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Comparing field inventory with mechanistic modelling and light-use efficiency modelling based approaches for estimating forest net primary productivity at a regional level

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Monitoring of forest carbon fluxes for the purpose of national greenhouse-gas inventorying and reporting are commonly based on repeated large-scale field measurements. Alternate approaches based on modelling of forest growth offers potential benefits such as cost savings and detailed assessments of involved carbon fluxes. We calculated the net primary productivity (NPP) of Swedish forests using two methods based on mechanistic and light use efficiency (LUE) modelling. The results were evaluated using data from traditional field inventories, and showed large variations in calculated NPP for the two methods. The national mean NPP for each method ranged between 0.35 and 0.59 kg C m^{-2} year^{-1}, with an average regional difference of ±50%. Despite the large differences in calculated NPP, mechanistic modelling was promising for estimating the spatial distribution with an r^2 value of 0.92 for predicting NPP of mainland Sweden.

Introduction

Forests play an important role in global climate change. They have potential to store large amounts of carbon both in soil and in living biomass (Pan *et al*. 2011), which helps offset part of human-induced CO_2 emissions and mitigates climate change. This potential is recognized in global climate politics such as those regulated by UNFCCC and the Kyoto protocol. Under article 4 of the UNFCCC, countries are committed to report national greenhouse gas (GHG) emissions and removals. This includes carbon emission due to forest clearing as well as emissions and uptake related to forest growth. The reported fluxes should encompass five defined forest carbon pools (above- and below ground living biomass, dead wood, litter, and soil organic matter) and be supported by inventories using comparable methods that are consistent with the IPCC guidelines (Eggleston *et al*. 2006). Several different methods, with various benefits and drawbacks, can be used for forest carbon inventorying.

A commonly used method to estimate forest carbon fluxes is the stock-change method (Richards and Stokes 1995), which is based on repeated measurements over time of forest stock at distinct locations. Measured tree dimensions are converted to whole-tree carbon using species-specific equations. Other carbon pools, such as deadwood, litter and soil organic carbon, can be measured at the sample location as well.

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Total forest carbon flux for each year is calculated as the interpolated change in carbon pools between two sample-events. Measurements at sample locations are assumed to be representable for larger regions, either by extrapolating the results of the field inventory or by relating emissions and uptake to land use categories that are determined using remote sensing and/or cadaster data (e.g. Hansen *et al*. 2010).

The stock-change methods relies on field inventorying to estimate carbon fluxes. Alternate methods are common within the scientific community that instead estimates carbon fluxes by modelling the processes involved in forest growth. Two distinct approaches can be distinguished, separated by what is measured related to forest carbon fluxes. Mechanistic or process-based modelling is driven by climate data, and simulates forest carbon fluxes based on an understanding of how processes such as photosynthesis, respiration and nutrient allocation are related to environmental variables (Prentice *et al*. 2007). Light use efficiency (LUE) modelling (Prince 1991) is used to relate forest growth to vegetation indexes which can be derived from remotely sensed satellite data. The measured vegetation index is converted to forest growth using a conversion efficiency parameter, which is dependent on both climate and vegetation.

Each of these two alternate methods has several potential benefits regarding forest monitoring compared with using traditional forest inventorying, by providing spatially and temporally detailed estimates of forest carbon fluxes (Table 1). A limiting factor to the applicability of the models is that empirical relationships often are highly site-specific and variations in parameter values may greatly affect model results (Gobron *et al*. 1997, Sitch *et al*. 2008, Galbraith *et al*. 2010). Successful use of mechanistic modelling and LUE-based approaches in describing forest processes relies on accurate parameterization (Knorr and Heimann 2001) as well as a correct representation of processes in the model design.

Those three approaches to forest carbon flux inventorying (field inventorying, mechanistic- and LUE modelling) are based on inherently different assumptions related to carbon monitoring. They rely on measurements of different metrics related to carbon fluxes: tree volume, climate or spectral radiation. This results in differences in the spatial distribution of calculated carbon fluxes depending on which method is used (e.g. Mitchard *et al*. 2014, Ometto *et al*. 2014, Réjou-Méchain *et al*. 2014), and also limits the inclusion/exclusion of measured carbon pools. Unless those differences are taken into account, compar-

Table 1. Potential advantages and disadvantages of different approaches for carbon monitoring.

Method		Benefits (+) and disadvantages (–)
Field inventorying	+	Reliable estimates of aboveground tree biomass
	+	High flexibility in what to measure
	–	Difficult to assess changes in soil C
	–	Low temporal resolution of measurements
	–	Hard to measure forest floor NPP
Mechanistic modelling	+	Detailed description of involved fluxes such as photosynthesis and respiration
	+	High temporal resolution of results
	+	Future predictions possible using climate scenarios or alternate management regimes
	–	Dependent on several uncertain parameters
	–	Hard to represent all aspects of spatial variability
	–	Dependent on weather and vegetation data
Light use efficiency	+	Saves manpower by directly monitoring large areas
	+	High spatial resolution, suitable for estimating the impact of e.g. harvest, storms
	+	and fires
	–	Soil fluxes hard to assess
	–	Susceptible to cloud interference

isons of results produced by different methods may be misguiding.

In this study, we compared the results of three methods for estimating carbon fluxes, with each method corresponding to one of the approaches mentioned above. Data on forest growth from the national Swedish forest inventory were used to calculate forest net primary productivity (NPP). This was compared with the results of two methods based on mechanistic and LUE modelling. The model results were evaluated for accuracy relative to the inventory results and regarding the spatial distribution of their results to highlight the effects of methodological differences.

