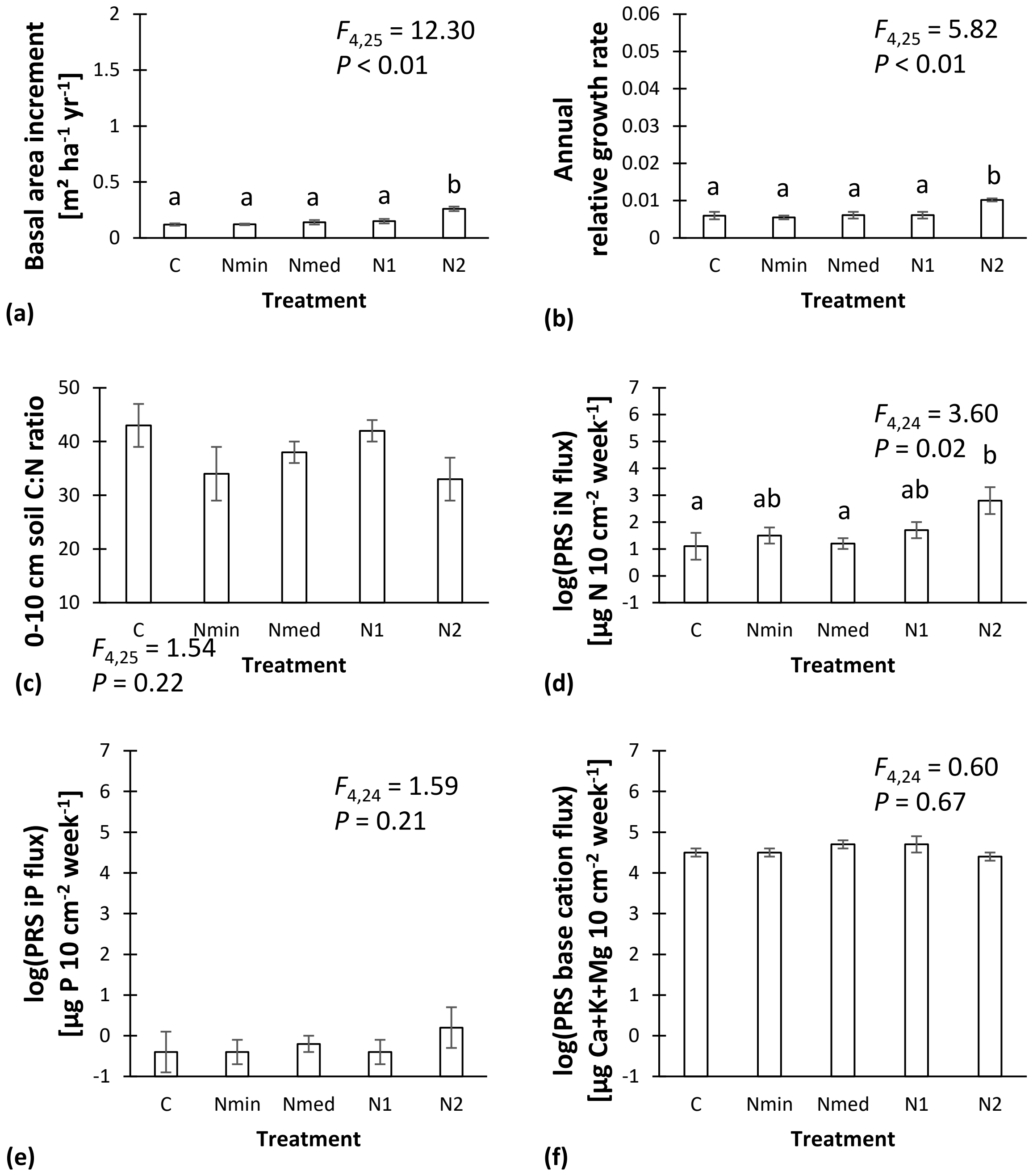

Figure S1 | Productivity (a,b) and selected soil variables (c-f) measured in summer 2016 for treatments at the Åheden experimental site (see Table 2 for site and treatment information). Abbreviations: PRS iN flux = inorganic nitrogen ($NH4^+$ + NO_3^-) supply rate measured with PRS probes; PRS iP flux = inorganic phosphorus supply rate measured with PRS probes; PRS base cation flux = base cation (Ca^{2+} + K^+ + Mg^{2+}) supply measured with PRS probes.

