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The influence of soil properties and nutrients on conifer forest growth in Sweden, and the first steps in developing a nutrient availability metric

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Abstract. The availability of nutrients regulates terrestrial carbon cycling and modifies ecosystem responses to environmental changes. Nonetheless, nutrient availability is often overlooked in climate-carbon cycle studies because it depends on the interplay of various soil factors that would ideally be comprised into one metric. Such a metric does not currently exist. Here, we used a Swedish forest inventory database that contains soil and tree growth data for >2500 forests across Sweden to test which combination soil factors best explains variation in plant growth, and to take the first steps in developing a nutrient availability metric. For the latter, we started from a (yet unvalidated) metric for constraints on nutrient availability that was previously developed by IIASA (Laxenburg, Austria). This IIASA-metric was developed for crops and uses only indirect indicators of nutrient availability. Our analyses revealed that soil organic carbon content (SOC) and the soil carbon to nitrogen (C:N) ratio were the most important factors explaining variation in "normalized" (climate-independent) productivity. Normalized productivity increased with decreasing soil C:N ratio ($R^2 = 0.02–0.13$), while SOC exhibited an empirical optimum ($R^2 = 0.05–0.15$). The IIASA-metric was unrelated to normalized productivity ($R^2 = 0.00–0.01$), because the soil factors under consideration were not well implemented, and because the C:N ratio was not included. We upgraded this metric by incorporating soil C:N and adjusting the relationship between SOC and nutrient availability in view of the observed relationship across our database. This upgraded metric explained a significant fraction of the variation ($R^2 = 0.03–0.21$; depending on the applied method) and thus opens up new opportunities to further validate and improve it with other datasets, from forests and from other ecosystem types, to ultimately develop a generic global nutrient availability metric.

1 Introduction

Nutrients determine structure and functioning at all levels of biological organization. The availability of mineral elements influences for example plant growth (von Liebig, 1840), patterns of biodiversity (Fraser et al., 2015) and ecosystem processes (e.g. Janssens et al., 2010; Vicca et al., 2012; Fernández-Martínez et al., 2014). Moreover, nutrient availability can modify ecosystem responses to global atmospheric and climatic changes, such as nitrogen (N) deposition (From et al., 2016), increasing CO_2 levels (Norby et al., 2010; Terrer et al., 2016), warming (Dieleman et al., 2012) and drought (Friedrich et al., 2012). Given the crucial role of nutrients in terrestrial carbon cycling and in shaping the magnitude and direction of its feedbacks to climate change, nutrient availability should be taken into account in global analyses and in Earth system models (Goll et al., 2012; Thomas et al., 2015; Wieder et al., 2015). This is, however, not yet common practice because we often lack the soil data and metrics needed to accurately account for nutrient availability.

Comparing nutrient availability among terrestrial ecosystems is thus difficult for two reasons: comprehensive and harmonized data on soil properties and nutrients are not usually available from experimental and observational sites, and no standardized quantitative metric exists to compare the nutrient statuses of terrestrial ecosystems at the global scale. In the absence of a standardized nutrient availability metric, studies comparing nutrient availability across sites have previously described soil fertility related approximations such as the height of 100 year old trees (Hägglund and Lundmark, 1977) or have manually classified sites as low, medium, and high nutrient availability based on existing site information (Vicca et al., 2012; Fernández-Martínez et al., 2014). The absence of a more nuanced expression impedes elucidating the role of nutrient availability in ecosystem processes and functioning (Cleveland et al., 2011) and how these respond to global change, and precludes investigating non-linear effects of nutrient availability.

Although various proxies exist to estimate soil N and phosphorus (P) availability at the local scale (e.g. “snapshots” of extractable pools), no perfect method exists to quantify N and P availability in a comparable way across ecosystems (Binkley and Hart, 1989; Holford, 1997; Neyroud and Lischer, 2003), which limits the potential for inter-site comparisons based on these data alone (Cleveland et al., 2011). Soil properties like soil texture, soil organic matter (SOM) quantity and quality, and pH, on the other hand, are more indicative, because together with environmental factors (temperature and moisture - Binkley and Hart, 1989), they control the size of the soil solution, exchange sites and unavailable soil pools and fluxes between them over longer time scales (Roy et al., 2006). For instance, 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), while SOM has a positive influence on nutrient availability by acting as a nutrient reserve (Grand and Lavkulich, 2015) and provides cation as well as anion exchange sites (IIASA and FAO, 2012). Finally, soil pH strongly influences availability of P and base cations (K^+, Ca^{2+} and Mg^{2+}). At low pH, P is bound to Fe and Al oxides, while at high pH, P is typically unavailable because of complex formation with Ca. P availability is thus maximal at intermediate pH (Chapin et al., 2002; Bol et al., 2016), while enhanced leaching of base cations occurs in acidic soils, thus lowering the amount of total exchangeable bases (TEB = cation equivalent of summed K, Ca, Mg and Na - IIASA and FAO, 2012). Hence, unlike temperature or precipitation, nutrient availability cannot be assessed by measuring one single parameter. It is determined by the interplay of various nutrients and soil conditions. A nutrient availability metric should thus combine critical soil properties and nutrients, while considering important non-linearities. To be widely applicable, such a metric is preferably constructed only of easy-to-obtain variables.

Only a few exploratory attempts to find an expression for nutrient availability at the global scale have been made. The most recent one was developed by the International Institute for Applied Systems Analysis (IIASA, Laxenburg, Austria) and FAO, who provide a recently developed, simple index in their Global Agro-ecological Zones report of 2012 (IIASA and FAO, 2012). 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:

$$\text{Actual productivity} = \frac{\text{Metric score [\%] x Attainable productivity}}{100}, \qquad (1)$$

The species-specific score of the metric depends on four measurable soil variables, related to soil fertility: soil organic carbon concentration (SOC - %), texture, total exchangeable bases (TEB - $\text{cmol}_+ \text{ kg}^{-1}$ dw) and pH measured in water (pH_w). The metric score combines the scores of each of these four attributes (provided in a look-up table), but giving more weight to the attribute with the lowest score. Together with the non-linear relationships (e.g. for pH and SOC - see Methods), this increases the realism of the metric.

To our knowledge, the accuracy of the IIASA-metric has not yet been tested against data from natural ecosystems, and it is not known to what extent the metric – aimed at describing constraints on nutrient availability – can describe variation in nutrient availability of non-agricultural soils. Evaluation of the IIASA-metric, and further development of a global metric of nutrient availability, requires datasets that combine the necessary information on soil properties and nutrients with data on plant productivity, while also covering a substantial variation in nutrient availability. Such a unique dataset – that comprises >2500 conifer forest plots and thus provides sufficient statistical power for an evaluation of the metric – is provided by the Swedish forest inventory service. Moreover, it contains additional variables of interest such as the soil C:N ratio, which we expected to be an important factor in explaining variation in nutrient availability. We used this dataset to address the following questions:

Question 1: which single soil variables can explain variation in normalized (i.e. climate-independent) productivity across Sweden? Which combination of soil factors best explains variation in normalized productivity?

Question 2: can the IIASA-metric of constraints on nutrient availability explain variation in normalized productivity? Are the soil variables already included in the metric (SOC, texture, TEB and pH_w) accurately implemented?

Question 3: can the IIASA-metric be upgraded to characterize nutrient availability in Swedish forests?

