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Towards comparable assessment of the soil nutrient status across scales – review and development of nutrient metrics

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40 **Abstract**

Nutrient availability influences virtually every aspect of an ecosystem, and is a critical modifier of ecosystem responses to global change. Although this crucial role of nutrient availability in regulating ecosystem structure and functioning has been widely acknowledged, nutrients are still often neglected in observational and experimental synthesis studies due to difficulties in comparing the nutrient status across sites. In the current study, we explain different nutrient-related concepts and discuss the potential of soil-, plant- and remote sensing-based metrics to compare the nutrient status across space. Based on our review and additional analyses on a dataset of European, managed temperate and boreal forests (ICP Forests dataset), we conclude that the use of plant- and remote sensing-based metrics that rely on tissue stoichiometry is limited due to their strong dependence on species identity. The potential use of other plant-based metrics such as Ellenberg indicator values and plant-functional traits is also discussed. We conclude from our analyses and review that soil-based metrics likely have the largest potential for successful inter-site comparison of the nutrient status. As an example, we used and adjusted a soil-based metric, previously developed for conifer forests across Sweden, against the same ICP Forests data. We suggest that this adjusted and further adaptable metric, which included the organic carbon concentration (SOC) in the upper 20 cm of the soil (including the organic fermentation-humus (FH) layer), the C:N ratio and $\text{pH}_{\text{CaCl}_2}$ of the FH layer, can be used as a complementary tool along with other indicators of nutrient availability, to compare the background nutrient status across temperate and boreal forests dominated by spruce, pine or beech. Future collection and provision of harmonized soil data from observational and experimental sites should facilitate further testing and adjustments of the metric.

Keywords: nutrient status, nutrient availability, nutrient limitation, tree growth, soil nutrients, stoichiometry, plant functional traits, leaf economics spectrum, remote sensing, ICP Forests

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1 | INTRODUCTION: RELEVANCE OF NUTRIENT AVAILABILITY TO GLOBAL CHANGE RESEARCH

85 Macronutrients like nitrogen (N), phosphorus (P), and potassium (K), as well as essential micronutrients (e.g. zinc, copper, manganese, iron etc.) are critical for plants, microbes, and all life on Earth. It is long known that scarcity of essential nutrients limits plant growth and yield (Liebig, 1841), but the influence of nutrients goes far beyond plant productivity. Nutrient availability influences virtually every aspect of an ecosystem. Ecosystem carbon cycling (Vicca et al., 2012; 90 Fernández-Martínez et al., 2016), plant phenology (Cleland et al., 2006), plant diversity and community composition (Peñuelas et al., 2013; Harpole et al., 2016; Bes et al., 2018), plant-herbivore (Borer et al., 2014) and plant-soil microbe interactions (Högberg et al., 2010), and the structure of trophic food webs (Elser et al., 2000; Laliberté et al., 2017) are all directly or indirectly influenced by nutrient availability. As a consequence, human activities that lead to for example soil 95 acidification (i.e. acid deposition), shifts in the water balance (e.g. drainage, wetting), increases in atmospheric nitrogen deposition or eutrophication (e.g. fossil fuel combustion and fertilization) can strongly impact ecosystem properties and functioning (Bobbink et al., 2010; Peñuelas et al., 2013; Niu et al., 2016; Fernández-Martínez et al., 2017; Averill et al., 2018; Schulte-Uebbing & de Vries, 2018).

100 In the context of global change, nutrient availability is also a critical modifier of ecosystem responses to various environmental changes. It has been widely shown that the effect of elevated atmospheric CO₂ depends on the nutrient status of the ecosystem. Under nutrient-rich conditions, plants are more likely to sustain a positive growth response to elevated CO₂ (Körner, 2006; Huang et al., 2015; 105 Terrer et al., 2016; 2018). Positive warming effects on plant growth can be intensified by enhanced nutrient availability following increases in mineralization (Strömberg & Linder, 2002; Dieleman et al.,

2012), and nutrients can be important modulators of ecosystem responses to altered rainfall. The latter can follow from changes in nutrient dynamics (White et al., 2004; Dreesen et al., 2012; Ren et al., 2017), as well as from differences in plant carbon allocation associated with the nutrient status of an ecosystem (Gessler et al., 2017; Shi et al., 2018; Wang et al., 2018a).

In spite of the central role of nutrients in ecosystem functioning and responses to climate change, nutrient availability is often not accurately accounted for in models, and in observational and experimental synthesis studies. N and P cycles are increasingly implemented in biogeochemistry models, but this still comes with high uncertainties related to data availability, understanding of nutrient cycling (Vicca et al., 2018), and quantification of nutrient limitations (Wang et al., 2010). In empirical studies, omission of nutrient availability from analyses of ecosystem functioning and its responses to global change can be deeply problematic, not only because it obfuscates our understanding, but also because it can even lead to misleading conclusions about the drivers of experimental results and of spatial and temporal variation (Cleveland et al., 2011). For example, Vicca et al. (2012) investigated factors underlying variation in forest biomass production efficiency (the ratio of biomass to GPP). By taking into account nutrient availability, they revealed that the direct (causal) influence of climate or stand age was being overestimated in earlier studies that did not include nutrient availability in their analyses (e.g. DeLucia et al., 2007).

There are at least two key reasons why taking nutrient availability into account is more complicated than e.g. climate: (i) comprehensive datasets are lacking (Vicca et al., 2018), and (ii) a standardized measure of the nutrient status does not exist. For standardized metrics of the nutrient status to be easily and widely applied, they should be constructed only from variables that can be obtained at reasonable costs, and do not demand extensive labor efforts. At the same time, metrics should be as complex as necessary, including all the variables essential for wide application and considering important nonlinearities and thresholds. Unfortunately, such metrics have not yet been developed.

In this study, we first clarify differences in concepts and clearly define the concept of the inherent nutrient status. Based on the available literature and our own analyses, we then discuss whether nutrient metrics should best be based on soil, plant or remote sensing data. As an example, we adjust an existing nutrient metric, such that it explains spatial variation in nutrient availability across temperate and boreal forests in Europe. Finally, we explore current limitations of this adjusted metric, and how it may be further improved in the future.

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2 | DEFINITION: WHAT IS THE NUTRIENT STATUS?

Different concepts have been described in the scientific literature to define nutrient availability, with particularly nutrient limitation being widely used. In the strict sense, nutrient limitation represents the plant response to addition of specific nutrients (Liebig, 1841; Augusto et al., 2017). For example, if plants respond strongly to P addition, but not to N addition, they are considered P-limited but not N-limited. The magnitude of limitation is usually expressed as a response ratio, i.e. productivity of fertilized plots compared to controls in fertilization experiments (e.g. Sullivan et al., 2014; Fay et al., 2015; Augusto et al., 2017). This plant response, and hence the magnitude of nutrient limitation, depends on the balance between the nutrient demand of the plants and nutrient supply (Fig. 1). The latter is determined by soil properties and nutrients as well as by species adaptations such as rooting

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strategy and investment in mycorrhizal or N₂-fixing symbionts. Because nutrient supply and demand vary among species and depend on climate and other environmental factors, nutrient limitation is not a constant value for a given soil (Legout et al., 2014).

155 An alternative concept is the inherent soil nutrient status. In contrast to nutrient limitation, the inherent soil nutrient status reflects the potential nutrient supply of a soil as characterized by soil properties and nutrients (Fig. 1). Hence, the soil nutrient status does not directly depend on the species growing on the soil (although soil properties are eventually also shaped by vegetation characteristics such as plant community structure, age, species, litter quality and quantity; Sardans & Peñuelas, 2012; Cools et al., 2014). This short-term independence of plant species greatly facilitates meaningful inter-site comparison of ecosystem responses while taking nutrients into account, and allows to determine the modulating role of the nutrient status in ecosystem responses to environmental change. The fact that the soil nutrient status does not capture effects of plant adaptations such as the rooting strategy or symbiotic associations allows to disentangle and quantify their role across a range of nutrient statuses.

