

Reconstruction and attribution of the carbon sink of European forests between 1950 and 2000

Valentin Bellassen, Nicolas Viovy, Sebastiaan Luyssaert, Guerric Le Maire,

Mart-Jan Schelhaas, Philippe Ciais

▶ To cite this version:

Valentin Bellassen, Nicolas Viovy, Sebastiaan Luyssaert, Guerric Le Maire, Mart-Jan Schelhaas, et al.. Reconstruction and attribution of the carbon sink of European forests between 1950 and 2000. Global Change Biology, 2011, 17, pp.3274-3292. 10.1111/j.1365-2486.2011.02476.x. cea-00853357

HAL Id: cea-00853357 https://cea.hal.science/cea-00853357

Submitted on 2 Jul2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés. Global Change Biology (2011) 17, 3274–3292, doi: 10.1111/j.1365-2486.2011.02476.x

Reconstruction and attribution of the carbon sink of European forests between 1950 and 2000

VALENTIN BELLASSEN*, NICOLAS VIOVY*, SEBASTIAAN LUYSSAERT*, GUERRIC LE MAIRE†, MART-JAN SCHELHAAS* and PHILIPPE CIAIS‡

*Commissariat a L'Energie Atomique, Laboratorie des Sciences du Climat et de l'Environnement, Centre d'Etudes de Orme des Merisiers, BAT 709, Gif sur Yvette, 91191, France, †CIRAD, UMR Eco&Sols, Ecosystèmes de plantations (UPR80), Montpellier, 34000, France, ‡Alterra, Wageningen UR, Droevedaalse steeg 3, P.O. Box 47, 6700, AA Wageningen, The Netherlands

Abstract

European forests are an important carbon sink; however, the relative contributions to this sink of climate, atmospheric CO₂ concentration ([CO₂]), nitrogen deposition and forest management are under debate. We attributed the European carbon sink in forests using ORCHIDEE-FM, a process-based vegetation model that differs from earlier versions of ORCHIDEE by its explicit representation of stand growth and idealized forest management. The model was applied on a grid across Europe to simulate changes in the net ecosystem productivity (NEP) of forests with and without changes in climate, [CO₂] and age structure, the three drivers represented in ORCHIDEE-FM. The model simulates carbon stocks and volume increment that are comparable – root mean square error of 2 m³ ha⁻¹ yr⁻¹ and 1.7 kg C m⁻² respectively – with inventory-derived estimates at country level for 20 European countries. Our simulations estimate a mean European forest NEP of 175 ± 52 g C m⁻² yr⁻¹ in the 1990s. The model simulation that is most consistent with inventory records provides an upwards trend of forest NEP of 1 ± 0.5 g C m⁻² yr⁻² between 1950 and 2000 across the EU 25. Furthermore, the method used for reconstructing past age structure was found to dominate its contribution to temporal trends in NEP. The potentially large fertilizing effect of nitrogen deposition cannot be told apart, as the model does not explicitly simulate the nitrogen cycle. Among the three drivers that were considered in this study, the fertilizing effect of increasing [CO₂] explains about 61% of the simulated trend, against 26% to changes in climate and 13% only to changes in forest age structure. The major role of $[CO_2]$ at the continental scale is due to its homogeneous impact on net primary productivity (NPP). At the local scale, however, changes in climate and forest age structure often dominate trends in NEP by affecting NPP and heterotrophic respiration.

Keywords: age structure, carbon sink, CO2 fertilization, Europe, forest management, NBP, NEP, wood demand

Received 5 March 2011; revised version received 19 May 2011 and accepted 20 May 2011

Introduction

Owing to the Kyoto Protocol and the takeoff of carbon markets, the carbon budget of European forests has become an economic reality. Although its current turnover is limited by conservative carbon accounting rules, its financial impact is likely to expand following the renegotiation of accounting rules and the development of voluntary carbon markets (Deheza & Bellassen, 2010). Several parties to the United Framework Convention on Climate Change (UNFCCC) are calling for 'forward-looking baselines' (UNFCCC, 2010). Such country-specific scenarios based on forest age structure would be used to credit only the part of the forest sink going beyond business-as-usual practices. This socioeconomic context is a pressing call for scientists to

Correspondence: Valentin Bellassen, CDC Climat, 47 rue de la Victoire, 75009 Paris, France, tel. + 33 1 58 50 19 75, fax + 33 1 58 50 00 00, e-mail: valentin.bellassen@lsce.ipsl.fr

refine estimates of the carbon balance of forest ecosystems at various scales and better understand its driving factors to correctly assess its business-as-usual baseline.

Carbon budgets of European forests are informed by a variety of methods: compilations of repeated forest inventories, upscaling of eddy-covariance measurements or intensive monitoring plots, atmospheric inversions, remote sensing and large-scale modelling (Lindner *et al.*, 2004; Luyssaert *et al.*, 2010). Regarding the possible drivers of this budget, however, large-scale process-based modelling, with its ability to simulate different environmental and management conditions, is best suited for understanding the relative importance of forest area, age structure, climate, [CO₂] and nitrogen deposition and their interactions.

Reported efforts between 2002 and 2010 to simulate the carbon budget of European forests were summarized (Table 1). We distinguished empirical, semi-empirical and process models according to the following characteristics:

Study	Model type	Model name	Period	Land-use change	Forest management	Natural disturbances	Climate and CO ₂	Nitrogen deposition
Bottcher et al. (2008)	Empirical	FORMICA	2050, 2013– 2017	No	Harvest	Yes	No	No
Schulp <i>et al.</i> (2008)	Empirical	No name	2000– 2030	Yes	No	No	No	No
Pussinen et al. (2009)	Semi- empirical	EFISCEN-SSW	2000– 2100	No	Yes	No	Yes	No
Eggers <i>et al.</i> (2008)	Semi- empirical	EFISCEN+LPJ	2000– 2100	Yes	Yes	No	Yes	No
Nabuurs <i>et al.</i> (2002) and Karjalainen <i>et al.</i> (2003)	Semi- empirical	EFISCEN+7 process-based models	2000– 2100	No	Yes	No	Yes	No
Luyssaert et al. (2010)	Process	LPJ, LPJd, ORCHIDEE, BIOME-BGC and CASA	1990– 2000	No	LPJd	LPJd and CASA	Yes	BIOME-BGC
Harrison et al. (2008)	Process	JULES	1980– 2005	Yes	No	No	Yes	No
Zaehle <i>et al.</i> (2007)	Process	LPJ	1990– 2100	Yes	No	No	Yes	No
Zaehle <i>et al.</i> (2006)	Process	LPJd	1940– 2000	Yes	Yes	Fire	Yes	No
Milne & Van Oijen (2005)	Process	EuroBiota	1990– 2050	No	Harvest	No	Yes	No