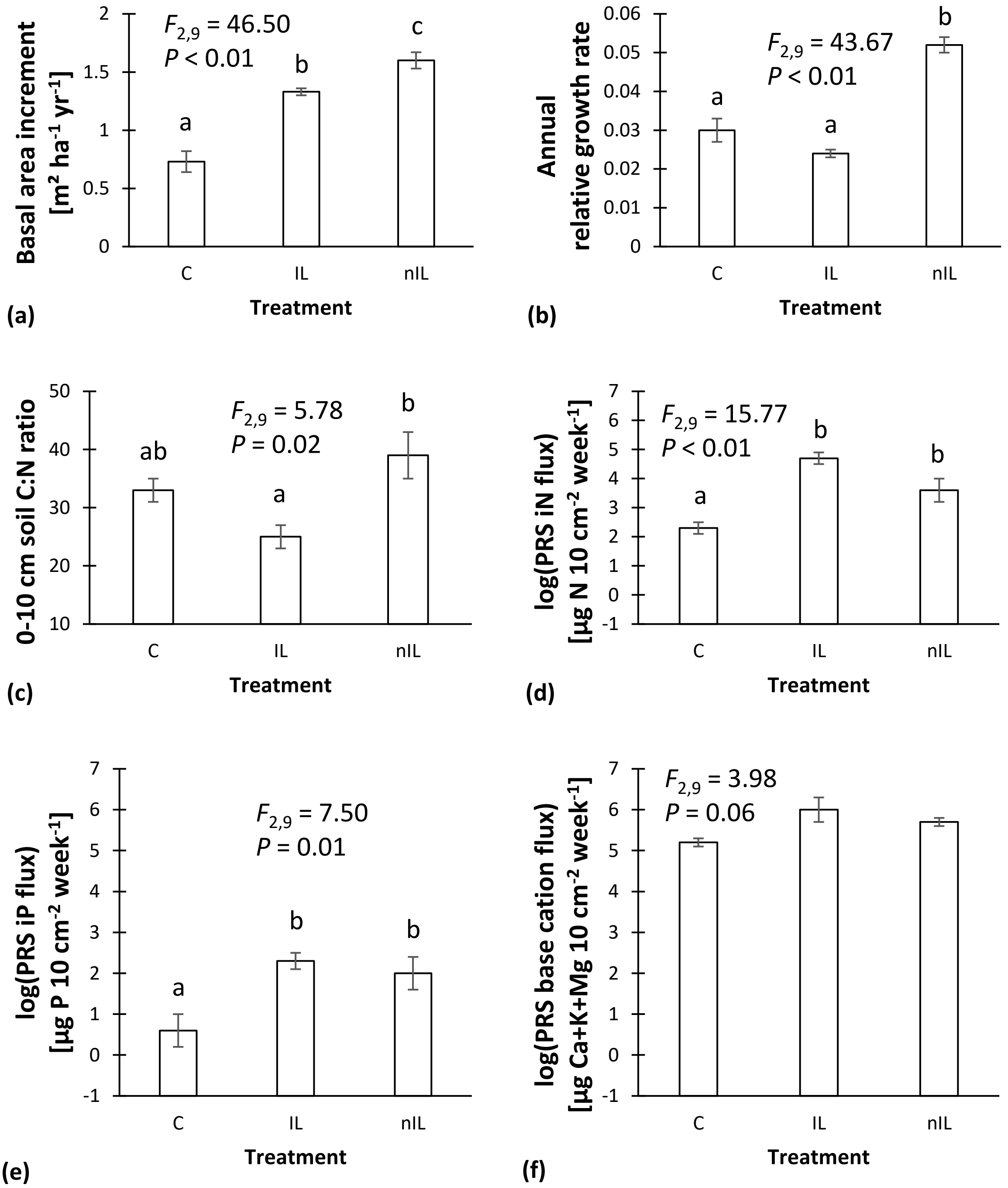

Figure S2 | Productivity (a,b) and selected soil variables (c-f) measured in summer 2016 for treatments at the Flakaliden experimental site (see Table 2 for site and treatment information). Abbreviations: PRS iN flux = inorganic nitrogen (NH4$^+$ + NO$_3^-$) supply rate measured with PRS probes; PRS iP flux = inorganic phosphorus supply rate measured with PRS probes; PRS base cation flux = base cation (Ca^{2+} + K$^+$ + Mg^{2+}) supply measured with PRS probes.