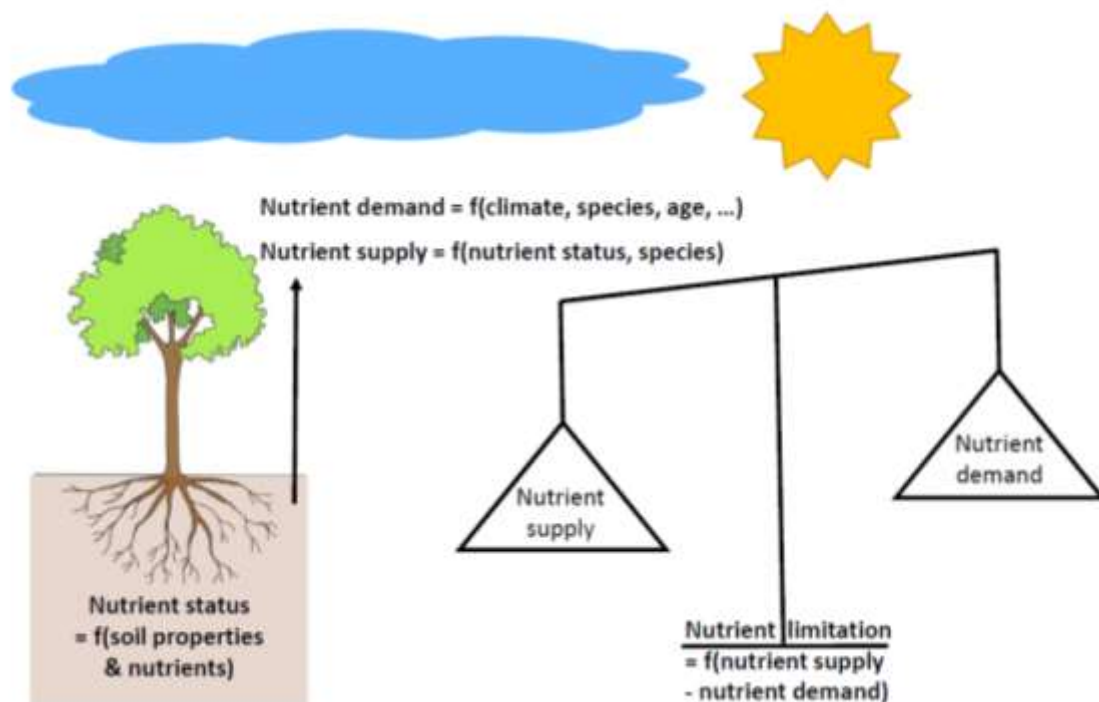


Figure 1 Conceptual diagram illustrating different concepts related to nutrients. For simplicity, the influence of N₂-fixing and mycorrhizal symbionts on nutrient supply is not explicitly included, but is in fact encompassed by “species”. In the present study, we discuss quantification of the soil nutrient status.

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Both nutrient limitation and nutrient status are of interest from an ecological perspective, and both concepts have their own advantages. While nutrient limitation may better clarify plant responses at the individual or population level, the nutrient status facilitates inter-site comparison of the role of nutrients and allows determining differences in sensitivities to variation in nutrient availability among species, ecosystems and biomes. In this study, the focus is on the comparison of soil-, plant- and remote sensing data in their potential to assess the nutrient status, and we propose a metric as a step forward in its quantification. For a recent synthesis of assessments of N and P limitation, we refer to Augusto et al. (2017).

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180 3 | SOIL- vs PLANT-DERIVED INDICATORS OF THE NUTRIENT STATUS

3.1 | SOIL-DERIVED INDICATORS OF THE NUTRIENT STATUS

185 Nutrient availability is rarely taken into account in large-scale studies focusing on inter-site comparison of ecosystem structure, functioning and responses to global change. From a soil perspective, quantifying the nutrient status to make such comparisons is complicated, in part, because nutrient availability is determined by the interplay of various nutrients and soil characteristics such as pH, texture, organic matter concentration and quality etc. Unlike temperature or precipitation, soil nutrient availability can therefore not be assessed by measuring one single variable. For example, at low pH, differences in N availability may be less influential than at optimal
190 pH because at low pH plant growth is commonly limited by Al toxicity and/or P deficiency (IIASA & FAO, 2012). In addition, the availability of the individual elements is difficult to determine because they can be bound with variable strengths to minerals, or are partly locked up in organic matter prior to being released in bio-available form through decomposition. Different procedures exist to estimate, for example, available N and P, but results can differ considerably among methods (Binkley & Hart, 1989; Holford, 1997; Neyroud & Lischer, 2003). Moreover, no sufficiently accurate methods
195 exist to quantify N and P availability in a comparable way across ecosystems.

Although quantifying the availability of different nutrients is not straightforward, there are soil characteristics that are very indicative of the soil nutrient status (Vicca et al., 2018). In particular, soil
200 organic matter concentration (SOM), texture (especially clay fraction), cation exchange capacity (CEC) and pH are critical. SOM is a source of nutrients and both organic matter and clay colloids are important exchange places for nutrients (Schroeder & Others, 1984; Roy et al., 2006). They determine the CEC of a soil, i.e. the capacity of the soil to store and exchange important nutrients such as NH_4^+ , K^+ , Mg^{2+} and Ca^{2+} . Soil pH is especially important for P availability: at $\text{pH} < 5$, P is strongly
205 bound to Fe and Al oxides, while at $\text{pH} > 7$, P becomes unavailable for most plants through complex formation with Ca^{2+} (Chapin et al., 2002; IIASA & FAO, 2012; Soil Survey Staff, 2014). Finally, the soil parent material and its weathering stage can also strongly influence the availability of nutrients such as P (Augusto et al., 2017) and even N (Houlton et al., 2018). Variation in the total bedrock concentration of P, and the presence of metal oxides or other soil substances that can bind P, have
210 also been found to influence nutrient availability (Bol et al., 2016). Hence, the governing role of these discussed soil factors implies that comparison and quantification of the nutrient status across distinct ecosystems requires that soil physical and chemical properties are taken into account.

The few studies that have taken the nutrient status into account have typically used an (indirect)
215 indicator of N availability (e.g. C:N ratio in Alberti et al., 2015 or N stock in Stevens et al., 2015). While such approach may suffice in particular regions where variation in other soil characteristics influencing nutrient availability may be limited, in general, thorough comparison of the nutrient status would require taking into account multiple interacting soil properties. Therefore, in an attempt to get a more comprehensive indication of the nutrient status, a nutrient availability
220 classification has been established based on the available but dispersed data (Vicca et al., 2012; Fernández-Martínez et al., 2014; Alberti et al., 2015; Campioli et al., 2015; Terrer et al., 2016). Although this approach, which separates nutrient-rich from nutrient-poor sites, has helped in gaining

225 a better understanding of the role of nutrient availability in terrestrial carbon cycling, it is a qualitative method based on distinct datasets. This has several limitations and it is, for example, not easily upscaled.

230 To our knowledge, only few initiatives have been taken to express the soil nutrient status in a quantitative manner, comparable across sites at larger spatial scales. In a report on global agro-ecological zones, the International Institute for Applied Systems Analysis (IIASA) and Food and Agricultural Organization of the United Nations (FAO – IIASA & FAO, 2012) present an adjustable metric of constraints on nutrient availability. The metric demands input on soil texture, SOM, pH and total exchangeable bases (TEB – cation equivalent of K, Ca, Mg, Na), which are then scored. The final metric value is then calculated by averaging the scores with a weighing function (weighing factors allow giving more weight to the most limiting factor, although the exact value of a weighing factor remains a subjective judgement). However, as this metric was primarily meant for agro-ecosystems, and only aimed to express constraints on nutrient availability, rather than the nutrient status itself, further testing of the metric was needed to e.g. evaluate its performance in non-agricultural systems, and assess potential adjustments.

240 In a recent study, Van Sundert et al. (2018) evaluated and adjusted the original IIASA-metric against an extensive database of Swedish conifer forests, ideal for exploring the link between soil characteristics (available from the Swedish Forest Soil Inventory – Olsson, 1999; Stendahl, 2019) and productivity (available from the Swedish National Forest Inventory – Stendahl, 2019). After concluding that the original IIASA-metric could not explain spatial variation in productivity normalized for climate, forest age and species, they adapted the metric based on the observation that across Sweden, soil C:N ratio was a key variable explaining variation in normalized productivity, while the soil organic carbon concentration (SOC) and pH explained additional variation. Their metric consisted of soil pH_{water}, SOM and the C:N ratio. The final metric score for a site was then calculated for each of these three soil factors by filling in regression equations obtained from part of the dataset. While a worthwhile effort to start developing a nutrient metric, the study by Van Sundert et al. (2018) only considered boreal forests, which have particular conditions (e.g. N limitation and deposition, low soil pH). Its application in other environments thus remains to be tested, and further adjustments are needed.