Table 1 Characteristics of recent modelling studies on the European forest carbon sink

- Empirical models such as EFISCEN rely on inventory data and forest yield tables (Bottcher *et al.*, 2008; Schulp *et al.*, 2008). For short simulations where climate and [CO₂] are expected to be similar to current conditions, these models are most reliable. They do not account, however, for changes in environmental factors, and they only simulate aboveground biomass and need to be complemented by soil models, soil data and/or biomass expansion factors (BEF) to produce complete carbon budgets.
- Process models such as ORCHIDEE, JULES, LPJ, • BIOME-BGC or EuroBiota (Milne & Van Oijen, 2005; Zaehle et al., 2006, 2007; Harrison et al., 2008; Luyssaert et al., 2010) rely on a set of equations describing eco-physiological processes such as photosynthesis, respiration and transpiration. As opposed to empirical models, process models are arguably more realistic for long simulations during which climate and [CO₂] change, because they explicitly account for the complex effect of these forcing variables on ecosystems, and their interactions. These process models usually simulate below-ground biomass and soil carbon content directly, but most of them do not represent stand growth processes and forest management (Le Quere et al., 2009).
- Semi-empirical models extract a productivity trend from process models and apply it to the simulations of empirical models (Nabuurs *et al.*, 2002; Karjalainen *et al.*, 2003; Eggers *et al.*, 2008; Pussinen *et al.*, 2009). This method allows applying empirical models over longer timeframes.

Previous studies highlight two patterns that earlier generations of global vegetation models (GVMs) - lacking age structure and forest management representation - struggled to simulate over Europe: the simulated carbon budget of the 1990s (Luyssaert et al., 2010) and the historical evolution of forest carbon stocks due to growth of young forests after World War II (Ciais et al., 2008). In particular, the uncertainty of data concerning past management and plantation history or the methods to reconstruct these data has often been highlighted as the weakest link in previous estimates (Nabuurs et al., 2000; Pussinen et al., 2009). To our knowledge, no GVM has successfully demonstrated its ability to meet these two challenges simultaneously for European forests, although LPJd (Zaehle et al., 2006) simulates a net ecosystem exchange that is close to estimates from inventories and upscaled eddy-covariance measurements for the 1990s (Luyssaert et al., 2010).

The latest generation of GVMs such as LPJ_d (Zaehle *et al.*, 2006), LM3V (Shevliakova *et al.*, 2009) or ORCHI-DEE-FM (Bellassen *et al.*, 2010) simulates forest management and age structure and therefore provides a fully integrative framework for attributing the observed decadal carbon sink of European forests that has been observed by repeated forest inventories. Compared with semi-empirical approaches, ORCHIDEE-FM simulates process-based responses to changes in climate and [CO₂] that may differ between age classes. In the near future, it will also allow for the assessment of the role of nitrogen deposition, a driver currently ignored by most modelling studies listed in Table 1.

Several studies aimed at separating the impact of changes in climate $[CO_2]$ and forest management on the future carbon balance of European forests (Nabuurs *et al.*, 2002; Eggers *et al.*, 2008; Pussinen *et al.*, 2009). They report that changes in forest management may have a stronger (Eggers *et al.*, 2008), similar (Pussinen *et al.*, 2009) or lower (Nabuurs *et al.*, 2002) impact than changes in climate and $[CO_2]$ on forest carbon stocks and net annual increment. These different studies are not necessarily contradictory, as they use various scenarios for future changes in management, climate and $[CO_2]$ which cannot be easily compared and of which credibility is difficult to assess.

Contrary to future scenarios, the credibility of the reconstruction of past changes should be easier to assess, at least for countries with a long history of forest inventories (Kurz & Apps, 1999; Nabuurs *et al.*, 2000). Age structure and forest management are responsible for a 600 g C m⁻² yr⁻¹ variation in net ecosystem productivity (NEP) over the course of a forest rotation, whereas the interannual variation of NEP due to climate variation is <300 g C m⁻² yr⁻¹ (Bellassen *et al.*, 2011a). Nevertheless, no study has so far attempted to simultaneously attribute the relative impact of climate, [CO₂] and management on past changes in the carbon balance at the scale of all European forests, this being the aim of this study.

Prior to using GVMs to discriminate among the possible drivers of the European forest sink, however, the carbon budgets they simulate must be consistent with existing data sources. In addition to evaluating ORCHI-DEE-FM simulations against forest inventory estimates of biomass stocks and increments in each country, this study provides a new estimate of the NEP of European forests in the 1990s at a resolution of 25 km \times 25 km, as well as a reconstruction of their carbon stocks between 1950 and 2000. Both results are evaluated against forest inventories. Factorial simulations that alter selectively climate or [CO₂] conditions are then performed to attribute the respective influences of historical changes in age structure, climate and [CO₂] on the trend in the European forest NEP between 1950 and 2000. Simulations cover the entire European continent except Turkey, Russia and Iceland. When specified, this spatial extent is reduced to the EU 25 or the EU 15 plus Norway and Switzerland and minus Luxemburg, to allow a meaningful comparison with previous studies. A index of abbreviations is available in Appendix S2.

Materials and methods

Data sources

Climate and soil datasets. We used climate and $[CO_2]$ data from the 0.25° resolution REMO reanalysis (Kalnay *et al.*, 1996; Vetter *et al.*, 2008), which covers Europe from 1861 to 2007. For simulations that go back to the year 1811, the 1861–1911 climate conditions are used as a proxy for the years 1811–1860 and a second time for the period 1861–1911. Maps of soil depth and texture were derived from FAO and IGBP products at the same resolution (Vetter *et al.*, 2008).

Data from forest inventories. For age-dependent vegetation models like ORCHIDEE-FM, age structure – maps of forest age for the period under study – is an essential input. The physiological processes and parameter values of ORCHIDEE-FM are specific to plant functional types – temperate/boreal, broadleaf/needleleaf, summergreen/evergreen for forests – which are therefore also the required level of aggregation for the age-structure maps.