We chose to use NPP as the base for method comparison even though it is only a part of the total forest carbon balance, omitting heterotrophic respiration. The choice was made since the methods differ distinctly in their potentials for measuring soil respiration, with e.g. the LUE method being unsuitable for directly measuring soil fluxes. Soil carbon fluxes are inherently difficult to measure (Liski 1995, Muukkonen *et al.* 2009) especially for countries lacking repeated large-scale forest/soil inventories and are sometimes excluded from GHG reports (e.g. Krtkova *et al.* 2016, Romano *et al.* 2016).

Material and methods

Methodological overview

This study utilized three methods for carbon monitoring which are based on various approaches (*see* Fig. 1). The first method calculates NPP using reported values of tree volume and growth from the Swedish national forest inventory (SNFI) in combination with biomass expansion factors and turnover rates, partly based on the methods described by Liski *et al.* (2006). This gives a baseline of NPP values against which the two other methods can be compared. The second method is a process-modelling based approach that combines the use of the model Biome-BGC, which is driven by climate input, with tree species- and age distribution data from the SNFI. The third method is MODIS yearly NPP product MOD17A3, which is based on satellite estimates of absorbed photosynthetically active radiation in combination with meteorological data and model-derived look-up tables. The three methods are henceforth referred to as "SNFI", "Biome-BGC" and "MODIS", respectively. They were compared using simple linear regression to show how the NPP values of the second and third methods compare to those of the SNFI. All data used are publicly available and free to use.

Study scope

Our NPP comparisons were limited to the Swedish forests. Those cover about 69% of the Swedish land area (Nilsson *et al.* 2013) and belong, from north to south, to the boreal, hemiboreal and nemoral vegetation zones, respectively. *Pinus sylvestris* and *Picea abies* are the dominant tree species constituting 39% and 41% of the total volume, respectively. Broad-leaved trees are often mixed with the conifers, with various species of *Betula* as most common (12% of total volume), but are also existing as pure broad-leaved stands. In the southernmost nemoral zone, *Quercus robur* and *Fagus sylvatica* forests are common. Most of the forests are managed, with a varying degree of intensity.

This study covers two consecutive five-year periods, 2000–2004 and 2005–2009. The units of the NPP comparisons were the Swedish counties: 21 administrative regions ranging in size between 0.29 and 9.73 Mha (*see* Fig. 2). Sometimes for analytical purposes the division between northern (6 northern counties) and southern Sweden (15 southern counties) was made (thicker black line in Fig. 2). This division corresponds approximately to boreal and hemiboreal zones. Before analysis and comparisons all spatially distributed data (D) used in this study were averaged on a county level. Each data gridcell (G) was given a weight proportional to the fraction of forest cover (F) in that gridcell, derived from the CORINE 2000 land-cover data set (Büttner *et al.* 2004). The weighted data were then used to calculate a county average as follows:

$$D_{\text{county}} = \frac{\sum(D_G F_G)}{\sum F_G} \quad (1)$$

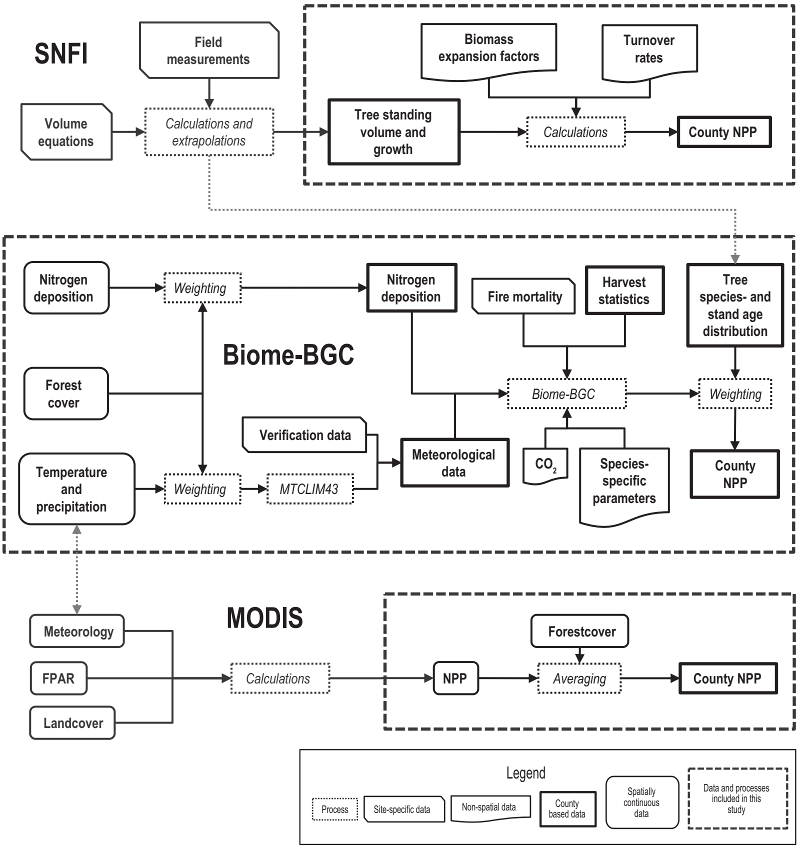

Fig. 1. Overview of the data and processes involved in calculating NPP according to the three methods used in this study.

National forest inventory

The Swedish national forest inventory is performed yearly by the Swedish University of Agricultural Science in about 30 000 permanent sample-plots that are inventoried with a five-year return interval. Tree species, age, height and diameter are measured together with a multitude of other variables. Using nationally developed formulas (Näslund 1947, Marklund 1988, Petersson and Ståhl 2006), several properties are calculated such as tree volume and division of tree biomass into subcompartments. Statistics for the Swedish counties based on the inventory results are made available online and published annually (Nilsson *et al*. 2013).