2 Methods

2.1 The Swedish forest and soil inventories (national database)

We combined a Swedish forest soil (Olsson, 1999; Lundin, 2011) and inventory database for the period 2003–2012 (Lundin, 2011) with a database with soil texture and climate information across Sweden. Precipitation data 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).

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 % basal area of 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):

$$\begin{aligned}\text{TSUM [°C days]}\\ &= 4203.212488 - 40.21083 * \text{latitude [° N]} - 2.564434 * \text{elevation [m]}\\ &+ 0.030492 * \text{latitude [° N]} * \text{elevation [m]} - 0.117532 * \text{latitude}^2\text{ [° N]} + 0.00188 * \text{elevation}^2\text{ [m]}\\ &- 0.000000556 * \text{latitude}^2\text{ [° N]} * \text{elevation}^2\text{ [m]}\,, \qquad (2)\end{aligned}$$

In order to facilitate between-site comparisons and to allow calculating the nutrient availability metric, we converted the soil measurements (SOC, texture, TEB, pH_w, 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 10–20 cm layer and combined these to obtain values for the 0–20 cm layer. To this end, we first calculated bulk densities (BD) as

$$BD_{\text{organic horizon}}\ [\text{kg m}^{-3}] = \frac{humus\ stock\ [kg/m^2]}{humus\ depth\ [m]}\,, \qquad (3)$$

for the organic horizons and

$$BD_{\text{mineral horizon}}\ [\text{kg m}^{-3}] = 1546.3 * \exp(-0.3130 * \sqrt{total\ carbon\ [\%]})\,, \qquad (4)$$

for the mineral soil (Nilsson and Lundin, 2006).

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

$$\begin{aligned}\text{Variable}_{x\text{-}ycm} &= (\text{soil mass}_{\text{horizon1}}/\text{soil mass}_{x\text{-}ycm}) * \text{variable}_{\text{horizon1}}\\ &+ (\text{soil mass}_{\text{horizon2}}/\text{soil mass}_{x\text{-}ycm}) * \text{variable}_{\text{horizon2}} + \ldots \qquad (5)\end{aligned}$$

The IIASA-metric of constraints on nutrient availability incorporates four crop specific scores (estimated for SOC, texture, TEB and pH_w), which can be assigned to any soil using look-up tables (IIASA and FAO, 2012). Given differences among species were minor and we are analyzing boreal forests and not crops, we used the average score of the different crop species for each of the four scores. In addition, we replaced the look-up table derived step functions by continuous empirical formulas, to facilitate its calculation as well as its modification (Fig. 1):

$$\text{SOC Score [\%]} = 38.94 + (100 - 38.94) * (1-\exp(-1.4192 * \text{SOC[\%]})) \,, \tag{6}$$

$$\text{Texture Score [\%]} = \max(100 + 0.4911 * (1-\exp(0.0522 * \text{SAND[\%]})), 35) \,, \tag{7}$$

$$\text{TEB Score [\%]} = 28.05 + (100 - 28.05) * (1-\exp(-0.4508 * \text{TEB}[\text{cmol}_+ \text{ kg}^{-1}])) \,, \tag{8}$$

$$\begin{aligned}\text{pH Score [\%]} &= \max(-17.228 * (pH_w - 4.04) * (pH_w - 8.84), 0) \\ &= \max(-17.228 * (pH_w - 6.44)^2 + 99.32, 0) \,,\end{aligned} \tag{9}$$

The total score for nutrient availability, which can be interpreted as the expected actual yield (i.e. aboveground productivity) proportional to the maximum attainable yield (i.e. without nutrient constraints), was then calculated as follows (IIASA and FAO, 2012):

$$\text{Total IIASA Score [\%]} = 0.5 * \text{Lowest Score} + 0.5 * \text{Average of other Scores} \,, \tag{10}$$

2.2 General approach

Forest productivity across Sweden depends not only on nutrient availability, but also on climate. Before evaluating the metric, we removed the influence of climate on forest productivity ("PRE" in Fig. 2). Normalized productivity was calculated in two alternative ways, each with its own advantages and drawbacks: (1) as the residuals of the regression model (of PRE) and (2) as the ratio of the original productivity relative to the theoretical maximum productivity. This theoretical maximum productivity, which was extracted from a map, provided by Bergh et al. (2005) with ArcGIS (ESRI, 2011), indicates the productivity that could be obtained under non-nutrient-limited conditions and is further referred to as attainable productivity. The second method is thus very similar to the IIASA approach (cf. Eq. (1)), but because an estimate for attainable productivity was only available for spruce, it could only be applied to this species.

Regression analysis was then used to elucidate how different available soil variables were related to normalized productivity (Q1). In addition, normalized productivity was fitted against the IIASA-metric to test its performance. The correlation between the residuals of this relationship and each of the four variables of the metric then indicated whether or not the variables were well implemented (Q2). Finally, the associations found in Q1 indicated how the metric could be upgraded (Q3). The upgraded metric was then evaluated in the same way as the original IIASA-metric in Q2. An overview of the methodology is presented in Fig. 2.

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2.3 Data analyses

The two methods for normalizing productivity each follow a different approach. The first method uses the residuals of a general linear model with productivity (Fig. S1a,b) dependent on climate and tree species (Fig. 3a, Tables S1 and S2 and Eq. (S1)). This approach considers the residuals to reflect deviations in productivity imposed by spatial variation in nutrient availability and in the absence of climate effects. However, residuals deviated more strongly from zero towards the warmer south (Fig. 3a), thus causing heteroscedasticity and a potential bias in the further analyses if not properly accounted for. For further analyses, we therefore we split the database into three TSUM groups (north, middle and south; Fig. 3a). For the alternative approach, actual productivities for spruce (Fig. S1b) were divided by hypothetical attainable productivities (Fig. S1c). In other words, while method 1 uses as response variable the residuals of the climate model per species, method 2 considers the ratio actual/attainable productivity (Fig. 3b).

2.3.1 *Question 1* - Normalized productivity vs single and combined soil variables

In order to understand how soil properties relate to normalized productivity, and to later verify if the IIASA-metric includes the best combination of variables, i.e. those explaining most variation while avoiding multicollinearity, we examined (1) correlations among the soil variables (SOC, total N, N stock, C:N ratio, sand fraction, clay fraction, TEB, pHw and pH_{KCl}), (2) the relationships between normalized productivity and single soil variables in the database, and (3) which combination of soil variables explains the largest proportion of variation in normalized productivity. We performed a principal component analysis (princomp function, package MASS - Venables and Ripley, 2002) for a visualization and constructed a correlation matrix with Pearson's *r* as correlation coefficients for each variable pair. In addition, soil moisture, which was available as a categorical variable, may act as a confounding factor for associations between productivity and the nutrient availability related soil variables (e.g. by inhibiting decomposition (Olsson et al., 2009), leading to reduced productivity and accumulating SOM at wet sites). We therefore tested if the selected soil variables differed among soil moisture classes (dry, fresh, fresh-moist and moist, as available from the database) using a two-way ANOVA with soil moisture and tree species as fixed factors.

Simple regression analysis was used to determine the relationship between single soil variables and normalized productivity, except for the categorical soil moisture for which we thus used ANOVA. Last, we tested which combination of continuous soil variables best explained variation in normalized productivity across Sweden (multiple regression analysis). 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 and Braun, 2015) each time indicated whether the variable in question could be removed. Interaction effects up to the first order were added if suggested by regression trees (package tree - Ripley, 2015). For method 1, 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).