255 **3.2 | PLANT-DERIVED INDICATORS OF THE NUTRIENT STATUS**

260 Plants are the ultimate sensors of nutrient availability integrated over a certain time, and thus plant-derived indicators may at first sight seem better candidates than soil-based metrics (Diekmann, 2003; Zelený & Schaffers, 2012). Plant-based metrics exist or could be developed based on the species composition of a site (e.g. Ellenberg indicator values), plant traits, nutrient stoichiometry or resorption. However, as we argue below, these plant-based approaches are of limited use for large-scale inter-site comparisons compared to soil-based metrics, primarily because of strong dependence on taxonomy and often limited distribution of scored species (Table 1).

265 In 1974, Heinz Ellenberg presented a set of vegetation-based indicator values for inter-site comparisons of environmental features (Diekmann, 2003), applicable to natural forests and grasslands in Central and Northwestern Europe (Ellenberg et al., 1992; Thompson et al., 1993;

270 Schaffers & Sykora, 2000). Knowledge of the link between species occurrence and the environment
allowed him to establish a system of species-specific scores on a nine-point scale for seven
environmental variables (i.e. Ellenberg indicator values or EIVs). In practice, EIVs for a site are
calculated by weighing species-specific EIVs based on their presence/absence or their abundance
(Schaffers & Sykora, 2000; Diekmann, 2003). In the context of nutrient metrics, the EIV for N or soil
fertility has most relevance. However, even though good performance of this EIV as a nutrient
availability indicator has been confirmed (e.g. Ewald & Ziche, 2017), caution is needed because EIV
275 would be influenced not only by the nutrient status, but also factors such as moisture, aeration and
disturbance (Schaffers & Sykora, 2000; Wagner et al., 2007). Other limitations of EIVs include that
they only apply to natural ecosystems, cannot be used for comparison outside the European
temperate zone (Godefroid & Dana, 2007), and problematic circularity emerges when EIVs are used
as variables explaining variation in vegetation structure or function (Zelený & Schaffers, 2012).

280 Plants have developed adaptations to grow and survive in specific environmental conditions,
including nutrient availability. Instead of directly using the species, we can therefore quantify plant-
functional traits, i.e. morpho-physio-phenological characteristics commonly shared among species
following similar growth strategies (McGill et al., 2006; Violle et al., 2007; Reich & Flores-Moreno,
285 2017). Within the framework of the plant economics-spectrum, root and stem tissue density, and in
particular leaf dry matter content (LDMC - Hodgson et al., 2011; Jager et al., 2015) emerge as
promising traits for retrieving the nutrient status; all three typically decrease with increasing nutrient
availability (Kramer-Walter et al., 2016).

290 Compared to EIVs, traits offer the advantage that application is not by definition restricted to a
particular region; plant traits are largely independent of plant functional type (but see He et al.,
2010; Hodgson et al., 2011; Roa-Fuentes et al., 2015) or biome (Wright et al., 2004). However,
multiple studies have shown that all traits - including LDMC - are sensitive to multiple environmental
factors, such as disturbance (Douma et al., 2012; Pakeman, 2013; Wigley et al., 2016) and climate
295 (Pakeman, 2013; Simpson et al., 2016), complicating the disentangling of the nutrient status effect
more than is the case with soil-based metrics. Disturbance and climate evidently modify soil
characteristics as well, but these translate into shifts in the actual nutrient status, whereas changes
in plant traits also reflect variation in e.g. light and water availability. Last, when measuring traits is
not possible for practical reasons, a posteriori assigned average trait values from databases such as
300 TRY (Kattge et al., 2011) may be used. This however comes with its further drawbacks such as
neglecting potentially considerable phenotypic plasticity of species traits (Pakeman, 2013; Roscher
et al., 2018). Related to this, while within-species plastic variation results from variation in nutrient
supply and status, genetic processes underlay average trait values, such that traits generally reflect
nutrient demand rather than nutrient supply (Peñuelas et al., 2019).

305 While the soil fertility EIV and plant economics-spectrum allow making a direct estimate of the
nutrient status, there is also the possibility of combining different nutrients in plants into one final
metric representing the 'general nutrient status', analogous to the metric based on soil
characteristics discussed in this article. Nutrient concentrations and stoichiometry of plant tissues
310 indeed inform about the soil nutrient status. As the concentration of a certain nutrient in a plant or
canopy typically increases with increasing availability in soil (as long as the nutrient is limiting – but
see Ostertag, 2010; Peñuelas et al., 2013; Zechmeister-Bolternstern et al., 2015), assessing tissue

315 concentrations and stoichiometry is common practice to evaluate the plant nutrient status in
 ecological and agronomical research (Sullivan et al., 2014). However, multiple studies have shown
 that factors like phylogeny, phenology and climate are proximal determinants of plant nutrient
 concentrations and stoichiometry, rather than the soil nutrient status (Kokaly et al., 2009; Sardans et
 al., 2015; Balzotti et al., 2016; Di Palo & Fornara, 2017). Indeed, in large scale studies including
 several species and strong climate gradients, plant stoichiometry is explained in great part by long-
 term evolutionary processes in which species adapted to soil nutritional conditions along the
 320 gradient (Asner et al., 2014; Sardans et al., 2015; 2016). As a result, two different species exhibiting
 high foliar N may be growing on soils with different soil nutrient status. Furthermore, stoichiometric
 flexibility strongly varies among species (Peñuelas et al., 2013; Zechmeister-Bolternstern et al., 2015;
 Peñuelas et al., 2019). Therefore, when comparing the nutrient status among ecosystems at large
 spatial scales, comprising large differences in species composition, plant stoichiometry is likely less
 325 suitable than soil characteristics (Vicca et al., 2018).

Trends in the degree to which plants resorb N and P from senesced leaves has also been proposed as
 an indicator of relative nutrient limitation (e.g. McGroddy et al., 2004). N and P resorption from
 senesced leaves is an important strategy for plants to conserve nutrients, with an increase in
 330 resorption with lower availability (Kobe et al., 2005; Vergutz et al., 2012; Reed et al., 2012; Han et
 al., 2013; Sullivan et al., 2014; Brant & Chen, 2015). In addition, results from experiments suggest
 that the ratio of N resorption versus P resorption generally increases when N is limiting and
 decreases when P is limiting (van Heerwaarden et al., 2003; Yuan and Chen., 2015). Thus, an index
 for relative N and P limitations has been proposed based on the difference of N and P resorptions for
 335 woody plants (Han et al., 2013). Although this is a promising field of study to map relative N and P
 limitations globally, these analyses are generally species-specific, and the global factors driving these
 patterns (e.g. climate) have not been found across species and biomes (Reed et al., 2012), thus
 failing to widely characterize and map the nutrient limitation or status.

340 **Table 1** Limitations of potential plant-derived indicators of the nutrient status.

Plant-derived indicator	Limitations
Ellenberg indicator value for N/soil fertility	<ul style="list-style-type: none"> - also influenced by environmental factors other than nutrients - applicable to natural ecosystems only - spatial extent restricted to region of species distribution - circularity limits applications
Plant-functional traits	<ul style="list-style-type: none"> - also influenced by environmental factors other than nutrients - laborious in species rich communities - database-derived mean values ignore phenotypic plasticity - rather represents nutrient demand than inherent nutrient status
Tissue stoichiometry	<ul style="list-style-type: none"> - controlled by phylogeny, phenology and climate - needs combining of different variables into one single metric
Nutrient resorption	<ul style="list-style-type: none"> - controlled by phylogeny and climate - needs combining of different variables into one single metric

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3.3 | SOIL OR PLANT DATA TO ASSESS NUTRIENT STATUS?

