Simulating ectomycorrhiza in boreal forests: implementing ectomycorrhizal fungi model MYCOFON into CoupModel (V5)

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Abstract

Ectomycorrhizal fungi (ECM), the symbiosis between a host plant and mycorrhizal fungi, are shown to considerably influence the C and N flux between the soil, rhizosphere, and plants in boreal forest ecosystems. However, ECM are either neglected or presented as an implicit, non-dynamic term in most ecosystem models which can potentially reduce their predictive power.

In order to investigate the necessity of an explicit consideration of ECM in ecosystem models, we implement the previously developed MYCOFON model into a detail process-based, soil-plant-atmosphere model, CoupModel MYCOFON, which explicitly describes the C and N fluxes between ECM and roots. This new Coup-MYCOFON model approach (ECM explicit) is compared with two simpler model approaches; one containing ECM implicitly as a non-dynamic N uptake function (ECM implicit), and the other a version where plant growth has a constant N availability (nonlim). Parameter uncertainties are quantified using Bayesian calibration where the model outputs are constrained to current forest growth and soil conditions for four forest sites along a climate and N deposition gradient in Sweden over a 100-year period.

Our results show that the nonlim approach does not describe both the forest growth and soil C and N conditions properly. The ECM implicit/explicit approaches are able to describe current conditions with acceptable uncertainty. Meanwhile, the ECM explicit Coup-MYCOFON model provides a more detailed description of internal ecosystem flux and feedback of C and N fluxes between plants, soil and ECM. Our modeling highlights the need to incorporate ECM into current ecosystem models. We also provide a key set of posterior fungal parameters which can be further investigated and evaluated in future ECM studies.

1. Introduction

Boreal forests cover large areas on the Earth's surface and are generally considered as substantial carbon (C) sinks (Dixon et al., 1994). The sink strength is determined through the balance between major C uptake and release processes, i.e., plant photosynthesis and both autotrophic and heterotrophic respiration, and is largely controlled by nitrogen (N) availability (Magnani et al., 2007). Numerous studies have shown that soil nitrogen availability is the main driver for plant and microbial growth (Klemedtsson et al., 2005; Lindroth et al., 2008; Luo et al., 2012; Mäkiranta et al., 2007; Martikainen et al., 1995). Thus, a proper description of N dynamics in ecosystem models

is prerequisite for precisely simulating plant-soil C dynamics and greenhouse gas (GHG) balance (Maljanen et al., 2010; Schulze et al., 2009; Huang et al., 2011). Ecosystem models, however, vary considerably in their representation of N fluxes: from very simplified presentations (e.g., the LPJguess model: Sitch et al., 2003; Smith et al., 2011) to very complex approaches which aim to capture the whole N cycle (e.g., LandscapeDNDC: Haas et al., 2012; CoupModel: Jansson and Karlberg, 2011).

Ectomycorrhizal fungi (ECM) are common symbionts of trees in boreal forests. ECM are more efficient than roots in taking up different N sources from the soil (Plassard et al., 1991), as well as store vast amounts of N in their tissues (Bååth and Söderström, 1979) and can cover a large fraction of their host plants' N demand (Leake, 2007; van der Heijden et al., 2008). Further, ECM are shown to respond sensitively to ecosystem N availability and are generally considered as adaptation measures to limited N conditions (Wallenda and Kottke, 1998; Read and Perez Moreno, 2003; Kjoller et al., 2012; Bahr et al., 2013). Previous research shows ECM can receive between 1 and 25% of the plants' photosynthates and constitute as much as 70% of the total soil microbial biomass, thus having a major impact on soil C sequestration in boreal forests (Staddon et al., 2003; Clemmensen et al.; 2013). Overall, the functions and abundance of ECM fungi constitute numerous pathways for N turnover in the ecosystem and considerably influence the magnitude and dynamics of C and N fluxes.

Nevertheless, ECM have rarely been considered in ecosystem models (for an overview about modeling ectomycorrhizal traits see Deckmyn et al., 2014). To our knowledge, only five ecosystem models have implemented ECM to various degrees: The ANAFORE model (Deckmyn et al., 2008), the MoBiLE environment (Meyer et al., 2012), the MyScan model (Orwin et al., 2011) and more recently the Moore et al. (2015) and Baskaran et al. (2016) ECM models. In the ANAFORE model, ECM are described as separate C and N pools. However, this model it does not distinguish between mycorrhizal hyphae and mantle. The C allocated from the host tree to ECM is simulated as a zero order function, further regulated by nutrient and water availability. ECM can also facilitate organic matter decomposition in the ANAFORE model. The MyScan model uses a similar approach for ECM C uptake and dynamics but does not, to our knowledge, include the influence of water availability on ECM. In both models, ECM transfer of N to the host is regulated by the C/N ratios of the plant and fungi. In the MoBiLE model, C allocation to ECM is more complex than that in ANAFORE and MyScan models, and the N allocation to the host by the ECM can feed back into their C gains. Although, the N allocation to the host plant is described similarly to the other two models. In MoBiLE, mycorrhiza are further distinguished between hyphae and mantle, but cannot degrade organic matter. Hyphae and mantle differ in their capacity to take up N, and the mantle has a slower litter production rate than that of hyphae. Both Moore et al. (2015) and Baskaran et al.'s (2016) ECM models represent the ECM as a separate model pool and explicitly simulate ECM decomposition, but with much simpler process descriptions, and the interaction with environmental functions are neglected.

The overall aim of this study is to present a new version of the CoupModel, coupled with an explicit description of ECM, to investigate how the explicit consideration of ECM affects overall model performance and uncertainty. Thus, we implement the previously developed MYCOFON model (Meyer et al., 2010; Meyer et al., 2012) into the well-established soil-plant-atmosphere model, CoupModel (Jansson, 2012). The implemented MYCOFON model contains a very detailed description of fungal C and N pools, and all major C and N exchange processes (i.e., litter production, respiration, C uptake, N uptake). Fungal growth and N uptake respond dynamically to environmental functions and plant C supply in the new Coup-MYCOFON model (Fig. 1). This detailed ECM

explicit modeling approach (hereafter called "ECM explicit") is further compared with two simpler modeling approaches – the "ECM implicit" and "nonlim" approaches – which already exist in CoupModel. The "ECM implicit" approach does not represent the ECM as a separate pool but incorporates ECM into the roots implicitly. Plants are thus allowed to take up additional organic N sources statically, and do not respond to environmental functions. The "ECM implicit" approach has been used in a similar way by Kirschbaum and Paul, (2002) and Svensson et al. (2008a). The "nonlim" approach assumes an open N cycle and plant growth are limited by a constant N availability (e.g., in Franklin et al., 2014). These three ECM modeling approaches constitute most of the current ECM representations in ecosystem models, and are tested by four forest sites situated along a climate and N fertility gradient across Sweden (Fig. 2). Bayesian calibration is used to quantify the uncertainty of model parameters and identify key parameter sets.

2. Methods

2.1 Model description

The CoupModel ("Coupled heat and mass transfer model for soil-plant-atmosphere systems", Jansson and Karlberg, 2011) is a one-dimensional process-oriented model, simulating all the major abiotic and biotic processes (mainly C and N) in the soil-plant-atmosphere system. The basic structure is a depth profile of the soil for which water and heat flows are calculated based on defined soil properties. Plants can be distinguished between understory and overstory vegetation, which allows simulating competition for light, water, and N between plants. The model is driven by measured climate data – precipitation, air temperature, relative humidity, wind speed, and global radiation – and can simulate ecosystem dynamics in hourly/daily/yearly resolutions. A general structural and technical overview of the CoupModel can be found in Jansson and Moon (2001) and Jansson and Karlberg (2011), and a recent overview of the model was also given by Jansson (2012). The model is freely available at www.coupmodel.com. The CoupModel is complemented with an ectomycorrhizal module (MYCOFON, Meyer et al., 2010) which allows the direct simulation of the C and N uptake processes of ECM. The MYCOFON model is described in detail by Meyer et al. (2010), and here only the key processes of plant and fungal growth, as well as littering and respiration are described.

2.1.1 Plant growth in CoupModel

An overview of model functions is given in Table A.1 in the Appendix. Plant growth is simulated according to a "radiation use efficiency approach" where the rate of photosynthesis is assumed to be proportional to the global radiation absorbed by the canopy, but limited by temperature, water conditions, and N availability (eq. 1, Table A.1(a)). Assimilated C is allocated into five different plant C compartments: C_{root}, C_{leaf}, C_{stem}, C_{grain}, and C_{mobile}. The same compartments also represent the corresponding N amounts. The "mobile" pool (C_{mobile}, N_{mobile}) contains embedded reserves which are reallocated during certain time periods of the year, e.g., during leafing. Respiration is distinguished between maintenance and growth respiration, where a Q_{10} function response is used for maintenance respiration (eqs. 2.1, 2.2, Table A.1(a)). Plant litter is calculated as fractions of standing biomass (eq. 3, Table A.1(a)).

2.1.2 Fungal C and N pools

The ECM are closely linked to the trees' fine roots and consist of C and N pools. The C pool is distinguished between the mycelia, which are responsible for N uptake, and the fungal mantle, which covers the fine roots tips. The C pool is the difference between C gains from plant supply and C losses due to respiration and litter production (eq. 8.1, Table A.1(b)). Accordingly, the fungal N pool is the result of the difference between N gains by uptake, N losses by litter production, and N transfer to the plant (eq. 8.2, Table A.1(b)). Fungal C and N pools distinguish between mycelia and mantle which is of importance when simulating N uptake (only the mycelia is able to take up N), and also litter production if a more complex approach for simulating fungal litter production is chosen (see section 2.1.4). The ratio between mycelia and mantle is determined by the parameter $FRAC_{MYC}$ which defines the fraction of mycelia C in total fungal C. For all other N and C exchange processes (growth, respiration, and N transfer to plant), the separation between mycelia and mantle is disregarded.

2.1.3 Growth of ectomycorrhizal fungi

ECM growth is limited by a defined maximum; i.e., only a certain amount of tree host assimilates are directed to the ECM. This maximum ECM growth is determined by a potential C supply from the plant, and limited by N availability (eq. 5.1, Table A.1 (b)). This is defined according to the results from field and laboratory studies that the ECM biomass of mycelia and mantle can be as much as 30-50% of fine root biomass. Besides, ECM growth is driven by sink strength (see overview by Smith and Read, 2008). Therefore, we use these observations as the bases for the calculation of actual ECM growth; i.e., the model aims to grow ECM biomass to a certain fraction of fine root biomass (eq. 5.2, Table A.1 (b): $FRAC_{OPT} * c_{frt}$). This is further dependent on the N supply from the ECM to the roots, $f(n_{supply})$. The model thus follows the assumption that plants feed the ECM with C as long as their investment is outweighed by the benefits obtained (Nehls et al., 2008). A minimum C supply to prevent fungi death during C shortage is guaranteed by the term during time periods when plant photosynthesis is limited, and belowground C supply to root and ECM becomes zero (eq. 5.3, Table A.1 (b)). The C supply is defined by a constant fraction of the root C gain and reduced by the function $f(c_{fungiavail})$ as soon as a defined value of soil available N is exceeded; i.e., in the model the potential ECM growth declines with rising soil N. This scaling function is based on observations from field and laboratory experiments which show that the majority of ECM decreases in abundance and functioning when the soil N levels are high (e.g., Wallander, 2005; Wallenda and Kottke, 1989; Högberg et al., 2010).

2.1.4 Respiration and litter production of ectomycorrhizal fungi

The same approach is used here for ECM and root respiration simulation, distinguishing between maintenance and growth respiration respectively (see eq. 2 and eq. 6, Table A.1). Two approaches are available to simulate fungal litter production which differ in complexity. The simple approach (eqs. 7.1, 7.2, Table A.1) uses one common litter rate L for both the fungal mantle and mycelia. Consequently, possible specific effects of the mantle and mycelia tissue on litter production are neglected. The alternative "detailed" approach (eqs. 7.3, 7.4, Table A.1) has specific litter rates for ECM mantle and mycelia (L_M, L_{MYC}). This set-up is recommended when investigating different biomass ratios between mycelia and mantle and their effects on overall litter production. The fraction between ECM mantle and mycelia is determined by the parameter $FRAC_{MYC.}$ Irrespective of the approach used for

litter production, ECM have the capability to retain a defined amount of N during senescence (eqs. 7.2, 7.5, Table A.1 (b): $nret_{fungi}$). In this study, the simple approach is applied.