2.3.2 *Question 2* - Evaluation of the IIASA-metric

Irrespective of the method applied, a well-functioning nutrient availability metric would be recognized by a clear, positive relationship with productivity. We used linear model analysis to test the significance of the relationship between the metric and normalized productivity, and its explanatory power (R^2). To test whether the variables included in the metric were accurately implemented, we also examined the correlation between the residuals of this linear model and each of the variables included in the metric (SOC, texture, TEB and pH_w). A significant correlation indicates that the soil variable under consideration is not optimally implemented in the metric.

2.3.3 *Question 3* - Upgrade of the IIASA-metric

Outcomes of *question 1* indicated which soil variables best explained variation in normalized productivity. This information was further used to i) assess if the relationships for variables already included in the IIASA-metric should be altered, ii) remove soil variables from the metric if their empirical associations with normalized productivity were opposite from their relationships in the original IIASA-metric due to indirect effects of other underlying mechanisms, complicating parametrization and iii) include additional soil variables to improve performance of the metric. As a starting point for upgrading the metric, regression equations containing normalized productivity of method 1 for half of the dataset for southern Sweden (where productivity varied most, cf. Fig. 3a) vs the most important single soil variables were adopted as partial metric scores (cf. the original Eqs. (6–9)). Moreover, the minimum and maximum normalized productivities observed in southern Sweden were included as lower and upper boundaries to the partial metric scores to avoid possible unrealistic values for future applications to other databases. Finally, an improved metric for nutrient availability was calculated as in Eq. (10). Performance of the upgraded metric was evaluated as described for the IIASA-metric under *question 2*, with the exception that for method 1 in southern Sweden, only the half of the data points not employed for constructing the metric served as input.

We examined the validity of the linear models' assumptions (linearity, normality of residuals, no influential outliers, homoscedasticity) with standard functions of R (R Core Team, 2015), 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. The variance inflation factor (package car - Fox and Weisberg, 2011) assessed possible multicollinearity. 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.

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3 Results

3.1 *Question 1* - Normalized productivity vs single and combined soil variables

In order to elucidate how soil variables affect nutrient availabilities across Sweden, we used their single and combined relationships with normalized productivity. In this database, pH_w and pH_{KCl} were strongly correlated. As pH_{KCl} has the practical advantage of showing less seasonal variation than pH_w (Soil Survey Staff, 2014), we opted to use only pH_{KCl} in the analyses for this research question. Similarly, TN and SOC largely shared the same information. We included SOC in the analyses and discarded TN because SOC is a component of the IIASA-metric of constraints on nutrient availability. Collinearity among other variables was minor ($|\text{Pearson's } r| < 0.65$; Fig. 4), and they were thus all included in the analysis.

Soil moisture may influence nutrient availability of ecosystems by – among other things – affecting the rate of decomposition, and consequently change other soil characteristics. In the database, each forest was originally assigned to a soil moisture category. Using these categories, we found that SOC and C:N ratio increased from dry to moist. A similar trend was observed for TEB, while the sand fraction and pH_{KCl} decreased from dry to moist. For clay, no significant differences among soil moisture classes occurred (Fig. S2). Hence, the wetness of a site could confound observed patterns in productivity associated with the five soil variables and is therefore taken into account in the further analyses and their interpretation.

For method 1, we found that most single soil variables were significantly related to normalized productivity (Table 2). Normalized productivity was significantly negatively correlated with the soil C:N ratio (Fig. 5b), for which the effect became more pronounced towards the south ($F_{2,2274} = 34.23$; $P < 0.01$). For both SOC (Fig. 5a) and pH_{KCl}, the relationship with normalized productivity was quadratic, while the associations with soil N stocks and clay were weak yet significantly positive. Normalized productivity and TEB did not significantly correlate, but the trend was weakly positive. Lastly, normalized productivity was highest in the “fresh” soil moisture class and lowest for the wettest forests (Fig. 5c). All these patterns were most pronounced 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 - $F_{7,2468} = 3.77$, $P < 0.01$). The strongest relationships were found for normalized productivity versus SOC, pH_{KCl} and soil C:N ratio (and moisture) and consequently these were among the variables selected for the model with multiple covariates (Table 3).

Results of method 2 were qualitatively similar to those of the other approach for SOC (Fig. 6a), N stock, C:N ratio (Fig. 6b), clay fraction, TEB and soil moisture ($F_{4,1054} = 24.90$, $P < 0.01$; Fig. 6c), although the N stock explained a larger proportion of the variation here and the curve for actual/attainable productivity decreased logarithmically rather than linearly with increasing C:N ratio. However, the function for pH_{KCl} was not quadratic, but linear with a significantly positive slope (Table 2). 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 thus included in the multiple regression models for both methods 1 and 2 (Table 3).

3.2 *Question 2* - Evaluation of the IIASA-metric

Both methods agreed on the poor performance of the IIASA-metric to elucidate patterns in nutrient availability, as the weakly positive correlation between normalized productivity and the metric was rarely significant, and explained < 1 % of the variation in normalized productivity in northern Sweden for method 1 (Fig. 7). Residual values of the relationship between normalized productivity of method 1 and the metric score (Fig. 7a) were significantly associated with all four input variables of the metric (SOC, texture, TEB and pH_w - Table 4). SOC and TEB correlated negatively with these residuals, while sand was significantly positively related to these same residuals, and productivities at low pH_w were overestimated (the quadratic functions were concave; not shown in Table 4). Residuals of method 2 (Fig. 7b) confirmed the negative trend with TEB, but showed no statistically significant relationship with SOC, texture or pH_w (Table 4). Overall, the fact that residuals were still correlated with the variables in the metric demonstrates that the input variables were not optimally implemented in the formula.

3.3 *Question 3* - Upgrade of the IIASA-metric

From *question 1*, we deduce that SOC, soil C:N and pH are important factors influencing nutrient availability in Sweden. Based on their relationships with normalized productivity in southern Sweden (Table S5), the following formulae were implemented in an upgraded nutrient availability metric (Fig. S3):

$$\text{SOC Score } [\text{m}^3\ \text{ha}^{-1}\ \text{yr}^{-1}] = \max(-0.18 * (\ln(\text{SOC}_{0\text{-}20\text{cm}}\ [\%]) - \ln(2.3))^2 + 0.525, -5.65)\ , \tag{11}$$

$$\text{C:N Score } [\text{m}^3\ \text{ha}^{-1}\ \text{yr}^{-1}] = \max(-0.08 * \text{C:N}_{0\text{-}20\text{cm}} + 2.1, -5.65)\ , \tag{12}$$

$$\text{pH Score } [\text{m}^3\ \text{ha}^{-1}\ \text{yr}^{-1}] = \max(-0.9 * (\text{pH}_{\text{w},0\text{-}20\text{cm}} - 4.67)^2 + 0.6, -5.65)\ , \tag{13}$$

In the same way as for the IIASA-metric, Eqs. (11–13) were combined in Eq. (10) to calculate the final nutrient availability score. Soil texture and exchangeable bases were not included here, as their empirical relationships with normalized productivity showed opposite trends as compared to their implementation in the IIASA-metric (Fig. 1 vs Tables 2 and 4), likely due to indirect effects of soil moisture and related organic matter accumulation.