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From the overview above, we deduce that soil characteristics are likely more feasible candidates for inter-site comparison of the nutrient status than plant-derived data, as the latter depend strongly on taxonomy. In order to reinforce or refute this conclusion, we contributed our own analyses by making use of the European ICP Forests database (ICP Forests, 2010; <http://icp-forests.net>) for which data on tree growth, soil properties and nutrients (from the European Forest Soil Inventory - Fleck et al., 2016) and leaf stoichiometry were available (Fig. 2). The ICP Forests database contains homogeneous monitored forest plots representative of the most important managed European forest types, and were previously selected for investigating the effects of acid rain (Table S1). Eventually, we compiled a dataset comprising 77 stands for which tree growth was previously calculated (Camino-Serrano et al., 2016), and measurements of soil properties and nutrients and leaf stoichiometry were available. The sites were dominated by either Common beech (*Fagus sylvatica* L.), Pedunculate oak (*Quercus robur* L.), Scots pine (*Pinus sylvestris* L.) or Norway spruce (*Picea abies* (L.) H. Karst.).

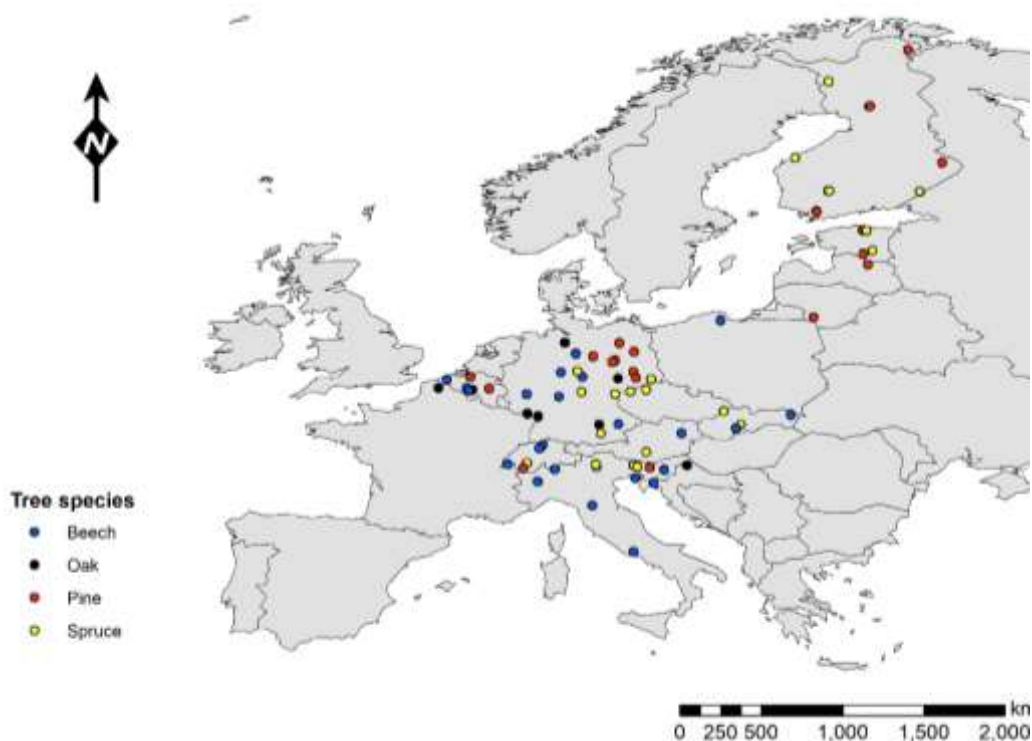


Figure 2 Location of the 77 ICP Forests sites used for the main analyses in this study. Dominant tree species growing on the sites were Common beech (*Fagus sylvatica* L.), Pedunculate oak (*Quercus robur* L.), Scots pine (*Pinus sylvestris* L.) or Norway spruce (*Picea abies* (L.) H. Karst.).

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We used the ICP Forests data to verify the use of soil data vs foliar nutrient concentrations and stoichiometry as indicators for the nutrient status across a range of forest, soil and climate types. Specifically, we (i) performed regression equations within and across species to link key soil vs leaf stoichiometry data with climate-, age- and species-normalized productivity (productivity was chosen as the response variable as it is well-known to respond strongly to increasing nutrient availability

(Chapin, 1980)), and (ii) performed principal component analysis (PCA) on the soil and leaf data to compare and visualize species dependence. More details regarding the ICP Forests data, and the normalization of productivity for climate, age and species are provided in the supplement.

Regression analyses per species indicated that for soil data, across beech forests, a model including soil organic carbon concentration (SOC – negative effect) and mineral soil C:P ratio (negative effect) performed best at explaining variation in normalized productivity ($R^2 = 57\%$; Table S10). In both European spruce (Table S11) and pine forests (Table S12), a model with only the negative influence of organic layer C:N ratio was selected ($R^2 = 43\%$ and 42% , resp.), and in an analysis combining all species, organic layer C:N, SOC and their interaction was selected ($R^2 = 17\%$, Table S13). We initially used exactly the same subset of the ICP Forests database to optimally compare the potential of leaf stoichiometry with that of soil characteristics. For beech and pine, these analyses indicated no potential of foliar data to explain variation in normalized productivity (Table S14 and S16), whereas for spruce, N:P ratio and N concentration (which showed no collinearity) exerted both a positive influence, together explaining 32% of the variation (Table S15). Finally, when combining all species in one analysis, no variation in normalized productivity was explained by any leaf nutrient or ratio (Table S17).

For stoichiometry, similar, but perhaps more clear results were obtained from an additional analysis on a more elaborate subset of the ICP Forests database (including sites that were lacking the necessary soil data, but with stoichiometry available): for beech, foliar nutrient concentrations were again not significantly related to normalized productivity, but for spruce and pine, foliar nutrients did relate to normalized productivity ($R^2 = 25\%$ and 28% , resp.). However, the combination of nutrients best explaining variation differed among species, such that in an analysis combining all species, foliar stoichiometry explained merely 4% of normalized productivity here (Table S18). Species differences in stoichiometry clearly lay at the base of the discrepancy in variation explained within vs across species, whereas species-dependence of soil characteristics was much less pronounced (Fig. 3a vs 3b). Our results thus confirm that when multiple species are involved, foliar elemental composition is primarily determined by taxonomy, therefore limiting the use of foliar stoichiometry as an indicator of large-scale variation in the nutrient status.

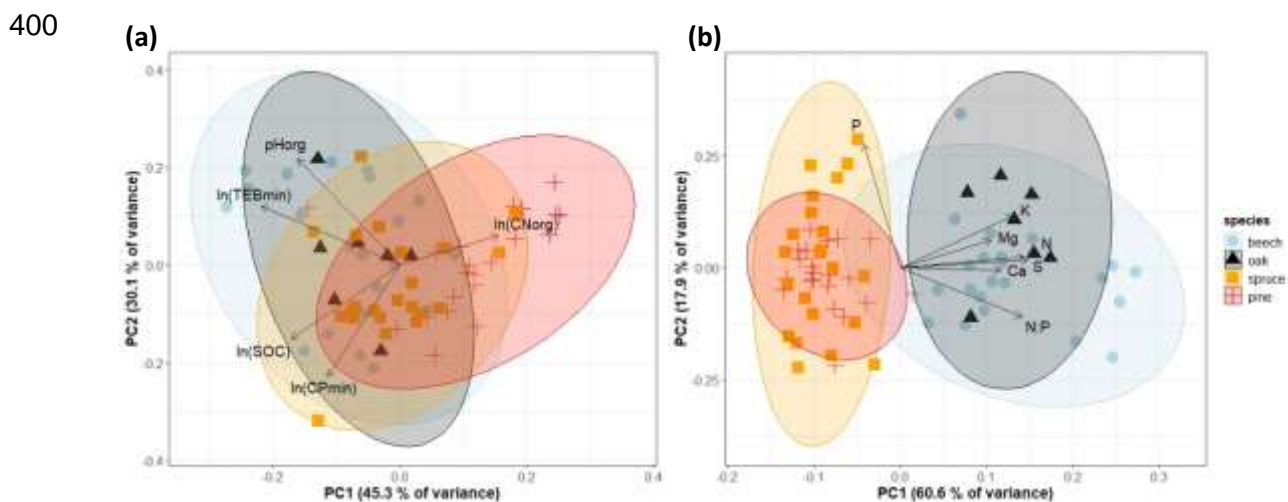


Figure 3 Principal component analysis on (a) key soil variables (sd for PC1 = 1.51, sd for PC2 = 1.23), and (b) foliar stoichiometry data in the European ICP Forests dataset (sd for PC1 = 2.06, sd for PC2 = 1.12). These soil variables in particular were chosen because of their link with the soil nutrient status (e.g. Van Sundert et al., 2018), and our observation during exploratory analyses that organic layer characteristics in particular explain

variation in normalized productivity (e.g. Table S11). Right-skewed variables were log-transformed. Abbreviations: SOC = soil organic carbon concentration (%) in the upper 20 cm of the soil, starting on top of the organic layer; CNorg = organic layer carbon to nitrogen ratio; pHorg = organic layer pH. Corresponding correlations are presented in Table S19 for panel a, and in Table S20 for panel b.