Using the single-tree biomass functions of Marklund (1988) in combination with the data from the Finnish national forest inventory, Lehtonen *et al*. (2004) developed biomass expansion factors (BEFs) based on stand age for Scots pine, Norway spruce and birch to convert stem volumes to biomass weight for whole trees (w) and different compartments (i) at a stand level. These BEFs were used together with the reported change in stem volume (ΔV, m^3) from the SNFI for the periods 2000–2004 and 2005–2009 to calculate yearly stand growth in kg biomass per m^2, with birch BEFs representing all broad-leaved forests. Litter production was calculated using turnover rates from Lisky *et al*. (2006) for different tree compartments (t_i; *see* Table 2) together with standing forest volumes (V, m^3) from the SNFI. NPP (kg C m^{-2} year^{-1}) was estimated, for all combinations of stand age (a) and tree species (s), as the sum of tree biomass increment and litter production assuming a biomass carbon content of 50% as follows:

$$\mathrm{NPP}_{\mathrm{county}} = 0.5\left[\Delta V \times \mathrm{BEF}_w + \sum\left(V \times \mathrm{BEF}_i \times t_i\right)\right. \quad (2)$$

Average NPP was calculated for each county based on the areas for specific stand ages and species reported in the SNFI as follows:

$$\mathrm{NPP}_{\text{county}} = \frac{\sum_{s,a}\left(\mathrm{NPP}_{s,a} \times \mathrm{Area}_{s,a}\right)}{\sum \mathrm{Area}} \quad (3)$$

Biome-BGC model

The model used in this study was the process-based model Biome-BGC ver. 4.2. It simulates carbon, nitrogen and water fluxes among compartments in the soil, vegetation and atmosphere on a daily time step (Golinkoff 2010). Processes covered in the model include photosynthesis, evapotranspiration, respiration, decomposition, nutrient allocation, and mortality. Biome-BGC uses temperature, precipitation, nitrogen deposition, atmospheric CO_2 concentration, altitude and latitude as input parameters, combined with site- and species-specific parameters (Table 3).

Meteorological data for the period 2000–2009 were acquired from the European Climate Assessment & Dataset project (Haylock *et al.* 2008); they included daily maximum- and minimum temperature and precipitation, available on a 0.25° grid. Those meteorological data were used as input to calculate incident shortwave radiation, humidity and day length with the program MTCLIM43 (Thornton and Running 1999, Thornton *et al.* 2000). The output shortwave radiation from MTCLIM43 was multiplied by 1.55 to better agree with the observations from two research sites, Norunda (Lundin *et al.* 1999) in central Sweden and Flakaliden (Linder 1995) in northern Sweden. Also, the snow correction factor was removed following the advice of Bohn *et al.* (2013). Nitrogen deposition values for the period 2000–2009 were acquired from the Swedish Meteorological and Hydrological Institute (SMHI). Historical N deposition values were based on deposition data from 1860 (Dentener 2006) and interpolated assuming that N-deposition patterns follow the atmospheric CO_2 concentrations until 1985 and then levels off (Schöpp *et al.* 2003). As the resolution of the 1860 data set was very coarse, 5° × 3.75°, it was linearly interpolated to the resolution of 25 × 25 km.

To simulate the effect of fire mortality, a linear relationship between latitude and fire occurrence (Fig. 3) was assumed based on stud-

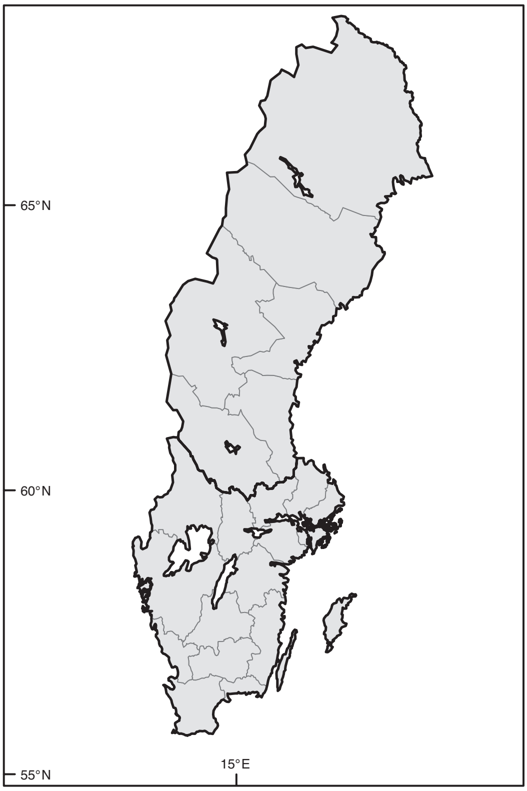

Fig. 2. The 21 Swedish counties that form the spatial basis for this study. The thicker border at 60°N is the border between northern and southern Sweden, which was introduced for analytical purposes and discussion.

Table 2. Tree-compartment yearly turnover rates (Liski *et al.* 2006).

	Spruce forest	Pine forest	Broad-leaved forest
Foliage	0.1	0.22	0.78
Branches and roots	0.0125	–*	0.0135
Stump bark	0	0.003	0.0001
Reproductive origins and stem bark	0.0027	0.0052	0.0029
Fine roots	0.811	0.868	1

* Turnover rates are related to stand age and calculated separately for each age group.

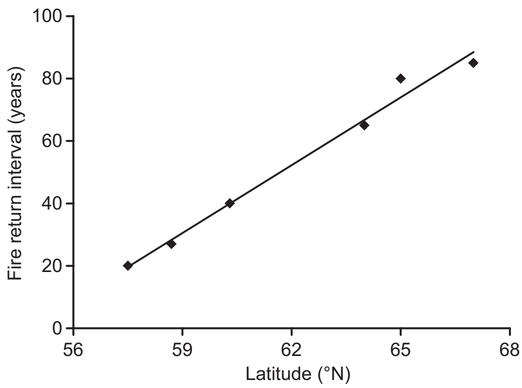

Fig. 3. Fire return interval (FRI) used in the Biome-BGC simulations. A linear relationship with latitude was assumed (FRI = 7.24 × latitude – 397, r^2 = 0.986, p = 0.00007) based on six studies of historical fire occurrence.

