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

Hongxing He[1], Astrid Meyer[1,a], Per-Erik Jansson[2], Magnus Svensson[2], Tobias Rütting[1], Leif Klemedtsson[1]

[1] Department of Earth Sciences, University of Gothenburg, Po Box 460, Gothenburg 40530, Sweden

[2] Department of Land and Water Resources Engineering, Royal Institute of Technology (KTH), Brinellvägen 28, Stockholm 100 44, Sweden

[a] now at: Institute of Groundwater Ecology, Helmholtz Zentrum München, Ingolstädter Landstraße 1, Neuherberg 85764, Germany

Correspondence to: Hongxing He (hongxing.he@gu.se)

Abstract

The symbiosis between plants and Ectomycorrhizal fungi (ECM) are shown to considerably influence the carbon (C) and nitrogen (N) fluxes 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 the predictive power of models.

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, Coup-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 dynamic uptake of organic N considering the plant roots to represent the ECM (ECM implicit), and the other a static N approach where plant growth is limited to a fixed N level (nonlim). Parameter uncertainties are quantified using Bayesian calibration where the model outputs are constrained to current forest growth and soil C/N ratio for four forest sites along a climate and N deposition gradient in Sweden and simulated over a 100-year period.

The "nonlim" approach could not describe the soil C/N ratio, due to largely overestimation of soil N sequestration but simulate the forest growth reasonably well. The ECM "implicit"/ "explicit" approaches both describe the soil C/N ratio well but slightly underestimate the forest growth. The "implicit" approach simulated lower litter production and soil respiration than the "explicit" approach. The ECM "explicit" Coup-Mycofon model provides a more detailed description of internal ecosystem fluxes and feedbacks of C and N between plants, soil and ECM. Our modeling highlights the need to incorporate ECM and organic N uptake into ecosystem models, and the "nonlim" approach is not recommended for future long-term soil C and N predictions. 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; Pan et al., 2011). 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; Högberg et al., 2017). Numerous studies have shown that soil N availability is the main driver for plant and microbial dynamics (Vitousek and Howarth, 1991; 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; Choma et al., 2017). Previous research showed that 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 (Table 1). In the ANAFORE model, ECM are described as separate C and N pools. However, this model does not distinguish between mycorrhizal mycelia 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 mycelia and mantle, but cannot neither degrade organic matter nor take up organic N forms. Mycelia and mantle differ in their capacity to take up N, and the mantle has a slower litter production rate than that of mycelia. 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 (Table 1).

The overall aim of this study is to improve understanding of ecosystem internal C and N flows related to symbiosis between ECM and host tree, in order to improve the model predictive power in assessment of C sequestration and climate change. This is done by presenting a new version of the CoupModel, coupled with an explicit description

of ECM. Specifically, we implement the previously developed MYCOFON model (Meyer et al., 2010) into the well-established soil-plant-atmosphere model, CoupModel (Jansson, 2012). We choose the MYCOFON model because; first, it contains a very detailed description of ECM fungal C and N pools, and all major C and N ECM exchange processes (i.e., litter production, respiration, C uptake, N uptake), and second, ECM can also additionally responses to the soil N availability (Table 1). Therefore, ECM growth and N uptake, both mineral and organic N forms, 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 from soil organic pools, 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 thus to a static fixed level (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. Data and Methodology

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 terrestrial ecosystem. 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 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 (V5) 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 ECM fungal growth, N uptake as well as litterfall and respiration are described.

2.1.1 Plant growth in CoupModel

An overview of model functions is given in the Appendix Table A.1. 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, respectively (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 ECM 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)). ECM 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 when simulating litter production if the more complex approach 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 ECM 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)). The C supply is defined by a constant fraction of the root C gain and is leveled off by the function $f(c_{fungiavail})$ as soon as a defined value of soil available total 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 showed that the ECM biomass of mycelia and mantle can be as much as 30-50% of fine root biomass, and 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). The actual ECM growth is limited by the maximum growth and calculated by a pre-defined fraction of assimilated root C, assuming that the production of an optimum mycorrhization degree requires a certain amount of ECM 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 ECM 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)).

2.1.4 Respiration and litter production of ectomycorrhizal fungi

Respiration is separated into two components (maintenance and growth) for both ECM and root respiration (see eq. 2 and eq. 6, Table A.1). Two approaches are available to simulate ECM 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. 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 Plant mycorrhization degree, plant N uptake, and ECM fungal N transfer to plant

According to field investigations, the mycorrhization degree can vary considerably between species. For spruce (*Picea abies*), 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, divided by the defined optimum mycorrhization degree (eq. 9, Table A1 (b)). It should be noted that 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. This is because plant ammonium and nitrate uptake is largely driven by the plant N demand (eqs. 4.1, 4.2, Table A.1), but also regulated 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 ECM 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 ECM fungal N transferred to the plant is determined by either the plant N demand or, if the plant N demands exceeds the ECM 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 calculated by the fungal C/N ratio (eq. 10.2, Table A.1). This relation is again based on the assumption that the ECM fungi will only supply the plant with N as long as its own demand is fulfilled (Nehls et al., 2008).

2.1.6 Ectomycorrhizal fungal N uptake

In the Coup-MYCOFON model, ECM can take up both mineral and organic N. For both N forms, the potential ECM uptake is first defined. This is determined by the size of ECM C pool, the fraction of ECM 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 ECM fungal mycelia can take up N. Values for $NO3_{RATE}$, $NH4_{RATE}$, and $NORG_{RATE}$ are derived from published values but with wide ranges (Table 2). The actual N uptake is dependent on the available soil N as well as the ECM 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 ECM fungal uptake, and is controlled by the parameters $NUPT_{ORGFRACMAX}$ (the fraction of organic N available for uptake) and $NUPT_{FRACMAX}$ (the fraction of mineral N available for uptake). N availability for ECM corresponds to the plant available N (eq. 16, Table A.1), but as ECM 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 ECM 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 (litter and humus). 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)).

2.2 Transect modeling approach

2.2.1 Three ECM modeling approaches

Three modeling approaches of different complexity were applied in this study. The basic "nonlim" approach was 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 the actual soil N availability, and N is used from a virtual source potentially exceeding the soil N availability, thus as an "open" N cycle. The ECM "implicit" approach simulates plant uptake of organic N which is assumed to be via ECM; i.e., ECM are considered implicitly as being responsible for N uptake, but are not physically represented 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, ECM fungi are fully physically considered as described above. ECM 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 3 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. 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 including the meteorological data, N deposition and soil data were used as input values (Table 3). 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 Brief description of Bayesian calibration

2.3.1 Observational constraints

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 plant and soil developments, also aiming at maximized

model flexibility. This allows us to compare the different model approaches in terms of explaining the measured data, and also to investigate distributions and uncertainty of key parameters. The previous modeling study by Svensson et al. (2008a) demonstrated that the changes of soil C in these sites were rather small over a 100-year period while the soil C/N ratio showed large variabilities with different N supply assumptions. Therefore, in this study the measured C/N ratio of soil organic matter and standing stock biomass were used as observational constraints. The measured error (also called relative uncertainty in Table 4) for both the soil C/N ratio and the standing stock biomass were difficult to assume due to lack of information. An uncertainty estimate of 30% was generally recommended under such conditions (van Oijen et al., 2005). In order to reduce the weight of values close to zero on behalf of large peaks, a minimum measured error that is 10% of the measured value was defined in this study (Klemedtsson et al., 2008). This is also because our intention was to force the model to simulate tree biomass and soil C/N ratio precisely, to better constrain posterior parameter distributions for the respective model approach and site. The Bayesian calibration as applied in this study is briefly described below, however for a detailed description of the general methodology see e.g., Klemedtsson et al. (2008) and van Oijen et al. (2005).