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4| REMOTE SENSING-DERIVED INDICATORS OF THE NUTRIENT STATUS

Three decades ago, researchers began using remote sensing to estimate leaf and canopy traits. While particular nutrients (mainly N – Filella et al., 1995; Serrano et al., 2002; Kokaly et al., 2009; Loozen et al., 2018) have been estimated frequently, other traits relevant to the nutrient status, such as LDMC, can be estimated as well but with low accuracy (Homolova et al., 2013). For this reason, the focus in this review section is merely on stoichiometry. By far the most common remote sensing method involves employment of passive hyperspectral sensors (but see Munoz-Huerta et al., 2013), on ground platforms (e.g. Peñuelas et al., 1994; Serbin et al., 2014), airplanes (e.g. Serrano et al., 2002; Mitchell et al., 2012; Wang et al., 2018b) or satellites (e.g. Ollinger et al., 2008; Loozen et al., 2018), depending on the desired resolution and scope of the study. Typically, concentrations of a particular element are estimated per pixel after an empirical calibration procedure in which reflectance in the 400-2400 nm range is matched with concentrations determined by standard lab procedures (Homolova et al., 2013). Although this method often yields high R^2 s within studies, estimating leaf and canopy nutrient concentrations at larger spatial scales is challenging not only because fine spatial resolution is needed to capture relevant and occasionally large small-scale variation in nutrient availability (e.g. Porder et al., 2005), but also because the empirical functions are typically overfitted to the data considered in the respective study (Verrelst et al., 2015). Alternatively to regressions, mechanistic radiative transfer models (RTMs) could be used in the future to avoid this problem, but research on RTM inversion to retrieve nutrient concentrations at the canopy level is still in its infancy (Wang et al., 2018b; but see Porder et al., 2005).

Using airborne based and satellite imagery, Ollinger et al. (2008) discovered a strong positive correlation between near infrared (NIR) reflectance (800-2500 nm) and %N in the canopy for North American forests. This was one of the first studies to remotely estimate %N of the canopy at a large spatial scale. The study was heavily criticized though, as the link between NIR reflectance and %N may be merely a correlation resulting from the influence of available N on vegetation structure (Knyazikhin et al., 2012 and e.g. Nunes et al., 2017). Even though indirect effects dominating the NIR reflectance-%N relationship are not necessarily problematic (Ollinger et al., 2013), caution is needed when using this remote sensing derived %N for a metric because biases may occur when for instance species composition (and therefore canopy structure) is modified by management, while N availability remains the same.

Although remote sensing is a promising tool for rapid assessment of plant tissue concentrations, its use for estimating stoichiometry at large spatial scales is currently limited because of biases and considerable uncertainties. Furthermore, the bulk of literature has so far focused on N (but see e.g. Porder et al., 2005), with remote sensing of nutrients such as P and K in leaves and canopies even less developed than for N (Homolova et al., 2013). In the context of nutrient metrics, remote sensing can be used as an alternative to lab-based measurements for determining plant tissue stoichiometry for purposes where the benefits of remote sensing (rapid estimation at large spatial scale) outweigh

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the disadvantages compared to destructive measurements. In the end, irrespective of whether stoichiometry was determined optically or destructively, the result is an estimate depending on (a mixture of) species. Therefore, as discussed earlier, the dependence of the nutrient status-stoichiometry link on species and their plasticity limits the use of large-scale remote sensing derived stoichiometry data.

Finally, Fisher et al. (2012) tried to estimate global nutrient limitation by comparing remotely-sensed productivity with modelled maximum productivity determined by light and water availabilities. However, this approach aims to quantify nutrient limitation rather than nutrient status, and more importantly, their proposed global map still contains considerable inaccuracies (e.g. it suggests no nutrient limitation in Eurasian boreal forests, where strong N limitation is in reality widespread – Högberg et al., 2017). We conclude that remote sensing may in some cases be a practical way to derive plant tissue stoichiometry (e.g. Asner et al., 2015), but at least for now, it is not possible to accurately compare the nutrient status among sites based on remote sensing data alone.

5 | EXAMPLE: A SOIL-BASED METRIC OF THE NUTRIENT STATUS

Based on our review and analyses above, we concluded that soil data likely have highest potential to develop metrics of the nutrient status. As an example of how such metric may be used and improved, we evaluate and adjust here a soil-based metric developed by Van Sundert et al. (2018), such that it explains considerable variation in normalized productivity not only in the original Swedish database it was developed from (Table S2), but also in the European ICP Forests. As mentioned in the section on soil indicators, their metric consisted of soil pH_{water} , SOM and the C:N ratio (all mass-based averaged over the top 20 cm of the soil, including the organic fermentation-humus (FH) layer; note that soil texture was not included in this metric because it was not significantly correlated with normalized productivity). Specifically, a score was calculated for each of these three soil factors by filling in the respective simple empirical regression equations, and including a minimum constraint representing the minimum climate-normalized productivity found across the dataset:

$$\text{SOC score} = \max(-0.18 * (\ln(\text{SOC}_{0-20\text{cm}}) - \ln(2.3))^2 + 0.525, -5.65) \quad (1)$$

$$\text{C:N score} = \max(-0.08 * \text{CN}_{0-20\text{cm}} + 2.1, -5.65) \quad (2)$$

$$\text{pH score} = \max(-0.9 * (\text{pH}_{\text{water},0-20\text{cm}} - 4.67)^2 + 0.6, -5.65) \quad (3)$$

The metric for any given (boreal) forest soil was then calculated by averaging the partial scores, giving more weight to the variable with the lowest score:

$$\text{Metric score} = 0.5 * \text{lowest score} + 0.5 * \text{mean (other 2 scores)} \quad (4)$$

This metric explained up to 21% of the variation in normalized productivity for forests in Sweden (Van Sundert et al., 2018).

To investigate the metric application for a wider range of conditions than merely boreal forests, we test and adjust here the soil-based metric against the ICP Forests data. Finally, we also evaluate the

495 metric against data from a global grassland database to explore its current performance for distinct
environments and identify soil parameters for future improvements of the metric.

5.1 | Evaluation of the earlier nutrient metric

5.1.1 | Performance of the earlier metric

500 The metric developed for Sweden by Van Sundert et al. (2018) could not significantly explain
variation in normalized productivity across European forests (Table 2), and neither could the original
metric proposed by IIASA (Table S21). Even when separately considering pine and spruce forests, for
which the metric was initially developed, the metric could not explain any variation in normalized
505 productivity. In other words, the metric provided in Van Sundert et al. (2018) cannot be used as a
general indicator of the nutrient status across European forests outside Sweden.

5.2 | Adjustment of the earlier metric

5.2.1 | Adjusting the earlier metric

510 One key difference between the Swedish forest soils and the forests elsewhere in Europe is the
organic layer thickness. While ~70% of the Swedish forest sites had an organic layer thicker than 5
cm, and for ~40% of the sites this layer was > 10 cm thick, most sites of the ICP Forests dataset used
here had an organic layer of 5 cm or less (Fig. S2). Given that the organic layer in the Swedish forests
dominated the earlier analyses for the development of the metric, and organic layer C:N ratio and
515 pH explained more variation than mineral soil C:N and pH (Table S22), we tested if an adjusted
metric including organic layer characteristics (1) performed similarly well for the Swedish dataset as
the metric of Van Sundert et al. (2018), and (2) whether this adjusted metric could explain variation
in normalized productivity for the ICP Forests dataset.