2.1.5 Ectomycorrhizal fungal N uptake

ECM can take up both mineral and organic N. For both N forms, the potential fungal uptake is first defined. This is determined by the size of fungal C pool, the fraction of fungal C which is capable of N uptake (the mycelia, $FRAC_{MYC}$), and an uptake rate ($NO3_{RATE}$, $NH4_{RATE}$, $NORG_{RATE}$ (eqs. 11.1, 11.3, 11.4, 11.6, Table A.1 (b)). This function is based on the assumption that only the fungal mycelia can take up N. Values for $NO3_{RATE}$, $NH4_{RATE}$, and $NORG_{RATE}$ are derived from published values (Table 1). The actual N uptake is dependent on the available soil N as well as the fungal N demand (eq. 11.2, Table A.1). The N availability function $f(n_{avfungi})$ determines the fraction of soil N which is available for fungal uptake, and is controlled by the parameters $NUPT_{ORGFRACMAX}$ and $NUPT_{FRACMAX}$. N availability for fungi corresponds to the plant available N (eq. 16, Table A.1), but as fungi are more efficient in the uptake of nutrients, the availability is enhanced for both mineral and organic N (eqs. 17.1, 17.2, 17.3, Table A.1). To prevent the fungal N demand being covered by only one N form, the parameters $r_{NO3,}$ $r_{NH4,}$ $r_{LIT,}$ and $r_{HUM,}$ are included, corresponding to the ratio of nitrate and ammonium in total available soil N. If the potential N uptake exceeds the available soil N, the actual uptake corresponds to the available N (eq. 11.2 and eq. 11.5, Table A.1 (b)).

2.1.6 Plant mycorrhization degree, plant N uptake, and fungal N transfer to plant

According to field investigations, the mycorrhization degree can vary considerably between species. For spruce, typical mycorrhization degrees of over 90% have been reported (Fransson et al., 2010; Leuschner, 2004). The impact of the ECM mantle on fine root nutrient uptake has been controversially discussed, but the majority of studies indicate that the root is isolated from the soil solution; i.e., the nutrient uptake is hampered so that the plant is highly dependent on ECM supplies (Taylor and Alexander, 2005). Therefore, the mycorrhization degree is of major importance when plant-ECM-soil N exchange and plant nutrition are of interest. In the explicit Coup-MYCOFON model, mycorrhization degree is calculated as the ratio between ECM C pool and the defined optimum ECM C pool, multiplied by the defined optimum mycorrhization degree (eq. 9, Table A1 (b)). However, the optimum mycorrhization degree needs to be defined with care as there is often a discrepancy between the applied root diameter in experimental studies and models: in experiments, mycorrhization degrees usually refer to fine roots ≤ 1 mm, whereas models often consider fine roots as roots with a diameter of up to 2 mm.

The mycorrhizal mantle has an impact on the mineral plant N uptake. Generally, plant ammonium and nitrate uptake is regulated by the plant N demand (eqs. 4.1, 4.2, Table A.1). The actual uptake is estimated by the N availability function (eqs. 15, 16, 17, Table A.1: $f(n_{avail})$, $f(n_{mhumavail})$) based on the assumption that only a certain fraction of soil ammonium and nitrate is available for plant uptake. The fungal mantle reduces this availability in such a way that reduction is highest at maximum biomass. In a balanced symbiosis, the fungus provides nutrients to the plant in exchange for the plant's C supply. In the Coup-MYCOFON model, the amount of fungal N transferred to the plant is determined by either the plant N demand or, if the plant N demands exceeds the fungal capacity, the available fungal N (eqs. 10.1, 10.2, Table A.1). This is the amount of "excess" N which is available after the ECM have fulfilled their defined minimum demand as defined by the fungal C/N ratio (eq. 10.2, Table

A.1). This relation is based on the theory that the fungi will only supply the plant with N as long as its own demand is fulfilled (Nehls et al., 2008).

2.2 Transect modeling approach

2.2.1 Three ECM modeling approaches

Three modeling approaches applied in this study differ in their complexity. The basic "nonlim" approach is conducted to test if plant N uptake can be described as proportional to the C demand of the plants of the respective sites. In this case, the plant N uptake is not regulated by N availability, and N is used from a virtual source exceeding the soil N availability, thus as an open N cycle. The "ECM implicit" approach simulates the plant taking up organic N which is assumed to be of ECM origin; i.e., ECM are considered implicitly as the N source but do not physically exist in the model. The rate of the organic N uptake is determined by the plant N demand and restricted by the availability of organic N in the soil humus pools (eqs. 4.4, 4.5, Table A.1). Plants can also additionally take up ammonium and nitrate (eqs. 4.1, 4.2, Table A.1). In the "ECM explicit" approach, fungi are fully physically considered as described above. Fungal growth interacts dynamically with plant growth and responds to changes in soil N availability and soil temperature. ECM fungi can take up both mineral and organic N forms.

2.2.2 Simulated regions and database

Simulations were performed for four forests sites – Lycksele, Mora, Nässjö, and Lungbyhed – situated along a climate and N deposition gradient in Sweden (Fig. 2). Climate and site information is given in Table 2 and the climate data were taken from the Swedish Meteorological and Hydrological Institute (SMHI). Data on forest standing stock volumes and forest management were derived from the database and practical guidelines of the Swedish Forest Agency (2005), and applied as previously described by Svensson et al. (2008a). Soil C content as well as soil C/N ratio, previously determined by Berggren Kleja et al. (2008) and Olsson et al., (2007), were used to describe soil properties in the initial model set up. For all simulated sites and modeling approaches, the development of managed Norway spruce forests was simulated in daily step over a 100-year period from a newly established to a closed mature forest. The measured 100-year old forest standing biomass and soil C/N ratio were used for model calibration. Climate input data were quadrupled in order to cover the entire period, and thus climatic warming effects are not considered here. A minimum of specific regional data were used as input values (Table 2). Otherwise, model parameters were kept identical between modeling approaches in order to evaluate the general model applicability. An overview of the parameter values is shown in Table A.1 (d) in the Appendix. For a more detailed site description and CoupModel setup, see Svensson et al. (2008a).

2.3 Bayesian calibration

2.3.1 Overview

We performed a Bayesian calibration for all modeling approaches and sites. In this study, we emphasize the models' predictability in precisely describing the long term C and N in the soils and standing forest stock, also aiming at maximized model flexibility. Measured data including tree biomass and the C/N ratio of soil organic matter are thus used as accepted criteria. This allows us to investigate the distributions and uncertainty of key

parameters of the respective ECM modeling approaches ("nonlim", "implicit", and "explicit"), as well as analyze model uncertainties and dependencies between parameters. Uncertainties in parameter values are expressed as probability distributions. The posterior probability distributions of parameters are estimated by considering the prior distribution and likelihood function in the calibration procedure. The likelihood function is determined by the measured data on output variables and the respective error estimates of the simulated model output. The Bayesian calibration as applied in this study is briefly described below, however for a detailed description of the general methodology see e.g., van Oijen et al. (2005) or Klemedtsson et al. (2008).

2.3.2 Bayesian calibration of models

The data likelihood function which determines the parameter sets being candidate of the posterior distributions is based on the assumption that the model errors, i.e., the differences between simulated and observed values, are normally distributed and uncorrelated (van Oijen et al., 2005). Furthermore, model errors are assumed to be additive so that the log-likelihood function reads:

$$\log L = \sum_{i=1}^{n} \left(-0.5 \left(\frac{y_i - f(\omega_i \cdot \theta_i)}{\sigma_i} \right) - 0.5 \cdot \log(2\pi) \right) - \log(\sigma_i)$$

where y_i = observed values, $f(\omega_i \cdot \theta_i)$ = simulated values for a given model input ω_i and parameter set θ_i, σ_i = standard deviation across the measured replicates, and n = number of variables measured.

In this study, a measured uncertainty of 10% for both the soil C/N ratio and the standing stock biomass data is used. The uncertainty estimate is low (van Oijen et al., 2005) as our intention is to force the model to simulate tree biomass and soil C/N ratio precisely, to better constrain posterior parameter distributions for the respective model approaches and sites. Candidate parameter sets are generated by investigating the parameter space using the Metropolis-Hastings random walk Markov Chain Monte Carlo algorithm (van Oijen et al., 2005). For each simulation, the model's likelihood is evaluated for a certain parameter set. After each run, a new parameter set is generated by adding a vector of random numbers ε to the previous parameter vector:

$$q_{i+1} = q_i + e$$

where θ_i = previous parameter vector, θ_{i+1} = new parameter vector, and ε = random numbers.

The normally distributed random numbers ε have a mean of zero and a step length of 0.05; i.e., 5% of the prior parameter range as proposed by van Oijen et al. (2005). We performed 10^4 runs for each ECM modeling approach and site to ensure posterior convergence.

2.3.3 Model parameters chosen for calibration

The different ECM modeling approaches are calibrated for a comprehensive set of key parameters which are chosen according to their function as regulating factors of the C and N fluxes in the plant-soil-mycorrhiza continuum (Table 3). In the "nonlim" approach, the constant N supply parameter *ConstantNsupply* for the spruce tree is a calibration parameter. In the "implicit" approach, the fraction of organic N available for plant uptake ($NUPT_{ORGFRACMAX}$) is included in the calibration based on Svensson et al. (2008a). For the ECM "explicit"

approach, all fungal parameters in MYCOFON including fungal growth (C and N assimilation and uptake, C and N losses), overall N uptake and plant N supply, respiration, and littering are calibrated. For all three approaches, the humus decomposition rate (K_H), the C/N ratio of microbes (CN_{mic}) regulating soil mineralization, and the fraction of plant C assimilates allocated to the rooting zone (F_{ROOT}) regulating fungal growth are also calibrated. Overall, we include a rather generous number of parameters for Bayesian calibration following Klemedtsson et al. (2008) who emphasize the importance of a holistic perspective when considering model parameters. Prior distributions of parameters are assumed to be uniform; i.e., each value is equally probable with given minimum and maximum values (Table 3). Values were chosen based on either previous modeling applications (e.g., plant parameters determined by Svensson et al. 2008a, b) or literature data (Table 3).

3. Results

3.1 Comparison of the three modeling approaches

3.1.1 General ability to reproduce tree growth and soil C/N

The three modeling approaches show different abilities in reproducing current plant growth and soil C/N ratio after calibration (Table 3B). The posterior model in the "implicit" and "explicit" approaches shows better performance of simulating soil C and N, as indicated by the soil C/N ratio, than the "nonlim" approach. The latter tends to simulate a lower soil C/N ratio, indicated by the negative mean errors (ME) in the posterior model (ME is the difference between the simulated and measured values) (Table 3B). The ME by the "nonlim" approach is also two to five times higher than that when using the "implicit" or "explicit" approach (Table 3B). The "nonlim" approach tends to overestimate plant growth as the posterior mean of ME for plant C is always positive, while the "implicit" and "explicit" approaches tend to show an underestimation (Table 3B).

All posterior models underestimate soil C/N for the northern sites which are generally more N limited, but gradually switch to overestimation at the southern sites. The model with the "nonlim" approach simulates better plant growth for the most southern site, Ljungbyhed, than the other sites. Further, modeled plant growth at Ljungbyhed is overestimated by the "implicit" approach, but underestimated when the "explicit" approach is used (Table 3B). The acceptance of model runs in posterior is higher for the "nonlim" (25 to 48%) and "implicit" approaches (42 to 50%), followed by the "explicit" approach (30 to 33%) which can be explained by model complexity; i.e. as more parameters are included for calibration, accepted combinations of parameter sets become less likely. No major differences are found for the summed log-likelihood for both calibration variables (Table 3B).

3.1.2 C and N budget

Modeled major ecosystem N fluxes, soil C, and N balance in the posterior are shown in Figure 3. In general, the "nonlim" approach shows much greater uncertainties in the modeled N fluxes than either the ECM "implicit" or "explicit" approaches. The "nonlim" approach simulates soil sequestration of N up to 2 g N m^{-2} yr^{-1} for all the sites, but much lower or close to zero values are found when using other two modeling approaches (Fig. 3). Soil N is expected to reach a steady state over a period of 100 years (Svensson et al., 2008a). Therefore, the "nonlim" approach largely overestimates soil N sequestration which can be attributed to the assumed "virtual" constant N uptake from the unlimited source. According to our model predictions, this "virtual" N fraction accounts for 20 to

30% of the total plant N uptake. The simulated soil C balance by the "nonlim" approach also contrasts with that of soil N, where the soil sequesters C at the most northern site, Lycksele, but loses C at a rate of 6 to 17 g C m^{-2} yr^{-1} for the other three sites (Fig. 3). Therefore, soil C and N are not in steady states and are decoupled in the "nonlim" approach over the simulated 100-year period.