In contrast to the IIASA-metric of constraints on nutrient availability, the upgraded metric explained a significant portion of the variation in normalized productivity, for both method 1 and 2 (Fig. 8). Only on few occasions did the soil variables included in the metric show a (borderline) significant correlation with the residuals of the relationship between normalized productivity and the upgraded metric (and the associated R^2 was always low; Table 5). We therefore conclude that SOC, soil C:N and pH are generally well implemented in the upgraded metric, at least for the database considered here.

4 Discussion

4.1 *Question 1* - Normalized productivity vs single and combined soil variables

Soil C:N ratio had a straightforward, negative effect on normalized productivity across both methods (Figs. 5b and 6b). Apart from high N concentrations at low C:N, increased productivities with decreasing C:N ratio can follow from its influence on litter decomposition and mineralization, and thus on nutrient availability: when the ratio in organic matter is high, microbes more strongly immobilize N to adjust their internal C to N stoichiometry. As a consequence, N is not easily 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). Last, the logarithmic relationship between actual/attainable productivity and soil C:N ratio indicates that in the lower range, close to the internal C:N stoichiometry microbes pursue (i.e. 5–17:1 - Cleveland and Liptzin, 2007), a small shift in C:N can have a large effect on mineralization rates and subsequent N supply to sustain plant biomass production. Where the C:N ratio is high, in contrast, microbial nutrient release is always low, and 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 make a larger difference to the equilibrium between mineralization and immobilization as compared to a change from 45:1 to 40:1.

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. The quadratic relationship between ln SOC and normalized productivity (Figs. 5a and 6a) 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. S2a), and moreover a reduced supply of newly available nutrients (Gorham, 1991), which in the end suppresses productivity (Figs. 5c and 6c). For intermediate soil moisture levels, on the other hand, SOC is lower while productivity is promoted, whereas for relatively dry soils with low SOC, productivity is reduced 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 and Schoenau, 2002) and lower retention (Larcher, 2003; Roy et al., 2006) and supply (Binkley and Hart, 1989) of nutrients by organic matter. Together, these results suggest that the empirical relationship between SOC and nutrient availability might have an optimum below which soil fertility is reduced due to a lack of sufficient organic matter itself, and above which high SOC indicates organic matter accumulation due to reduced decomposition and thus limited nutrient supply through mineralization. The first aspect is thus included in the IIASA-metric (Fig. 1), while the decreasing part of the curve should be included in the empirical relationship of SOC with nutrient availability if the effect of reduced decomposition is not captured by any of the other soil variables 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 2). N stocks could explain variation across both methods, but their explanatory power was rather modest for method 1. We anticipate that including N stock in a nutrient availability metric will be of limited value, as this variable is only loosely related to N availability at the continental or global scale (cf. Binkley and Hart, 1989). 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 influence 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 and FAO, 2012). Effects of TEB and pH were dependent on the method, possibly reflecting differences between regional (method 1) and national (method 2) variation in nutrient availability.

All equations resulting from multiple regression analysis combining different soil variables contained the soil C:N ratio and SOC (Table 3), confirming that these are key and complementary determinants of nutrient availability in northern coniferous forests. Qualitatively considered, associations of C:N ratio (-), SOC (concave quadratic after log-transformation), N stock (+) and clay fraction (+) with normalized productivity were consistent for both approaches (Table 2). Together with their abilities to explain variation, the consistent effects of C:N and SOC suggest these soil variables have most potential for inclusion in an improved nutrient availability metric.

4.2 *Question 2* - Evaluation of the IIASA-metric

The IIASA-metric of constraints on nutrient availability, originally designed for evaluating constraints on nutrient availability of arable lands, does not clarify much variation in normalized productivity among Swedish forests: only in the north, the metric was significantly positively associated with normalized productivity of method 1, but the explained variation was minor ($R^2 = 0.008$). In middle and southern Sweden, and for actual/attainable productivity across the country (method 2), the IIASA-metric was not significantly correlated with the response (Fig. 7).

Although the IIASA-metric was not or only weakly related to normalized productivity, the variables it includes did exhibit significant relationships with the residuals obtained from the relationship between normalized productivity and the metric. In other words, SOC, soil texture, TEB and pH_w were not optimally implemented in the IIASA-metric. For example, SOC and TEB were negatively associated with productivity (residuals) instead of positively as suggested by the metric (Table 4). In Sweden, the high organic matter contents are very likely not the direct reason for the suppressed productivity. As reasoned under *question 1*, organic matter probably accumulated in places where decomposition rates are low (Minderma, 1968), giving rise to almost purely organic topsoils. This slow decomposition, in turn, may arise from high soil moisture contents (Olsson et al., 2009 - see *question 1* for evidence) and/or low temperatures (Larcher, 2003). Similarly, the organic matter typically retains exchangeable base cations (IIASA and FAO, 2012), explaining the association of TEB with residuals.

4.3 *Question 3* - Upgrade of the IIASA-metric

Based on results of the analyses for *question 1*, the nutrient availability metric was improved by i) including an empirical optimum in the influence of SOC on normalized productivity and ii) including soil C:N, thus more explicitly incorporating the availability of N. In the current analysis, soil texture and TEB were excluded from the metric, as they exhibited negative instead of the expected positive associations with normalized productivities (IIASA and FAO, 2012), probably due to indirect effects of reduced decomposition and suppressed productivity where the proportion of sand is low and TEB is high.

In contrast to the original metric developed by IIASA, the upgraded metric significantly described variation across all approaches (Fig. 8), and variables were generally properly implemented (Table 5). In order to further enhance performance of the metric, other nutrient status related data, such as stable N isotope signatures (e.g. Craine et al., 2009, 2015; Wolf et al., 2011) or information from ion exchange resin bags or membranes (e.g. Lundell, 2001; Qian and Schoenau, 2002), may well be necessary.

5 Conclusions

The present study has shown that SOC and the soil C:N ratio are key soil properties explaining variation in productivity of Swedish conifer forests. The empirical relationship between SOC and normalized productivity showed an optimum, reflecting the soil characteristic's direct positive effect on nutrient availability only at low soil carbon 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 showed the expected negative correlation with normalized productivity in the present database. Based on the resulting regression equations, we upgraded the IIASA-metric by adjusting the relationship between soil organic carbon concentration and nutrient availability, and by incorporating soil C:N.

In order to eventually obtain a sufficiently accurate, globally applicable nutrient availability metric that enables comparison of the nutrient status across experimental and observational sites worldwide, and that may even be used in terrestrial biosphere and Earth system models (e.g. based on a world map of nutrient availability), the upgraded metric developed in this study should in the first place be validated and further improved based on other forest data for which the necessary soil information is available. In a later stage, this approach can then be expanded to other ecosystem types.

Code and data availability

The Swedish national database and R scripts with statistical analyses are available at https://www.dropbox.com/s/ba088p790tbigwr/KevinVanSundert_etal_Biogeosciences_2017.7z?dl=0.

Supplementary information is available online at doi: XXX.

Author contribution

SV and KVS conceived the study. KVS performed the analyses and wrote the manuscript. JAH provided statistical advice and JS provided data. All authors contributed to the discussions and the writing of the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

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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; pH_w = pH measured in water; pH_{KCl} = pH measured in KCl solution; TN = total nitrogen; C:N ratio = carbon to nitrogen ratio.