520 This adjusted metric was developed as in Van Sundert et al. (2018), but using the C:N ratio and pH of
the organic FH layer instead of the top 20 cm of the soil profile (including FH layer). We opted to use
south Sweden as the calibration dataset (similar to Van Sundert et al., 2018), because variation in
both productivity and soil characteristics was largest for that region, and because more data were
available for south Sweden than for ICP Forests. Regressions were thus fitted to the data, but now
525 using organic-layer variables to calculate the partial scores. Additionally, we fixed the optimum for
soil $\text{pH}_{\text{CaCl}_2, \text{org}}$ a priori to 4.5, since this value was more clearly suggested by the European ICP data
than the Swedish data, given a wider range of soil types with higher pH (Fig. S3a vs b; note that this
pH optimum is low at the global scale, suggesting that further adjustments may be necessary if the
metric would be updated for wider application). Finally, for SOC, we kept the top 20 cm layer (where
530 most fine roots are found - Göransson et al. 2006), which can be regarded as the contribution of the
organic layer to the upper 20 cm of the soil, or the abundance of nutrient supplying organic matter
mixed in the upper 20 cm of mineral soil where an organic layer is (nearly) absent. The adjusted
metric consisted of the following equations (note that $\text{pH}_{\text{CaCl}_2}$ was used here instead of pH_{water}
because of data availability):

$$535 \text{ SOC score} = \max(-0.18 * (\ln(\text{SOC}_{0-20\text{cm}}) - \ln(2.3))^2 + 0.525, -5.65) \quad (5)$$

$$\text{C:N score} = \max(-1.8 * \ln(\text{CN}_{\text{org}}) + 5.7, -5.65) \quad (6)$$

$$\text{pH score} = \max(-0.52 * (\text{pH}_{\text{CaCl}_2, \text{org}} - 4.5)^2 + 0.9, -5.65) \quad (7)$$

540 The final score of the adjusted metric is then calculated as in Eq. 4. For the southern Swedish validation dataset, performance of this adjusted metric was similar to that of the metric presented in Van Sundert et al. (2018; see Table 2). Moreover, for some natural gradients in soil characteristics and productivity representing subsets of this Swedish dataset, the adjusted metric even performed better than the original one (Table S23).

545 5.2.2 | Performance of the adjusted metric

For the ICP Forests dataset, the adjusted metric explained 12% of the variation in normalized productivity when including all plots in the analysis, i.e. combining forests dominated by spruce, pine, beech and oak. When analyses were performed per species, this increased up to 19% for spruce, 61% for pine and 31% for beech (Fig. 4; Table 2; for oak, the number of sites ($n = 8$) and associated variation in normalized productivity were too small for a robust analysis). Note that even with a perfect metric, R^2 would be unlikely to approach 1 because even though direct influences of climate and stand age were removed, there is still uncertainty in the response variable. Such uncertainty may for example arise from variation in soil water and oxygen availability, the normalization procedure of productivity for climate and age, and uncertainty in estimates of productivity and soil characteristics. Hence, especially the rather high species-specific R^2 values increase the confidence in this metric. For a more elaborate discussion on uncertainties, we refer to Van Sundert et al. (2018).

560 Even though across all species, the organic layer C:N ratio was typically most influential in the final metric score (i.e. the C:N score had the highest weight in equation 4), species-specific analyses may be more appropriate. Relationships between productivity and the metric can differ among species (Table 2, Fig. 4), hence confounding the analysis combining all species. Moreover, species also influence soil characteristics (e.g. Cools et al., 2014), such that low vs high values along the horizontal axis of Fig. 4a may be influenced by different species (e.g. metric values for pine were generally lower than values for beech – Fig. 4c vs 4d).

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Table 2 Comparison of nutrient metric abilities to explain variation in normalized productivity across different datasets. The adjusted metric refers to the metric presented in the current paper (Eqs. 5-7 in Eq. 4), whereas the regression equation represents a multiple regression model using the same soil variables as the adjusted metric (Eq. 8). All three metrics were calibrated using data of southern Sweden. For the Swedish data, a validation subset (228 plots) of southern Swedish forests was used instead of the dataset of entire Sweden to avoid heteroscedasticity-induced artifacts (see Van Sundert et al. (2018)). Hence, the results for Sweden here represent the validation subset for southern Sweden. Errors represent the s.e.m.

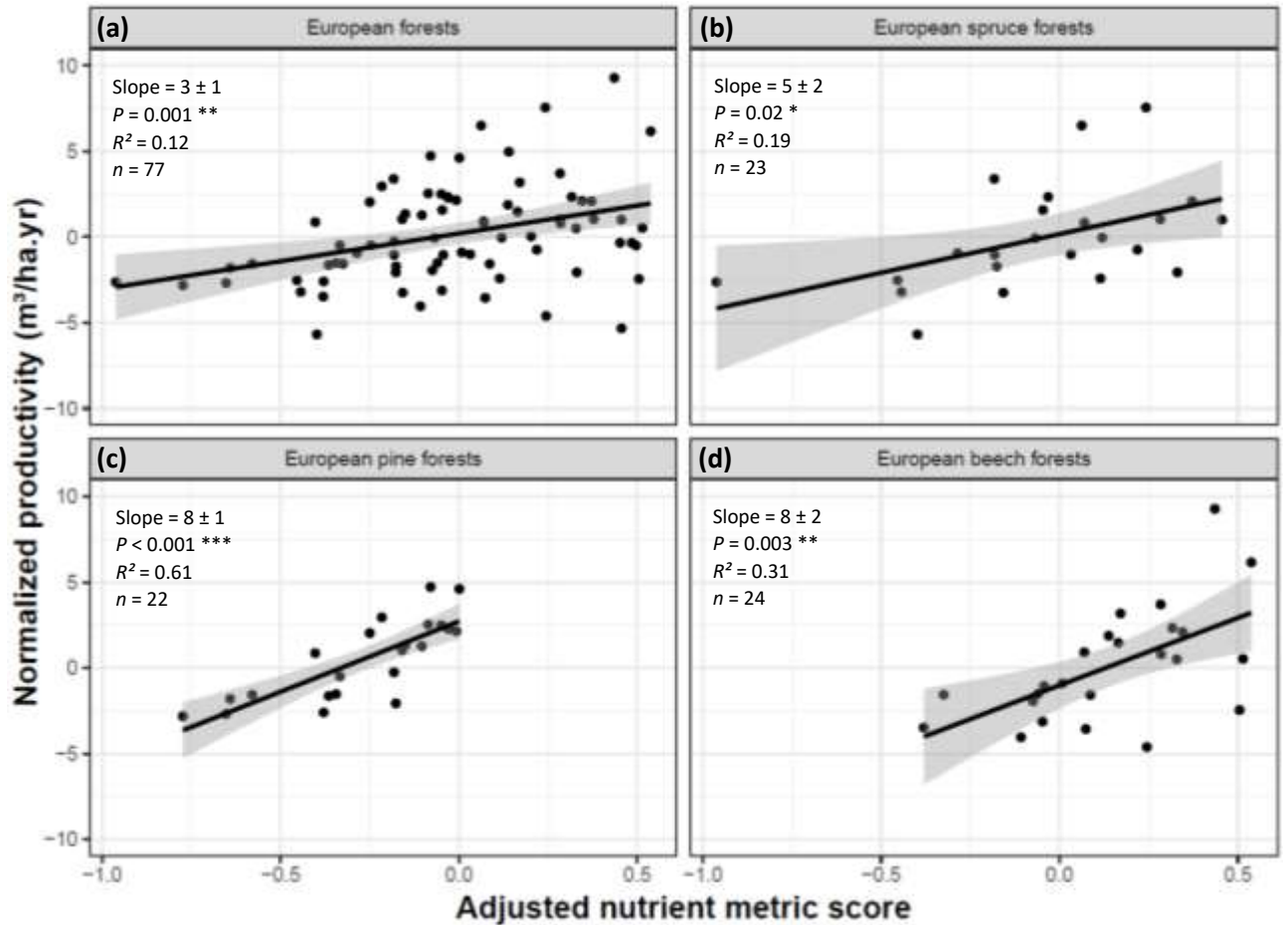
Dataset	Explanatory power of metric presented in Van Sundert et al. (2018)	Explanatory power of adjusted metric	Explanatory power of regression equation
Swedish conifer forests (southern Sweden only)	slope = 1.4 ± 0.2 $P < 0.001$ *** $R^2 = 0.19$ $n = 228$	slope = 1.6 ± 0.2 $P < 0.001$ *** $R^2 = 0.17$ $n = 228$	slope = 0.9 ± 0.1 $P < 0.001$ *** $R^2 = 0.22$ $n = 228$
European forests	$P = 0.32$ $n = 71$	slope = 3 ± 1 $P = 0.001$ ** $R^2 = 0.12$ $n = 77$	slope = 1.7 ± 0.5 $P = 0.002$ ** $R^2 = 0.11$ $n = 77$
European spruce forests	$P = 0.65$ $n = 22$	slope = 5 ± 2 $P = 0.02$ * $R^2 = 0.19$ $n = 23$	slope = 2 ± 1 $P = 0.03$ * $R^2 = 0.17$ $n = 23$
European pine forests	$P = 0.86$ $n = 21$	slope = 8 ± 1 $P < 0.001$ *** $R^2 = 0.61$ $n = 22$	slope = 5 ± 1 $P < 0.001$ *** $R^2 = 0.50$ $n = 22$
European beech forests	slope = 2 ± 1 $P = 0.09$ (*) $R^2 = 0.10$ $n = 21$	slope = 8 ± 2 $P = 0.003$ ** $R^2 = 0.31$ $n = 24$	slope = 2.0 ± 0.9 $P = 0.04$ $R^2 = 0.14$ $n = 24$
Grasslands worldwide	slope = 0.16 ± 0.06 $P = 0.01$ * $R^2 = 0.07$ $n = 77$	slope = 0.23 ± 0.08 $P = 0.008$ ** $R^2 = 0.08$ $n = 77$	slope = 0.08 ± 0.03 $P = 0.006$ ** $R^2 = 0.09$ $n = 77$