Forest ages per species, reported in the compilation of one of the most recent cycles of national forest inventories in Europe by Schelhaas *et al.* (2006), were gap-filled by the reported values of an older and less detailed study (Kuusela, 1994). From these gap-filled observations, forest plant functional types in ORCHIDEE and their surface area for each age class were determined for the 1990s. Depending on the country, the most recent inventory cycle dates from 1985 to 2000, and the spatial scale of the age class data varies from administrative region – e.g. Aquitaine in France, Bavaria in Germany – to the whole country. For broader groupings of countries – e.g. Nordic, Mediterranean – Kuusela (1994) also gives information on recommended rotation lengths that was used in one of our age reconstruction algorithms (see Supply driven algorithm).

The Corine Land Cover map with a resolution of 100 m (Buchroithner *et al.*, 2000) was used to downscale the regional or national estimates of each plant functional types to the finer spatial scale input datasets (Fig. S1) used by ORCHIDEE-FM (0.25 \times 0.25°, see Initial conditions).

Age-structure information with European coverage is absent before 1990: data on age classes from past inventory campaigns are readily available for only a few countries such as Sweden or Finland (Nabuurs *et al.*, 2000; Swedish National Forest Inventory, 2010). This missing information must therefore be reconstructed based on justifiable hypotheses. In this study, we use three different hypotheses and test them against historical carbon stock data (see Reconstruction of the agestructure distribution of European forests and Model evaluation against historical forest inventory data).

Model description

The ORCHIDEE GVM ('ORganizing Carbon and Hydrology In Dynamic Ecosystems') is designed to operate from regional to global scales (Krinner et al., 2005). ORCHIDEE typically represents an average mature forest at steady-state equilibrium in a 'big-leaf' manner. For a given climatology, it simulates the carbon, water and energy budget at the scale of an ecosystem, assumed homogeneous. For carbon, ORCHIDEE computes its fixation [gross primary productivity (GPP)], allocates photosynthates to the different biomass compartments where they are respired or stored and recycles carbon through constant tree mortality and soil respiration. The version of OR-CHIDEE used in this study is ORCHIDEE 1.8. It uses the carbon allocation framework of Friedlingstein et al. (1999), which relies on competition for nutrient, light and water to prioritize allocation between roots, leaves and stem. ORCHIDEE 1.8 does not simulate the nitrogen cycle, recently included in ORCHIDEE-N, also called O-CN, by Zaehle & Friend (2010). ORCHIDEE 1.8, hereafter referred to as the standard version, is intended to simulate forests that have reached a steady-state equilibrium between growth and mortality.

The standard version does not represent important processes driving the evolution of stand structure such as competition, forest management or the age-limitation of net primary productivity (NPP), and is therefore not suited to simulate managed forests or forests recovering from past disturbance.

To simulate forest management, a management module has been added to the standard version of ORCHIDEE and runs at a yearly time step (Bellassen et al., 2010). This forest management module is inspired by the stand-level model FAGACEES (Dhôte & Hervé, 2000). The key concept is to add to the 'bigleaf' representation of ORCHIDEE, an explicit distribution of individual trees, which is the basis for a process-based simulation of mortality. The aboveground 'stand-scale' wood increment simulated by ORCHIDEE is distributed on a yearly time step among individual trees according to the rule of Deleuze et al. (2004): the basal area of each individual tree grows proportionally to its circumference. Tree mortality is then determined by the density and size distribution of the stand. Mortality due to natural competition relies on the self-thinning rule of Reineke (1933), whereas another set of rules drives the mortality processes due to human interventions such as thinnings and clearcuts when the stands matures. As a result, this new version of the model, called ORCHIDEE-FM, is able to simulate the aboveground biomass growth for typical even-aged stands, and hence the carbon budget, and the stand density and size distribution structure of forests are composed of even-aged stands with a distribution of varying age. Its equations are fully described in Bellassen et al. (2010), and validated for the European context in Bellassen et al. (2011b).

Bellassen *et al.* (2010, 2011b) also quantify the uncertainty of ORCHIDEE-FM simulations and their sensitivity to key parameters at the site level. At present, uncertainty assessment neither exists for the sensitivity of ORCHIDEE-FM variables at the continental scale, nor for an assessment of the model's sensitivity to different sets of climate data. As an alternative, we use a fixed percentage obtained from other GVMs for estimating the standard deviation of our estimates, consistently with Luyssaert *et al.* (2010): 25% for GPP (Jung *et al.*, 2007), 40% for NPP (Zhao *et al.*, 2006) and 30% for heterotrophic respiration (HR) and NEP (Zaehle *et al.*, 2005).

Reconstruction of the age-structure distribution of European forests

Supply driven algorithm (FM_s). Similar to Vetter et al. (2005) and Bottcher et al. (2008), the FMs hypothesis assumes a constant rotation length for each forest plant functional type (PFT) in each region, which is then applied backward in time from the known 1990s age structure. The region and PFT-specific rotation length was set according to Kuusela (1994). As an example, 100 000 ha of forest reported to be between 10 and 20 years old in the inventory of 1985, and a rotation length of 85 years. Following the supply driven FMs algorithm, these 100 000 ha of forest were aged between 0 and 10 years in 1975, and between 80 and 90 years back in 1965. If the national forest area has changed between 1965 and 1975, the fractional area of each age class is adjusted as described in Change in forest area to account for deforestation and afforestation. The fractional area of each PFT is kept constant due to the lack of relevant information at European scale.

Demand-driven algorithm (FM_d). The FM_d hypothesis resembles that of Zaehle et al. (2006) and Eggers et al. (2008). It relies on the FAO statistics on domestic wood harvest (FAO, 2010) to reconstruct the age structure of European forests since 1950. From 1960 onwards, all European countries have reported annual wood harvest statistics at the national level. Missing harvest statistics between 1950 and 1960 are gap-filled by assuming that the harvest was equal to the average harvest in the 1960s. In the FM_d algorithm, each decade, the volume of simulated thinned wood according to the ORCHIDEE-FM rules is complemented with simulated clear-cuts: forests in the oldest age class are harvested first, followed by just younger age classes, until the cumulated volume from thinnings and clear-cuts matches the wood harvest data. Stands younger than a minimal age - set at 40 years - are considered too young to be clear-cut. In this method, an initial age structure for 1950 is needed. This initial age map in 1950 was prescribed from the age reconstruction method described in the Supply driven algorithm. The FM_d algorithm may therefore result in a 1990 age structure that differs from observations for this date.