Available data	location	climate	soil	vegetation
	latitude [° N] longitude [° E] elevation [m]	MAP [mm] TSUM[a] [° 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_w, pH_{KCl} TN, C:N ratio, moisture	age [yrs], tree species composition [%] productivity[b] [$m^3 ha^{-1} yr^{-1}$]

[a] TSUM was calculated for each data point based on its latitude, longitude and elevation.

[b] Productivities (site quality) or mean annual volume increments (MAI) over a full rotation were estimated based on height development curves. *In situ* productivities may be lower, depending on the management.

Table 2. Associations between single soil variables and normalized productivity for Swedish spruce and pine 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: N = north; M = middle; S = south; SOC = soil organic carbon concentration; 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 actual/attainable MAI, the model including 0-10 cm soil C:N performed better than the one with 0-20 cm soil C:N (ms = 173 vs 159).

Normalized productivity response	**Region**	**ln SOC** **0-20cm** **[%]**	**ln N stock** **0-20cm** **[g m^{-2}]**	**C:N** **0-20cm**	**ln C:N** **0-10 cm**	**Mineral soil sand [%]**	**Mineral soil clay [%]**	**ln TEB stock** **0-20cm** **[cmol$_+$ m^{-2}]**	**pH$_{KCl}$** **0-20cm**
Residual MAI (method 1)	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 = 0.29 ± 0.06 $P < 0.01$ intercept = -1.5 ± 0.3 $P < 0.01$ $R^2_{tot} = 0.012$	slope = -0.014 ± 0.004 $P < 0.01$ intercept = 0.3 ± 0.1 $P < 0.01$ $R^2 = 0.021$	N/A	slope = 0.003 ± 0.001 $P = 0.01$ intercept = -0.2 ± 0.1 $P = 0.03$ $R^2_{tot} = 0.008$	slope = 0.009 ± 0.004 $P = 0.02$ intercept = -0.05 ± 0.03 $P = 0.14$ $R^2_{tot} = 0.002$	$P = 0.11$	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 = 0.29 ± 0.06 $P < 0.01$ intercept = -1.5 ± 0.3 $P < 0.01$ $R^2_{tot} = 0.012$	slope = -0.027 ± 0.005 $P < 0.01$ intercept = 0.7 ± 0.2 $P < 0.01$ $R^2 = 0.029$	N/A	slope = 0.003 ± 0.001 $P = 0.01$ intercept = -0.23 ± 0.09 $P = 0.01$ $R^2_{tot} = 0.008$	slope = 0.009 ± 0.004 $P = 0.02$ intercept = -0.05 ± 0.03 $P = 0.14$ $R^2_{tot} = 0.002$	$P = 0.11$	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 = 0.29 ± 0.06 $P < 0.01$ intercept = -1.5 ± 0.3 $P < 0.01$ $R^2_{tot} = 0.012$	slope = -0.082 ± 0.007 $P < 0.01$ intercept = 2.0 ± 0.2 $P < 0.01$ $R^2 = 0.112$	N/A	slope = 0.003 ± 0.001 $P = 0.01$ intercept = 0.00 ± 0.08 $P = 0.98$ $R^2_{tot} = 0.008$	slope = 0.009 ± 0.004 $P = 0.02$ intercept = -0.05 ± 0.03 $P = 0.14$ $R^2_{tot} = 0.002$	$P = 0.11$	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 (method 2)	entire Sweden	quad = -2.6 ± 0.4 $P < 0.01$ lin = 11 ± 2 $P < 0.01$ intercept = 32 ± 2 $P < 0.01$ $R^2 = 0.048$	slope = 10.7 ± 0.8 $P < 0.01$ intercept = -18 ± 5 $P < 0.01$ $R^2 = 0.146$	N/A	slope = -19 ± 5 $P < 0.01$ intercept = 100 ± 5 $P < 0.01$ $R^2 = 0.131$	slope = -0.04 ± 0.02 $P = 0.01$ intercept = 42 ± 1 $P < 0.01$ $R^2 = 0.005$	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 3. 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. Abbreviations: MAI = mean annual increment [m³ 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; quad = parameter estimate for quadratic term; lin = parameter estimate for linear term of a quadratic function. Output of the model selection procedures for methods 1 and 2 is shown in Tables S3 and S4. Data for method 1 are for both spruce and pine, whereas actual/attainable MAI (method 2) was only available for spruce.

Normalized productivity response	**Region**	**ln SOC** $_{0\text{-}20cm}$ **[%]**	**ln N stock** $_{0\text{-}20cm}$ **[g m^{-2}]**	**C:N** $_{0\text{-}20cm}$	**ln C:N** $_{0\text{-}10\ cm}$	**Mineral soil sand [%]**	**ln TEB stock** $_{0\text{-}20cm}$ **[cmol$_+$ m^{-2}]**	**pH$_{KCl}$** $_{0\text{-}20cm}$	**intercept**	***P* and R^2**
Residual MAI (method 1)	N	quad = -0.16 ± 0.02 $P < 0.01$ lin = 0.34 ± 0.08 $P < 0.01$	not selected	lin = -0.004 ± 0.007 $P = 0.58$	N/A	not selected	lin = 0.13 ± 0.04 $P < 0.01$	quad = 0.3 ± 0.2 $P = 0.22$ lin = -2 ± 2 $P = 0.22$	4 ± 3 $P = 0.27$	$P < 0.01$ $R^2_{tot} = 0.180$
	M	quad = -0.16 ± 0.02 $P < 0.01$ lin = 0.34 ± 0.08 $P < 0.01$		lin = -0.014 ± 0.006 $P = 0.03$	N/A		lin = 0.13 ± 0.04 $P < 0.01$	quad = 0.0 ± 0.1 $P = 0.88$ lin = 0.2 ± 0.9 $P = 0.86$	0 ± 2 $P = 0.81$	
	S	quad = -0.16 ± 0.02 $P < 0.01$ lin = 0.34 ± 0.08 $P < 0.01$		lin = -0.050 ± 0.008 $P < 0.01$	N/A		lin = 0.13 ± 0.04 $P < 0.01$	quad = -0.40 ± 0.08 $P < 0.01$ lin = 2.7 ± 0.6 $P < 0.01$	-3 ± 1 $P < 0.01$	
Actual/attainable MAI (method 2)	entire Sweden	quad = -2.3 ± 0.4 $P < 0.01$ lin = 9 ± 2 $P < 0.01$	lin = 6 ± 1 $P < 0.01$	N/A	lin = -15 ± 2 $P < 0.01$	lin = -0.02 ± 0.02 $P = 0.20$	not selected	lin = -3 ± 1 $P < 0.01$	64 ± 13 $P < 0.01$	$P < 0.01$ $R^2 = 0.215$

Table 4. Associations between residuals of normalized productivities in Fig. 7 and soil variables in the IIASA-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; pH_w = pH measured in water; quad = parameter estimate for quadratic term; lin = parameter estimate for linear term of a quadratic function. Note that TEB is expressed here according to the standard definition (per kg dry weight as defined for the IIASA-metric), whereas elsewhere in this paper, TEB is referred to as a stock, i.e. an amount per m² in the upper 20 cm of the soil, thus better representing the actual number of base cations available to plants. Error bars represent the s.e.m.