Table 4. Forest ages (years) simulated by Biome-BGC and corresponding age classes reported by the Swedish national forest inventory (SNFI).

Biome-BGC	SNFI
3–7	0–10
13–17	11–20
23–27	21–30
33–37	31–40
48–52	41–60
68–72	61–80
88–92	81–100
108–112	101–120
138–142	121–160
168–172	> 161

ies of historical fire frequencies (Zackrisson 1977, Engelmark 1984, Page *et al*. 1997, Niklasson and Granström 2000, Niklasson and Drakenberg 2001, Granström and Niklasson 2008). This relationship and an average fire mortality rate of 10% per occasion, estimated using values obtained from Linder *et al*. (1998), were combined to acquire the annual fire mortality fractions used in the model during the spin-up phase. The fire return interval (FRI) value from the southernmost site was assumed to be representative for all counties at lower latitude (< 57°N) to avoid extrapolation into unrealistic values of a FRI close to 0.

Soil depth was assumed to be a constant 1 m across all simulation areas, which is generally the case except for the coastal regions of Sweden between 57° and 60° latitude where soil depth is often below 0.7 m according to the Swedish survey of forest soils. To test the effects of this assumption, a sensitivity test was carried out by running simulations with soil depths of 0.75 m and 0.5 m. Those showed soil depth to have little effect on the final results (less than 3.5% NPP reduction).

For each county NPP was modelled for three tree species classes: *Pinus sylvestris*, *Picea abies* and deciduous broad-leaved forest (DBF), as well as for ten forest ages corresponding to the reported SNFI age classes (Table 4). Species-specific parameters (Table 5) from Pietsch *et al*. (2005) were used in the simulations, with the exception of deadwood C/N ratios. Deadwood C/N values influence the amount of plant available nitrogen, and when performing a sensitivity test with variable deadwood C/N values these were found to have a high influence on the model results. The reported C/N values from Pietsch

Table 3. Biome BGC input parameters.

Parameters	Source
Temperature (max and min, °C)	ECAD, Haylock *et al.* (2008)
Incoming radiation (W m^{-2})	MTCLIM43
Precipitation (cm day^{-1})	ECAD, Haylock *et al.* (2008)
Nitrogen deposition (kg m^{-2} $year^{-1}$)	SMHI, Dentener (2006)
Atmospheric CO_2 (ppm)	
Altitude (m a.s.l.)	
Latitude (degrees, °)	
Soil depth (1 meter fixed)	
Soil composition (percentages of size fractions)	Lagergren *et al.* (2006)
Species parameters	Pietsch *et al.* (2005), White *et al.* (2000)

were very high for *P. sylvestris*, which caused it to grow unrealistically well compared with *P. abies*. These C/N values were based on a study of another species of Pine (*Pinus contorta*), and were in the highest end of C/N values found in literature. To reduce the growth gap between the species we choose to use mean values of dead-wood C/N ratios for evergreen coniferous forests

Table 5. Species-specific parameters used in Biome-BGC.

Parameters	*Picea abies*	*Pinus sylvestris*	DBF
Phenological parameters			
Transfer growth period (%)	30	30	20
Litterfall period (%)	30	30	20
Annual turnover rates			
Leaves and fine roots (year^{-1})	0.195	0.18	1.0
Live wood (year^{-1})	0.7	0.7	0.7
Whole plant mortality (year^{-1})	0.005	0.005	0.005
Fire mortality (year^{-1})	0.0*	0.0*	0.0*
Allocation ratios			
Fine root C/leaf C (DIM)	0.622	0.523	1.2
Stem C/leaf C (DIM)	3.03	2.5	2.2
Live wood C/total wood C (DIM)	0.076	0.059	0.16
Coarse root C/ stem C (DIM)	0.19	0.29	0.22
Growth C/storage C (DIM)	0.5	0.5	0.5
C/N ratios			
C/N of leaves (DIM)	58.8	33.1	25.0
C/N of falling leaf litter (DIM)	116	132.0	55.0
C/N of fine roots (DIM)	58.0	38.0	48.0
C/N of live wood (DIM)	50.0	50.0	50.0
C/N of dead wood (DIM)	730	730	550
Leaf litter proportions			
Labile proportion (DIM)	0.44	0.257	0.38
Cellulose proportion (DIM)	0.35	0.493	0.44
Lignin proportion(DIM)	0.21	0.25	0.18
Fine roots proportions			
Labile proportion (DIM)	0.427	0.252	0.34
Cellulose proportion (DIM)	0.381	0.495	0.44
Lignin proportion (DIM)	0.192	0.253	0.22
Dead wood proportions			
Cellulose proportion (DIM)	0.71	0.71	0.77
Lignin proportion (DIM)	0.29	0.29	0.23
Canopy parameters			
Water interception coefficient (LAI^{-1} d^{-1})	0.036	0.051	0.045
Light extinction coefficient (DIM)	0.67	0.51	0.54
Average specific leaf area (m^2 kg^{-1} C)	10.2	13.0	32.0
Ratio of sunlit to shaded LAI (DIM)	2.0	2.0	2.0
Ratio of all sided to projected LAI (DIM)	2.6	2.6	2.0
Fraction of leaf N in Rubisco (DIM)	0.0457	0.0457	0.088
Conductance parameters			
Maximum stomatal conductance (m s^{-1})	0.002	0.0010	0.006
Cuticular conductance (m s^{-1})	0.00006	0.00001	0.00006
Boundary layer conductance (m s^{-1})	0.009	0.009	0.009
Boundaries for conduction reduction			
Leaf water potential: start of reduction (Pa)	–500	–500	–334
Leaf water potential: complete reduction (Pa)	–2500	–2200	–2200
VPD: start of reduction (Pa)	50	50	1100
VPD: complete reduction (Pa)	1500	2500	3600

* During the spin-up phase of the simulation the fire mortality value was county-specific and dependent on latitude.

as reported by White *et al*. (2000) for both *P. sylvestris* and *P. abies*.