Combined algorithm (FM_c). The FM_c hypothesis assumes that the former age distribution can be calculated backward from the observed age structure of the 1990s, just like FM_s , but uses the wood harvest statistics for this backward computation, just like FM_d . A similar approach is taken by Kurz & Apps (1999). Assume, as an example, that 100 000 ha of forest were between 0 and 10 years old during the 1990 inventory. This area of forest has been harvested between 1980 and 1990, but we have to estimate the age of these 100 000 ha of forests at the time of this last harvest. To do so, we first subtract the wood supply from thinning simulated by ORCHIDEE-FM for the 1990s to the wood harvest statistics of the same decade.

The remaining wood supply was then assumed to have come from clear cuts. Given the constraint of the surface area, we can calculate the growing stock per hectare in the harvested forest. We can then match this with the average growing stock per age class to determine which age class has been harvested.

Decades with a larger demand per area of surface thus require older forests to be harvested, because older forests contain more wood. Minimal and maximal ages of, respectively, 40 and 150 years are set for this age guess, and the cohort of clear-cut forest can be distributed among two neighbouring age classes to improve the match to harvest statistics. Unlike the former algorithm, this combined algorithm matches exactly the observed 1990 age structure.

Change in forest area. In all the reconstruction algorithms, the evolution of total forest area (Gold, 2003; FAO, 2006) is also accounted for: a decrease in forest area between two decades is proportionally downscaled to all age classes, whereas an increase is entirely realized in the 0–10 age class, that corresponds to new plantations.

Simulations, postprocessing, attribution

ORCHIDEE-FM simulations. We set-up a modelling experiment, consisting of the six scenarios described in Table 2, to quantify and separate the effects of increasing [CO2], climate variability and trends and forest management, on the NEP of European forests. For the three scenarios with management (FMs_clim_co2, FMd_clim_co2 and FMc_clim_co2), 19 runs of ORCHIDEE-FM are combined - with forests starting to grow in each grid point, every 10 years from 1811 onward - to reproduce the carbon stocks and fluxes of European forests over 1950-2000. The simulation starting in 1901, for example, represents forests of the 50-60 age class in the 1950s, and forests of the 90-100 age class in the 1990s. All forests older than 140 years are represented by a single simulation corresponding to the 140-150 age class in ORCHIDEE-FM. This maximum age threshold was used because the model structure does not account for older forests where recruitment and agerelated mortality are taking place (Bellassen et al., 2010). This model limitation does not strongly affect the European stocks and fluxes because forests older than 150 years represent just 0.03% of the total European forest area. Subsequently, maps of carbon stocks and fluxes are obtained by calculating the weighted averaging of age classes for each PFT in each grid cell that is provided by the age reconstruction algorithms (Fig. 1).

Attribution. The relative importance of climate, [CO₂] and age structure in the evolution of NEP is tracked through the slope of the linear regression of annual NEP against year in each scenario (e.g. *a*_{STD clim} for scenario STD_clim). We use the STD scenario as a baseline for the evolution of NEP under constant [CO2] and climate conditions. The individual effect of climate and the combined effect of climate and [CO₂] on NEP are then estimated as, respectively, $a_{STD \ clim} - a_{STD}$, and $a_{STD_clim_co2} - a_{STD_clim}$. The effect of age structure is estimated for each age-resolving scenario as $a_{FMx \ clim \ co2} - a_{STD \ clim \ co2}$. Our approach to separate the contribution of each factor to changes in NEP is an additive method, similar to the method used by Gervois et al. (2008) and Ciais et al. (2009). It does not enable disentangling the interactions between the different factors. The current implementation of age-class structure in ORCHIDEE-FM is computationally expensive, hence, a full factorial experiment similar to, for example, that of Luo et al. (2008) will only be feasible for future computationally more efficient versions of ORCHIDEE-FM.

Initial conditions. Following a common practice in global vegetation modelling, a model 'spinup' is performed to set the initial steady-state conditions of the STD simulation. These initial conditions determine the soil carbon and biomass pools and as such have a large effect on the outcome of the simulations. The spin-up continues until equilibrium is reached between litter input and decomposition output (which takes several thousands of years, due to the long residence time of passive soil carbon in ORCHIDEE). As it only takes several hundreds of years, the biomass pools have also reached an equilibrium between NPP input and natural mortality at the end of the spin-up. For a 'forest spin-up', ORCHIDEE is repeatedly run for the relevant forest PFT and for the years 1861-1870. The resulting initial conditions of carbon and water pools represent the state of pristine, unmanaged forests everywhere at the beginning of the simulation. In our modelling framework, it can be considered as the maximum reachable soil and vegetation carbon content in each grid cell for a given PFT and preindustrial conditions in terms of climate and [CO₂].

For the ORCHIDEE-FM simulations – used in the $FM_{s_clim_co2}$, $FM_{d_clim_co2}$ and $FM_{c_clim_co2}$ scenarios – these initial conditions overestimate biomass, litter and soil carbon, as

Table 2	Characteristics of the six	scenarios used for	or the attribution o	of changes in the forest sink
---------	----------------------------	--------------------	----------------------	-------------------------------

Scenario	Model		Climate	[CO ₂]	Age reconstruction algorithm
STD	ORCHIDEE		Constant (1951–1960)	Constant (1951 value)	na
STD_clim	ORCHIDEE		Historical (1951–2000)	Constant (1951 value)	na
STD_clim_co2	ORCHIDEE		Historical (1951–2000)	Historical (1951–2000)	na
FMs_clim_co2	ORCHIDEE-FM	(19 runs)	Historical (1811–2000)	Historical (1811–2000)	FMs
FMd_clim_co2	ORCHIDEE-FM	(19 runs)	Historical (1811–2000)	Historical (1811–2000)	FMd
FMc_clim_co2	ORCHIDEE-FM	(19 runs)	Historical (1811-2000)	Historical (1811–2000)	FMc

© 2011 Blackwell Publishing Ltd, Global Change Biology, 17, 3274–3292



Fig. 1 Flowchart of datasets (italic) and modelling steps (bold) used to reconstruct the evolution of carbon stocks and fluxes between 1950 and 1990.

most European forests even in 1811 were grown from either clear-cut managed forests or abandoned farmlands, and not from mature forests (Pongratz *et al.*, 2009). Therefore, more realistic initial conditions, in terms of biomass and soil carbon, were constructed for the ORCHIDEE-FM simulations by combining two sets of initial conditions (Fig. 2):

- A 'forest INIT' set with a forest in each grid point. The age of the forest is the locally relevant standard rotation length defined in the *FMs* algorithm for each grid cell and PFT (see Supply driven algorithm). This set is obtained by clear-cutting a mature forest and letting ORCHIDEE-FM simulate its re-growth until the given age. Climate and [CO₂] conditions follow the historical reconstructions. The retained values for initial conditions in terms of soil and biomass carbon thus correspond to a managed forest having reached maturity.
- A 'cropland INIT' set with a C3 type of cropland, representative in ORCHIDEE of common crops in Europe such as wheat (Gervois *et al.*, 2008), in each grid point. The retained values for soil and biomass carbon thus correspond to steady-state equilibrium of a cropland.