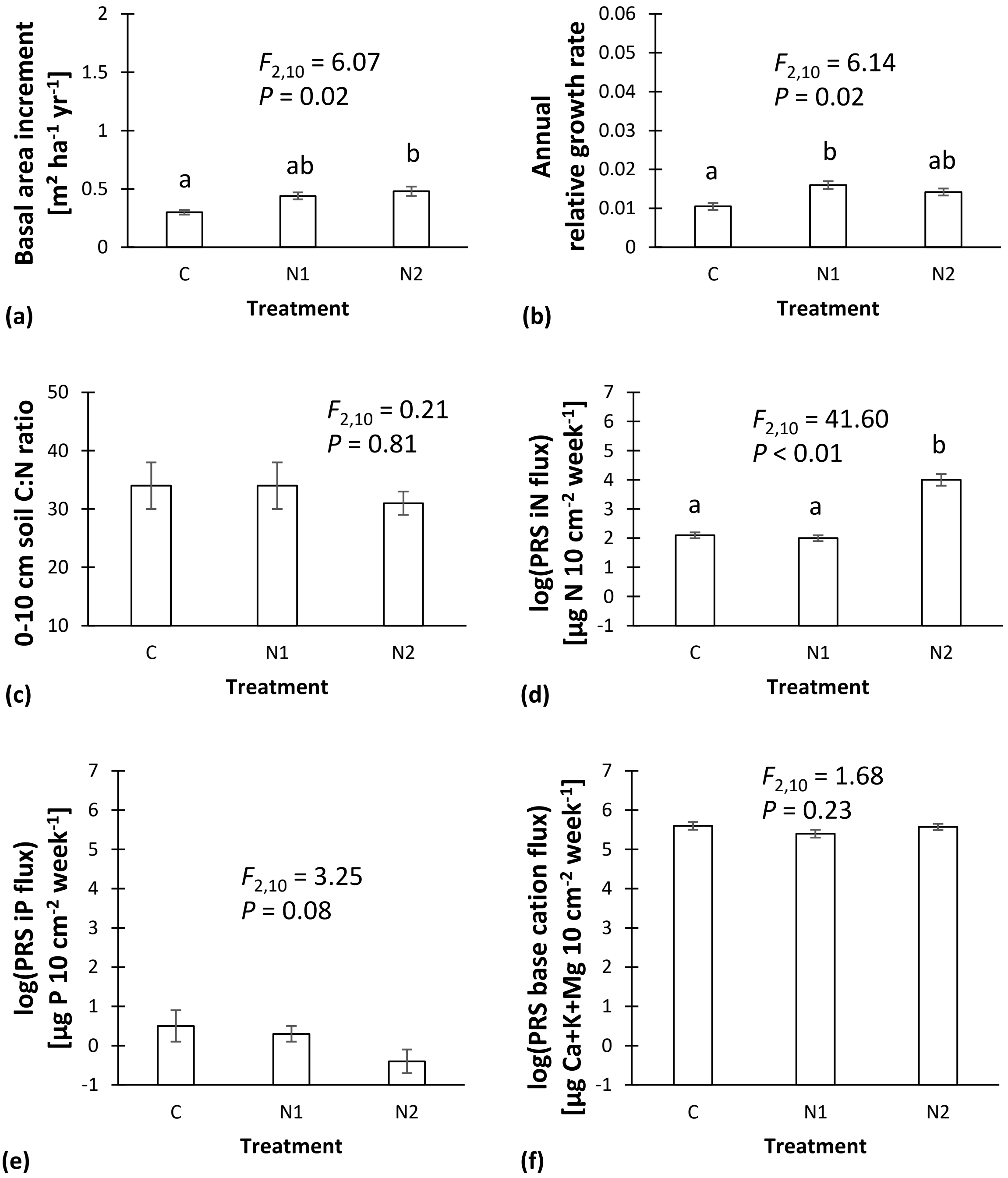

Figure S3 | Productivity (a,b) and selected soil variables (c-f) measured in summer 2016 for treatments at the Svartberget experimental site (see Table 2 for site and treatment information). Since plots were organized in a randomized complete block design along a hydrological gradient, blocks (*n* = 6) were included in a separate main effect in the analyses for the reported F and P values. Abbreviations: PRS iN flux = inorganic nitrogen ($\mathrm{NH4}^{+}$ + $\mathrm{NO_3}^{-}$) supply rate measured with PRS probes; PRS iP flux = inorganic phosphorus supply rate measured with PRS probes; PRS base cation flux = base cation (Ca^{2+} + K^{+} + Mg^{2+}) supply measured with PRS probes.