However, the "implicit" and "explicit" approaches show a strong coupling between soil C and N (Fig. 3). That is, for the "implicit" approach, Lycksele and Mora soils lose 6 and 5 g C m^{-2} yr^{-1} respectively, while Nässjö and Ljungbyhed soils gain 3 and 13 g C m^{-2} yr^{-1} respectively. Similarly, Lycksele and Mora lose N by 0.2 and 0.1 g N m^{-2} yr^{-1}, while Nässjö and Ljungbyhed gain N by 0.3 and 0.6 g N m^{-2} yr^{-1}. For the "explicit" approach, soil C and N losses at the two northern sites are slightly higher than that in the "implicit" approach (Fig. 3). In contrast to the "implicit" approach, the two southern sites also show overall minor C and N losses with large standard deviations (Fig. 3). Modeled N litter production increases by 1 to 30% compared to the "implicit" approach, but N losses due to uptake and leaching also increase by 10 to 50% for Lycksele and Ljungbyhed respectively (Fig. 3). The increased litter addition of easily degradable C and N stimulates microbial activity, thus leading to a higher microbial respiration which explains the minor losses of C and N in the southern sites in the "explicit" model. The higher N leaching in the "explicit" model can be attributed to a higher uptake from organic N (eqs. 11.5, 11.6, Table 1.B) and a stimulated microbial growth thus increases net mineralization, both of which leave more mineral N in the soil (Fig. 4).

Simulated plant gross primary production (GPP) using the "explicit" and "implicit" approaches shows an increasing trend from the North to South due to more favorable climates and N availability for spruce forest growth, but the "explicit" approach shows a higher predicted GPP than the "implicit"; i.e., 7% in Ljungbyhed to 12% in Lycksele (Fig. 5). C losses from autotrophic respiration are lower in the "explicit" approach (Fig. 5). Trees in the northern regions seems slightly more efficient in taking up C shown by the higher biomass efficiency (NPP/GPP, Fig. 5). Overall, our results show that explicitly accounting for ECM in boreal forest ecosystems can have a considerable impact on the predicted C and N dynamics both for the plants and soil.

3.2. Posterior parameter distributions

3.2.1. Posterior distributions of common parameters

The posterior distributions differ from the prior uniform distributions for all modeling approaches and parameters, reflecting the efficiency of Bayesian calibration (Fig. 6 and Fig. 7). The posterior *constantNsupply* parameter in the "nonlim" approach shows the lowest values at Lycksele and the highest at Ljungbyhed. This means a higher N supply is necessary at the southern sites to explain the observed tree biomass and soil C/N ratio. No significant differences in parameter values – microbial C/N ratio (CN_{MIC}), humus decomposition coefficient (K_H), and the fraction of C allocated to roots, F_{ROOT} – in the "nonlim" approach are found for the different sites (data not shown). The organic N uptake parameter in the "implicit" and "explicit" approaches ($NUPT_{ORGFRACMAX}$) shows an opposite pattern with the highest values for Lycksele and lowest for Ljungbyhed (Fig. 6). Similar posterior distributions of $NUPT_{ORGFRACMAX}$ parameters are found in both approaches, except for larger uncertainties in the "explicit" approach. Besides, a much wider range of posterior parameter values are found for the northern sites than for the southern sites (Fig. 6). This also explains the smaller simulated ME of soil C/N in the southern sites (Table 3). Both approaches demonstrate that the plant and soil conditions at the northern sites could not be simulated without an enhanced uptake of organic N.

When the "implicit" approach is used, the posterior humus decomposition coefficient K_H shows higher values for the northern sites and decreases along the studied transect, demonstrating a modeled higher organic matter turnover and thus soil mineralization for northern sites (Fig. 7). A less clear tendency is identified for the fraction of C allocated to roots, F_{ROOT} parameter, but with a slight tendency towards higher values at the southern sites. Microbial C/N ratio and CN_{MIC} parameters for both "implicit" and "explicit" approaches show similar posterior distributions for the three northern sites. However, much lower values are obtained for the southernmost Ljungbyhed site (Fig. 7), reflecting a more soil N rich environment. Overall, parameters are less constrained and only minor differences between sites are found when the "explicit" approach is used (Fig. 7).

3.2.2 Fungal specific parameters

The posterior distributions of all fungal specific parameters are constrained to log-normal or normal distributions (data not shown). The mean values of N uptake parameters ($NORG_{RATE}$, $NH4_{RATE}$, $NO3_{RATE}$) show a decreasing trend from the northern to southern sites (Fig. 8). This again means a higher ECM fungal N uptake rate is necessary to explain the observed soil and plant data at the more N-limited northern sites. Similarly, lower values for the northern and higher values for the southern regions are also found for the minimum fungal C/N ratio parameter (CN_{FMIN}). The optimum ratio between fungal and root C content, $FRAC_{OPT}$, tends to be higher at the northern sites and lower at the southern sites, also implying a modeled higher ECM biomass at the northern sites (Fig. 8). MIN_{SUPL}, the minimum supply of N from fungi to the host plant parameter, does not show a clear trend. Further, differences of the other ECM parameters for the four regions are minor (Fig. 8).

3.2.3 Correlation between parameters

An overview of correlations for all posterior model parameters can be found in the Appendix in Tables A2, A3, and A4. Parameters showing correlation with each other (defined here as a Pearson correlation coefficient $r \geq 0.3$ or ≤ -0.3) are identified as the key parameter sets, shown in Figure 9. When the "implicit" approach is used, a significant positive correlation is obtained between the humus decomposition rate, K_H, and the fraction of C allocated to rooting zone, F_{Root}. The organic N uptake parameter, $NUPT_{ORGFRACMAX}$ and microbial C/N ratio, CN_{MIC} are negatively correlated, except for a weak correlation for Ljungbyhed (Fig. 9). A weak correlation between $NUPT_{ORGFRACMAX}$ and F_{ROOT} is found for the Nässjö site only (see Table A2 Appendix). For the "explicit" approach, the correlation coefficients between K_H and F_{ROOT} are decreased, and there is also a weaker correlation between $NUPT_{ORGFRACMAX}$ and CN_{MIC} for all sites compared to the "implicit" approach (Fig. 9). No clear correlation between common and fungal parameters is obtained. Further, a negative correlation occurred between microbial C/N ratio, CN_{MIC}, and the fungal N uptake rates ($Norg_{RATE}$, $NH4_{RATE}$, $NO3_{RATE}$), but only for the Northern sites Lycksele and Mora (Table A4). A moderate correlation is found for K_H and the fungal litter rate, L for Ljungbyhed. Among fungal parameters, the N uptake rates moderately correlate to the litter production rate, L at the northern sites, but correlations at Nässjö and Ljungbyhed are either non-existent or weak (Table A4). Our identified inter-connections and correlations between the parameters in general reflect the complex and interrelated nature of ECM, soil, and plant interactions. But more importantly, they also highlight the need to calibrate a number of parameters simultaneously rather than calibrating just one single parameter when applying such detailed ecosystem models (He et al., 2016; Klemedtsson et al., 2008).

4. Discussion

Our new version of the CoupModel provides a detailed model predictive framework to explicitly account for ECM in the plant-soil-ECM continuum. Model comparison to two earlier ECM modeling approaches show that ECM have to be included in ecosystem models ("implicitly or explicitly") to be able to describe the long term plant and soil C and N development. Overall, the models perform similarly in the "implicit or explicit" approaches, while the "nonlim" approach significantly overestimates soil N uptake. Our results thus confirm that ECM have a substantial effect on soil C and N storage, and can also impact forest plant growth. But more importantly, including them into ecosystem models is both important and feasible.

4.1 ECM alter plant-soil C and N dynamics

The "nonlim" model in this study shows overestimations of plant growth and also larger biases in soil N than "implicit and explicit" approaches even after calibration (Table 3). A previous CoupModel application by Wu et al. (2012) demonstrated that the "nonlim" approach could possibly describe short term carbon and water dynamics for a Finnish forest site. The same approach with open N cycle was also used in Franklin et al. (2014) to simulate Swedish forest biomass growth and its competition with ECM. It therefore seems that plant growth and thus the C cycle can be simulated reasonably with the "nonlim" approach, although a slight trend of overestimation is exhibited. However, our modeling further indicates that this simplified approach has an uncoupled soil C and N in its model structure (Fig. 3) and is thus not recommended for future long term soil C and N predictions. This is also reflected in the posterior model parameter distributions where the *constantNSupply* rate parameter shows primary control on the modeled plant growth and soil conditions. Other parameters have minor or no importance for the model results, reflecting an oversimplified soil C and N model structure. Thus, the following discussion focuses on the other two modeling approaches.

Moore et al. (2015) demonstrate that ECM substantially affect soil C storage, and the impact is largely dependent on plant growth. The present study additionally shows that ECM representation in ecosystem models could also feedback into the predicted plant growth through N. As when ECM are implicitly included, the model simulates a 78 (average of four sites, std: 102) g C m^{-2} lower plant biomass compared to the "nonlim" approach. Further, when they are explicitly included, the difference becomes even larger, 214 (50) g C m^{-2} (Table 3). Including ECM in the model thus shows decreased plant growth. This somehow differs from the generally assumption that growth should be higher in mycorrhized plants, i.e., boreal forests, due to optimized nutrient supply (Pritsch et al., 2004; Finlay et al., 2008, see also review by Smith and Read, 2008). This discrepancy could be possibly due to: *1)* an enhanced root litterfall due to a higher turnover of fungal mycelia, shown by a higher litter turnover rate (calibrated litter rate of ECM is 0.0075 d^{-1}, Fig. 8, whereas the litter rate of roots is 0.0027 d^{-1}, Table A1(d)). When ECM is explicitly considered, litter production is modeled higher than in the "implicit" approach (difference from 50 to 110 g C m^{-2} yr^{-1}, data not shown). These two modeling approaches thus show large differences in simulating litter production. Field data are further needed to clarify this. The discrepancy could also be due to: *2)* an enhanced N immobilization in ECM under N-limited conditions because ECM retain more N in their own biomass in response to plant allocation of newly assimilated C (Nehls et al., 2008). The constrained optimum fungi C allocation fraction parameter shows an increasing trend towards the more northern sites (Fig. 8). This indicates a higher proportional C "investment" by the forest plants on ECM in northern, N limited conditions. The resulting ECM-plant competition for N could then potentially result in decreased plant N uptake, and thus plant growth (Näsholm et al.,

2013). Finally, the discrepancy could be due to *3)* biases in simulating ECM N uptake due to model/parameter uncertainties caused by high variability among fungal species and the scarcity of direct measurements in the field (Smith and Read, 2008; Clemmensen et al., 2013). The current "explicit" approach implements many biotic interactions and internal feedbacks within the plant-soil-ECM continuum. However, increasing the number of processes and interactions in an already complex ecosystem model will not necessarily generate more reliable model predictions; as shown here, the parameters in the "explicit" approach have a larger uncertainty range even after calibration. Thus, future model evaluation, together with more detailed ECM data, are needed to better understand the tightly coupled soil-ECM-plant continuum.

Both approaches simulate the soil C and N stock well (Table 3). The respective net change in the soil C pools of the "implicit" approach corresponds well to the results by Svensson et al. (2008a) who also suggest a small loss of soil C in the north while a gain in the south. However, when the "explicit" approach is used, the soils in the south are also predicted to lose C and N, mostly due to enhanced soil respiration (see section 3.1.2). It is difficult to evaluate which approach gives a more realistic prediction as field data are not available. However, Lindroth et al. (2008), who measured C fluxes at three sites in Sweden at comparable latitudes and on comparable soils, found a similar trend in the soil net C change as simulated by the "explicit" approach here, but with a higher loss rate of between 24 and 133 g C m^{-2} $year^{-1}$ (Table 4).