The initial conditions of the subsequent ORCHIDEE-FM simulations are estimated by a weighted average of the soil and biomass pools from these two INIT simulations in each grid cell:

- For the five ORCHIDEE-FM runs starting after 1950, the relative weight *p* (Fig. 2) of the cropland INIT set corresponds to the fraction of afforestation in the age class of 0–10 years, as defined by the *FM*_s algorithm for each PFT and grid cell.
- For the 14 ORCHIDEE-FM runs starting before 1950, when reliable data on forest area change is lacking, the relative weight of the cropland simulation is set to zero for each pixel. This coarse approximation for older stands is tolerable, as the most important impact of initial conditions on carbon fluxes occurs within the first 20 years of simulated growth (Bellassen *et al.*, 2011a).

Model evaluation against historical forest inventory data. Despite an uneven spatial coverage across countries, estimates of average standing volume and average volume



Fig. 2 Initial conditions of ORCHIDEE-FM simulations for soil and biomass carbon. p is the proportion of afforestation at the start of the ORCHIDEE-FM simulation. The carbon pools of a 'managed forest' and a 'wheat field' simulations are averaged (in proportion to the newly forested area at the start of the ORCHIDEE-FM simulation) to determine the initial conditions of ORCHIDEE-FM simulations.

increment at country level are available from forest inventories, and can be used for model evaluation. The homogenized compilation of such estimates by Kuusela (1994) is used to evaluate the ORCHIDEE-FM simulation results for the 1980s. Standing commercial volume from inventories is converted to total aboveground biomass using the relevant default BEF for branches and wood densities of ORCHI-DEE-FM for conifers and broadleaves.

Performance of the three historical reconstructions is evaluated for carbon stocks and NPP against the aggregated estimates used by Ciais *et al.* (2008) and updated by Schelhaas (2010), based on a compilation of forest inventories from Norway, Switzerland and each EU 15 country excluding Luxembourg. The different components of the carbon budget of European forests [GPP, NPP, HR, NEP, net biome productivity (NBP)] are compared with the various estimates synthesized by Luyssaert *et al.* (2010).

NBP (NEP minus harvest, natural disturbances and carbon losses to rivers) cannot be entirely derived from ORCHIDEE-FM, which does not simulate natural disturbances and carbon losses to rivers. The simulated value of NEP minus harvest is therefore adjusted for fire induced losses using the regional estimates of Schelhaas *et al.* (2003) and for river losses using a constant value of 9 g C m⁻² yr⁻¹ derived from Luyssaert *et al.* (2010). Both fluxes being 4–10 times lower than harvest in Europe (Luyssaert *et al.*, 2010), this *in situ* NBP estimate – it does not account for NBP in the wood product pool – can still be considered to be an output of ORCHIDEE-FM as the applied adjustments are only minor.

Results

Evaluation of model performance

Simulation of carbon stock and volume increment. Simulations (FMs_clim_co2 scenario) and inventories are in partial agreement for harvestable volume increment and total aboveground biomass (Fig. 3). For harvestable wood increment, we obtained a root mean square error (RMSE) of 2 m³ ha⁻¹ yr⁻¹ (or 36% of the average inventory estimate) and a slope of 0.44 between simulations and observations at the national and PFT-level. For aboveground biomass, the corresponding RMSE is 1.7 kg C m⁻² (43% of the average inventory estimate) and the slope is 0.32. The Nordic countries are the region for which the model-data lack of fit is clearly not random: ORCHIDEE-FM underestimates both harvestable volume increment and aboveground biomass for needleleaves, and overestimates them for broadleaves. A few other regions have a particularly poor match: the average aboveground biomass of Swiss and Italian broadleaves for example (black and light grey circles



Fig. 3 Simulated (*FMs_clim_co2* scenario) and inventoried harvestable volume increment and biomass stocks in the 1980s. Each point represents the national average for either broadleaves or needleleaves in one European country. Countries are then labelled according to their ecological zone as defined by Kuusela (1994): alpine (Austria, Switzerland), atlantic (Belgium, France, Ireland, Netherlands, UK), continental (Denmark, Hungary, Germany, Poland, Romania), Mediterranean (Bulgaria, Greece, Italy, Portugal, Spain) and Nordic (Norway, Finland, Sweden). The name of individual outliers (as opposed to outliers belonging to the same group of countries) which are discussed in the main text is added next to their corresponding dot. Luxemburg is excluded from the figure as a clear outlier, probably due to its small forest area (sampling effect).

most on the right of Fig. 3) is largely underestimated by ORCHIDEE-FM.

Reconstruction of changes in NPP and aboveground biomass. We assessed the ability of ORCHIDEE-FM and its postprocessing algorithms to simulate the history of carbon stocks and fluxes in European forests (Fig. 4). As reported by Ciais et al. (2008), the standard version of ORCHIDEE simulates a positive trend in NPP between 1950 and 2000 driven only by climate and [CO₂]. The inventory-derived trend is also positive, although the observed variation in NPP - from 220 to $350 \text{ g} \text{ C} \text{ m}^{-2} \text{ yr}^{-1}$ for needleleaves and from 250 to 430 g C m⁻² yr⁻¹ for broadleaves – is three times bigger than the simulated values with only a 50 g C m⁻² yr⁻¹ difference between the 1950s and the 1990s. The standard version of ORCHIDEE simulated a stable or slightly decreasing trend of above-ground biomass which, in the light of the observations, is unrealistic.