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For pine and spruce, residual variation of the relationship of normalized productivity and the nutrient metric was not significantly explained by any of the three soil factors included in the metric (Table 3), indicating that the adjusted metric developed for Sweden can also be used for central and western European pine and spruce forests. For beech, the residual variation correlated significantly with SOC (Table 3), suggesting that despite the strong correlation between normalized productivity and the adjusted metric for these forests, the influence of SOC may not be accurately implemented. The negative relationship between the residual variation and SOC points towards a potential bias in

the incorporated influence of SOC, with the SOC influence being increasingly overestimated as the metric value increases.



605 **Figure 4** Normalized productivity versus the adjusted soil nutrient metric for (a) all forests, (b) spruce forests,
 610 (c) pine forests and (d) beech forests. Errors on the slope estimates represent the s.e.m. Shaded areas around
 615 the regression lines represent 95% confidence intervals.
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Table 3 Tests of variable implementation in the adjusted nutrient metric presented in this study. Species-specific associations between residuals of normalized productivities in Fig. 4 and soil variables in the metric are shown. Aggregated results for all forests, dominated by varying species, are not shown because of differential performance of the metric and its variable implementation among species. Abbreviations: SOC = soil organic carbon concentration; soil C:N ratio = soil carbon to nitrogen ratio. For the grassland dataset, mineral soil data were used to calculate the metric because no organic layer data were available. Errors represent the s.e.m.

Dataset	Residuals of Fig. 4 panel	ln SOC (%)	ln organic layer C:N ratio	pH
European spruce forests (<i>n</i> = 23)	b	<i>P</i> = 0.29	slope = -5 ± 2 <i>P</i> = 0.08 (*) <i>R</i> ² = 0.10	<i>P</i> = 0.11
European pine forests (<i>n</i> = 22)	c	<i>P</i> = 0.43	<i>P</i> = 0.69	<i>P</i> = 0.68
European beech forests (<i>n</i> = 24)	d	slope = -1.7 ± 0.8 <i>P</i> = 0.04 * <i>R</i> ² = 0.14	<i>P</i> = 0.17	<i>P</i> = 0.64
Grasslands worldwide (<i>n</i> = 77)		<i>P</i> = 0.28	<i>P</i> = 0.58	<i>P</i> = 0.96

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5.2.3 | The adjusted metric versus multiple regressions

The nutrient metric follows the rationale that nutrient availability depends more strongly on the soil factor that is most limiting, as that factor receives a higher weight (see equation 4; note however that the exact value of weighing factors is subjective). This is meaningful from a biogeochemical point of view, because, for example, differences in N availability may be more influential at optimal pH than at low pH where plant growth is commonly limited by Al toxicity and/or P deficiency. But does this metric indeed perform better than a multiple regression based on the same variables, or does it only make calculations more complicated? To test this, we fitted a multiple regression using the same three soil factors as the adjusted metric to normalized productivity (Norm) of the calibration dataset for southern Sweden (quadratic terms were included for SOC and pH to represent likely optima – e.g. Van Sundert et al., 2018):

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$$\text{Norm} = a * \ln(\text{C:N}_{\text{org.}}) + b * \ln^2(\text{SOC}_{0-20\text{cm}}) + c * \ln(\text{SOC}_{0-20\text{cm}}) + d * \text{pH}_{\text{CaCl2,org.}}^2 + e * \text{pH}_{\text{CaCl2,org.}} + f, \quad (8)$$

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with $a = -1.1 (\pm 0.4)$, $b = -0.21 (\pm 0.08)$, $c = 0.5 (\pm 0.4)$, $d = -0.5 (\pm 0.2)$, $e = 4 (\pm 1)$, and $f = -4 (\pm 4)$.

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Not surprisingly, performance of this regression equation for the metric calibration dataset of southern Sweden and gradients in Sweden was similar, or even slightly better, than that of the metric (Tables 2 and S23). However, the multiple regression explained consistently less variation than the metric for the ICP dataset (Table 2). Moreover, variable implementation in the metric was better according to the ICP data per species (Table 3 vs S24). Finally, use of the metric instead of a

multiple regression approach has the advantage that future updating based on other datasets is more practical. In the metric, additional soil variables can simply be introduced by a new partial equation (cf. Eqs. 1-3 and 5-7) without necessarily modifying the equations of pre-existing variables in the metric. Furthermore, the final weighing in the metric (Eq. 4) represents a type of interaction in which the worst scoring soil parameter gains most importance. This is much more complicated to achieve with multiple regression.

6 | APPLICATIONS OF THE SOIL-BASED METRIC AND FUTURE PROSPECTS

Based on a literature review and additional analyses, we illustrated that strong species-dependence limits the use of plant and remote sensing data when performing inter-site comparisons of the nutrient status. We therefore suggest that soil data offer more potential for use in nutrient status metrics, and presented a soil-based metric for temperate and boreal forests as an example. In this section, we discuss applications of this metric and potential for future improvements.

Our analysis indicated that the adjusted metric developed for pine and spruce forests explains a significant proportion of the variation in normalized productivity of beech forests. However, our analyses on beech suggested that the influence of SOC may not be accurately implemented and further adjustments to the metric may be needed in this regard. Interestingly, we also found that for beech, the organic layer and especially mineral soil C:P ratio (but not soil total P – Table S25) correlated negatively with normalized productivity (Fig. 5, see also Table S10), while for the other species the influence of C:P was much less pronounced (Table S19). This result is in agreement with studies showing that P limitation in European beech forests is common (e.g. Talkner et al., 2015; Lang et al., 2017). Adding the C:P ratio to the metric and perhaps modifying the relationship for SOC may thus further improve metric performance. However, further adjusting the metric based on the ICP Forests database alone is not possible because of the limited number of sites.