To produce initial carbon and nitrogen pools, the model was run with a spin-up phase using repetitions of the 2000–2009 period climate data until reaching a carbon equilibrium. After the spin-up phase, fire mortality was set to zero and an additional 290 years were simulated (years 1810–1999) during which the area was clear-cut twice, by removing 99% of all living biomass and converting leaf and 10% of removed woody biomass to litter. The year of the second clearcut was determined by the stand age to be achieved, i.e. if the purpose was to simulate a 33-year-old forest in year 2000, the second clearcut had to occur in 1967. The periods 2000–2004 and 2005–2009 were modelled separately, making it a total of 60 model runs for each county (3 species classes × 10 age classes × 2 periods). Just as for the SNFI method, average NPP was calculated for each county based on the distribution of stand ages and species reported from the national forest inventory (Eq. 3).

MODIS remote sensing NPP product

The Moderate Resolution Imaging Spectroradiometer (MODIS) sensor was designed to measure ocean and atmospheric characteristics as well as terrestrial properties. It was launched first on the Terra satellite in 1999 and later also on the Aqua satellite in 2002. The resulting data are available for download in the form of radiation measurements as well as more processed products such as vegetation indices and productivity estimates.

For our NPP comparisons, the MODIS product MOD17A3 was used, which is distributed by the LP DAAC and available for download free of charge. It contains annual NPP values with a 1-km^2 resolution. Those values are calculated using multi-spectral satellite data to produce estimates of FPAR (Knyazikhin *et al*. 1999) in combination with PAR measurements. The conversion efficiency parameter (ε) is estimated with the help of look-up tables (BPLUT) which are derived from simulations with the Biome-BGC model. The BPLUT contains parameters related to meteorological limits on productivity, which are used together with temperature and VPD data to calculated ε (Running *et al*. 2004). The BPLUT also contains parameters related to growth and maintenance respiration used to calculate NPP. All parameters are land-cover specific, determined by the MODIS land-cover product. GPP and NPP are calculated as follows:

$$\mathrm{GPP} = \varepsilon \times \mathrm{FPAR} \times \mathrm{PAR} \quad (4)$$

$$\mathrm{NPP} = \mathrm{GPP} - \mathrm{respiration} \quad (5)$$

Since the NPP values from the MOD17A3 product cover all terrestrial areas they were weighted according to the amount of forest cover in each MODIS pixel, in the same way as the BIOME-BGC climate data were using Eq. 1. This allowed pixels with low forest cover to affect the result, but due to the weighting this had a minor effect on the results. Sensitivity tests showed that NPP values varied by $< 2\%$ only when pixels with forest cover lower than 75% were excluded as compared with when all pixels were included.

Method interdependence

The three methods we used for NPP estimates were not fully independent of each other. Biome-BGC and MODIS both use similar meteorological data in their processes, and they also depend on data derived using another method. The Biome-BGC modelling approach used data on forest age and species distribution obtained from the SNFI (Fig. 1). The MODIS NPP product used lookup tables calculated by Biome-BGC to estimate vegetation light-use efficiency (ε) and respiration rates. This interdependence causes the results to be more similar, especially regarding spatial patterns of the NPP values. To quantify some of this effect, we introduced extra scenarios for the Biome-BGC and the MODIS methods. In each scenario, we kept some variables constant to assess the variation in NPP related to other variables.

To determine the influence of species and age distributions, obtained from the SNFI, on Biome-BGC simulated NPP we assumed two different scenarios. In each scenario, either species productivity (i.e. $\mathrm{NPP}_{s,a}$ in Eq. 3) or species and age distributions (i.e. $\mathrm{Area}_{s,a}$ in Eq. 3) was replaced

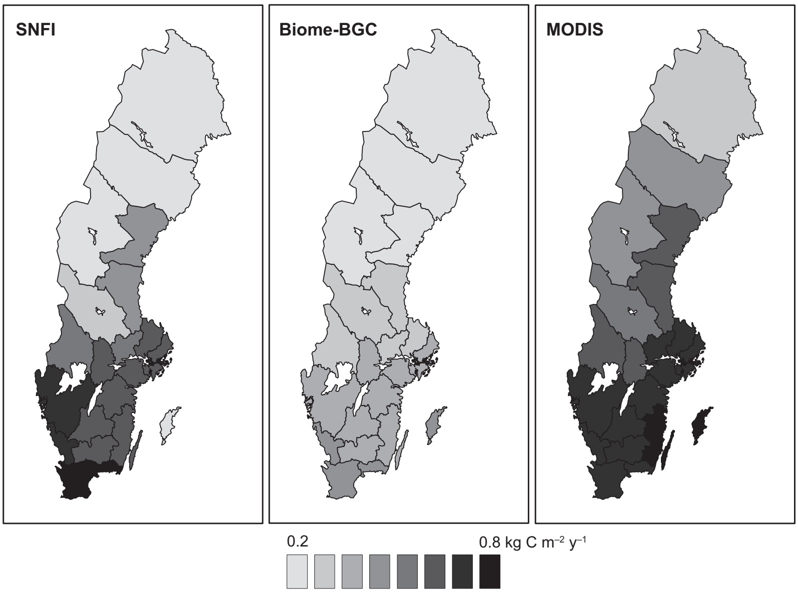

Fig. 4. Forest net primary productivity (NPP) for the Swedish counties, calculated by the three methods used in this study.

by a national average and thus constant across all counties. With one factor held constant all remaining variation in county NPP can be attributed to the other, and by comparing the relative variation related to the two scenarios the influence of species and age distribution could be estimated.