Similar to the standard version, ORCHIDEE-FM simulates a positive NPP trend although with a smaller than observed variability. In addition, ORCHIDEE-FM simulates a positive trend in aboveground biomass. The *FMs_clim_co2* scenario is consistent with the inventory mean biomass estimate for the last decade, but does not reproduce the positive trend. The *FMd_clim_co2* scenario simulates the observed biomass trend, but leads to an overestimate of aboveground biomass in the 1990s. The *FMc_clim_co2* reconstruction better compares with both the trend and current values of aboveground biomass, although the temporal variation of aboveground biomass is about half of the inventory based estimate. The *FMc* age structure can therefore be considered as the 'best available reconstruction' to simulate the European forest carbon balance (both NPP and stocks changes). The *FMs* and *FMd* age maps can be used to quantify the possible bias owing to the necessary reconstruction of the evolution of age distribution between 1950 and 2000.

Carbon balance of European forests in the 1990s

A set of maps shows our 'best available estimate (*FMc_clim_co2*)' of the spatial distribution of 36 variables related to the carbon balance of European forests in the 1990s. We selected the four variables we considered most informative to discuss (Fig. 5); however, the entire set is provided in the supporting information (Figs S1–S10).

The impact of age structure is reflected in the NEP and aboveground biomass: regions and countries with younger forests such as Brittany, Flanders or Wales, tend to have a higher forest NEP (larger sink) and a lower biomass than their immediate neighbours. Conversely, lower NEP (smaller sink) and higher biomass are simulated for regions and countries with older forests such as Switzerland and northern Finland. In other regions such as Italy, Spain or eastern Europe, the impact of age structure on NEP is overridden by local climate and soil variability: the strong North–South gradient of NEP in Italy is probably due to the North–South climate gradient, as the age structure and PFT composition are similar along this North–South gradient.

Over the EU 25, the simulated fluxes of the 'best available scenario (*FMc_clim_co2*)' agree well with estimates



Fig. 4 Simulated 1950–2000 reconstruction of net primary productivity (NPP) and aboveground biomass. Each point corresponds to a decadal average in NPP and aboveground biomass for (a) needleleaves and (b) broadleaves. Chronology can be derived from this graphic as aboveground biomass happens to be monotonously increasing from decade to decade. Four simulations and one inventory-derived estimate are presented: STD_clim_co2 , using the standard version of ORCHIDEE with changing climate and [CO₂] and FM_s , FM_d and FM_c using ORCHIDEE-FM with the 'supply driven', 'demand-driven', and 'combined' age reconstruction algorithms respectively. *Inventories* is the inventory-derived estimate published by Ciais *et al.* (2008), updated by Schelhaas (2010). The changes in NPP and aboveground biomass due to changes in climate and [CO₂] are derived from the STD_clim_co2 results and are reported in dashed red at the level of the FMc_clim_co2 results. The residual changes are due to changes in age structure and reported in dashed green. The spatial domain of all four reconstructions is restricted that of the inventory-derived estimate, that is the EU 15 countries, excluding Lux-embourg, and adding Norway and Switzerland.

from other methods and models (Fig. 6): all are within the uncertainty ranges of data-derived estimates, in particular, HR which was particularly high in the standard version of ORCHIDEE. Only the two GVMs that reconstruct age structure, namely LPJ_d and ORCHIDEE-FM, are able to simulate the large positive NEP of 160–200 g C m⁻² yr⁻¹ as observed. LPJd estimates an NEP values 125 ± 38 and ORCHIDEEE-FM of 175 ± 52 g C m⁻² yr⁻¹. The detailed values of the forest carbon balance of each European country are listed in Appendix S1. For each country, the observed forest age structure in the 1990s, the FAO statistics for wood harvest, the simulated wood supply and the simulated volume increment between 1950 and 2000 are presented in Fig. S16.

Attribution of the European forest sink between 1950 and 2000

[CO₂] effect dominates at the aggregated European scale. For our 'best available estimate (*FMc_clim_co2*)', the European forest NEP increased on average by 1 ± 0.5 g C m⁻² yr⁻² or 0.7% yr⁻¹ (Table 3) between 1950 and 2000. Climate is largely responsible for the inter-annual NEP variability that is therefore similar for all scenarios, but *STD* (Fig. 7a). The mean increase in NEP hides a considerable variability between scenarios; NEP under the *STD* simulation increased by 0.4 ± 0.4 g C m⁻² yr⁻² whereas NEP under the *FMs_clim_co2* scenario increased by 1.1 ± 0.5 g C m⁻² yr⁻². A similar trend analysis was applied to the simulated time series of NPP and HR, and the results are summarized in Appendix S3.

As expected from the simulated carbon budget for the 1990s, most of the *absolute value* of the NEP is due to forest management that keeps HR below NPP by removing wood that would otherwise be delivered to the litter pools (Fig. 7b): in the 1990s, the NEP of the *STD_clim_co2* scenario is only slightly higher than the NEP of the *STD* scenario (16 g C m⁻² yr⁻¹ vs. -3 g C m⁻² yr⁻¹), a difference due to the effect of [CO₂] and



Fig. 5 Carbon balance of European forests in the 1990s. (a) Net ecosystem productivity (NEP), (b) average aboveground biomass, (c) stand age and (d) total aboveground biomass. For NEP, positive values correspond to a carbon sink. The coloured version of this figure is available in the supporting information (Fig. S14).



Fig. 6 Compilation of estimates of carbon fluxes in European forests (EU 25) in the 1990s. All estimates, but ORCHIDEE and ORCHIDEE-FM simulations are derived from Luyssaert *et al.* (2010). Model estimates rely on the same climate and [CO₂] drivers as the simulations in this study. Similar to ORCHIDEE-FM, LPJd (Zaehle *et al.*, 2006) simulates different age classes. Error bars represent uncertainty (standard deviation), as estimated by Luyssaert *et al.* (2010). For models, uncertainty is restricted to driver uncertainty [gross primary productivity (GPP), net primary productivity (NPP)] or parameter uncertainty [heterotrophic respiration (HR), net ecosystem productivity (NEP), NBP], and is probably an underestimate of total uncertainty, especially for NEP for which most models are knows to be structurally erroneous.

climate. However, the *FMc_clim_co2* scenario averages 175 ± 52 g C m⁻² yr⁻¹, a difference with the standard model that is entirely due to wood removal. Note that

the interannual variability of NPP and NEP is comparable in the *STD_clim_co2* and *FMc_clim_co2* scenarios, whereas the interannual variability of HR is a third

Slope Uncertainty $(g\dot{C} m^{-2} vr^{-2})$ $(g C m^{-2} vr^{-2})$ Simulation STD 0.4 0.4 STD clim 0.0 0.5 STD clim co2 0.8 0.6 FMs_clim_co2 1.1 0.5 FMd clim co2 0.50.5 FMc_clim_co2 1.0 0.5

Table 3Average annual change in NEP for the EU 25between 1950 and 2000

Slope is the estimated value of slope of the linear regression of annual NEP against year and its associated uncertainty (95% confidence interval). Slope values significantly different from 0 - that is >0 \pm *uncertainty* – are highlighted in grey. NEP, net ecosystem productivity.