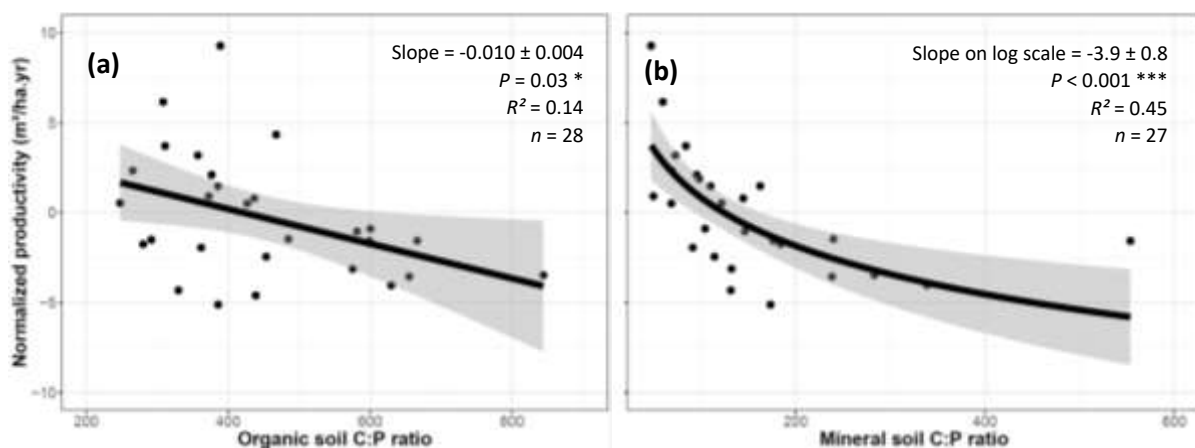
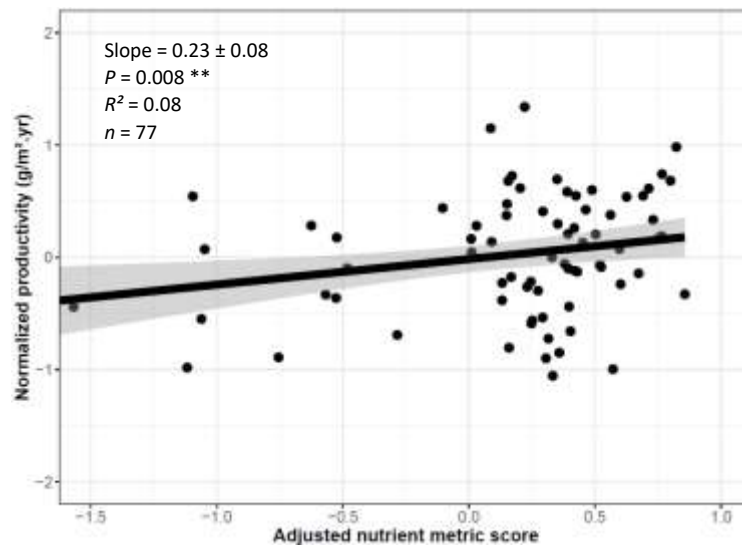


Figure 5 Normalized productivity of European beech forests versus (a) organic and (b) mineral soil C:P ratio. Aqua regia extractable P was taken here as the best available proxy for soil total P, such that actual total P as derived from the acid digestion method may have been underestimated (ISO 11466, 1995; Ivanov, 2012). Errors on the slope estimates represent the s.e.m. Shaded area around the regression curve represents 95% confidence intervals.



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Figure 6 Normalized productivity versus the adjusted metric in worldwide distributed grasslands. Since SOC data were not available for most grassland sites, total C was used to calculate equation 5 instead (grasslands on calcareous soils were omitted from the analysis to ensure total C approximated SOC). Because of positive skewness, grassland productivity was log-transformed before normalizing (Table S7). Although model assumptions of normality of residuals, linearity, homoscedasticity and absence of outliers were met, nutrient metric scores in this dataset were negatively skewed. We therefore verified robustness of the result by transforming the X-axis to $\log(-\text{Adjusted nutrient metric score} + 1)$, which yielded similar results ($P = 0.004^{**}$; $R^2 = 0.09$). The error on the slope represents the s.e.m. Shaded area around the regression line represents 95% confidence intervals.

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To test the application of the metric in ecosystems other than forests, we collected data from grasslands worldwide (Table S3). Via a literature search on web of science (see SI) we collected ANPP and the necessary combination of soil data for 77 grasslands. After normalizing ANPP using the SEM approach (see Table S7), and calculating the metric (using upper mineral soil data in equations 5-7 since grasslands usually lack an organic layer), we found a significantly positive relationship between normalized ANPP and the adjusted metric, albeit with a low R^2 (Fig. 6; Table 2). Residual variation was not explained by any of the variables included in the metric, hence supporting their correct implementation. Interestingly, we found a borderline significant positive correlation between residual variation and soil total P ($R^2 = 0.04$). This suggests that adding soil P to the metric may further improve its performance. More data, preferably across local gradients to avoid confounding effects of e.g. climate, are needed to explore the incorporation of soil P in the metric.

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The new nutrient metric presented here can be used in observational and experimental temperate and boreal (conifer) forests with an organic soil horizon. Application in other ecosystems remains to be tested, and especially tropical forests may pose a key challenge because these systems often lack organic soil layers and there is often efficient nutrient recycling from litter while the infertile mineral soil is largely bypassed (Legout et al., 2014; Grau et al., 2017). Nevertheless, the positive effect of P on normalized productivity in both beech forests and grasslands worldwide indicates further potential for improvement of the metric by more explicitly incorporating P (which was not possible within this study because no P data are available for the Swedish dataset used for the metric development).

725 The inclusion of additional parameters (e.g. soil P, or texture, which did not have an effect in the
current datasets but might in others), further testing of the metric (e.g. against data from tropical
forests, and unmanaged ecosystems), and later applications of the metric (e.g. meta-analyses
incorporating the influence of the nutrient status) require comprehensive and harmonized soil
datasets. At a national scale, country-wide (forest) soil inventories may be used also in future
studies, as we exemplified with the Swedish dataset. At larger spatial scales, however, combining
730 national inventories may become complicated, because of incompatible procedures, different
variables measured etc. For large-scale modeling studies, initiatives such as SoilGrids (Hengl et al.,
2017) might prove useful for upscaling (Dai et al., 2018), although finer spatial resolutions may be
needed depending on the aim of the model and study. In general, harmonized soil datasets are
rarely available and we therefore call on the scientific community to collect and provide these data
for existing and future experiments and field sites. For more information regarding data needed to
735 create harmonized datasets, useful for both data-synthesis and modeling communities, we refer to
Vicca et al. (2018).

The (current) components of the nutrient metric respond only slowly to environmental changes,
such that it cannot be used to capture quick changes in the soil nutrient status, for example induced
740 by (experimentally imposed or natural) global change. Determining the variables included in the
metric would nevertheless still be useful in such experiments to investigate long-term changes that
eventually occur (e.g. Jandl et al., 2012; Zechmeister-Boltenstern et al., 2015). For capturing quick
(sometimes transient) changes in the nutrient status, also other data should be collected, such as
supply rates derived from resin membranes in the soil (Qian & Schoenau, 2002; Meason et al., 2009;
745 Dijkstra et al., 2012; Andersen et al., 2014), data from soil based nutrient extractions (e.g. Vicca et
al., 2018) and/or from shifts in tissue stoichiometry (Dijkstra et al., 2012; Sardans & Peñuelas, 2012;
Peñuelas et al., 2013; Urbina et al., 2014). Global change induced shifts in such variables are
however difficult to compare across sites in a quantitative manner (e.g. Sardans et al., 2017). Ideally,
future metrics should not only grasp large-scale spatial variation in the nutrient status, but also
750 responses to environmental change.

7 | CONCLUSIONS

A wide range of research shows that nutrient availability strongly influences terrestrial ecosystems
and shapes their responses to atmospheric, climatic and other environmental changes. Nonetheless,
755 our understanding of nutrient controls remains poorly quantified, because we lack the tools for such
quantification. There is thus a clear need for nutrient metrics that allow comparing the nutrient
status across experimental and observational sites. Through a literature review and data analyses,
we demonstrated that such a metric is best based on soil characteristics, rather than on plant- or
remote sensing-derived indicators, because the link between plant traits and nutrient status strongly
760 depends on factors like phylogeny, phenology and climate. Here, we presented a soil-based metric,
demanding data on SOC, organic layer C:N ratio and pH, that explains considerable variation in the
nutrient status across northern and central European managed spruce, pine and beech forests. We
propose that this nutrient metric can, in combination with other measures of nutrient availability, be
used in inter-site comparisons across spruce and pine (and with caution also beech) forests in the
765 temperate and boreal biomes. Application of our adjusted metric to other ecosystem types such as

tropical forests and grasslands remains to be verified, and future improvements may be possible through for example more explicit incorporation of P.

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775 Environmental Protection Agency. EC–JRC–MARS provided precipitation data used in combination with the Swedish database. Data of the global grassland dataset were collected by DR, based on references given in the supplementary material. The study was supported by the Fund for Scientific Research – Flanders (FWO aspirant grant to KVS; FWO postdoctoral fellowships to SV and MFM) and by the European Research Council grant ERC-SyG-610028 IMBALANCE-P. CT acknowledges financial
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