4.2 Parameter and model responses to different environmental conditions

Our modeling results show a consistent pattern with observations (e.g., Hyvönen et al., 2008; Näsholm et al., 2013) that at the northern N limited sites, organic N uptake by ECM is highly important for plant growth, becoming less important as N availability increases southwards. As indicated by the "explicit" approach, the mycorrhization degree of tree roots at Lycksele and Mora (> 90%) is much higher than that of Ljungbyhed (15%), thus the majority of modeled N uptake is through fungal mycelia in northern sites. The constrained fungal organic and mineral N uptake parameters also show a decreasing trend (Fig. 8). Similarly, the organic N uptake parameter, $NUPT_{ORGFRACMAX}$, in the "implicit" approach decreases from north to south, but with a clearer site to site difference; thus indicating a stronger response to environmental conditions (Fig. 6). This is expected as more detailed ECM processes in the "explicit" approach should result in more internal interaction and feedback, thus damping the direct environmental regulations. Current modeling also indicates a higher mineralization shown by the humus decomposition coefficient, K_H, in the northern sites. However, the decomposition of mineralization is also enhanced when ECM is "explicitly" considered (Fig. 7). This collaborates well with findings from field measurements and recent modeling studies that ECM are able to degrade complex N polymers in humus layers, thus enhancing soil N transformation under low N conditions (Moore et al., 2015; Lindahl and Tunlid, 2015; Baskaran et al., 2016).

In the "implicit" approach, the humus decomposition coefficient, K_H, was found to correlate with the fraction of C that allocates to the rooting zone, F_{ROOT}. As ECM are implicitly included in the roots, this correlation therefore indirectly indicates a strong connection of the root-ECM symbiosis and soil N availability. But when ECM are explicitly considered, this becomes less important, again due to a more detailed internal cycling of N supply and uptake from the fungi; i.e., plant N supply is further regulated by simulated higher litter input and N uptake from the soil in the "explicit" model (Fig. 3, Fig. 9). Our modeling shows that fungal litter rates correlate to fungal N uptake rates in the "explicit" model, and that fungal N uptake rates have significant correlations to the microbial

C/N ratio, CN_{MIC}, for the northern sites (Fig. 9). This indicates the close coupling between fungal N uptake (N loss from the soil) and fungal litter production (N input to the soil). Such an incorporated tight cycle is of major importance for the overall plant N supply, and thus C and N dynamics of plant and soil at the N limited sites in the boreal forests.

Most fungal parameters in the "explicit" approach are not – or only weakly – dependent on the differing environmental conditions along the modeled transect, except for the N uptake parameters and fungal minimum C/N ratio, CN_{FMIN}, which show different mean values (Fig. 8). As such, these parameters need to be calibrated carefully when further applying the model to other sites with different soil nutrient levels or climate conditions.

One of the major difficulties of the explicit inclusion of ECM in ecosystem models is the unknown turnover of fungal mycelia (Ekblad et al., 2013). Previously reported turnover rates of newly formed mycelia vary from days to weeks, even up to 10 years (Staddon et al., 2003; Wallander et al., 2004), mostly due to the high variability in ECM species and structures (see review by Ekblad et al., 2013). Besides, root turnover rates can also vary considerably between species, soils, and climate zones (Brunner et al., 2012). Thus far, very few studies have reported parameterization of C and N cycling for ECM in boreal forests. Our calibration study thus provides a key set of ECM parameters that can be further tested through field observation, and more importantly, together with the identified correlations with the variables, can act as a guidelines for future ECM modeling studies.

5. Conclusions

The key components and features of the Coup-MYCOFON model have been described. The new version of CoupModel simulates C and N fluxes and pools, with the capacity of explicitly accounting for the links and feedback between the ECM, soil, and plant. The comparison of three common ECM modeling approaches which differ in complexity demonstrates that the simple "nonlim" approach cannot describe the measured soil C/N ratio, and also overestimates measured forest growth. When including ECM either implicitly or explicitly, both models deliver accurate long-term quantitative predictions on forest C and N cycling with simultaneous considerations of the impact of ECM fungi on ecosystem dynamics. However, they slightly underestimate forest growth. The ECM explicit Coup-MYCOFON model provides a more detailed description of internal ecosystems flux and feedback of C and N. The constrained ECM parameter distributions presented in this study can be used as guidelines for future model applications. Overall, our model implementation and comparison suggest ecosystem models need to incorporate ECM fungi into their model structure for a better prediction of ecosystem C and N dynamics, and the new version of CoupModel provides such an option.

6. Code and data availability

The model and extensive documentation with tutorial excises are freely available from the CoupModel home page http://www.coupmodel.com/ (CoupModel, 2015). The source code can be requested for non-commercial purposes from Per-Erik Jansson (pej@kth.se). CoupModel is written in the C programming language (code also available in Fortran) and run mainly under Windows/Linux systems. Inputs and outputs are in binary format. The version used as the basis for the present development was version 5 from 12 April 2017. The simulation files including the model and calibration set-up, the used parameterization, and corresponding input and validation files can be requested from Hongxing He (hongxing.he@gu.se). However, the majority of the input and output data used for

the current modeling is available publicly through SMHI or previous publications, i.e., Svensson et al. (2008). Please contact the first author of this publication or Per-Erik Jansson if you plan an application of the model and further collaboration.

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APPENDIX:

Table A.1 Model functions describing plant growth, fungal growth, model parameters, and response functions of plant and ECM. Parameters are always entitled with capital letters

Table A.1 (a) Description of plant model functions. (i = fine roots, coarse roots, stem, leaves, grain, mobile)

No.	Equation

Plant photosynthesis (g C m^{-2} d^{-1}):

1 $$c_{atm \rightarrow plant} = \varepsilon_L \times f(T_1) \times f(CN_1) \times f(\frac{E_{ta}}{E_{tp}}) \times r_S$$

ε_L= coefficient for radiation use efficiency, $f(T_l)$, $f(CN_l)$, $f(E_{ta}/E_{tp})$ = response functions to leaf temperature, leaf CN, and air moisture (see Table A.1 (c)), r_s = global radiation absorbed by canopy.

Plant maintenance respiration (g C m^{-2} d^{-1}):

2.1 $$c_{plantM \rightarrow atm} = c_i \times K_{RMi} \times f(T_l)$$

c_i = C content of each respective plant compartment i (g C m^{-2}) and K_{RMi} is a coefficient.

Plant growth respiration (g C m^{-2} d^{-1}):

2.2 $$c_{plantG \rightarrow atm} = c_{m \rightarrow i} \times K_{RGi}$$

$c_{m \rightarrow i}$ = C gain (growth) of each plant compartment i (g C m^{-2} d^{-1}) and K_{RGi} is a coefficient.

Plant litter production (g C m^{-2} d^{-1}):

3 $$c_{i \rightarrow lit} = c_i \times L_i$$

where C_i is the C content of each plant compartment i (g C m^{-2}) and L_i (= 0.0027 d^{-1}) is a coefficient.

Plant nitrate and ammonium uptake (g N m^{-2} d^{-1}) (only shown for nitrate, equivalent for ammonium):

4.1 $$n_{NO3 \rightarrow plant} = dem_{Nplant} \times r_{NO3}$$ if $f(n_{minavail})$ x $n_{NO3soil} \geq dem_{Nplant}$ x r_{NO3}

4.2 $$n_{NO3 \rightarrow plant} = f(n_{minavail}) \times n_{NO3soil} \times dem_{Nplant}$$ if $f(n_{minavail})$ x $n_{NO3soil} \leq dem_{Nplant}$ x r_{NO3}

and where

4.3 $$dem_{Nplant} = \sum \frac{c_{a \rightarrow i} - c_{i \rightarrow atm}}{CN_{iMIN}}$$

$f(n_{NO3avail})$ = fraction of soil NO_3 available for plant uptake (see response functions Table A.1 (d)), $n_{NO3soil}$ = soil NO_3-N content (g N m^{-2}), dem_{Nplant} = plant N demand (g N m^{-2} d^{-1}), r_{NO3} = fraction of soil NO_3-N in total mineral soil N, $c_{a \rightarrow i}$ = plant C gain (g C m^{-2} d^{-1}), $c_{i \rightarrow atm}$ = respiration of respective plant compartment i (g C m^{-2} d^{-1}), CN_{iMIN} = defined minimum C:N ratio of each plant compartment i.

Plant organic N uptake (g N m^{-2} d^{-1}) from the humus layer:

4.4 $$n_{hum \rightarrow plant} = dem_{Nplant} \times r_{hum}$$ if $f(n_{humavail})$ x $n_{humsoil} \geq dem_{Nplant}$ x r_{hum}

4.5 $n_{hum \rightarrow plant} = f(n_{humavail}) \times n_{humsoil}$ if $f(n_{humavail})$ x $n_{humsoil} < dem_{Nplant}$ x r_{hum}

$f(n_{humavail})$= response function for plant available N from the humus layer, $n_{humsoil}$ = soil N content in humus layer (g N m^{-2}).

Table A.1 (b) Functions describing processes related to fungal growth and N exchange to plant

Fungal maximum C supply (g C m^{-2} d^{-1}):

5.1 $c_{a \rightarrow fungi} = c_{a \rightarrow root} \times FRAC_{FMAX} \times f(c_{fungiavail})$

Fungal actual growth (g C m^{-2} d^{-1}):

5.2 $c_{a \rightarrow fungi} = ((c_{frt} \times FRAC_{OPT}) - c_{fungi}) \times f(n_{supply})$

$c_{a \rightarrow root}$ = C available for root and mycorrhiza growth (g C m^{-2} d^{-1}), $FRAC_{FMAX}$ = maximum fraction of total root and mycorrhiza available C which is available for ECM, $f(c_{fungiavail})$ = response function which relates fungal growth to N availability, c_{frt} = total root C content (g C m^{-2}), $FRAC_{OPT}$ = optimum ratio between root and fungal C content, c_{fungi} = total ECM C content (g C m^{-2}), $f(n_{supply})$ = response function of fungal growth to the amount of N which is transferred from ECM to plant.

Minimum fungal C supply (g C m^{-2} d^{-1}):

5.3 $c_{a \rightarrow fungi} = c_{fungi \rightarrow atm}$ if $c_{a \rightarrow root} \leq 0$

Total fungal respiration (g C m^{-2} d^{-1}):

6.1 $c_{fungi \rightarrow atm} = c_{mfungi \rightarrow a} + c_{gfungi \rightarrow a}$

where $c_{mfungi \rightarrow a}$ = fungal maintenance respiration and $c_{gfungi \rightarrow a}$ = fungal growth respiration (all in g C m^{-2} d^{-1}).

Fungal maintenance respiration (g C m^{-2} d^{-1}):

6.2 $c_{mfungi \rightarrow a} = c_{fungi} \times K_{RM} \times f(T_l)$

c_{fungi} = total ECM C content (g C m^{-2}), K_{RM} = maintenance respiration coefficient, $f(T_l)$ = temperature response function.

Fungal growth respiration (g C m^{-2} d^{-1}):

6.3 $c_{gfungi \rightarrow a} = c_{a \rightarrow fungi} \times K_{RG}$

$c_{a \rightarrow fungi}$ = fungal growth (g C $m^{-2}d^{-1}$), K_{RG} = growth respiration coefficient.

Fungal C and N litter production ($c_{fungi \rightarrow lit}$: g C m^{-2} d^{-1}, $n_{fungi \rightarrow lit}$: g N m^{-2} d^{-1}):

If fungal growth = simple

7.1 $c_{fungi \rightarrow lit} = c_{fungi} \times L$

7.2 $n_{fungi \rightarrow lit} = n_{fungi} \times L - nret_{fungi}$

7.3 $nret_{fungi} = n_{fungi} \times L \times (1 - N_{RET})$

c_{fungi} = ECM C content (g C m^{-2}), n_{fungi} = fungal N content (g N m^{-2}), L = litter rate, $nret_{fungi}$: fungal N which is retained in fungal tissue, N_{RET} = fraction of N retained in fungal tissue from senescence.

If fungal growth = detailed

7.4 $$c_{fungi \rightarrow lit} = c_{fungi} \times (FRAC_{MYC} \times L_{MYC} + ((1 - FRAC_{MYC}) \times L_M))$$

7.5 $$n_{fungi \rightarrow lit} = n_{fungi} \times (FRAC_{MYC} \times L_{MYC} + ((1 - FRAC_{MYC}) \times L_M)) - nret_{fungi}$$

7.6 $FRAC_{MYC}$ = fraction of mycorrhizal hyphae in total fungal biomass, L_{MYC} = litter rate of mycorrhizal hyphae, L_M= litter rate of fungal mantle tissue.

Fungal biomass (g C m^{-2}, g N m^{-2})

8.1 $$c_{fungi} = c_{a \rightarrow fungi} - c_{fungi \rightarrow litter} - c_{fungi \rightarrow a}$$

8.2 $$n_{fungi} = n_{N \rightarrow fungi} - n_{fungi \rightarrow litter} - n_{fungi \rightarrow plant}$$

Mycorrhization degree

9 $$m = \frac{c_{fungi}}{c_{frt} \times FRAC_{OPT} \times M_{OPT}}$$

c_{frt} = fine root biomass (g C m^{-2}), $FRAC_{OPT}$ = coefficient defining optimum ratio between fungal and fine root biomass, M_{OPT} = optimum mycorrhization degree.