Fig. 7 Simulated reconstruction of net ecosystem productivity (NEP), net primary productivity (NPP) and heterotrophic respiration (HR) in the EU 25. Six scenarios are presented for NEP simulation (a) and two only for NPP and HR (b). For a description of the different scenarios, see Table 2.

lower in the *FMc_clim_co2* due to the lower mass of litter and soil carbon stocks that are available as a substrate for HR.

Furthermore, we analysed which factors were responsible for the changes in NEP between 1950 and 2000. Our modelling framework does not permit to tell apart the potentially large impact of nitrogen deposition. Among the three factors analysed, increasing [CO₂] was found to be the most important driver of the trend in modelled forest NEP, explaining between 56% and 61% of the total trend, depending on the age reconstruction algorithm (Fig. 8a). The contribution of changing climate and changing age structure are comparable, between 24% and 26% for climate, and 13-20% for age structure. Note that the change in age structure can contribute both negatively or positively to the change in NEP, and this highlights the importance of obtaining accurate age reconstructions in this attribution. NEP is the balance between NPP and HR. Although the impact of management is largest on HR, the impact of climate is particularly important for NPP (Fig. 8b).

The large inter-annual variability of NEP is reflected in the uncertainties of the estimated values of the long-term trends. Increasing trends of NEP in all simulations are nevertheless found to be significant (P = 0.05), except for *STD* and *STD_clim* (Table 3). When the individual contributions of climate, [CO₂] and age structure to NEP change are separated from one another, none is clearly greater than its associated



Fig. 8 Impact of changing climate, [CO₂] and management on the average change in carbon fluxes between 1950 and 2000. The impact of each factor is represented for three scenarios with different age-structure reconstruction hypothesis (a) and for three carbon fluxes for the 'best available estimate (*FMc_clim_CO2*)' (b).



Fig. 9 Disaggregated impact of changing climate, $[CO_2]$ and age structure on the net ecosystem productivity (NEP) change between 1950 and 2000. The impact of each factor is calculated as the difference between the slopes of the relevant linear regressions: $a_{STD_clim} - a_{STD}$ for climate (a), $a_{STD_clim_co2} - a_{STD_clim}$ for $[CO_2]$ (b), $a_{FMc_clim_co2} - a_{STD_clim_co2}$ for age structure (c) and $a_{FMc_clim_co2} - a_{STD}$ for all three factors combined (d). See Attribution for a full explanation of the attribution method and the meaning of the slopes. The corresponding maps for NPP and HR are available in the supplementary materials (Figs S11 and S12).

uncertainty. This does not invalidate the fact that these potential causes have a significant impact on NEP change when combined, but calls for caution when discussing their quantitative assessment (Gervois *et al.*, 2008; Ciais *et al.*, 2009).

Importance of climate change and age structure at local scale. The dominant effect of the [CO₂] increase on the NEP increase at the European scale is due to its spatial homogeneity (Fig. 9b). However, at local scale, the effect of changing climate or age structure tends to dominate the modelled NEP trend (Figs 9 and 10). Climate change is found to be driving NEP down (smaller sink) in southern Europe and up (larger sink) in eastern European countries (Fig. 9b). The impact of changes in age structure on changing NEP is specific to the spatial unit at which it is defined (countries or regions). The trend towards increasing ages is driving NEP down in ageing, more mature, forests (e.g. Germany, Switzerland, northern Sweden). On the contrary, countries

with younger forests (e.g. Scotland, Ireland, eastern Europe) show an increasing NEP along with ageing forests. Part of this positive effect can be attributed to the build up of soil carbon following large-scale afforestation. Other exceptions may be simulation artefacts: in Finland, the age reconstruction algorithm assigns simulated cuts to the North, where older forests are located, whereas in reality, these cuts may have been concentrated in the more accessible south of Finland.

Environmental drivers (climate and $[CO_2]$) are driving NPP upwards (larger sink) everywhere in Europe, by an average 1.3 g C m⁻² yr⁻², with the exceptions of southern Europe because of increasingly dry conditions, and Ireland where the massive reforestation undertaken since 1950 overwhelms the effects of climate forcing (Fig. 10a). In contrast, the upwards HR trends are largely driven by changes in age structure (Fig. 10b). This combination of drivers for NEP shows contrasting regions across Europe (Fig. 10c and d).



Fig. 10 Dominant factors explaining the changes in carbon fluxes of European forests change between 1950 and 2000. The impact of each factor is calculated as the difference between the slopes of the relevant linear regressions: $a_{STD_clim} - a_{STD}$ for climate (CLIM), a_{STD_-} . $c_{lim_co2} - a_{STD_clim}$ for [CO₂] (CO₂), $a_{STD_clim_co2} - a_{STD}$ for the combination of climate and [CO₂] (ENV), and $a_{FMc_clim_co2} - a_{STD_clim_co2}$ for age structure (AGE). The dominant factor is the factor with highest impact in absolute value. The signs indicate whether the impact of the dominant factor is a positive (+) or negative (-) change in the flux. See Attribution for a full explanation of the attribution method and the meaning of the slopes.

Discussion

Impact of age structure on the European forest sink

Separating drivers at the continental scale. Our 'best available estimate (FMc_clim_co2)' for the attribution of the increase in European forest NEP between 1950 and 2000 stresses the effects of rising [CO₂] as the most important factor, explaining 61% of the trend. The impact of changes in climate and age structure is lower, with 26% and 13% respectively. To our knowledge, no modelling study has so far distinguished simultaneously at the EU-25 scale and with gridded results, between climate, [CO₂] and management as potential causes of the historical European forest sink. Several modelling studies, however, quantified the impact of one or multiple of these factors on future carbon fluxes, based on different projection scenarios. Gervois et al. (2008) - for croplands - and Harrison et al. (2008) - for all land uses - report the dominant role of [CO₂] changes in explaining changes in NPP and NEP, outweighing the impact of climate change. Using a bookkeeping approach at European scale with no climate or [CO₂] variation, Bottcher et al. (2008) estimates, just as we do, that differences in age structure can alter the trend of NEP by about 0.2 g C m⁻² yr⁻². For future climate and management scenarios, Karjalainen et al. (2003) report a lower importance of 'climate and [CO₂]' changes relative to management, both with values between 0.3 and 0.4 g C m⁻² yr⁻². The relatively lower impact of management in our results comes from opposite trends across Europe that cancels one another, whereas Karjalainen et al. (2003) apply uniform changes in management across the continent. Moreover, they report a future negative impact of climate and [CO₂] changes over most of southern Europe, an impact that remains limited to Spain in our historical simulations (Fig. 10a). At the continental scale of Africa, Ciais et al. (2009) report a pattern similar to our findings, with climatic changes levelling off and therefore leaving [CO₂] increase as the main driver of GPP change (although not of NEP due to a proportional increase in HR in the simulated steady-state equilibrium ecosystems). A homogeneous effect of $[CO_2]$ is also described by Gloor *et al.* (2009) for the Amazon.