Residuals of	**Region**	**ln $SOC_{0\text{-}20cm}$ [%]**	**$Sand_{0\text{-}20cm}$ [%]**	**ln $TEB_{0\text{-}20cm}$ [$cmol_+ kg^{-1}$]**	**$pH_{w,0\text{-}20cm}$**
Residual MAI (method 1)	N	slope = -0.11 ± 0.03 $P < 0.01$ $R^2 = 0.022$	slope = 0.005 ± 0.001 $P < 0.01$ $R^2 = 0.025$	slope = -0.04 ± 0.02 $P = 0.09$ $R^2 = 0.003$	quad = -0.3 ± 0.1 lin = 2.7 ± 0.9 $P < 0.01$ $R^2 = 0.019$
	M	slope = -0.31 ± 0.03 $P < 0.01$ $R^2 = 0.092$	slope = 0.012 ± 0.002 $P < 0.01$ $R^2 = 0.065$	slope = -0.20 ± 0.03 $P < 0.01$ $R^2 = 0.052$	quad = -0.4 ± 0.1 lin = 4 ± 1 $P < 0.01$ $R^2 = 0.055$
	S	slope = -0.56 ± 0.04 $P < 0.01$ $R^2 = 0.141$	slope = 0.015 ± 0.002 $P < 0.01$ $R^2 = 0.076$	slope = -0.39 ± 0.04 $P < 0.01$ $R^2 = 0.099$	quad = -0.86 ± 0.07 lin = 8.4 ± 0.6 $P < 0.01$ $R^2 = 0.166$
Actual/attainable MAI (method 2)	entire Sweden	$P = 0.41$	$P = 0.33$	slope = -0.6 ± 0.4 $P = 0.08$ $R^2 = 0.002$	$P = 0.73$

Table 5. Associations between residuals of normalized productivities in Fig. 8 and soil variables in the upgraded nutrient availability metric. 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; C:N = soil carbon to nitrogen ratio; pH_w = pH measured in water. Error bars represent the s.e.m.

Residuals of	**Region**	**ln $SOC_{0\text{-}20cm}$ [%]**	**$C{:}N_{0\text{-}20cm}$**	**$pH_{w,0\text{-}20cm}$**
Residual MAI (method 1)	N	$P = 0.40$	$P = 0.24$	$P = 0.28$
	M	slope = -0.06 ± 0.03 $P = 0.08$ $R^2 = 0.003$	slope = 0.011 ± 0.005 $P = 0.03$ $R^2 = 0.005$	$P = 0.14$
	S	$P = 0.36$	$P = 0.73$	$P = 0.28$
Actual/attainable MAI (method 2)	entire Sweden	slope = 1.7 ± 0.4 $P < 0.01$ $R^2 = 0.016$	slope = -0.33 ± 0.07 $P < 0.01$ $R^2 = 0.021$	$P = 0.17$

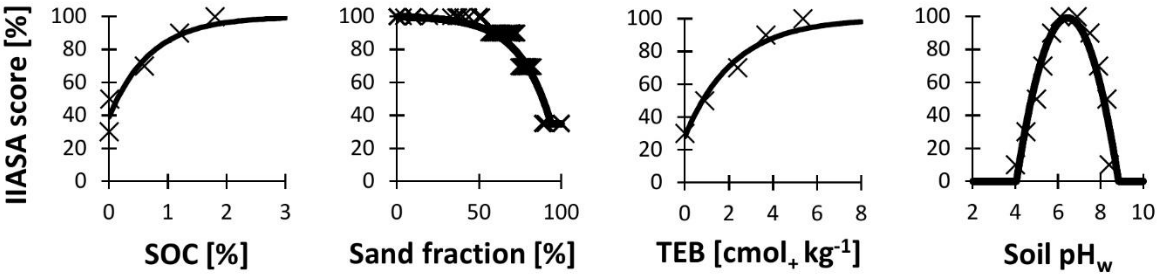


Figure 1. Species-averaged IIASA soil scores for soil organic carbon concentration (SOC), texture, total exchangeable bases (TEB) and pH measured in water (pH_w). The curves indicate approximate functions through the points, which represent values from a look-up table (IIASA and FAO, 2012). For texture, scores were originally assigned based on FAO texture classes (e.g. sand, loamy sand, …). Since 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.

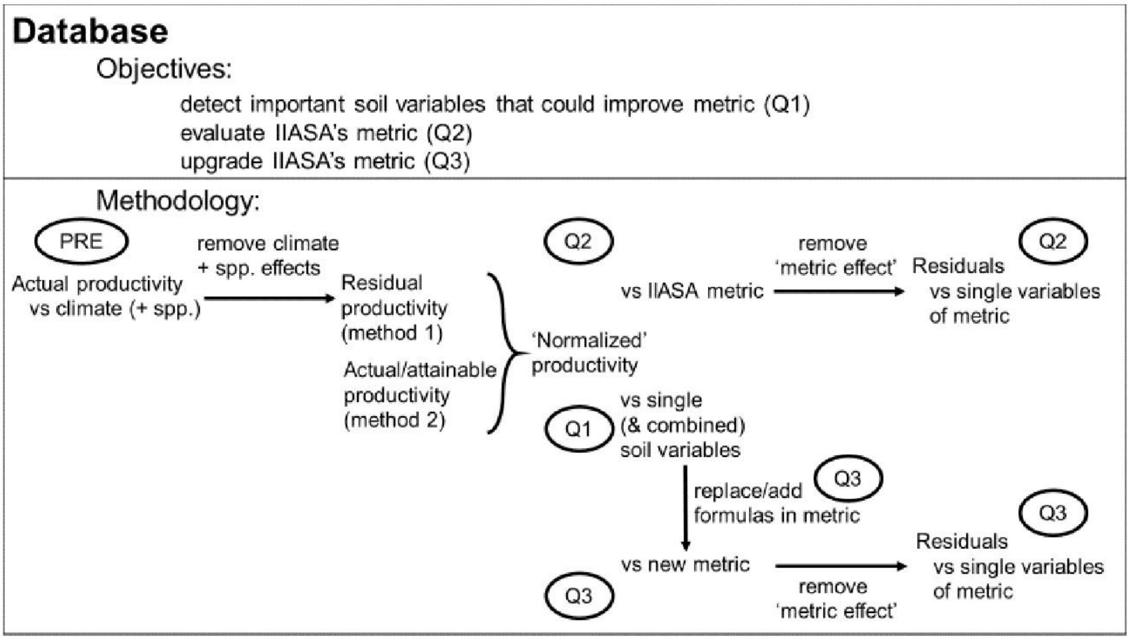


Figure 2. Objectives and methods followed in the current paper. PRE refers to a regression model of productivity vs climate and species; Q1, Q2 and Q3 refer to the research questions.