Uptake and transfer processes of ECM and plant

N transfer from ECM to plant (g N m^{-2} d^{-1})

10.1 $$n_{fungi \rightarrow plant} = dem_{Nplant} \quad \text{if } dem_{Nplant} \leq n_{fungiavail}$$

$$n_{fungi \rightarrow plant} = n_{fungiavail} \quad \text{if } dem_{Nplant} > n_{fungiavail}$$

dem_{Nplant} = plant N demand, $n_{fungiavail}$ = fungal available N for transfer to plant (all g N m^{-2} d^{-1})

10.2 $$n_{fungiavail} = n_{fungi} - \frac{c_{fungi}}{CN_{FMAX}}$$

c_{fungi} = ECM biomass (g C m^{-2}), CN_{FMAX} = maximum C:N ratio of fungal tissue, which allows N transfer to plant.

Fungal nitrate and ammonium uptake (given for nitrate, equivalent for ammonium with ammonium specific parameter)

11.1 $$n_{NO3 \rightarrow fungi} = n_{NO3pot \rightarrow fungi} \times r_{NO3} \times f(n_{demfungi}) \quad \text{if } N_{NO3pot \rightarrow fungi} < n_{NO3soil} \, x \, f(n_{avfungi})$$

11.2 $$n_{NO3 \rightarrow fungi} = n_{NO3soil} \times f(n_{avfungi}) \quad \text{if } N_{NO3pot \rightarrow fungi} > n_{NO3soil} \, x \, f(n_{avfungi})$$

11.3 $$n_{NO3pot \rightarrow fungi} = NO3_{RATE} \times c_{fungi} \times FRAC_{MYC}$$

$n_{NO3pot \rightarrow fungi}$=potential ECM nitrate uptake (g N m^{-2} d^{-1}), r_N = fraction of ammonium-N and total mineral-N in the soil, $f(n_{demfungi})$= N uptake response to N demand, $n_{NO3soil}$ = soil nitrate content (g N m^{-2}), $f(n_{avfungi})$ = N uptake response to soil availability, $NO3_{RATE}$ = nitrate specific uptake rate (g N m^{-2} d^{-1}), c_{fungi} = fungal biomass (g C m^{-2}), $FRAC_{MYC}$ = fraction of mycorrhizal mycelia in total fungal biomass.

Fungal organic N uptake from litter and humus (given for litter, equivalent for humus with humus specific parameter)

11.4 $$n_{lit \rightarrow fungi} = n_{litpot \rightarrow fungi} \times r_{lit} \times f(n_{demfungi})$$ if $n_{litpot \rightarrow fungi} \times r_{lit} < n_{litsoil} \times f(n_{litavfungi}) \times r_{lit}$

11.5 $$n_{lit \rightarrow fungi} = n_{litsoil} \times f(n_{litavfungi}) \times r_{lit}$$ if $n_{litpot \rightarrow fungi} \times r_{lit} > n_{litsoil} \times f(n_{litavfungi}) \times r_{lit}$

11.6 $$n_{litpot \rightarrow fungi} = LIT_{RATE} \times c_{fungi} \times FRAC_{MYC}$$

where $n_{litpot \rightarrow fungi}$ = potential ECM organic N uptake from litter (g N m^{-2} d^{-1}), r_{lit} = fraction of litter-N in total organic-N in the soil, $f(n_{demfungi})$= N uptake response to N demand, $n_{litsoil}$ = soil litter content (g N m^{-2}), $NLIT_{RATE}$ = litter specific uptake rate (g N g C^{-1} d^{-1}), c_{fungi} = fungal biomass (g C m^{-2}), $FRAC_{MYC}$ = fraction of mycorrhizal mycelia in total fungal biomass.

Table A1 (c) Overview of response functions of plant and fungal growth and N uptake

No.	Equation		
Plant response to air temperature			
12	$f(T_l) =$	0	$T_l < P_{mn}$
		$(T_1 - p_{mn}) / (p_{O1} - p_{mn})$	$p_{mn} \leq T_1 \leq p_{O1}$
		1	$p_{O1} < T_l < p_{O2}$
		$1- (T_1 - p_{O2}) / (p_{mx} - P_{O2})$	$p_{O2} < T_l < p_{mx}$
		0	$T_l > p_{mx}$

where T_l = leaf temperature (°C) and P_{MN} (-4°C), PO1 (10°C), PO_2 (25°C), P_{MX} (40°C) are coefficients.

Photosynthetic response to leaf C/N ratio

13	$f(CN_l) =$	1	$CN_l < p_{CNOPT}$
		$1 + (\frac{cn_l - p_{CNOPT}}{p_{COPT} - p_{CNTH}})$	$p_{CNTH} \leq CN_l \geq p_{CNOPT}$
		0	$CNl > p_{CNTH}$

where CN_l = leaf C:N ratio and p_{CNOPT} (25) and p_{CNTH} (75) are parameters.

Plant response to soil moisture

14 $$f(\frac{E_{ta}}{E_{tp}}) = \frac{E_{ta}}{E_{tp}}$$

where E_{ta} = actual transpiration and E_{tp} = potential transpiration (mm d^{-1}).

Plant mineral N uptake response to N availability and fungal mantle

15 $$f(n_{\min avail}) = NUPT_{FRACMAX} \times e^{(-FM \times m)}$$

Where $NUPT_{FRACMAX}$, coefficient describing fraction of soil N available, and FM, uptake reduction due to fungal mantle.

630 Plant organic N uptake response to N availability and fungal mantle (given for litter, equivalent for humus)

16 $$f(n_{humavail}) = NUPT_{ORGFRACMAX} \times e^{(-FM \times m)}$$

Where $NUPT_{FRACMAX}$ is the respective uptake coefficient for N from humus (included in calibration), and FM the uptake reduction due to fungal mantle.

635 ECM N uptake response to N availability

17.1 $$f(n_{avfungi}) = NUPT_{FRACMAX} \times UPT_{MINENHANCE}$$ for nitrate

17.2 $$f(n_{avfungi}) = NUPT_{FRACMAX} \times UPT_{MINERAL} \times UPT_{NH4}$$ for ammonium

17.3 $$f(n_{orgavfungi}) = NUPT_{ORGFRACMACX} \times UPT_{ORG}$$ for litter/humus

640 ECM N uptake response to N demand

18 $$f(n_{demfungi}) = 1 - \frac{CN_{FMIN}}{cn_{fungi}}$$

where CN_{FMIN} = minimum ECM C/N ratio.

19 $$f(c_{fungiavail}) = e^{(-N_{AVAILCOEF} \times n_{\min soil}^{2})^{3}}$$

645 Where $NAVAIL_{COEF}$ is a coefficient and $N_{minsoil}$ is the total soil content of ammonium and nitrate (g N m^{-2}).

20.1 $$f(n_{supplyfungi}) = 1$$ if $\min_{NPlant} < n_{fungi \rightarrow plant}$

20.2 $$f(n_{supplyfungi}) = \frac{n_{fungi \rightarrow plant}}{n_{fungi \rightarrow plant} + n_{soil \rightarrow plant}}$$ if $\min_{NPlant} > n_{fungi \rightarrow plant}$

20.3 $$\min_{NPLant} = MIN_{SUPL} \cdot (n_{fungi \rightarrow plant} + n_{soil \rightarrow plant})$$

650 Where $\min_{NPlant}$ = defined minimum fungal N supply in plant N uptake, $n_{fungi \rightarrow plant}$ = actual ECM N supply to plant (g N m^{-2} d^{-1}), $n_{soil \rightarrow plant}$ = total plant N uptake from mineral and organic fraction (g N m^{-2} d^{-1}).

Table A1 (d) Overview of model parameters; previous CoupModel parameters are mostly from Svensson et al. (2008a) and ECM parameters are from literature value (references in the paper text)

655 Parameter	Description	Value	Unit
CN_{FMIN}	Minimum fungal C/N ratio for fungal N demand	18	gC gN^{-1}
CN_{FMAX}	Maximum fungal C/N ratio for N transfer to plant	30	gC gN^{-1}
CN_{iMIN}	Minimum C/N ratio of fine roots	40	gC gN^{-1}
	Needles/leaves	22	gC gN^{-1}
660	Coarse roots and stem	450	gC gN^{-1}

	E_L	Coefficient for radiation use efficiency	8	
	E_{NH4}	Fungal NH_4 uptake enhancement factor	5	
	FM	Plant N uptake reduction due to ECM mantle	0.5	
	$FRAC_{FMAX}$	Maximum fraction of C allocated to rooting	0.5	
665		zone which is made available for ECM		
	$FRAC_{MYC}$	Fraction of fungal mycelia in total biomass	0.5	
	$FRAC_{OPT}$	Optimum fraction between root and fungal biomass	0.3	
	K_{RGF}	Growth respiration coefficient of ECM	0.21	d^{-1}
	K_{RMi}	Maintenance respiration coefficient of plant compartment i		
670		(i = fine roots, coarse roots, stem, leaves)	0.001	d^{-1}
	K_{RGi}	Growth respiration coefficient of	0.21	d^{-1}
		plant compartment i		
	L_{FRT}	Litter rate of fine roots	0.0027	d^{-1}
	L_{CRT}	Litter rate of coarse roots	0.000027	d^{-1}
675	L_{LEAF}	Litter rate of needles	0.0002	d^{-1}
	L_{STEM}	Litter rate of stem	0.000027	d^{-1}
	L	Litter rate of ECM (if fungal growth = simple)	0.004	
	L_M	Litter rate of fungal mantle		
		(if fungal growth = detailed)	0.0014	d^{-1}
680	L_{MYC}	Litter rate of fungal mycelia	0.01	d^{-1}
		(if fungal growth = detailed)		
	M_{OPT}	Optimum mycorrhization degree		
		of fine roots < 2 mm	0.5	
	N_{RET}	N retained by ECM from senescence	0.54	d^{-1}
685	$NUPT_{FRACMAX}$	fraction of mineral N available for uptake	0.08	d^{-1}

690 **Table A2 Correlation between common model parameters for all simulated sites with the "implicit" and "explicit" approaches respectively. Correlation is given as the Pearson correlation coefficient**

		implicit				explicit			
		K_H	$NUPT_{OFM}$	F_{ROOT}	CN_{MIC}	K_H	$NUPT_{OFM}$	F_{ROOT}	CN_{MIC}
Lycksele	K_H	1	-0.20	0.67	0.23	1	-0.08	0.28	0.21
	$NUPT_{OFM}$		1	0.24	-0.57		1	0.02	-0.35
	F_{ROOT}			1	0.18			1	0.02
	CN_{MIC}				1				1
Mora	K_H	1	-0.13	0.73	0.11	1	0.08	0.22	0.04
	$NUPT_{OFM}$		1	0.18	-0.64		1	0.10	-0.46
	F_{ROOT}			1	0.13			1	0.12
	CN_{MIC}				1				1
Nässjö	K_H	1	0.03	0.70	-0.08	1	0.13	0.29	0.16
	$NUPT_{OFM}$		1	0.31	-0.60		1	0.29	-0.53
	F_{ROOT}			1	0.02			1	0.12
	CN_{MIC}				1				1
Ljungbyhed	K_H	1	0.03	0.66	-0.18	1	0.33	0.26	-0.19
	$NUPT_{OFM}$		1	0.17	-0.28		1	0.23	-0.26
	F_{ROOT}			1	0.24			1	0.07
	CN_{MIC}				1				1

Table A3 Correlation between fungal and common model parameters with "explicit" approach for all sites. Correlation is given as the Pearson correlation coefficient