2.3.2 Model parameters chosen for calibration

The different ECM modeling approaches were 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 2). In the "nonlim" approach, the constant N supply parameter *ConstantNsupply* for the spruce tree was a calibration parameter. In the "implicit" approach, the fraction of organic N available for plant uptake ($NUPT_{ORGFRACMAX}$) was included in the calibration based on Svensson et al. (2008a). For the ECM "explicit" approach, all ECM fungal parameters in MYCOFON including ECM growth (C and N assimilation and uptake, C and N losses), overall N uptake and plant N supply, respiration, and littering were calibrated. For all three approaches, the humus decomposition rate (K_H), the C/N ratio of microbes (CN_{mic}) regulating soil mineralization thus soil N availability, and the fraction of plant C assimilates allocated to the rooting zone (F_{ROOT}) regulating ECM fungal growth were additionally calibrated.

2.3.3 Bayesian calibration of models

The prior distributions of the parameters were chosen as uniform and non-correlated, with wide ranges of possible values (Table 2). Bayesian calibration combines the prior information about the parameters, and the observational constraints on model outputs to obtain a revised probability distribution or called posterior distribution (Yeluripati et al., 2009). The posterior probability of any parameter vector is proportional to the product of its prior probability and its corresponding data likelihood (eq. (1)). The data likelihood function which determines acceptance of the parameter sets as the posterior distributions, is based on the assumption that the model errors (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:

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

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

To construct the posterior parameter distribution, many sets of parameter θ were sampled. In this study, candidate parameter sets were generated using the Metropolis-Hastings random walk Markov Chain Monte Carlo (MCMC) algorithm (van Oijen et al., 2005; Vrugt, 2016). Briefly, a parameter ensemble of "walkers" move around randomly and the integrand value at each step was calculated. A few number of tentative steps may further be made to find a parameter space with high contribution to the integral. MCMC thus increases the sampling efficiency by using information about the shape of the likelihood function to preferentially sample in regions where the posterior probability is high (Rubinstein and Kroese, 2016). For each simulation, the model's likelihood was evaluated for a certain parameter set. After each run, a new parameter set was generated by adding a vector of random numbers ε to the previous parameter vector:

$$q_{i+1} = q_i + e \tag{2}$$

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). After a sufficiently long iteration (referred to as the "burn-in" period), the Markov chain reaches a stationary distribution that converges to the joint parameter posterior (Ricciuto et al., 2008). Van Oijen et al. (2005) recommended chain lengths in the order of 10^4–10^5 for modelling forest ecosystems with many observational constraints. In this trial study, we performed 10^4 runs for each ECM modeling approach and site. This is because a length of 10^4 model runs with a burn-in length of around 10^3 runs results in numerically stable results for our current considered problem. The step sizes used in this study result in acceptance rates between 25 to 50% (Table 4), which is also generally the most efficient range for the MCMC algorithm (Harmon and Challenor, 1997).

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 accuracies in reproducing current plant growth and soil C/N ratio after calibration (Table 4B). 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, difference between the simulated and measured values) in the posterior model (Table 4B). The ME by the "nonlim" approach is also two to five times higher than that when using the "implicit" or "explicit" approach (Table 4B). 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 4B).

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 southernmost 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 4B). 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%). No major differences are found for the summed log-likelihood for both calibration variables (Table 4B).

3.1.2 Ecosystem N and C fluxes and comparison to measured data

Modeled major ecosystem N fluxes in the posterior are shown in Figure 3. The modeled N litterfall, uptake and leaching fluxes differ significantly from one modeling approach to another where the "nonlim" approach always gives the highest fluxes. The "explicit" and "implicit" approaches show similar modeled N fluxes for the northernmost site, Lycksele. However, the differences between these two approaches become larger when moving towards south where higher fluxes are simulated by the "explicit" approach (Fig. 3). For instance, modeled N litter production in "explicit" approach 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 modeled N pool sizes for these two sites also differ where the "explicit" approach shows a larger mineral N in the soil and a smaller organic N pool compare to the "implicit" approach (Fig. 4).

Figure 5 shows the modeled major ecosystem C fluxes and comparison with previous results by Svensson et al. (2008a) and measured data from three other Swedish sites (Flakaliden, Knottåsen and Asa, Fig. 2) at comparable latitudes and on comparable soils by Lindroth et al. (2008). The simulated plant gross primary production (GPP) using three approaches all show an increasing trend from the northern sites to the southern sites, due to a more favorable climates and N availability for spruce forest growth. For the studied four sites, the "nonlim" approach simulates the highest GPP followed by the "explicit" and lastly the "implicit" approach. The variation of modeled GPP between the "explicit" and "implicit" approach ranges from 12% in northernmost Lycksele site to 7% in the southernmost Ljungbyhed site (Fig. 5). Simulated GPP in this study are generally higher than that by Svensson et al. (2008a) but comparable with the measured data from Lindroth et al. (2008). It should be noted that the GPP at the southern site, Asa was only measured for one year thus can associated with large uncertainties due to annual variations. Modeled ecosystem respiration generally follows the pattern of GPP. The net ecosystem exchange (NEE) predicted by the three approaches all show an overall atmospheric C uptake for all the sites where the "explicit" approach seems to have a higher uptake strength than the others (Fig. 5). Current estimates of NEE are again within the measured range by Lindroth et al., (2008), although a small net release of C was measured at Knottåsen, likely caused by the abnormal high temperature during those measured years. In addition, explicitly including ECM also increase the soil respiration for the four sites except the northernmost Lyckesele site. The simulated ranges however are somehow smaller than that by Svensson et al. (2008a).