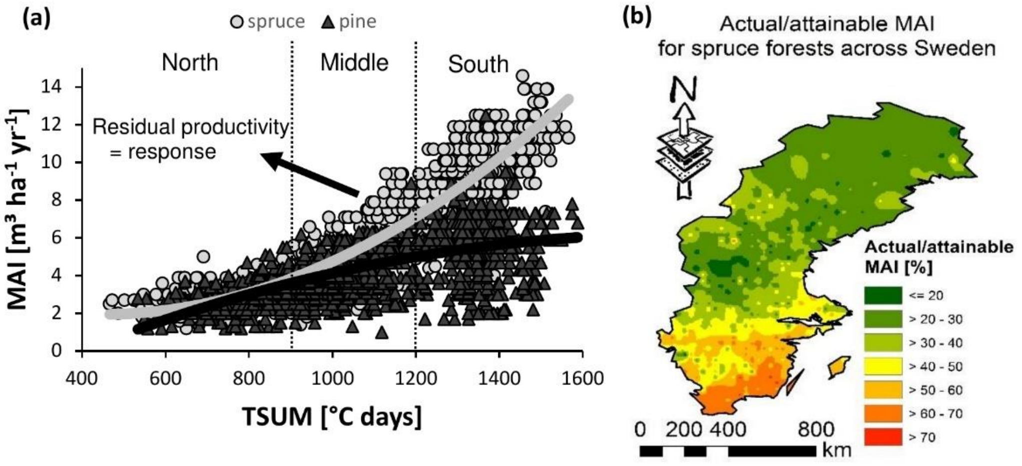
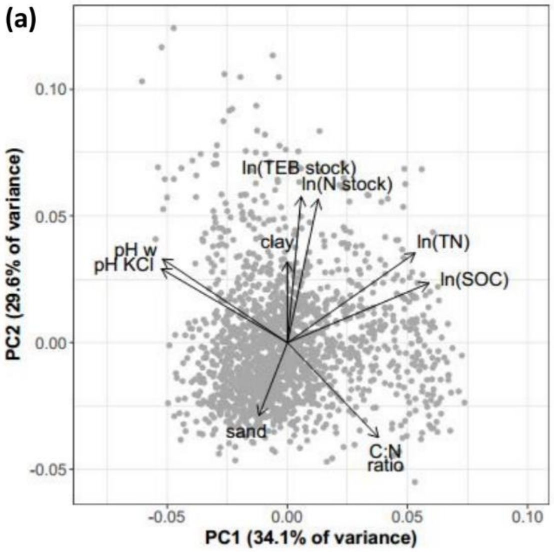


Figure 3. Normalized productivity was calculated in two alternative ways. (a) In method 1, residual values were taken from a regression model, explaining variation in mean annual increments (MAI) by climate (growing season temperature sum or TSUM and precipitation) and species. The selection procedure, equation and parameter estimates are given in the supplementary information (resp. Table S1, Eq. (S1) and Table S2). In order to avoid heteroscedasticity-induced artefacts, the dataset was split in a northern (TSUM < 900 °C days), middle (900 °C days < TSUM < 1200 °C days) and southern (TSUM > 1200 °C days) region for this approach. (b) In method 2, actual productivities for spruce were divided by theoretically attainable productivities, provided by Bergh et al. (2005).



(b)

soil variable	ln TN	ln N stock	C:N ratio	sand	clay	ln TEB stock	pH_w	pH_{KCl}
ln SOC	0.97	0.38	0.39	-0.18	0.05	0.33	-0.45	-0.45
ln TN		0.52	0.15	-0.21	0.10	0.43	-0.34	-0.34
ln N stock			-0.42	-0.16	0.19	0.58	0.11	0.12
C:N ratio				0.06	-0.16	-0.23	-0.52	-0.53
sand					-0.44	-0.20	0.01	0.03
clay						0.21	0.11	0.10
ln TEB stock							0.39	0.22
pH_w								0.89

Figure 4. Correlation structure of a set of potential key soil variables for a soil depth of 0-20 cm. (a) = PCA biplot (sd for PC1 = 1.75, sd for PC2 = 1.63). (b) = correlation matrix, showing Pearson's r for the variable pairs. Abbreviations: SOC = soil organic carbon concentration [%]; TN = soil total nitrogen [%], N stock = amount of nitrogen in the layer [g m^{-2}]; C:N ratio = soil carbon to nitrogen ratio; sand = % sand in the mineral soil; clay = % clay in the mineral soil; TEB = total exchangeable bases [$cmol_+$ m^{-2}]; pH_w = pH measured in water; pH_{KCl} = pH measured in KCl solution.

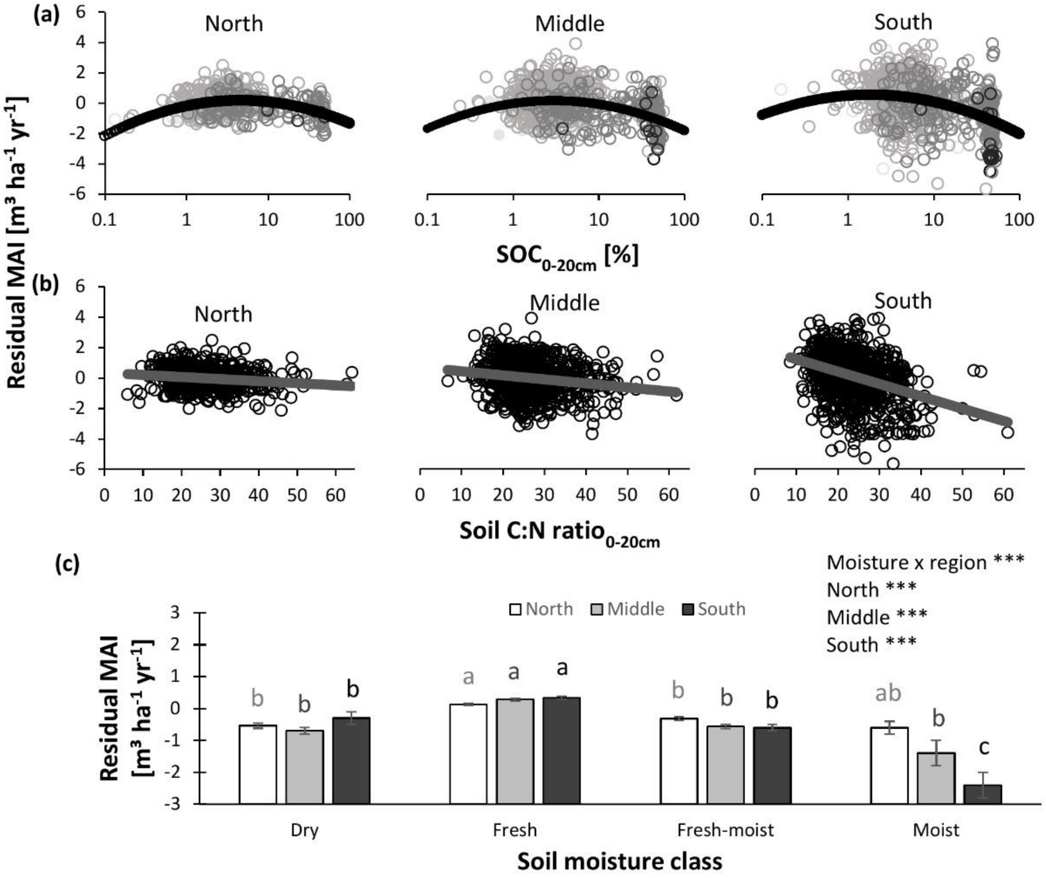


Figure 5. Relationship between normalized productivity of method 1 (residual mean annual increment - MAI) and, (a) log-transformed soil organic carbon (SOC) concentration, (b) soil carbon to nitrogen (C:N) ratio at depth 0-20 cm and (c) soil moisture class. Separate analyses were performed for northern, middle and southern Sweden, as the SOC, C:N and moisture effects differed among regions. Point darkness in panel a represents soil moisture (darker = moister). Statistics corresponding to panels a and b are presented in Table 2. *** indicates significant differences at the $P < 0.01$ level. Error bars represent the s.e.m.