		$Norg_{RATE}$	$NH4_{RATE}$	$NO3_{RATE}$	K_{RM}	L_{MYC}	L_M	CN_{FMIN}	MIN_{SUPL}	$FRAC_{OPT}$	$NAVAIL_{COEF}$
Lycksele	K_H	0.17	0.16	0.16	0.01	-0.30	-0.27	0.02	0.00	-0.17	-0.13
	$NUPT_{OFM}$	-0.32	-0.28	-0.28	0.09	0.13	0.13	0.18	0.10	0.01	0.02
	F_{ROOT}	0.06	0.03	0.03	-0.05	0.03	0.03	0.00	0.06	-0.04	-0.15
	CN_{MIC}	-0.33	-0.34	-0.34	0.00	0.21	0.21	0.23	0.03	-0.12	-0.01
Mora	K_H	0.22	0.20	0.20	-0.09	-0.25	-0.21	-0.02	0.08	-0.14	-0.04
	$NUPT_{OFM}$	-0.15	-0.09	-0.09	0.08	0.02	0.02	0.05	0.11	-0.08	0.00
	F_{ROOT}	-0.11	-0.12	-0.12	0.06	0.26	0.26	0.25	-0.06	-0.01	0.01
	CN_{MIC}	-0.38	-0.40	-0.40	-0.03	0.29	0.29	0.33	-0.10	-0.08	-0.08
Nässjö	K_H	0.20	0.18	0.18	-0.06	-0.33	-0.32	-0.13	0.08	-0.03	-0.08
	$NUPT_{OFM}$	-0.07	-0.03	-0.03	-0.05	-0.11	-0.11	-0.12	-0.03	0.18	-0.06
	F_{ROOT}	-0.06	-0.03	-0.03	0.01	0.08	0.08	0.09	-0.08	0.14	-0.08
	CN_{MIC}	-0.23	-0.20	-0.20	0.05	0.11	0.11	0.15	-0.02	-0.17	0.09
Ljungbyhed	K_H	0.34	0.36	0.36	-0.08	-0.51	-0.53	-0.13	0.18	-0.22	-0.20
	$NUPT_{OFM}$	0.10	0.16	0.16	0.05	-0.21	-0.21	-0.24	0.06	-0.13	-0.07
	F_{ROOT}	-0.11	-0.07	-0.07	0.19	0.10	0.10	0.11	0.04	0.02	-0.02
	CN_{MIC}	-0.22	-0.21	-0.21	0.01	0.15	0.15	0.18	-0.05	0.02	0.07

Table A4 Correlation between fungal model parameters with the "explicit" approach for all sites. Correlation is given as the Pearson correlation coefficient

		$Norg_{RATE}$	$NH4_{RATE}$	$NO3_{RATE}$	K_{RM}	L_{MYC}	L_M	CN_{FMIN}	MIN_{SUPL}	$FRAC_{OPT}$	$NAVAIL_{COEF}$
Lycksele	$Norg_{RATE}$	1	0.91	0.91	0.01	-0.55	-0.59	-0.10	-0.07	0.07	-0.03
	$NH4_{RATE}$		1	0.99	0.01	-0.50	-0.56	-0.07	-0.05	0.07	-0.03
	$NO3_{RATE}$			1	0.01	-0.50	-0.56	-0.07	-0.05	0.07	-0.03
	K_{RM}				1	-0.1	-0.1	-0.06	-0.07	-0.03	-0.04
	L_{MYC}					1	0.95	0.04	0.07	-0.17	-0.03
	L_M						1	0.04	0.07	-0.13	-0.02
	CN_{FMIN}							1	0.05	0.07	0.05
	MIN_{SUPL}								1	0	0.05
	$FRAC_{OPT}$									1	0.17
	$NAVAIL_{COEF}$										1
Mora	$Norg_{RATE}$	1	0.88	0.88	-0.09	-0.40	-0.48	0.02	-0.05	0.04	0.06
	$NH4_{RATE}$		1	0.99	-0.08	-0.32	-0.43	0.01	-0.03	0.09	0.08
	$NO3_{RATE}$			1	-0.08	-0.32	-0.43	0.01	-0.03	0.09	0.08
	K_{RM}				1	-0.07	-0.06	0.01	-0.15	0.05	0.05
	L_{MYC}					1	0.95	-0.08	0.05	-0.21	-0.02
	L_M						1	-0.07	0.07	-0.19	-0.03
	CN_{FMIN}							1	-0.08	-0.01	0.04
	MIN_{SUPL}								1	0.06	0.13
	$FRAC_{OPT}$									1	0.02
	$NAVAIL_{COEF}$										1

Table A4 (continued)

		$Norg_{RATE}$	$NH4_{RATE}$	$NO3_{RATE}$	K_{RM}	L_{MYC}	L_M	CN_{FMIN}	MIN_{SUPL}	$FRAC_{OPT}$	$NAVAIL_{COEF}$
Nässjö	$Norg_{RATE}$	1	0.86	0.86	0.05	-0.13	-0.20	-0.08	-0.10	0.09	-0.02
	$NH4_{RATE}$		1	0.99	0.11	0.00	-0.07	-0.09	-0.07	0.15	-0.02
	$NO3_{RATE}$			1	0.11	0.00	-0.07	-0.09	-0.07	0.15	-0.02
	K_{RM}				1	-0.05	-0.06	0.01	0.05	-0.01	0.01
	L_{MYC}					1	0.96	0.07	0.06	-0.11	-0.02
	L_M						1	0.06	0.07	-0.11	-0.05
	CN_{FMIN}							1	-0.07	-0.07	0.08
	MIN_{SUPL}								1	-0.05	-0.04
	$FRAC_{OPT}$									1	0.02
	$NAVAIL_{COEF}$										1
Ljungbyhed	$Norg_{RATE}$	1	0.86	0.86	-0.13	-0.32	-0.40	-0.06	0.07	0.04	-0.03
	$NH4_{RATE}$		1	0.99	-0.07	-0.21	-0.28	-0.05	0.02	0.06	0.00
	$NO3_{RATE}$			1	-0.07	-0.21	-0.28	-0.05	0.02	0.06	0.00
	K_{RM}				1	-0.09	-0.08	-0.01	0.01	-0.03	-0.05
	L_{MYC}					1	0.96	0.01	-0.08	-0.04	0.12
	L_M						1	0.02	-0.10	-0.04	0.10
	CN_{FMIN}							1	-0.03	0.16	0.04
	MIN_{SUPL}								1	-0.07	-0.03
	$FRAC_{OPT}$									1	0.01
	$NAVAIL_{COEF}$										1

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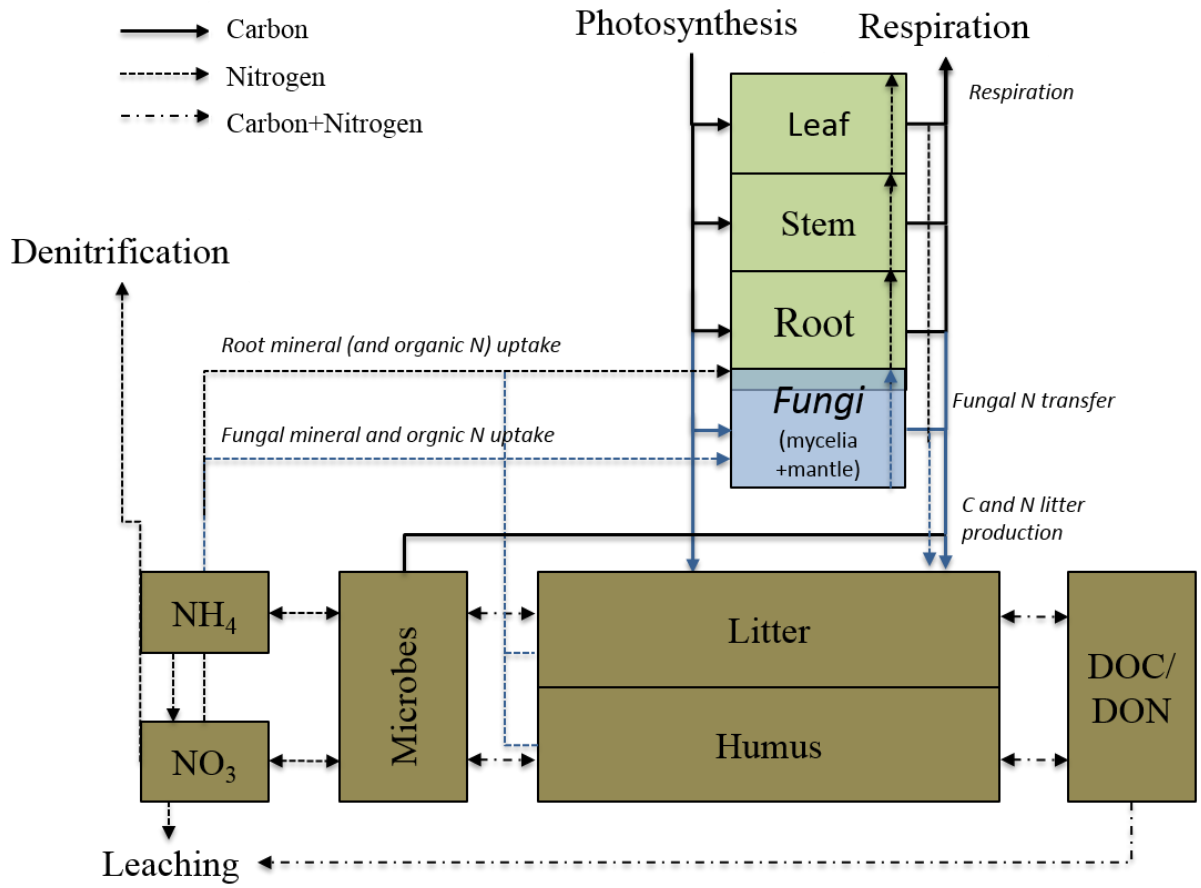


Figure 1 A simplified overview of C and N fluxes between plants, mycorrhiza fungi, and the soil in the Coup-MYCOFON model. Light blue indicates the newly implemented MYCOFON model