The "nonlim" approach generally shows much higher uncertainties in the modeled N fluxes than either the "implicit" or "explicit" approaches. The "nonlim" approach simulated soil N sequestration up to 2 g N m^{-2} yr^{-1} for all the sites, but much lower or close to zero values were found when using the other two modeling approaches (Fig. 5). The simulated soil C balance by the "nonlim" approach also contrasts with that of soil N, where the soil sequesters C at the northernmost site, Lycksele, but loses C at a rate of 6 to 17 g C m^{-2} yr^{-1} for the other three sites (Fig. 5). Therefore, soil C and N are not in steady state and are decoupled in the "nonlim" approach over the simulated 100-year period. The "implicit" and "explicit" approaches, however, show a strong coupling between soil C and N (Fig. 5). 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. The respective net change in the soil C and N 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 whereas soils in the south gain C. However, when the "explicit" approach is used, the soils in the south are also predicted to lose C and N. Lindroth et al. (2008) found a similar trend in the soil net C change as simulated by the "explicit" approach here, but with a higher loss rate between 24 and 133 g C m^{-2} yr^{-1} (Fig. 5). Overall, our results show that accounting 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 ($NUPT_{ORGFRACMAX}$) show an opposite pattern with the highest values for Lycksele and lowest for Ljungbyhed and larger parameter uncertainties are found for the "explicit" approach (Fig. 6). Parameter values for the northern sites also have a much wider range compared with the southern sites (Fig. 6) which also explains the larger simulated ME of soil C/N in the northern sites (Table 4). 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 enhancement of organic matter decomposition and soil mineralization for northern sites (Fig. 7). A less clear tendency towards higher values at the southern sites is identified for the fraction of C allocated to roots, F_{ROOT} parameter. Microbial C/N ratio CN_{MIC} parameter 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 ECM fungal specific parameters

The posterior distributions of all ECM 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 an enhanced ECM fungal N uptake 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 ECM fungal C/N ratio parameter (CN_{FMIN}). The optimum ratio between ECM and root C content, $FRAC_{OPT}$, tends to be higher

375 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 ECM to the host plant parameter, does not show a clear trend. Further, differences of the other ECM parameters for the four sites are minor (Fig. 8).

3.2.3 Correlation between parameters

An overview of correlations for all posterior model parameters can be found in the supplementary in Tables A2,
380 A3, and A4. Key parameter sets showing correlation with each other (defined here as a Pearson correlation coefficient $r \geq 0.3$ or ≤ -0.3) are 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 significantly negative correlated, except for a weak correlation for Ljungbyhed (Fig. 9). A weak correlation between $NUPT_{ORGFRACMAX}$
385 and F_{ROOT} is also found for the Nässjö site (Table A2). 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 ECM 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
390 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 weak or non-existent (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 (He et al., 2016; Klemedtsson et al., 2008). But more importantly, they also highlight the different
395 process interactions and explanations provided by the applied modeling approaches, for the observational constraints.

4. Discussion

Our new version of the CoupModel provides a detailed predictive model framework to explicitly account for ECM in the plant-soil-ECM continuum. Model comparison to two simpler ECM modeling approaches show large
400 variations in N dynamic simulations, and that ECM and organic N uptake have to be included in ecosystem models to be able to describe the long-term plant and soil C and N development. Our results 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 Comparison of the three ECM modeling approach

405 The "nonlim" approach in this study shows an overestimation of plant growth and also larger biases in soil N than the "implicit" and "explicit" approaches even after calibration (Table 4). 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.
410 A previous CoupModel application by Wu et al. (2012) demonstrated that the "nonlim" approach could possibly

describe short-term C and water dynamics for a Finnish forest site. The same "nonlim" approach was also used in Franklin et al. (2014) to simulate Swedish forest biomass growth and its competition with ECM. These seem to suggest that plant growth and the C cycle can be simulated reasonably with the "nonlim" approach, although a slight trend of overestimation is exhibited. However, our modeling exercise further indicates that in this simplified approach soil C and N are uncoupled (Fig. 5) and therefore this approach is 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 model structure of N. Thus, the following discussion focuses on the other two modeling approaches.

Moore et al. (2015) demonstrated that accounting ECM in ecosystem models would substantially affect soil C storage, and that the impact is largely dependent on plant growth. Our study additionally shows that ECM representation in ecosystem models could further feedback into the predicted plant growth through N. When ECM are implicitly included, the model simulates a 48 g C m^{-2} (average of four sites, ±std: 86) lower plant biomass compared to the measured data. When they are explicitly included, the difference becomes even larger, 185 (±35) g C m^{-2} (Table 4). Including ECM explicitly in the model therefore results in decreased plant growth. This somehow differs from the general assumption that growth should be higher in mycorrhized plants, i.e., boreal forest trees, due to optimized nutrient supply (Pritsch et al., 2004; Finlay et al., 2008, see also review by Smith and Read, 2008). This discrepancy can be possibly due to: *1)* an enhanced root litterfall due to a higher turnover of ECM mycelia. Simulated litter production is 50 to 110 g C m^{-2} yr^{-1} higher by the "explicit" approach compared to the "implicit" approach. This could be explained by the conceptually considering the ECM implicitly into the roots where the litterfall rate of roots is c.a. three times lower than that of ECM (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)). These two approaches thus show large differences in simulating litter production. The discrepancy could also be due to: *2)* an enhanced N immobilization in ECM under N-limited conditions based on the assumption that ECM retain more N in their own biomass in response to plant allocation of newly assimilated C (Nehls et al., 2008). The increasing trend towards the northern sites shown by the constrained optimum ECM fungi C allocation fraction parameter (Fig. 8) also indicates a higher proportional C "investment" by the forest plants in 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 ECM 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. This is also shown by the smaller accepted ratio in the calibration (Table 4) which can be explained by model complexity; i.e. as more parameters are included for calibration, accepted combinations of parameter sets become less likely.

It should also be noted that the "explicit" and "implicit" approaches show considerable difference in estimating soil respiration. Compared to the "implicit" approach, the "explicit" approach simulates a 15% higher soil respiration for the northernmost site and 40% for the southernmost site. The measured soil respiration at Flakaliden

is 400 to 590 g C m^{-2} yr^{-1} (Coucheney et al., 2013) and 460 to 520 g C m^{-2} yr^{-1} at Asa (Von Arnold et al., 2005) and these data generally align better with the modeled results by the "explicit" approach (Fig. 5). The estimated higher soil respiration is partly due to the higher litter production and consequently soil respiration in the "explicit" approach, but also due to a higher decomposition of the old organic matter (humus) as shown by the constrained higher humus decomposition coefficient, K_H in the "explicit" approach (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 (Hartley et al., 2012; Moore et al., 2015; Lindahl and Tunlid, 2015; Parker et al., 2015; Baskaran et al., 2016). The modeled higher soil respiration further explains the minor losses of soil C and N in the southern sites, and also a higher mineral N pool thus higher N leaching in the "explicit" approach (Fig. 3 and Fig. 4).

4.2 Constrained parameters

Our constrained parameters generally indicate a shift in the role of ECM from northern to southern sites with a corresponding shift in both climate and soil conditions (Fig. 6, Fig. 7 and Fig. 8). The ECM N uptake parameters show a decreasing trend with increasing soil N availability in the "explicit" approach. This is consistent with observations 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 (e.g., Hyvönen et al., 2008; Näsholm et al., 2013). Shown 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. Similar trend is also found for the organic N uptake parameter in the "implicit" approach, but with a larger site to site difference, thus indicating a stronger response to soil N conditions (Fig. 6). This is expected as more detailed ECM processes in the "explicit" approach should result in more internal interactions and feedbacks, thus more resilience to the change of environmental conditions.

Most ECM 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, $NORG_{RATE}$ and ECM 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.