To show how remotely sensed data and climate data contributed to the spatial variation of the MODIS NPP, we calculated new NPP values following the same procedure as described for the MOD17A3 product but with new input data. As input data we used the MODIS FPAR and LAI product, MOD15A2, and the same climate data as were used for the BIOME-BGC modelling. Two scenarios were assumed, in which we alternately replaced the remotely sensed data (MOD15A2) or the climate data with a spatially constant average for Sweden. By comparing the relative variation of scenario NPP values we could assess their influence on MODIS NPP values.

Results

NPP estimates

The county NPP values calculated using the SNFI method averaged 0.5 kg C m^{-2} $year^{-1}$, ranging between 0.20 and 0.81 for northern and southern Sweden, respectively (Table 6). The NPP values followed, roughly, a linear latitudinal trend with two notable exceptions: the NPP values for three southernmost counties were higher than expected, and NPP for Gotland (the eastern island in the Baltic sea) was much lower than for other counties at the same latitude (Fig. 4). NPP for coastal counties was slightly higher, 0.1 kg C m^{-2} $year^{-1}$ on average, as compared with that for adjacent inland counties.

The Biome-BGC method produced similar NPP values for northern Sweden as did the SNFI method, and much lower NPP values (ca. 50%) for central and southern Sweden. Despite the large difference in absolute values, the spatial NPP patterns produced by the Biome-BGC and the SNFI methods were similar (Fig. 5). The coefficient of determination (r^2) for the linear regression between SNFI NPP and Biome-BGC

Table 6. County estimates of forest NPP (kg C m^{-2} $year^{-1}$) for each of the three methods used in this study. Root mean square error (RMSE) was calculated in relation to the SNFI values.

	Min	Max	Mean ± SD	RMSE
SNFI	0.21	0.78	0.50 ± 0.16	–
Biome-BGC	0.24	0.43	0.35 ± 0.06	0.19
MODIS	0.32	0.76	0.59 ± 0.11	0.16

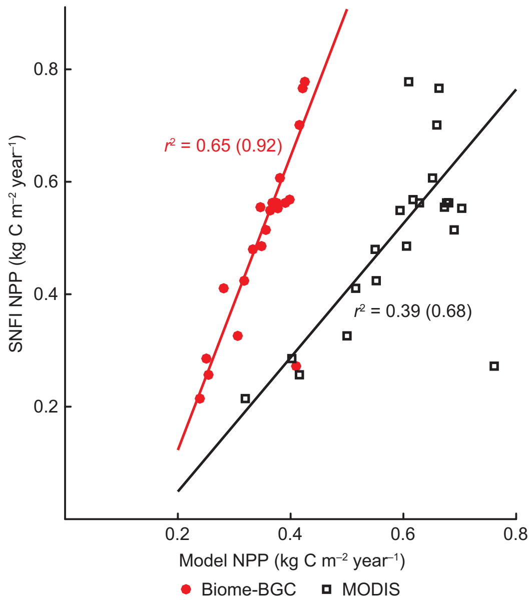

Fig. 5. Net primary productivity (NPP) calculated by the Biome-BGC and the MODIS methods, compared to NPP calculated by the SNFI method; r^2 values written inside parentheses were derived for mainland Sweden, excluding the county of Gotland as an outlier. The regression equations are $NPP_{SNFI} = 0.89NPP_{MODIS} - 0.03$, $p = 0.002$, and $NPP_{SNFI} = 2.26NPP_{Biome\text{-}BGC} - 0.29$, $p = 0.00001$.

NPP equalled 0.65, and increases to 0.92 if the outlier Gotland is excluded.

The MODIS NPP values ranged between 0.32 and 0.76 kg C m^{-2} year^{-1}. The NPP values were generally 10%–50% higher than those from the SNFI method, except for the three southernmost counties for which MODIS NPP instead was much lower (Fig. 5). The spatial distribution was different and had a weaker latitudinal gradient than the other two methods, with the MODIS method resulting in highest NPP values along the eastern Baltic coast. The coefficient of determination (r^2) for the linear regression between SNFI and MODIS NPP values equalled 0.39 only, or 0.68 if excluding Gotland.

The change in NPP during the two studied periods, 2000–2004 and 2005–2009, differed considerably between the SNFI and the other two methods (Fig. 6). Both Biome-BGC and MODIS showed a higher increase in NPP for the southeastern region than for the rest of the country. The SNFI method showed a high increase in NPP, 10% as compared with ±2% given by Biome-BGC and MODIS. This increase was present across all counties except for central southern Sweden where this time SNFI indicated an equally large reduction in NPP.

Method interdependence

Method interdependence was estimated by comparing data contribution to standard deviation. The relative effect of species distribution *vs*. climate data for the Biome-BGC method, as well as the effect of climate data *vs*. remotely sensed data for the MODIS method, was assessed using scenario variations. The scenarios for Biome-BGC showed that the variation in county NPP caused by the climate data (i.e. scenario 2) was several times higher than the variation caused by the species-distribution data (0.052 compared with 0.008 kg C m^{-2} year^{-1}, respectively; Fig. 7a). For the MODIS scenarios, variation in county NPP was caused to the same extent by the spatial data (SD = 0.12 kg C m^{-2} year^{-1}, scenario 1) and remotely sensed data (SD = 0.09 kg C m^{-2} year^{-1}, scenario 2; Fig. 7b). Within-county variation in NPP was high for MODIS scenario 1, on average 0.9 kg C m^{-2} year^{-1}, and relatively low for all the other scenarios.