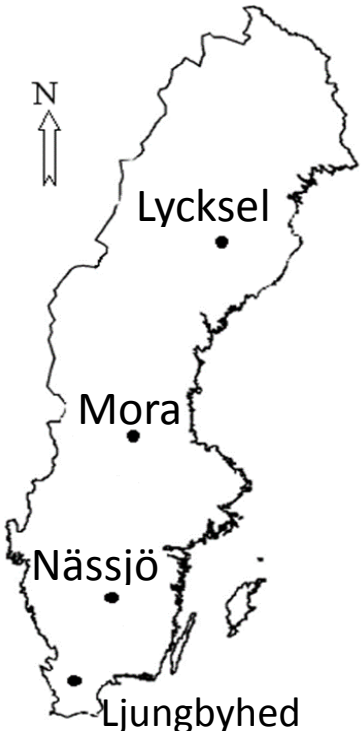


Figure 2 Position of the four study sites in Sweden

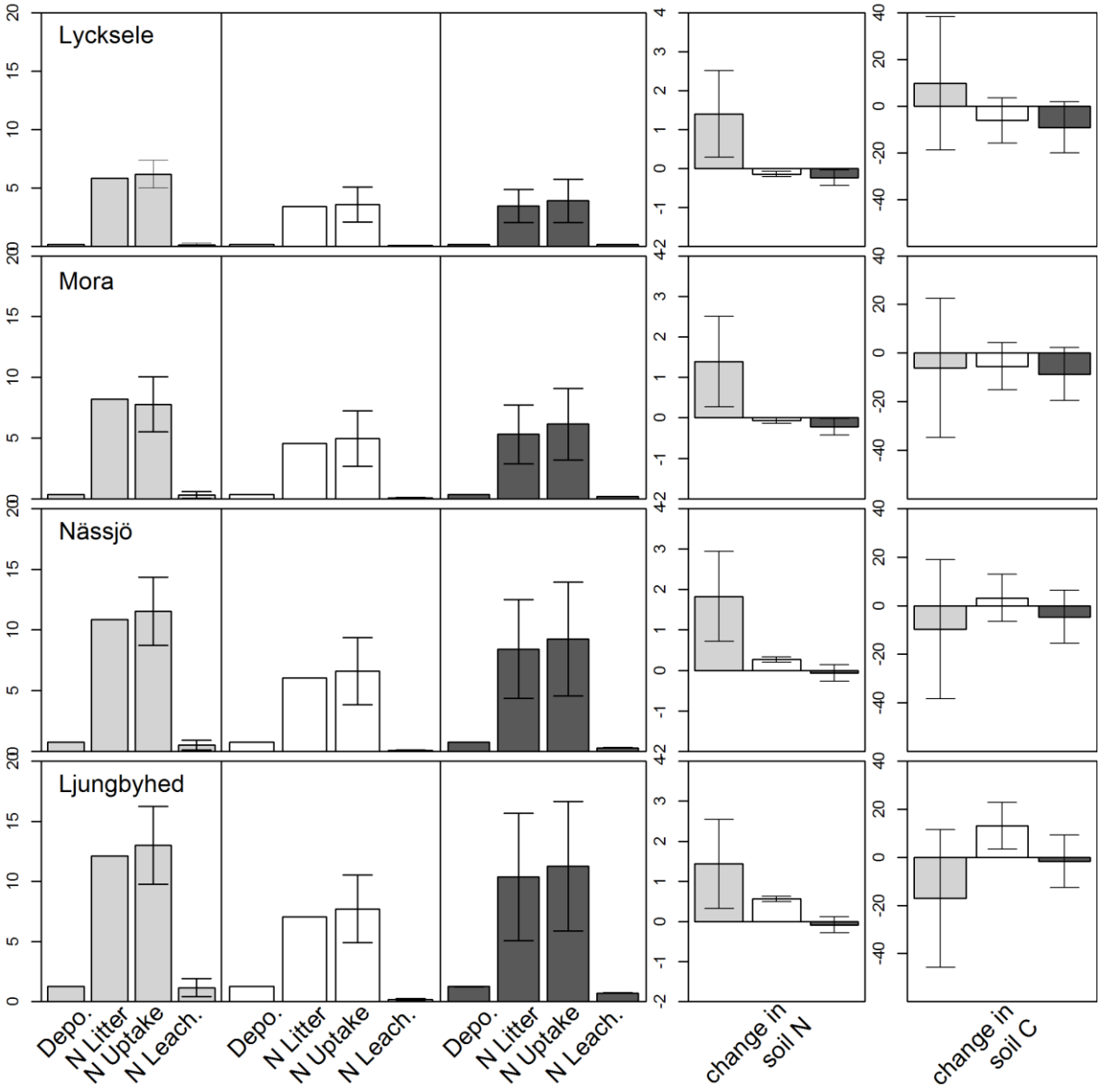
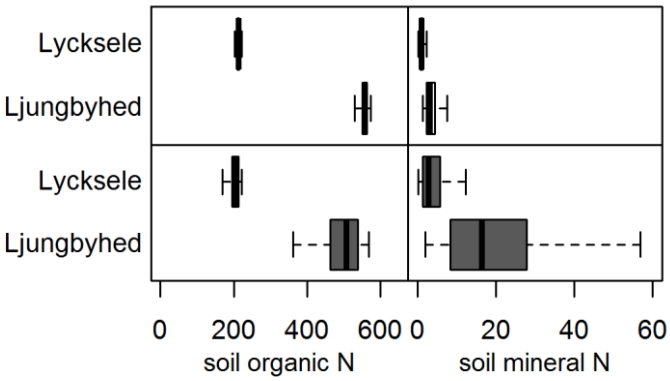


Figure 3 Soil N fluxes for the nonlim (grey columns, left), implicit (white, 2nd left column), and explicit (black, 3rd left column) model approaches. Presented are the major N inputs (N deposition, total N litter production), outputs (N uptake from the plant/fungi, N leaching), and the net change in the total soil N pool (mineral and organic). For C, the net change is presented (right column). Error bars indicate the 90th percentile of accepted model runs (posterior). Units for N are g N m^{-2} $yr^{-1}$and g C m^{-2} yr^{-1} for C



915 **Figure 4 Average soil organic and mineral (ammonium and nitrate) content (g N m^{-2}) in the implicit ECM model (upper graph) and explicit ECM model (lower graph) for the two sites Lycksele and Ljungbyhed. Box plots indicate the median (bold line), the 25th and 75th percentile (bars), and the 10th and 90th percentile (whiskers)**

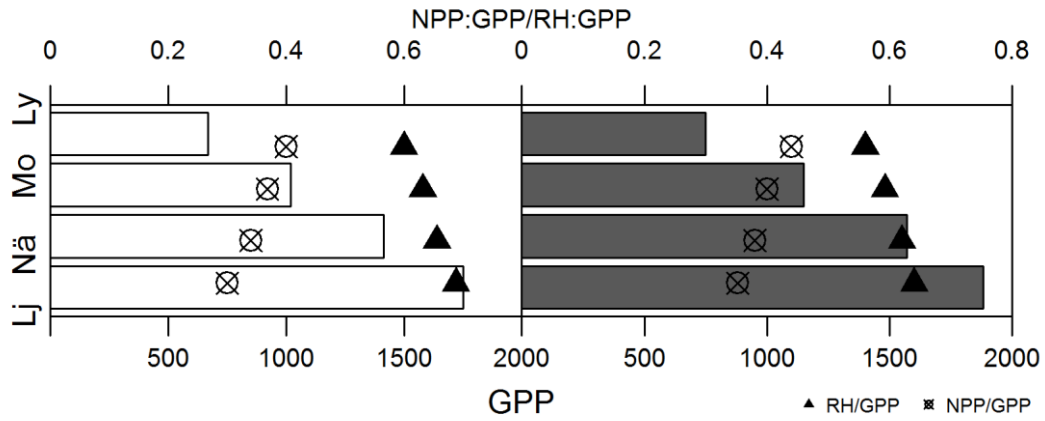


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Figure 5 GPP (bars), Rh/GPP ratio (triangle), and NPP/GPP ratio (cross circles) for all four sites simulated with the implicit (left) and explicit (right) ECM model approach

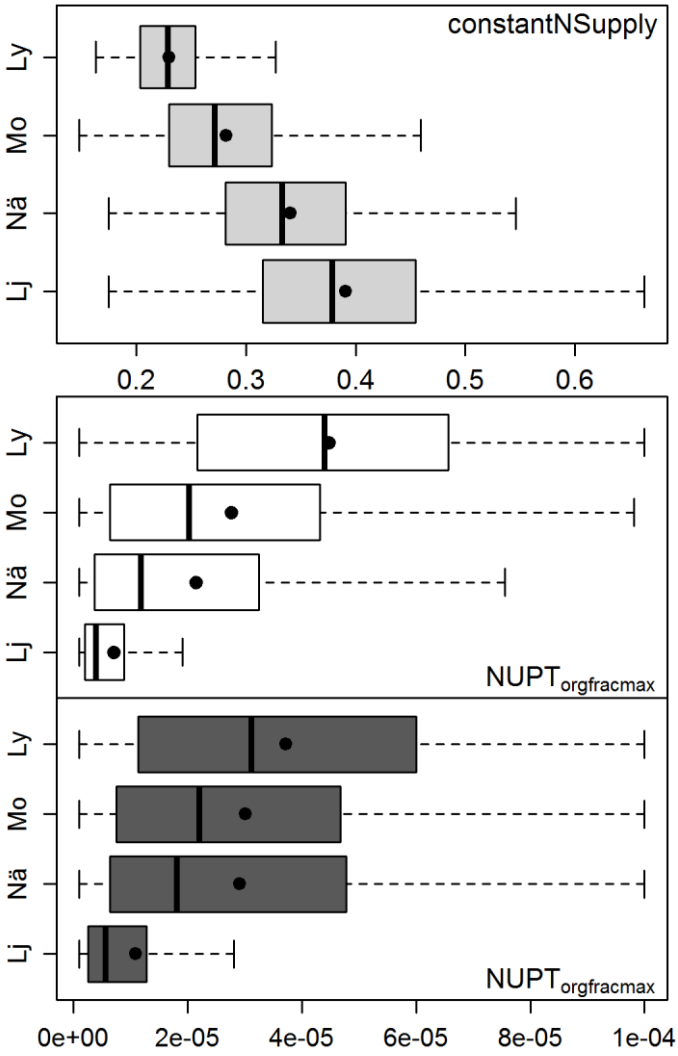

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Figure 6 Posterior parameter distributions for N uptake parameters: constant N supply rate in the "nonlim" approach (light grey) and organic N uptake capacity in the implicit (white) and explicit (dark grey) ECM model approaches. Distributions are presented as box plots over the prior range of variation (corresponding to the range in the x-axis). Box
930 **plots depict the median (bold line), the 25th and 75th percentile (bars), and the 10th and 90th percentile (whiskers)**