Table S5 | Associations between single soil variables and relative growth rate at the experimental sites mentioned in Table 2. For (near) significant variables (i.e. $P < 0.10$), parameter estimates ± s.e.m. and the proportion of variation explained (R^2) are given. Abbreviations: SOC = soil organic carbon concentration; TEB = total exchangeable bases; TN = total nitrogen; C:N = soil carbon to nitrogen ratio; CEC = cation exchange capacity; PRS iN flux = inorganic nitrogen ($NH_4^+ + NO_3^-$) supply rate measured with PRS probes; PRS iP flux = inorganic phosphorus supply rate measured with PRS probes; PRS base cation flux = base cation ($Ca^{2+} + K^+ + Mg^{2+}$) supply measured with PRS probes.

Site	Åheden (*n* = 30)	Flakaliden C & IL treatments (*n* = 8)	Flakaliden C & nIL treatments (*n* = 8)	Svartberget (*n* = 18)
log SOC$_{0\text{-}20cm}$ [%]	*P* = 0.15	*P* = 0.25	slope = 0.012 ± 0.006; *P* = 0.09 intercept = 0.024 ± 0.009; *P* = 0.03 R^2 = 0.316	*P* = 0.31
Clay$_{10\text{-}20cm}$ [%]	*P* = 0.83	t_6 = -0.80	*P* = 0.95	*P* = 0.23
log TEB$_{0\text{-}20cm}$ [cmol$_+$ kg^{-1}]	slope = 0.005 ± 0.003; *P* = 0.08 intercept = 0.010 ± 0.002; *P* < 0.01 R^2 = 0.073	*P* = 0.76	*P* = 0.15	slope = -0.005 ± 0.002; *P* = 0.02 intercept = 0.0145 ± 0.0009; *P* < 0.01 R^2 = 0.312
pH$_{KCl,0\text{-}20cm}$	*P* = 0.11	slope = 0.008 ± 0.002; t_6 = 3.50 intercept = 0.000 ± 0.008; t_6 = 0.003	*P* = 0.32	quad = 0.03 ± 0.01; *P* = 0.03 lin = -0.17 ± 0.07; *P* = 0.03 intercept = 0.3 ± 0.1; *P* = 0.02 R^2 = 0.247
log TN$_{0\text{-}20cm}$ [%]	slope = 0.002 ± 0.001; *P* = 0.08 intercept = 0.013 ± 0.003; *P* < 0.01 R^2 = 0.071	*P* = 0.21	*P* = 0.11	*P* = 0.14
C:N$_{0\text{-}10cm}$	*P* = 0.55	*P* = 0.19	*P* = 0.38	*P* = 0.63
log CEC$_{0\text{-}20cm}$ [cmol$_+$ kg^{-1}]	slope = 0.002 ± 0.001; *P* = 0.04 intercept = 0.004 ± 0.002; *P* = 0.03 R^2 = 0.109	*P* = 0.25	slope = 0.015 ± 0.004; *P* = 0.02 intercept = 0.013 ± 0.009; *P* = 0.18 R^2 = 0.597	*P* = 0.34
log TEB$_{0\text{-}20cm}$ [cmol$_+$ m^{-2}]	*P* = 0.88	*P* = 0.74	*P* = 0.44	*P* = 0.42
log P$_{Bray,0\text{-}20cm}$ [mg kg^{-1}]	*P* = 0.89	t_6 =-1.96	*P* = 0.15	*P* = 0.17
log PRS iN flux [µg 10cm^{-2} week^{-1}]	slope = 0.0009 ± 0.0005[1]; *P* = 0.07 intercept = 0.0053 ± 0.0009 *P* < 0.01 R^2 = 0.081	*P* = 0.14	slope = 0.011 ± 0.004; *P* = 0.03 intercept = 0.01 ± 0.01; *P* = 0.47 R^2 = 0.516	*P* = 0.39
log PRS iP flux [µg 10cm^{-2} week^{-1}]	slope = 0.0020 ± 0.0008[1]; *P* = 0.03 intercept = 0.0073 ± 0.0005; *P* < 0.01 R^2 = 0.136	*P* = 0.39	slope = 0.009 ± 0.003; *P* = 0.03 intercept = 0.029 ± 0.005; *P* < 0.01 R^2 = 0.514	*P* = 0.88
log PRS base cation flux [µg 10cm^{-2} week^{-1}]	*P* = 0.24[1]	*P* = 0.51	slope = 0.033 ± 0.007; *P* < 0.01 intercept = -0.14 ± 0.04; *P* < 0.01 R^2 = 0.781	*P* = 0.94

Table S6 | Overall mean squared error (mse) after 10-fold cross-validation for the most relevant candidate model structures that explain variation in absolute growth rate (AGR - m^2 ha^{-1} yr^{-1}) by soil variables for the Åheden experimental forest. The selected model is marked in gray. Only models with up to three parameters were tested, since the number of data points was limited (*n* = 30). Interactions were only added in cases where they were suggested by a regression tree (not shown). Abbreviations: PRS iN FLUX = inorganic nitrogen ($NH4^+$ + NO_3^-) supply rate measured with PRS probes; PRS iP FLUX = inorganic phosphorus supply rate measured with PRS probes.