Discussion

NPP estimates

Field-based studies of NPP in Sweden and Finland reported NPP values between 0.22 and 0.46 kg C m^{-2} year^{-1} (Gower *et al*. 2001, Havas 2013), and Lisky *et al*. (2006) estimated mean NPP of Finnish forests to be 0.38 kg C m^{-2} year^{-1} using an inventory-based method. This is comparable to our results from the SNFI method for counties in the same latitudinal range, 0.26–0.55 kg C m^{-2} year^{-1}, suggesting that those results are valid for the middle and northern parts of Sweden. In the southern parts, NPP for three counties were higher than might be expected from the latitudinal trend. These counties are characterized by higher temperatures, high nitrogen deposition rates and a large fraction of

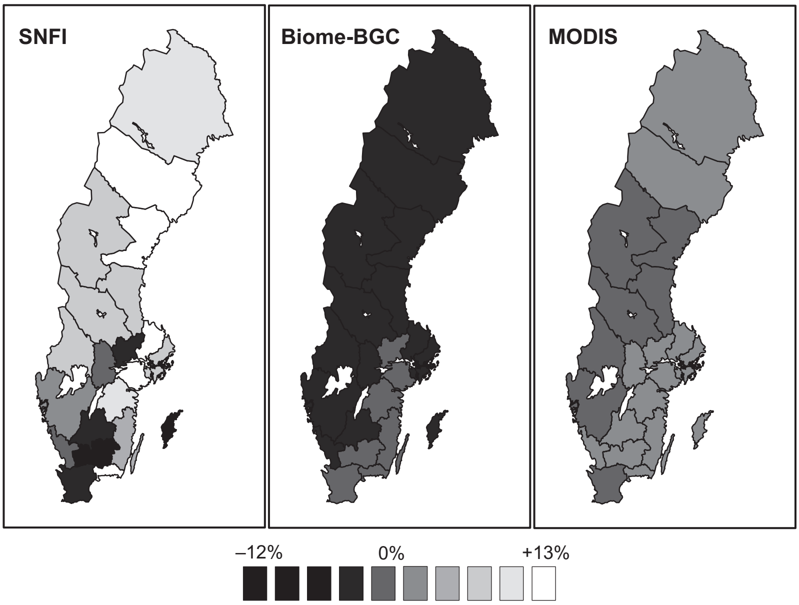

Fig. 6. Changes in net primary productivity (NPP) when comparing the studied period 2005–2009 with the period 2000–2004.

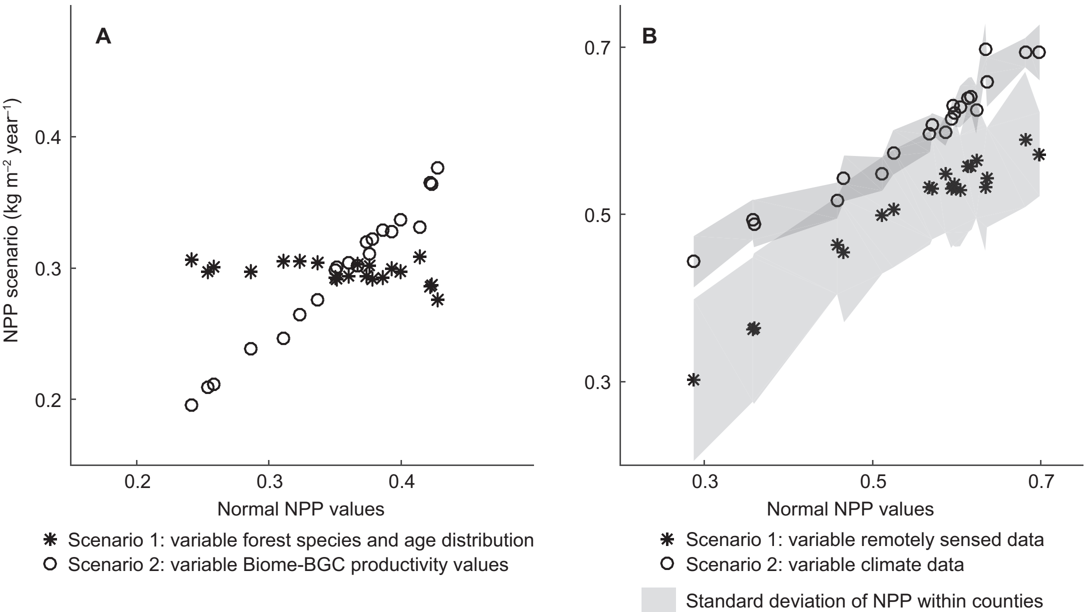

Fig. 7. (**A**) Biome-BGC and (**B**) MODIS net primary productivity (NPP) calculated for different scenarios. For Biome-BGC, scenario 1 represents the variability in NPP caused by tree age and species composition which were obtained from the national forest inventory and scenario 2 represents variability in NPP caused by simulated forest growth. For MODIS, scenario 1 represents variability in NPP related to climate input and scenario 2 represents variability related to remotely sensed data. The standard deviation was calculated for within-county variation in 1 × 1-km pixel NPP values.

broad-leaved forest. Productivity there is likely higher than in the rest of the country, but might still have been overestimated by the SNFI method. According to Lehtonen *et al*. (2004), the biomass expansion factors (BEFs) used in our study for converting measured stem volume increases to NPP values are only valid for coniferous-forest densities of less than 250 m^3 ha^{-1}

and broad-leaved forests densities of less than 200 m^3 ha^{-1}. Stand densities in several regions in southern Sweden exceed those values, especially so in the three southernmost counties. Jalkanen *et al*. (2005) reported overestimation of biomass of Norway spruce of up to 30% for southern Sweden when using same BEFs as in our study as compared with when using single-tree-biomass equations. This indicates that our NPPs might be overestimated. Interestingly the same pattern of relatively higher productivity was found when using Biome-BGC even though this model does not use the BEFs.