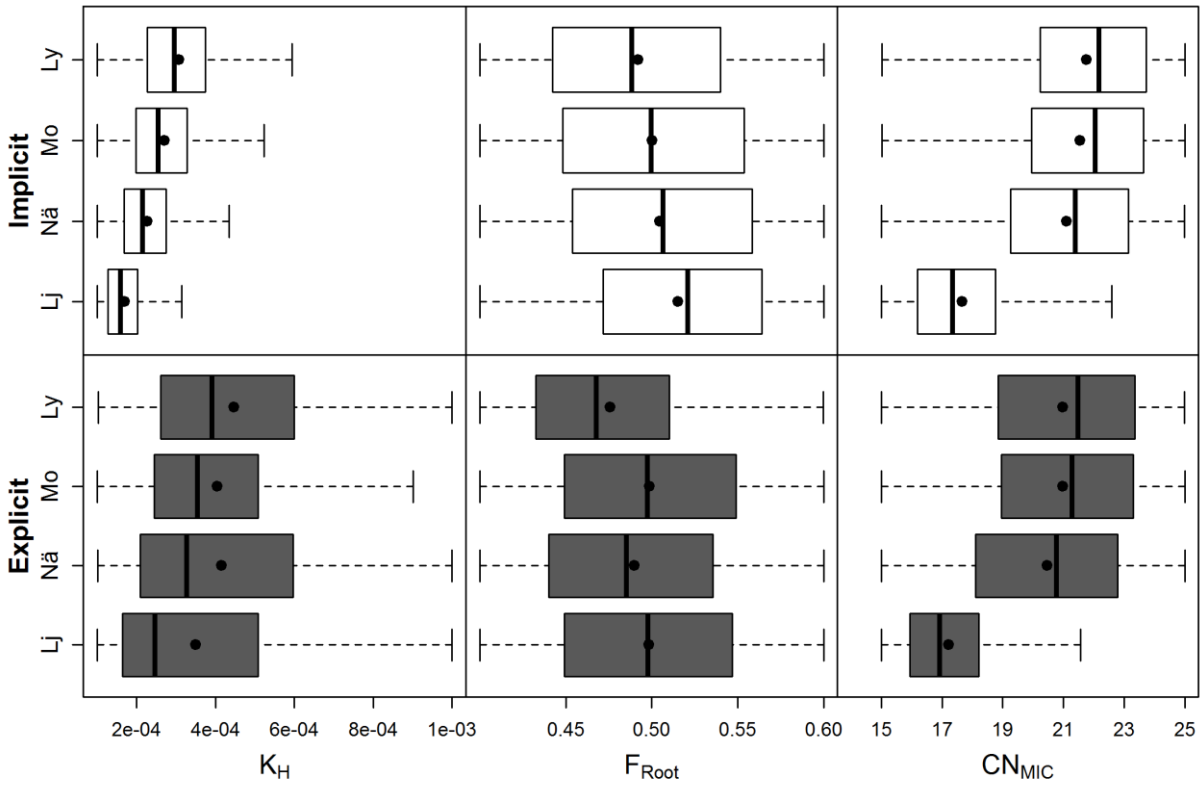

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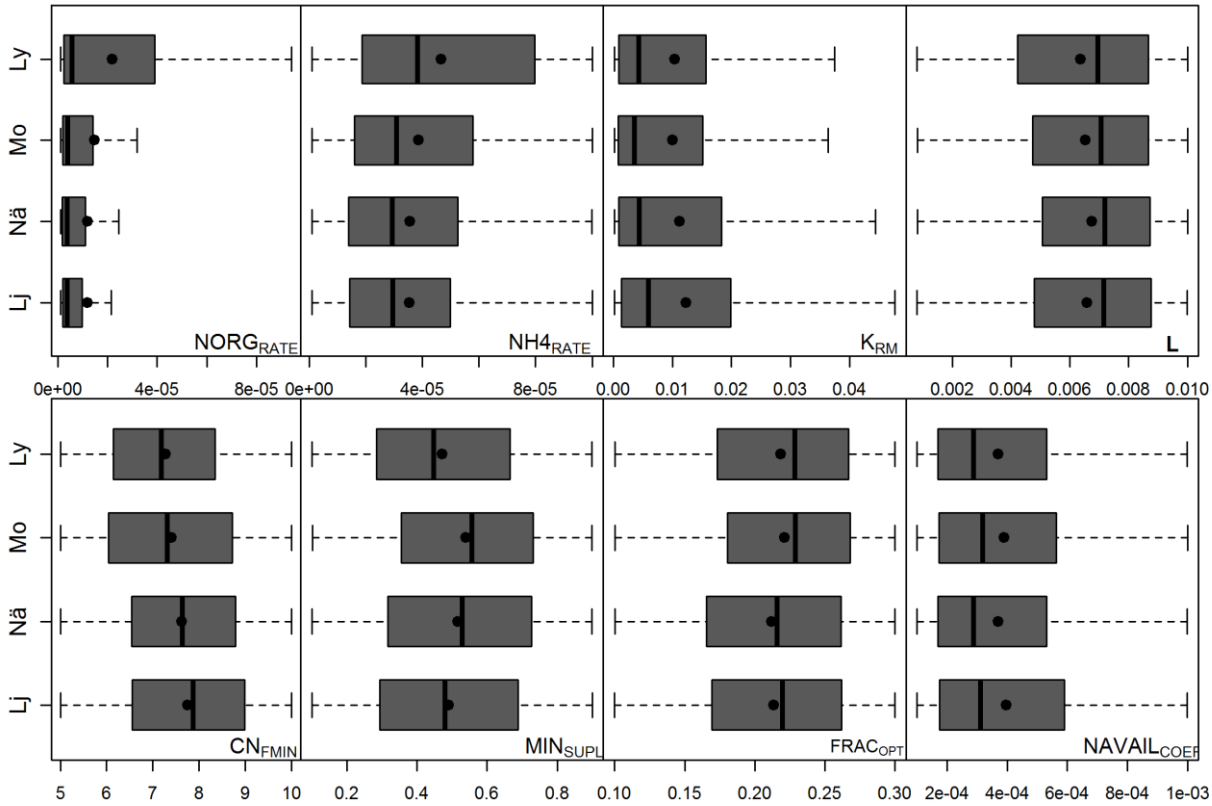
Figure 7 Posterior parameter distributions for common parameters using the implicit (top: white boxes) and explicit (bottom: dark grey boxes) ECM approaches for four different sites from North to South. Distributions are presented as box plots over the prior range of variation (corresponding to the range in the x-axis). Box plots depict the median (bold line), the 25th and 75th percentile (bars), and the 10th and 90th percentile (whiskers). The parameters shown are: 940 **K_H: the humus decomposition coefficient, F_{Root}: the fraction of C assimilates distributed to the roots, and EM, CN_{MIC}: the microbial C/N ratio**



945 **Figure 8 Posterior parameter distributions of fungal specific parameters (from top left to bottom right): organic N uptake rate (*NORG*$_{RATE}$), ammonium uptake rate (*NH4*$_{RATE}$), respiration coefficient (*K*$_{RM}$), fungal litter rate coefficient (*L*), minimum fungal C/N ratio (CN$_{FMIN}$), fungal minimum N supply to plant (*MIN*$_{SUPL}$), optimum ratio between fungal and root C content (*FRAC*$_{OPT}$), and N sensitivity coefficient (*NAVAIL*$_{COEF}$). Distributions are presented as box plots over the prior range of variation (corresponding to the range in the x-axis). Box plots depict the median (bold line), the**
950 **mean (black point), the 25th and 75th percentile (bars), and the 10th and 90th percentile (whiskers)**

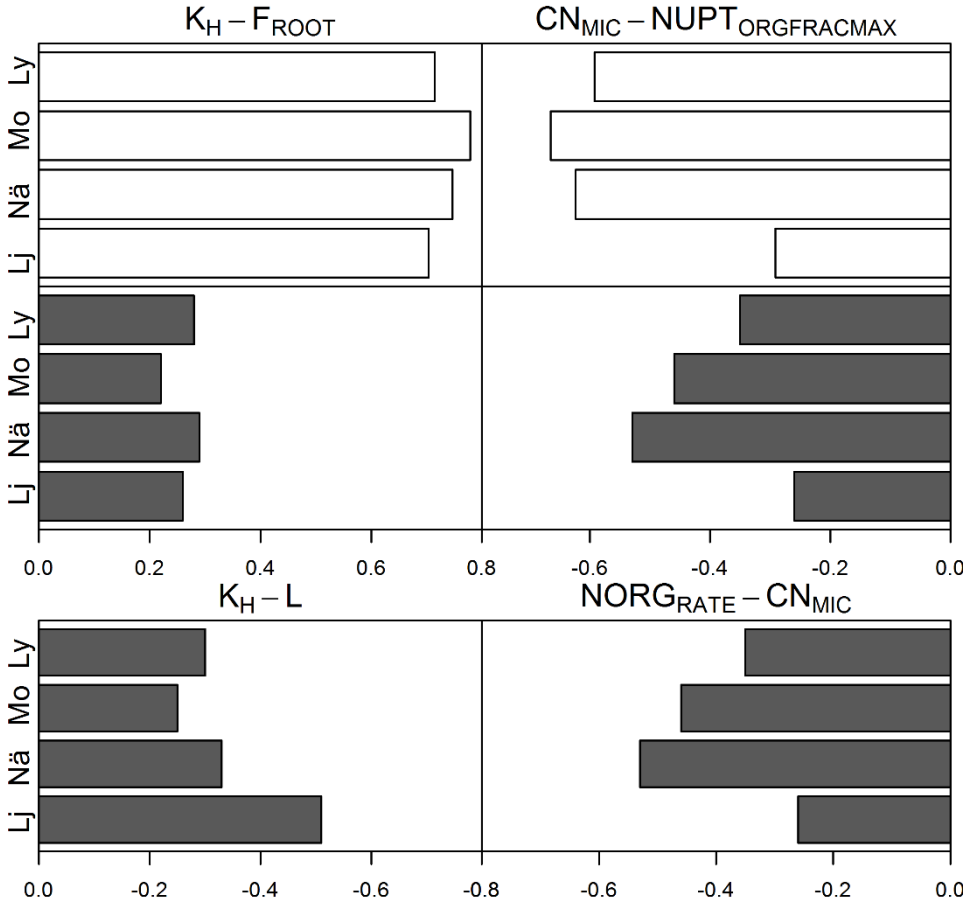


Figure 9 Correlation between model parameters, given as the Pearson correlation coefficient, for the implicit and explicit ECM approaches. Top left: correlation between humus decomposition coefficient (K_H) and the fraction of C assimilates directed to EM and roots (F_{ROOT}). Top right: C/N of microbes (CN_{MIC}) and fraction of organic N available for uptake ($NUPT_{ORGFRACMAX}$). Correlation between fungal parameters: bottom left: humus decomposition coefficient (K_H) and fungal litter rate (L). Bottom right: fungal organic N uptake ($NORG_{RATE}$) and C/N of microbes (CN_{MIC})

Table 1 Maximum and minimum parameter values prior to Bayesian calibration for the nonlim, implicit, and explicit model approaches

A. Common parameters (all three approaches, including the "implicit" approach)

Parameter	Unit	Min	Max
Humus decomposition			
K_H	d^{-1}	0.0001	0.001
Fraction of organic N available for uptake			
$NUPT_{ORGFRACMAX}$	d^{-1}	0.000001	0.0001
Fraction of root C allocation in mobile C			
F_{ROOT}	d^{-1}	0.4	0.6
C/N ratio of decomposing microbes			
CN_{MIC}	d^{-1}	15	25

B. Parameters of the "nonlim" approach

Parameter	Unit	Min	Max
Plant N Supply			
ConstantNSupply	-	0.1	0.7

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C. Fungal parameters of the "explicit" approach

Parameter	Unit	Min	Max
Fungal N uptake			
$NORG_{RATE}$	g N gdw^{-1} d^{-1}	0.000001[a]	0.0001
$NH4_{RATE}$	g N gdw^{-1} d^{-1}	0.000001[a]	0.0001
$NO3_{RATE}$	g N gdw^{-1} d^{-1}	0.000001[a]	0.0001
Fungal respiration coefficient			
K_{RM}	d^{-1}	0.0002 [b]	0.05
Fungal litter rate			
L	d^{-1}	0.0008 [c]	0.01
Minimum fungal C/N ratio			
CN_{FMIN}	d^{-1}	5 [d]	10
Fungal minimum N supply to plant			
MIN_{SUPL}	d^{-1}	0.1[e]	0.9
Optimum fungi C allocation fraction			
$FRAC_{OPT}$	d^{-1}	0.1[f]	0.3[f]

N sensitivity coefficient			
$NAVAIL_{COEF}$	d^{-1}	0.0001	0.001

[a] Plassard et al. (1991), Chalot et al. (1995), and Smith and Read (2008)

[b] Set equally to trees according to Thornley and Cannell (2000)

[c] Staddon et al. (2003) and Ekblad et al. (2013)

[d] Högberg and Högberg (2002) and Wallander and Nilsson (2003)

[e] Estimated

[f] Leake (2007), Staddon et al. (2003), and Johnson et al. (2005)

975 **Table 2 Climatic and soil data, and initial settings of the four study soils applied in all model approaches**

Sites	Location	Altitude (m asl)	Air temperature[a] (°C)	Precipitation[a] (mm)	Soil C (g C m^{-2})	Soil N (g N m^{-2})	Soil C/N[c]	Standing stock (g C m^{-2})[c]	N deposition (kg N ha^{-1} $year^{-1}$)[d]
Lycksele	64°59'N 18°66'E	223	0.7	613	7006	223	31.5	5371	1.5
Mora	61°00'N 14°59'E	161	3.3	630	8567	295	29.1	7815	3.5
Nässjö	57°64'N 14°69'E	305	5.2	712	9995	367	27.2	10443	7.5
Ljungby-hed	56°08'N 13°23'E	76	7.1	838	10666	539	19.8	11501	12.5

[a] 30-year average/sum
[b] According to Skogsdata for a 100-year-old forest (2003: http://www.slu.se/en/webbtjanster-miljoanalys/forest-statistics/skogsdata/)
[c] Used as calibration parameter
980 [d] Used as driving data

Table 3 Prior values of variables used for model calibration and accepted relative uncertainty (A), and posterior model performance indicators (B): mean error (ME) between simulated and measured values, standard variation of ME (std), and summed log-likelihood of all accepted runs for simulated standing plant biomass (g C m^{-2}) and soil C/N ratio after the 100 year simulation period

A	PRIOR			
	Plant biomass (g C m^{-2})		Soil C/N ratio	
	Mean	Relative uncertainty (%)	Mean	Relative uncertainty (%)
Lycksele	5371	0.1	32	0.1
Mora	7815	0.1	29.1	0.1
Nässjö	10443	0.1	27.2	0.1
Ljungbyhed	11501	0.1	19.8	0.1

B		POSTERIOR						
		Plant biomass (g C m^{-2})			Soil C/N ratio			Runs
		ME	std	loglike	ME	std	loglike	accepted (%)
nonlim	Lycksele	37.6	531.1	-7.7	-5.8	1.3	-3.8	25
	Mora	38.7	1098.2	-8.4	-3.9	1.4	-3.0	41
	Nässjö	42.2	1021.3	-8.3	-2.7	1.6	-2.6	48
	Ljungbyhed	1.0	1155.6	-10.2	0.3	1.8	-2.1	48
implicit	Lycksele	-107.2	535.0	-7.7	-1.1	3.3	-2.7	42
	Mora	-98.3	787.1	-8.1	-1.1	2.7	-2.5	45
	Nässjö	-86.0	1036.2	-8.0	-1.0	2.5	-2.4	46
	Ljungbyhed	100.1	1143.2	-8.5	0.5	1.6	-2.0	50
explicit	Lycksele	-162.3	534.9	-7.7	-0.5	3.4	-2.7	29
	Mora	-215.4	809.1	-8.2	-0.3	2.7	-2.4	32
	Nässjö	-222.3	1041.2	-8.1	0.0	2.5	-2.3	30
	Ljungbyhed	-139.0	1137.6	-8.5	1.0	1.7	-2.1	32

Table 4 Comparison between modeled soil C and N of this study and literature value

Reference	Site	Ecosystem type	Forest age (years)	Soil C change (g C m^{-2} yr^{-1})	Soil N change (g N m^{-2} yr^{-1})
Svensson et al. 2008a	Lycksele	Coniferous on podzol	100	-5	
	Mora			-2	
	Nässjö			9	
	Ljungbyhed			23	
Lindroth et al. 2008	Flakaliden	Coniferous on podzol	39-42 (in 2002)	-79[a]	
	Knottåsen			-133[a]	
	Asa			-24	
This study	Lycksele	Coniferous on podzol	100	-6 to 13.1[b]	-0.2 to 0.6[b]
	Mora			-8.7 to -1.6[c]	-0.2 to -0.1[c]
	Nässjö				
	Ljungbyhed				

[a] Mean of the highest and lowest error estimates

[b] Implicit approach

[c] Explicit approach

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