Variables in model	Overall ms
LOG(PRS iN FLUX)	0.00322
LOG(PRS iN FLUX), LOG(PRS iP FLUX), LOG(PRS iN FLUX):LOG(PRS iP FLUX)	*0.00283*
LOG(PRS iN FLUX), LOG(PRS iP FLUX)	0.00324

Table S7 | Estimates ± s.e.m. for parameters of the selected multiple regression equations linking soil variables to relative growth rate (RGR) at the Åheden experimental site. Degrees of freedom (*df*), significance of the pattern (*P* values) and proportion of variation explained (R^2) are given as well. Interactions were added if suggested by a regression tree (not shown). Multiple regression was not performed for Flakaliden and Svartberget owing to an insufficient number of data points. Output of the model selection procedure is shown in Table S8. Abbreviations: CEC = cation exchange capacity; PRS iN flux = inorganic nitrogen (NH_4^+ + NO_3^-) supply rate measured with PRS probes; PRS iP flux = inorganic phosphorus supply rate measured with PRS probes; PRS base cation flux = base cation (Ca^{2+} + K^+ + Mg^{2+}) supply measured with PRS probes.

Site	Response	log $CEC_{0\text{-}20cm}$ [$cmol_+$ kg^{-1}]	log PRS iN flux [µg N 10^{-1} cm^{-2} $week^{-1}$]	log PRS base cation flux [µg Ca+K+Mg 10^{-1} cm^{-2} $week^{-1}$]	intercept	*P* and R^2
Åheden (*df* = 25)	RGR	0.003 ± 0.001	0.0013 ± 0.0004	-0.003 ± 0.001	0.015 ± 0.006	$P < 0.01$ $R^2 = 0.349$

Table S8 | Overall mean squared error (mse) after 10-fold cross-validation for the most relevant candidate model structures that explain variation in relative growth rates (RGR) by soil variables for the Åheden experimental forest. The selected model is marked in gray. Only models with up to three parameters were tested, since the number of data points was limited (*n* = 30). Interactions were only added in cases where they were suggested by a regression tree (not shown). Abbreviations: PRS iP FLUX = inorganic phosphorus supply rate measured with PRS probes [µg 10 cm^{-2} $week^{-1}$]; PRS iN FLUX = inorganic nitrogen ($NH4^+$ + NO_3^-) supply rate measured with PRS probes [µg 10 cm^{-2} $week^{-1}$]; CEC = cation exchange capacity [$cmol_+$ kg^{-1}]; TEB = total exchangeable bases [$cmol_+$ m^{-2}]; TN = total nitrogen [%]; PRS base cation flux = base cation (Ca^{2+} + K^+ + Mg^{2+}) PRS measured supply rate [µg 10 cm^{-2} $week^{-1}$].

Variables in model	Overall ms (x 10^{-6})	Variables in model	Overall ms (x 10^{-6})
LOG(PRS iP FLUX)	6.94	LOG($CEC_{0\text{-}20cm}$), LOG(PRS iN FLUX)	6.01
LOG(PRS iN FLUX)	6.82	LOG($CEC_{0\text{-}20cm}$), LOG(PRS iP FLUX)	6.39
LOG($CEC_{0\text{-}20cm}$)	6.73	LOG($CEC_{0\text{-}20cm}$), LOG(PRS BASE CATION FLUX), LOG($CEC_{0\text{-}20cm}$):LOG(PRS BASE CATION FLUX)	7.43
LOG($TEB_{0\text{-}20cm}$)	7.63	LOG($CEC_{0\text{-}20cm}$), LOG(PRS BASE CATION FLUX)	6.76
LOG($TN_{0\text{-}20cm}$)	7.32	LOG($CEC_{0\text{-}20cm}$), LOG(PRS iN FLUX), LOG(PRS iP FLUX)	6.19
LOG(PRS BASE CATION FLUX)	7.99	*LOG($CEC_{0\text{-}20cm}$), LOG(PRS iN FLUX), LOG(PRS BASE CATION FLUX)*	*5.32*
LOG($CEC_{0\text{-}20cm}$), LOG(PRS iN FLUX), LOG($CEC_{0\text{-}20cm}$):LOG(PRS iN FLUX)	6.92	LOG(PRS iN FLUX)	5.92