Our Biome-BGC results compare well with the SNFI values for northern Sweden, but NPP for southern counties was severely underestimated (by up to 50%). Using another mechanistic model, Smith *et al*. (2008) reported NPP estimates for Swedish conifer forests ranging between 0.22 and 0.41 C m^{-2} $year^{-1}$ which is similar to our BIOME-BGC results. Both models underestimated NPP for southern Sweden, which could have several explanations. Notably, most species-specific parameters used in our simulations were calibrated for either North America or central Europe (White *et al*. 2000, Pietsch *et al*. 2005) even though some originated from studies carried out in Sweden or Finland. The parameters' inability to accurately capture species differences is apparent when comparing spruce and pine growth across Sweden. A comparative study showed that in northern Sweden spruce grows slightly slower than pine, but about 60% faster in the south (Bergquist *et al*. 2005). The BIOME-BGC model failed to capture this difference with the species parameters used in our study, perhaps partly due to uncertainties in the C:N ratios of dead wood as was mentioned in the 'Material and methods' section. Even though the Biome-BGC model failed to calculate the same NPP values as the SNFI method, it performed well in predicting the spatial variation in mainland NPP explaining 92% of the variation.

The MODIS NPP values were consistently higher than the SNFI values, except for the southernmost counties. This overestimation of forest productivity was shown in other studies as well. Turner *et al*. (2006) concluded that the MODIS NPP and GPP products tend to overestimate in low- and underestimate in high-productivity areas. This overestimation can have several explanations. Neumann *et al*. (2016) showed that the coarse-resolution global climate data used for the MOD17A3 product cause an overestimation of NPP, which they solved by using local high-resolution climate date instead. Peltoniemi *et al*. (2015) found that MODIS GPP was 50%–100% higher than their simulated values for large parts of Finland, which they explained partly as the effect of understory vegetation. This could also be true in our case, as understory vegetation NPP was not included in either of the BIOME-BGC or SNFI based method. Despite the low fraction of forest biomass made up by understory vegetation, studies show that it can account for 30% or more of the total forest NPP due to the high biomass turnover rates (Goulden and Crill 1997, O'Connell *et al*. 2003, Nilsson and Wardle 2005). Understory NPP is also often inversely proportional to overstory NPP (O'Connell *et al*. 2003) which corresponds well to MODIS NPP being relatively greater for the northern parts of Sweden where forest productivity is lower. The spatial distribution of MODIS NPP values identifies that the productivity in the eastern counties along the Baltic coast is the highest, which contrasts with the other two methods giving higher values for the southwest. The main regional differences between southeastern and southwestern Sweden were nitrogen deposition rates and species composition, both which are considered in the SNFI and the Biome-BGC methods but not in MODIS.

The differences among the three methods are particularly evident in the case of Gotland. It is an island in the Baltic sea with poor soil conditions and slow-growing forests. This is evident in the SNFI results where NPP for Gotland was much lower as compared with that for counties at a similar latitude, whereas both Biome-BGC and MODIS predicted high productivity as none of them includes information on local soil characteristics.

When comparing NPP between the two simulated periods, both Biome-BGC and MODIS indicated increasing productivity in the southeastern region whereas the SNFI method indicated large losses in NPP in central-southern Sweden. This difference may be explained by the two storms hitting southern Sweden in 2005

(Svensson *et al*. 2006) and 2007 (Alexandersson and Edquist 2007). They caused severe forest damages by felling more than 90 million m^3 of trees, mainly in the same regions for which the SNFI method indicated lower NPP values.

The results of the scenario simulations for Biome-BGC and MODIS showed that method interdependence effects on the spatial distribution of NPP values are limited. Biome-BGC used the data on tree species and age distributions obtained from the Swedish national forest inventory to calculate NPP values for each county. This may have contributed to NPP values given by the SNFI and Biome-BGC methods being spatially distributed in a similar way. But as shown by the scenarios, variation in county NPP caused by age and species distribution is much smaller than variation related to the model simulation results. For MODIS the variation was more equally attributed to each scenario, indicating similarity to the Biome-BGC results as both methods relied on climate data and common parameters. Despite this, the spatial distribution of MODIS NPP values differed distinctly from that of the Biome-BGC method.

Implications for carbon accounting

We compared three methods for calculating NPP, with the intention that they should be distinctly separable in approach. There are large differences among the resulting NPP values, showing that both Biome-BGC and MODIS are inadequate for estimating Swedish forest productivity with their current calibration. Overall accuracy can be improved for all three methods by improvement of e.g. BEFs for conversion of volume to biomass and species parameters for the BIOME-BGC model simulation, or by using local models based on MODIS data (Turner *et al*. 2006, Sjöström *et al*. 2011, Schubert *et al*. 2012).

BIOME-BGC simulated NPP results show spatial variations similar to that of the SNFI method. This indicates that, with proper calibration and parameterization, the model can produce results of reasonable quality. Input data obtained from the SNFI could presumably be replaced by remotely sensed estimates of forest composition (e.g. tree species, age or density), which would produce results with higher spatial resolution and reduce the amount of required fieldwork.

The light use efficiency approach, such as used for the MODIS NPP product, suffers from several inherent limitations. Vegetation index saturation is a well-known problem (Sellers 1985, Birky 2001) which makes it hard to correctly scale LAI and FPAR for dense forests. Understory vegetation strongly affects the results in sparse stands as previously mentioned. These problems might be reduced to some extent by using specially derived vegetation indexes (e.g. Jin and Eklundh 2014) or by inclusion of stand density data (Hasenauer *et al*. 2012, Neumann *et al*. 2015). The distinctly different spatial distribution of MODIS NPP as compared with that of the SNFI method indicate that those limitations strongly affect the results and must be addressed for the method to be reliable. The factors affecting methods may also vary among regions, e.g. in Sweden nitrogen limitation and soil conditions are affecting the results but this is not necessarily the case in other countries.

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