The correlation between the humus decomposition coefficient, K_H and the fraction of C that is allocated to the rooting zone, F_{ROOT}, reflects the strong connection of the root-ECM symbiosis and also soil N availability. When ECM are explicitly modeled, this becomes less important, which can be explained by a more detailed internal cycling of N supply and uptake from the ECM; i.e., plant N supply is further regulated by simulated higher root litter input and N uptake from the soil (Fig. 3, Fig. 9). The correlations between the ECM fungal litter rate and ECM fungal N uptake rates in the "explicit" model, and that between fungal N uptake rates, $NORG_{RATE}$ and the microbial C/N ratio, CN_{MIC}, for the northern sites (Fig. 9) further indicate the close coupling between ECM fungal N uptake (N loss from the soil) and litter production (N input to the soil). Such an incorporated tight cycle is of major importance for the overall plant N supply, and thus for the C and N dynamics of plant and soil at the N limited sites in the boreal forests. One of the major difficulties of explicitly including ECM in ecosystem models is the unknown turnover of ECM 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). Additionally, 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. The present model calibration thus provides a key set of ECM parameters that can be further tested by field observations, and more importantly, can in combination with the identified model parameter correlation, act as a guideline 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 explicitly accounts for the links and feedback between the ECM, soil, and plant. The comparison of three modeling approaches which differ in complexity demonstrates that the simple "nonlim" approach cannot describe the soil C/N ratio, and also overestimates the 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 on ecosystem dynamics. However, the "implicit" approach shows a much lower litter production and soil respiration than the "explicit" approach, and both approaches 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 that ecosystem models need to incorporate ECM into their model structure for a better prediction of ecosystem C and N dynamics.

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 will be available to download from the home page and a link to a repository for MS Visual studio can also be provided. CoupModel is written in the C programming language and runs mainly under Windows systems. 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).

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APPENDIX:

Table A.1 Model functions describing plant growth, ECM 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 ECM fungal growth and N exchange to plant

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

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

ECM 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 ECM growth to N availability, c_{frt} = total root C content (g C m^{-2}), $FRAC_{OPT}$ = optimum ratio between root and ECM 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 (both mineral and organic N) which is transferred from ECM to plant.

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

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

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

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

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

ECM 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.

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

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

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

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

If ECM 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 mycelia in total fungal biomass, L_{MYC} = litter rate of mycorrhizal mycelia, L_M= litter rate of ECM fungal mantle tissue.

ECM 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 ECM fungal and fine root biomass, M_{OPT} = optimum mycorrhization degree, and m=1, when $\frac{c_{fungi}}{c_{frt} \times FRAC_{OPT}} \geq M_{opt}$

Uptake and transfer processes of ECM and plant

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

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

$n_{fungi \rightarrow plant} = n_{fungiavail}$ 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.

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

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

11.2 $n_{NO3 \rightarrow fungi} = n_{NO3soil} \times f(n_{avfungi})$ 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} = ECM fungal biomass (g C m^{-2}), $FRAC_{MYC}$ = fraction of mycorrhizal mycelia in total ECM biomass.

ECM 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} = ECM fungal biomass (g C m^{-2}), $FRAC_{MYC}$ = fraction of mycorrhizal mycelia in total ECM biomass.

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

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

where T_l = leaf temperature (°C) and P_{min} (-4°C), P_{O1} (10°C), P_{O2} (25°C), P_{max} (40°C) are coefficients.

Photosynthetic response to leaf C/N ratio

		1	$CN_l < p_{CNOPT}$
13	$f(CN_l) =$	$1 + (\frac{cn_l - p_{CNOPT}}{p_{COPT} - p_{CNTH}})$	$p_{CNTH} \leq CN_l \geq p_{CNOPT}$
		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 ECM 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 ECM fungal mantle.

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

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

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

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

670 17.3 $$f(n_{orgavfungi}) = NUPT_{ORGFRACMACX} \times UPT_{ORG}$$ for litter/humus

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.

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

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 $\min_{NPlant} < n_{fungi \rightarrow plant}$

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

Where $\min_{NPlant}$ = defined minimum ECM 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}).

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Table A1 (d) Overview of model parameters; previous CoupModel parameters are mostly from Svensson et al. (2008a) and ECM parameters are from literature value (Meyer et al. (2012) and references therein)

Parameter	Description	Value	Unit
CN_{FMIN}	Minimum ECM C/N ratio for fungal N demand	18	gC gN^{-1}
690 CN_{FMAX}	Maximum ECM 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}
	Coarse roots and stem	450	gC gN^{-1}
E_L	Coefficient for radiation use efficiency	8	
695 E_{NH4}	ECM 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 zone which is made available for ECM	0.5	
	$FRAC_{MYC}$	Fraction of ECM mycelia in total biomass	0.5	
	$FRAC_{OPT}$	Optimum fraction between root and ECM biomass	0.3	
	K_{RGF}	Growth respiration coefficient of ECM	0.21	d^{-1}
	K_{RMi}	Maintenance respiration coefficient of plant compartment i (i = fine roots, coarse roots, stem, leaves)	0.001	d^{-1}
	K_{RGi}	Growth respiration coefficient of plant compartment i	0.21	d^{-1}
	L_{FRT}	Litter rate of fine roots	0.0027	d^{-1}
	L_{CRT}	Litter rate of coarse roots	0.000027	d^{-1}
	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 ECM mantle (if fungal growth = detailed)	0.0014	d^{-1}
	L_{MYC}	Litter rate of ECM mycelia (if fungal growth = detailed)	0.01	d^{-1}
	M_{OPT}	Optimum mycorrhization degree of fine roots < 2 mm	0.5	
	N_{RET}	N retained by ECM from senescence	0.54	d^{-1}
	$NUPT_{FRACMAX}$	fraction of mineral N available for uptake	0.08	d^{-1}

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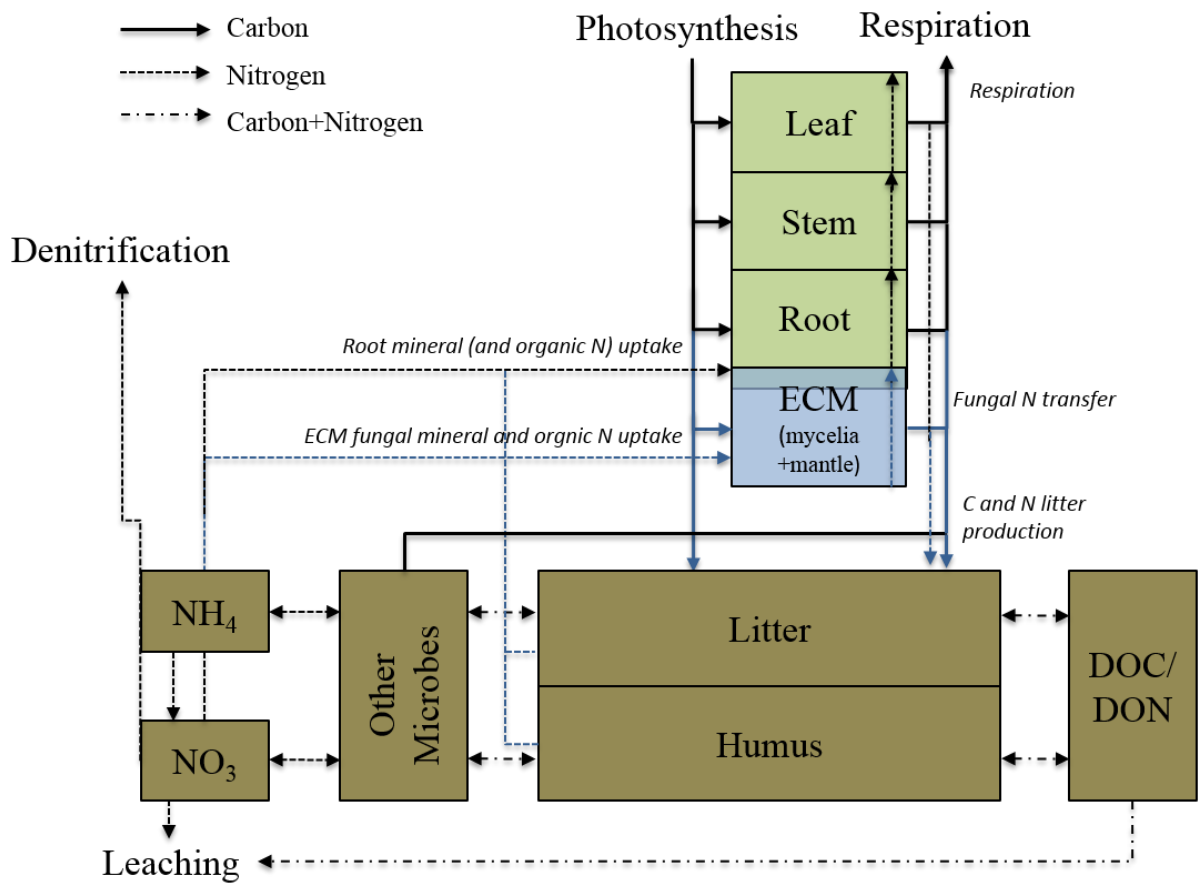