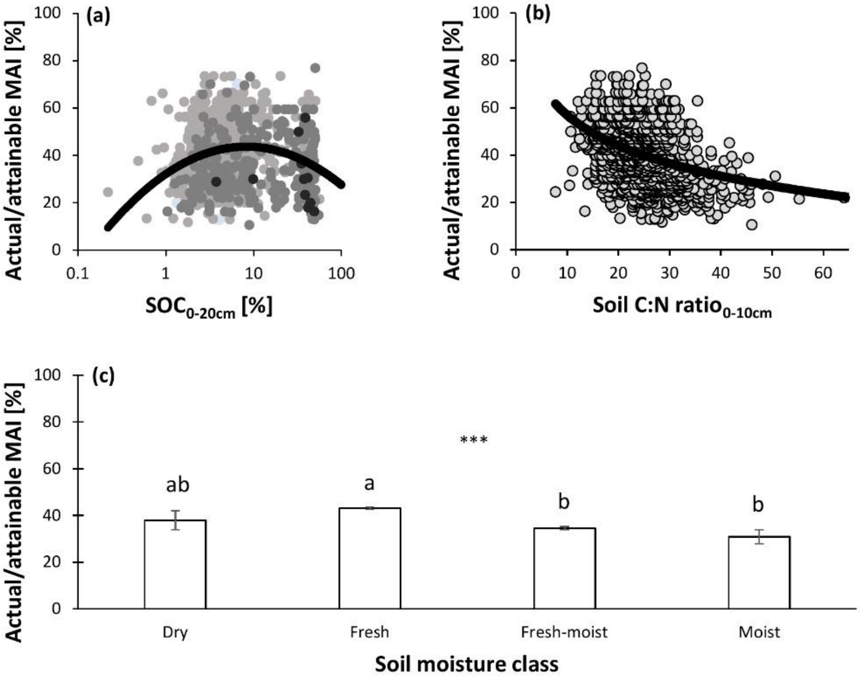


Figure 6. Relationship between normalized productivity of method 2 (actual/attainable mean annual increment – MAI for spruce) and, (a) log-transformed soil organic carbon (SOC) concentration, (b) soil carbon to nitrogen (C:N) ratio and (c) soil moisture class. Point darkness in panel a represents soil moisture (darker = moister). Statistics corresponding to panels a and b are presented in Table 2. *** indicates significant differences at the $P < 0.01$ level. Error bars represent the 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 decreased southwards (Fig. S1d), 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$_{0\text{-}10cm}$).

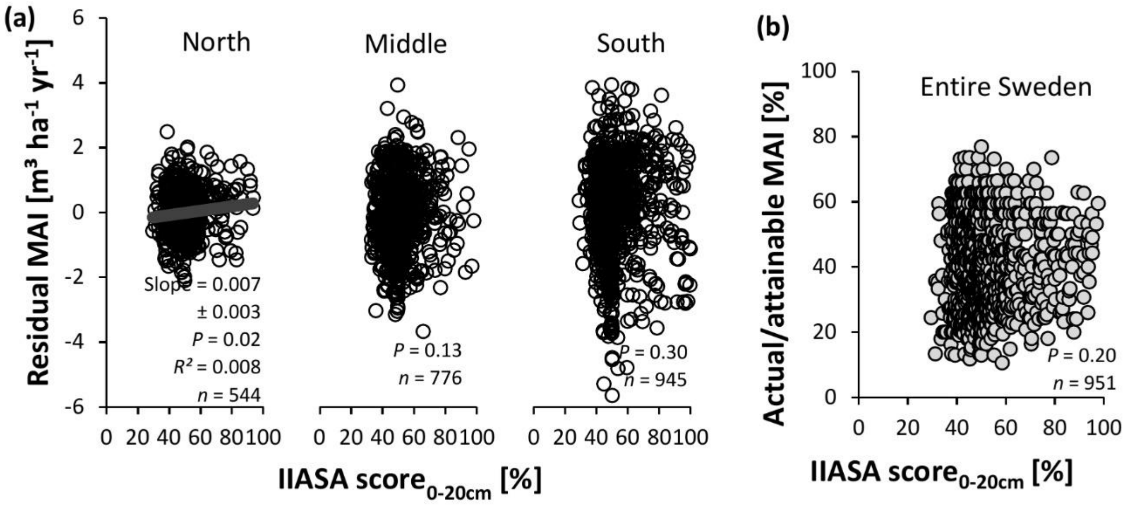


Figure 7. Evaluation of the IIASA-metric of constraints on nutrient availability for Swedish conifer forests. (a) Method 1 - association with residual mean annual increments (MAI) of the productivity-climate regression model (Fig. 3a, Eq. (S1) and Table S2), distinguishing northern, middle and southern Sweden. (b) Method 2 - association with actual/attainable MAI for the entire Swedish land area (Fig. 3b). 5 Full line = significant slope ($P < 0.05$).

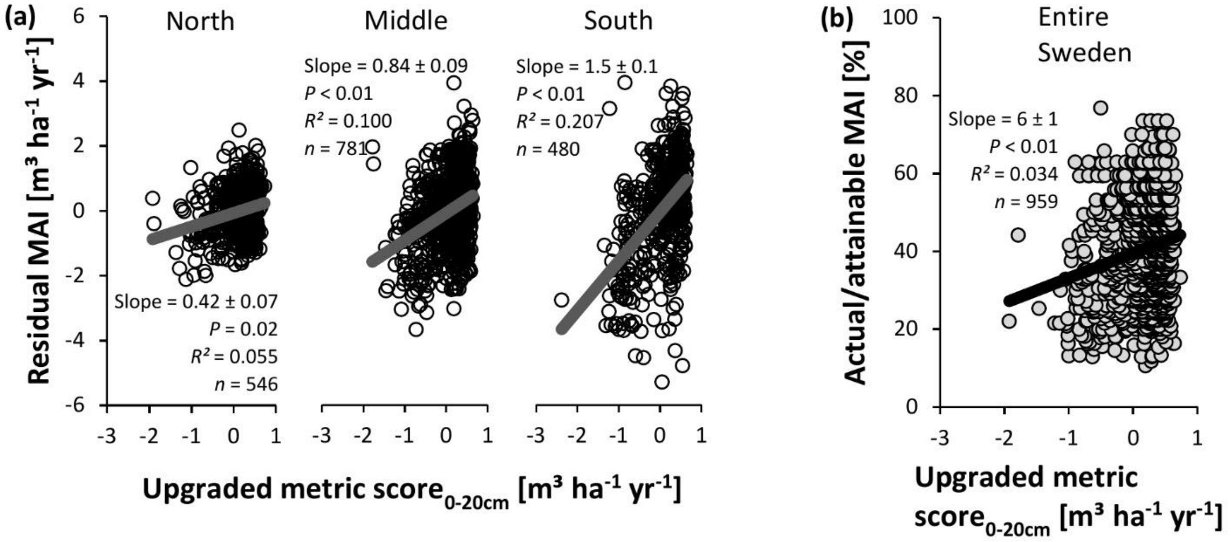


Figure 8. Evaluation of the upgraded nutrient availability metric for Swedish conifer forests. (a) Method 1 - association with residual mean annual increments (MAI) of the productivity-climate regression model (Fig. 3a, Eq. (S1) and Table S2), distinguishing northern, middle and 10 southern Sweden. (b) Method 2 - association with actual/attainable MAI (Fig. 3b) for the entire Swedish land area. Full line = significant slope ($P < 0.05$).