Figure 1 A simplified overview of C and N fluxes between plants, mycorrhiza fungi, and the soil in the Coup-MYCOFON model. Light blue indicates the newly implemented MYCOFON model

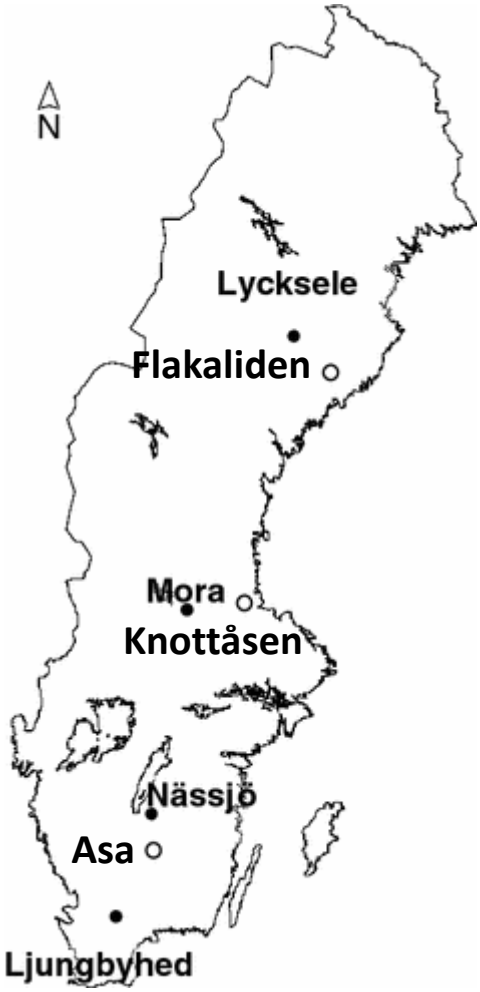
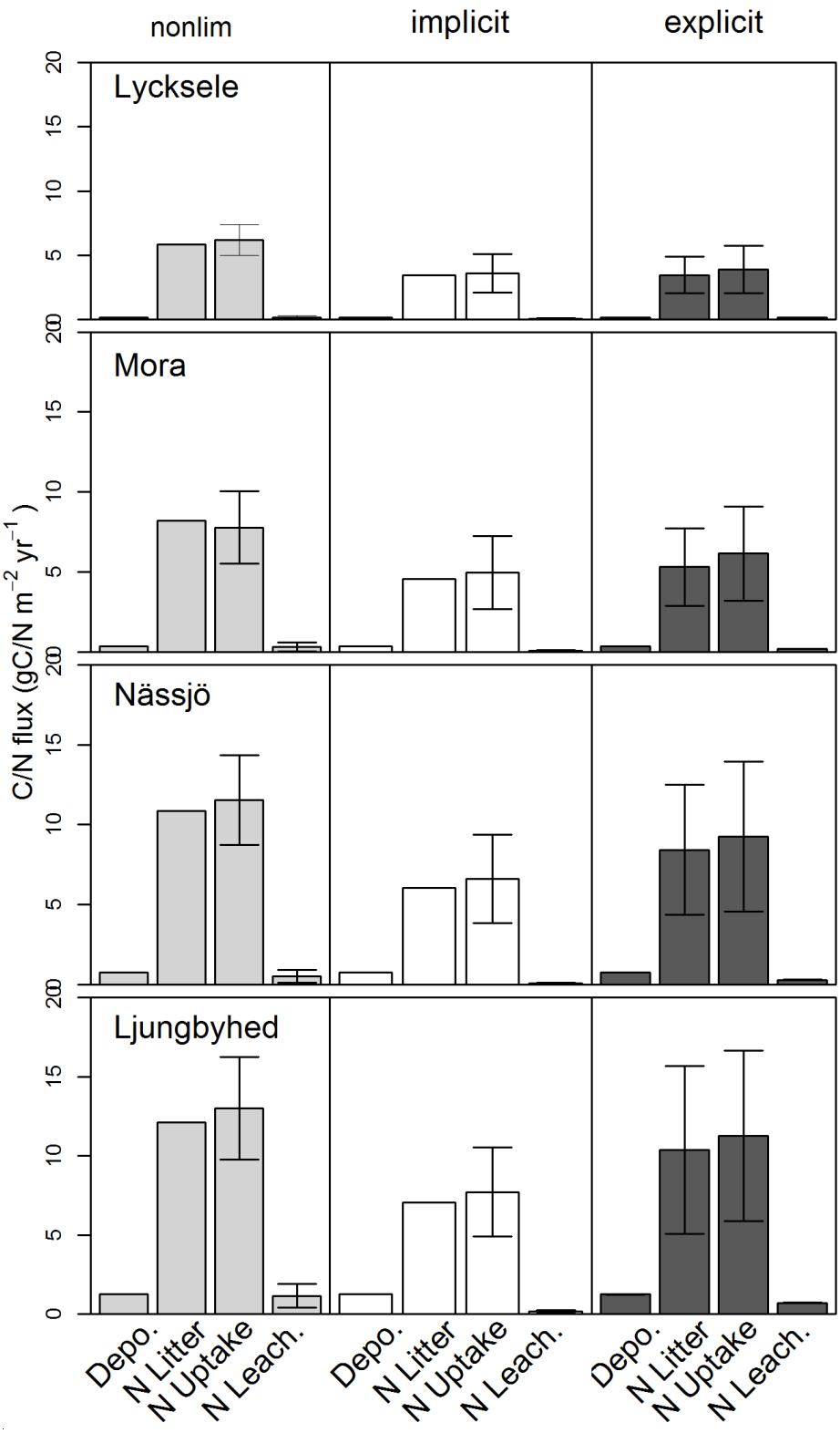


Figure 2 Location of the four study sites in Sweden modified from Svensson et al. (2008a). Filled cycles represent the studied four sites. Open circles are the measured sites reported in Lindroth et al. (2008) used for comparison



960 **Figure 3 Soil N fluxes for the nonlim (grey columns), implicit (white), and explicit (black) model approaches, same color scheme used for the other figures. Presented are the major N inputs (N deposition, total N litter production, added to the soil litter pool by fresh litter), and outputs (N uptake from the plant/ECM fungi, N leaching), 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**

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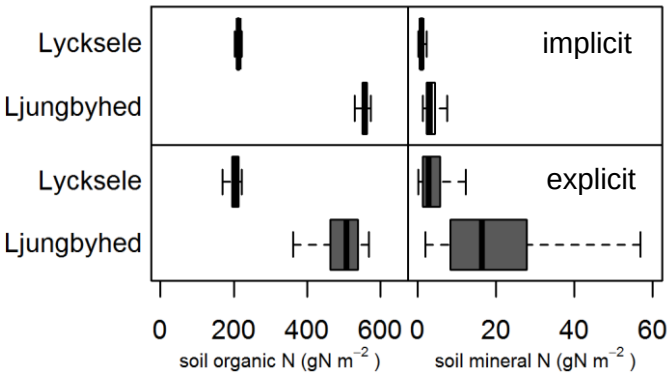

Figure 4 Average soil organic and mineral content in the implicit ECM model (upper graph) and explicit ECM model (lower graph) for the two sites Lycksele and Ljungbyhed. Box plots indicate the median (bold line), the 25th and 75th percentile (bars), and the 10th and 90th percentile (whiskers)

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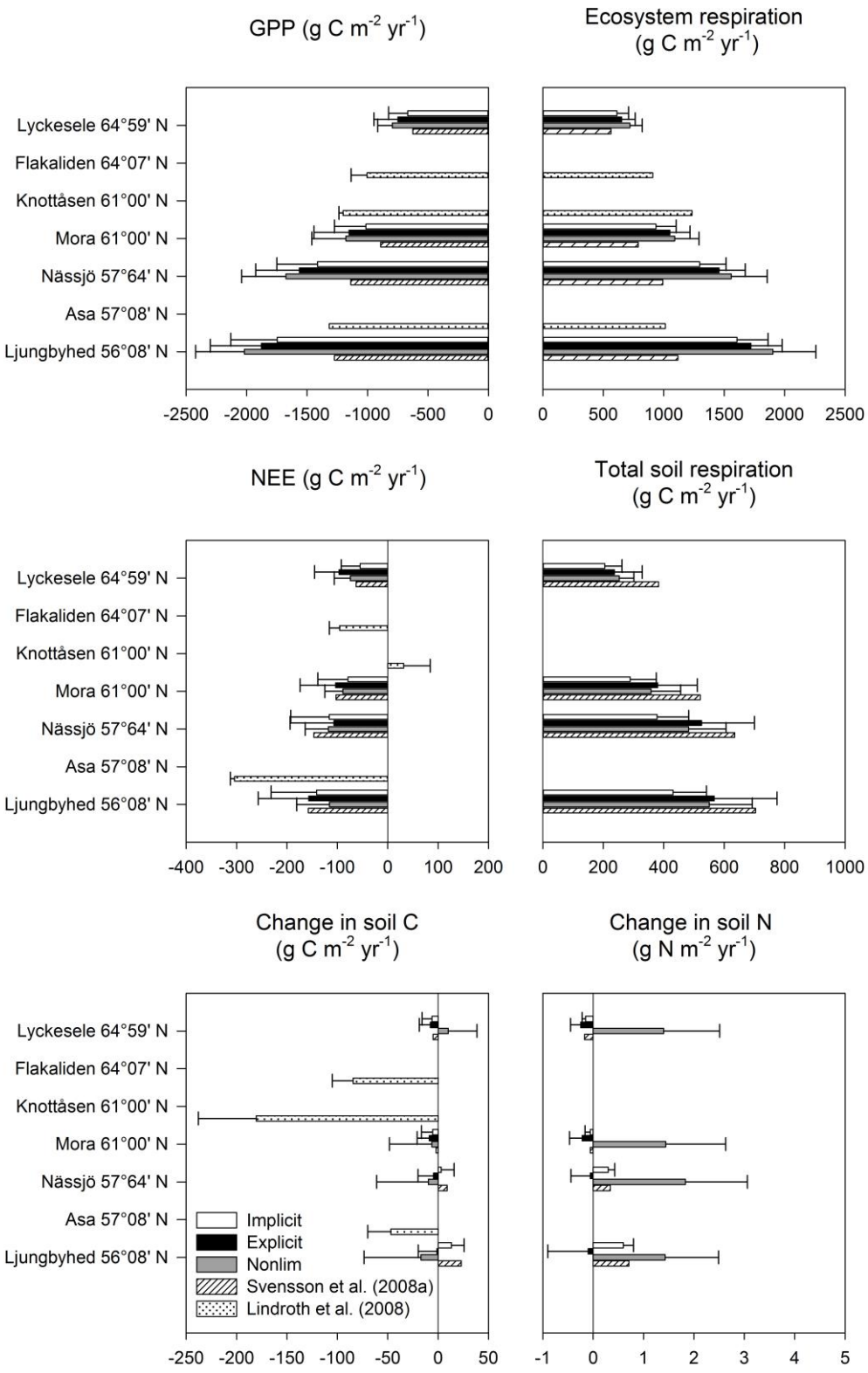

Figure 5 Simulated GPP, ecosystem respiration, NEE, soil respiration, change in soil C and change in soil N for all four sites with the three ECM modeling approaches and also compared with modelled data by Svensson et al. (2008a) and measurements by Lindroth et al. (2008)

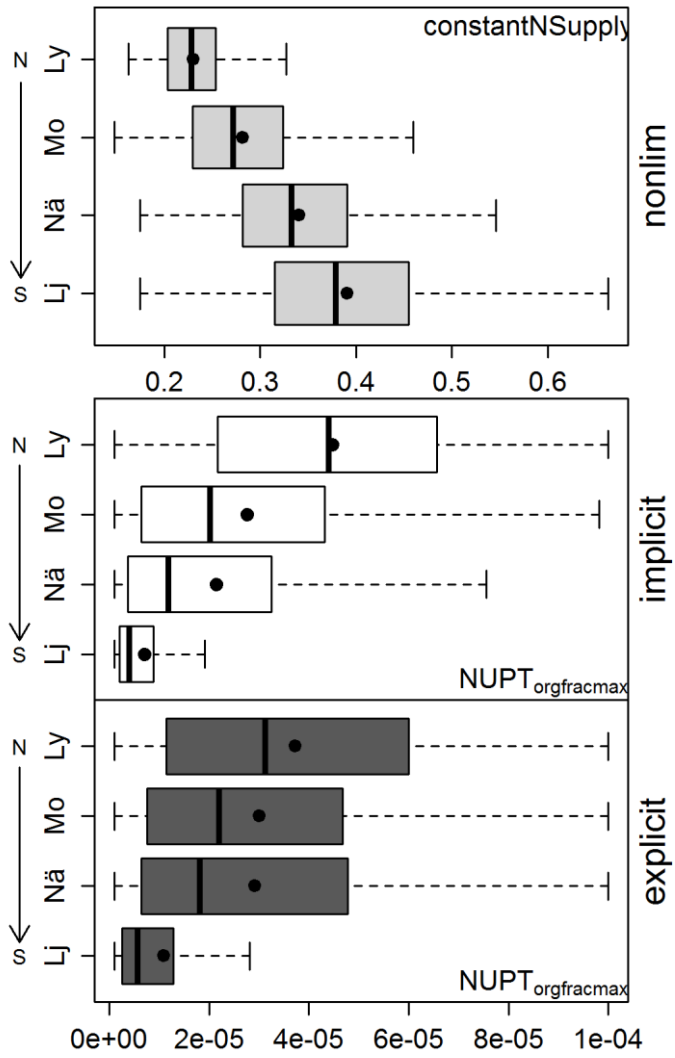

Figure 6 Posterior parameter distributions for N uptake parameters: constant N supply rate in the "nonlim" approach (grey) and organic N uptake capacity in the implicit (white) and explicit (black) ECM model approaches. Distributions are presented as box plots over the prior range of variation (corresponding 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)

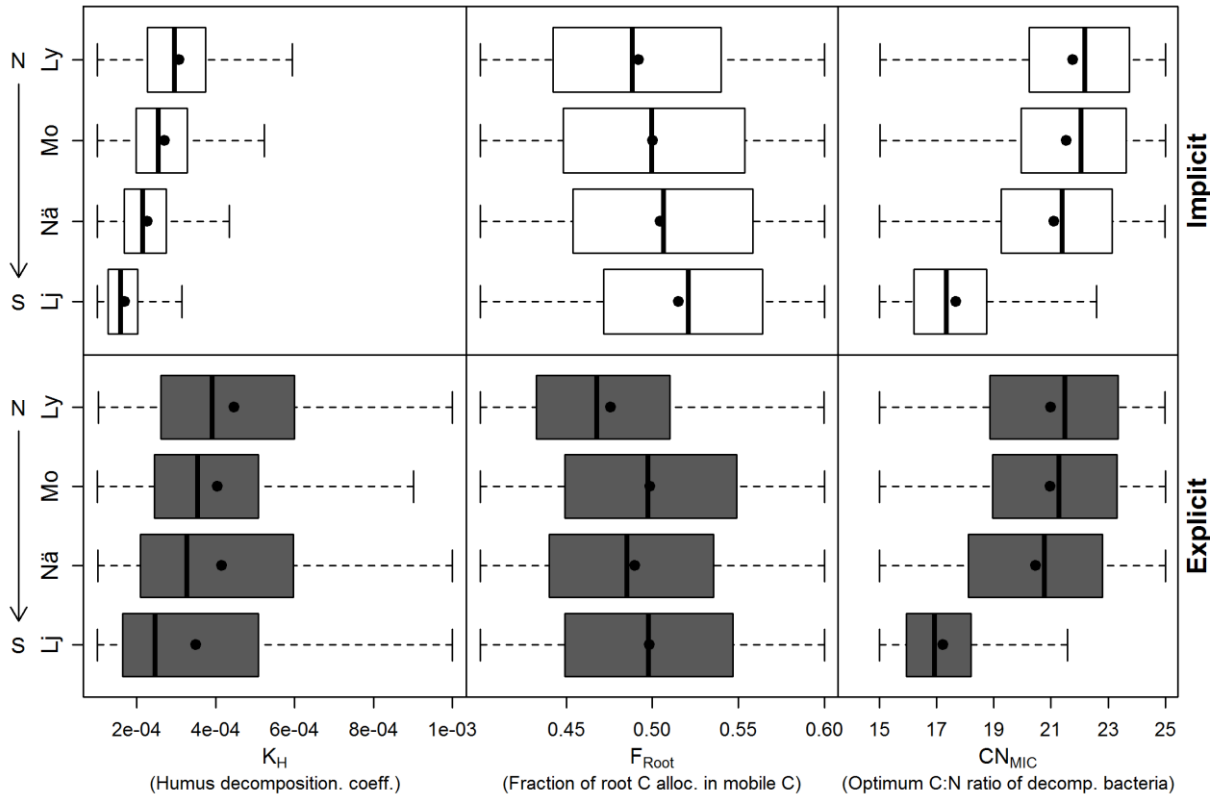

Figure 7 Posterior parameter distributions for common parameters using the implicit (top: white) and explicit (bottom: black) ECM approaches for four different sites from North to South. Distributions are presented as box plots over the prior range of variation (corresponding to the range in the x-axis).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

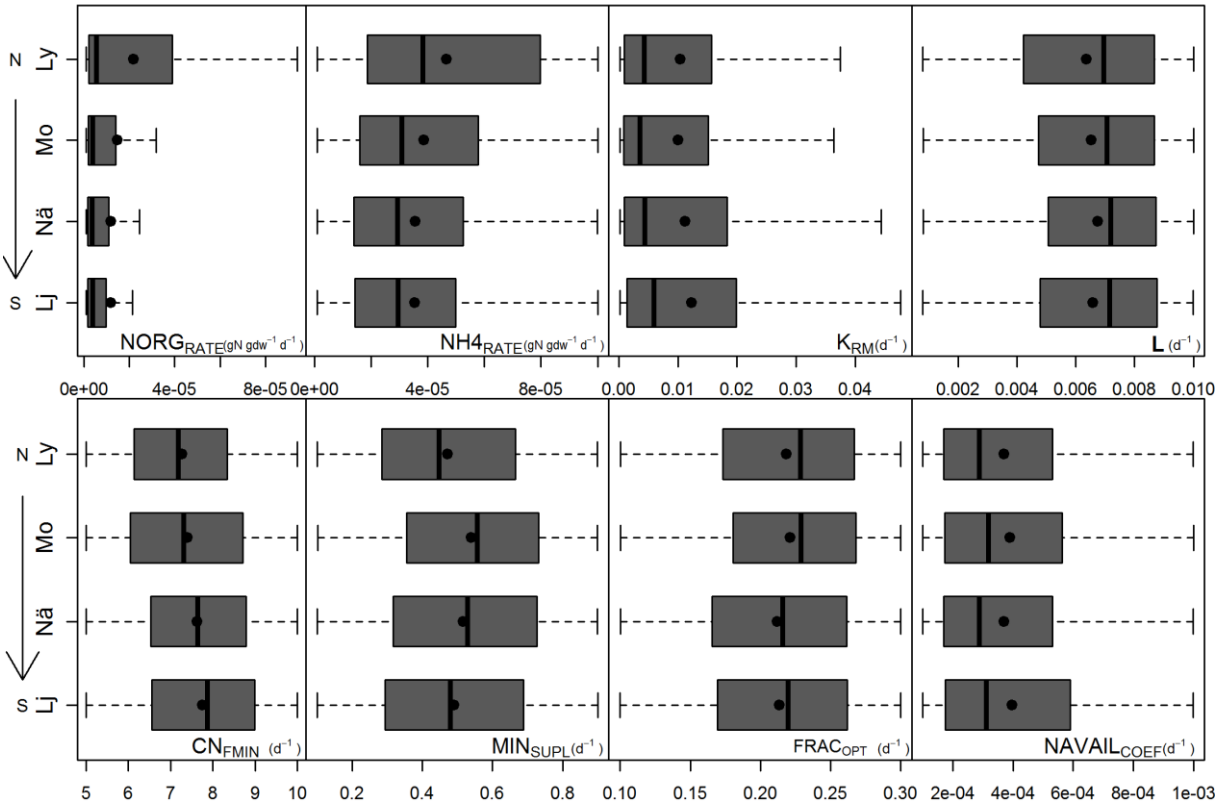

Figure 8 Posterior parameter distributions of ECM fungal specific parameters (from top left to bottom right): organic N uptake rate (*NORG*$_{RATE}$), ammonium uptake rate (*NH4*$_{RATE}$), respiration coefficient (*K*$_{RM}$), ECM fungal litter rate coefficient (the rate at which mycelia and mantle die and add to the soil litter pool, *L*), minimum ECM fungal C/N ratio (CN$_{FMIN}$), ECM minimum N supply to plant (*MIN*$_{SUPL}$), optimum ratio between ECM 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 mean (black point), the 25th and 75th percentile (bars), and the 10th and 90th percentile (whiskers)

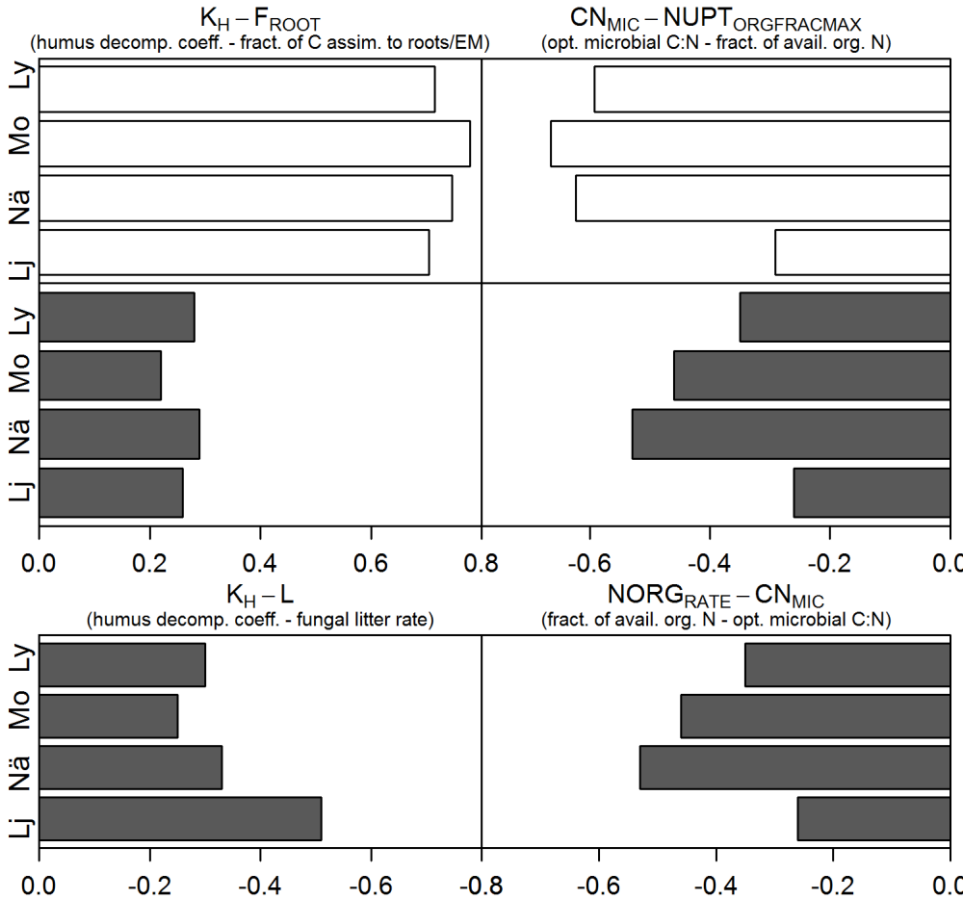

Figure 9 Correlation between model parameters, given as the Pearson correlation coefficient, for the implicit (white) and explicit ECM (black) approaches. Top left: correlation between humus decomposition coefficient (K_H) and the fraction of C assimilates (GPP) directed to ECM and roots (F_{ROOT}).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

Table 1 Main characteristics of previous ecosystem models include ECM

Models	Time step	Elements included	Differentiation in mycelia and mantle	Organic matter decomposition	C allocation	Plant N uptake	Is ECM sensitive to soil N
ANAFORE, Deckmyn et al. (2011)	hourly	C, N	No	Yes	Fraction of C allocated to roots, regulated by water and N	Function of the available mineral and organic N pools	No
MoBiLE and Mycofon, Meyer et al. (2010, 2012)	Daily	C, N	Yes	No	A certain ratio between root and ECM biomass exists to reach the optimum degree of mycorrhization, regulated by soil N and temperature	Separated root and mycelia mineral N uptake and regulated by plant and ECM N demand	Yes
MySCaN, Orwin et al. (2011)	Daily	C, N, P	No	Yes	Constant fraction of plant C assimilates, modified by nutrients	Driven by C to nutrient ratios in pools	No
Moore et al. (2015) model	Monthly	C	No	Yes	Constant fraction of plant C assimilates		No
Baskaran et al. (2016) model	Annual	C, N	No	No	Constant fraction of plant C assimilates	Root inorganic N uptake by Michaelis-Menten function and ECM N uptake by ECM C to N ratio	No
Coup-MYCOFON (This study)	Daily	C, N	Yes	No	Similar to MoBiLE	Similar to MoBiLE, but allows organic N uptake for ECM	Yes

Table 2 Maximum and minimum parameter values prior to Bayesian calibration for the nonlim, implicit, and explicit model approaches

A. Common parameters (all three approaches)

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

C. ECM fungal parameters of the "explicit" approach

Parameter	Unit	Min	Max
ECM 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
ECM respiration coefficient			
K_{RM}	d^{-1}	0.0002[b]	0.05
ECM litter rate			
L	d^{-1}	0.0008[c]	0.01
Minimum ECM fungal C/N ratio			
CN_{FMIN}	d^{-1}	5[d]	10
ECM minimum N supply to plant			
MIN_{SUPL}	d^{-1}	0.1[e]	0.9
Optimum ECM 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)

Table 3 Climatic and soil data, and initial settings of the four study soils applied in all model approaches

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

[a] 30-year (1961 to 1991) annual average [b] According to Skogsdata for a 100-year-old forest (2003: http://www.slu.se/en/webbtjanster-miljoanalys/forest-statistics/skogsdata/)

Table 4 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	10	32	10
Mora	7815	10	29.1	10
Nässjö	10443	10	27.2	10
Ljungbyhed	11501	10	19.8	10

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