Part of this large effect of [CO₂] is explained by the formulation of photosynthesis in the model (Farquhar et al., 1980; Collatz et al., 1992). As our additive modelling design attributes these interactions to [CO₂], part of the observed effect could be due to interactions between [CO₂] and climate. The formulation of stomatal conductance (Ball et al., 1987) and phenology (Botta et al., 2000) lead to positive interaction effects between, respectively, water stress and [CO₂] and temperature and [CO₂]: a higher [CO₂] mitigates the impact of stomatal closure under water stress conditions and a longer growing season because warmer days allows temperate trees to benefit longer from [CO₂] enhanced photosynthesis. Luo et al. (2008) used a full factorial design to show that these interaction effects can be as large as the effect of $[CO_2]$ alone.

What would be changed by explicitly simulating the nitrogen cycle? The finding of the dominant role of [CO₂] could be partly due to the formulation of ORCHIDEE 1.8 whose NPP is known to strongly respond to [CO₂] changes (Friedlingstein et al., 2006), a reaction that could have been and may continue to be limited by nitrogen availability (Hungate et al., 2003; Churkina et al., 2010; Norby et al., 2010). Recent evidence shows that heterotrophic respiration is also impacted by nitrogen (Janssens et al., 2010). ORCHIDEE-N, also called O-CN, the new version of ORCHIDEE that includes the nitrogen cycle, only simulates a terrestrial sink similar to ORCHIDEE 1.8 in the temperate zone when nitrogen deposition is accounted for (Zaehle et al., 2010). Accounting for nitrogen deposition may therefore reduce the impact attributed to [CO₂] in this study rather than simply adding to the overall increase in NEP. It would not, however, alter our finding that at continental scale, [CO₂] has a homogeneous and positive impact, whereas the heterogeneous impacts of climate and age structure become more or less balanced at the continental scale.

Regional changes. European forests are found to have a positive NEP all across Europe (Fig. 5a), although this sink tends to decrease in countries with older and still ageing forests (Fig. 9d). This is consistent with the empirical findings of Luyssaert *et al.* (2008). At the scale of Thuringen, a German *Bundesland* or region, Vetter *et al.* (2005) found an average forest NEP of 142 g C m⁻² yr⁻¹, which is comparable to our results of ca. 200 ± 60 g C m⁻² yr⁻¹ in this region. Their estimate that age-structure legacy accounted for 17% of the forest sink in Thuringen is more difficult to put on par

with our values, as we estimate the impact of management against past age structure rather than an evenage-class distribution.

In relative terms, our NBP inferred from NEP at country level also compares well with Bottcher et al. (2008). They studied seven countries, ranking in the following order from higher to lower NBP: Italy, Poland, France, Germany, Sweden, Finland and Slovenia. In our results, only Italy and Slovenia are misplaced in this list, both of which are strongly impacted by changes in environmental conditions in our model (Fig. 10c), a factor unaccounted for by Bottcher et al. (2008). However, we find a positive NBP (sink) in every European country in the 1990s (Appendix S1), whereas Bottcher et al. (2008) find a mix of positive and negative NBP (although their methodology is designed to highlight the effect of age legacy rather than to provide realistic NBP estimates). This difference is explained by the driving mechanism for harvest: in the FMc clim co2 scenario, harvest is driven by FAO statistics instead of stand age in Bottcher et al. (2008). The consistency between our estimates and independent NBP estimates from other sources (Fig. 6) increases our confidence in our results.

Net primary productivity changes are found to be dominated by environmental changes (Fig. 10a), mostly the increase in [CO₂] except for parts of western France, parts of central Europe, the Alps and eastern Spain (see Fig. S13c). For the 1980–2000 period, the modelling experiment conducted by Piao *et al.* (2006) simulates similar spatial pattern in leaf area index dominated by [CO₂]. The NPP increase simulated in our study therefore probably comes from an increase in growing season leaf area index.

In contrast to NPP trends, HR trends are most impacted by climate and age structure (Figs 10b and S13d). In over restricted areas like France, however, where our simulations indicate an impact of climate on HR close to zero, $[CO_2]$ increase may be driving the trend in HR through increased litterfall (Davi *et al.*, 2006).

Our simulation showed that climate change is driving a larger decrease in NEP over western Europe than over northern Europe, whereas the impact of [CO₂] is positive everywhere. Harrison *et al.* (2008) come to a similar conclusion making use of JULES, another DGVM without any age-structure parameterization. Where they find a negative impact of climate change over central Europe, we find a very contrasted pattern in this region, with strong negative impact (less sink) in the Baltic states and south-eastern Europe, but a positive impact (more sink) in central Poland and Ukraine. These patterns are most likely explained by temperature change, which was moderate over central Poland and Ukraine, but much stronger in south-eastern Europe and the Baltic states wherein addition rainfall has slightly decreased since 1950. In our results, the HR component of NEP is dominated by local changes in NEP (Figs 9 and S12). The local picture contrasts with the continental scale results for which the more homogeneous increase in $[CO_2]$ drives the increase in NPP which in turn dominates the NEP increase (Fig. 8b). This increase in NEP is slightly higher in north-western Poland and the Baltic states, probably due to the positive interaction between $[CO_2]$ and temperature increase, which is strongest in these regions (Fig. S15).

Impact of modelling strategy

Impact of management representation on NPP and HR. Interestingly, the large difference between NPP and HR flux, which is essential to simulate a large positive NEP (Fig. 6) is not obtained similarly across the two agedependent GVMs, i.e. LPJd and ORCHIDEE-FM. In LPJ_d, HR is largely unaffected by introducing an age structure, whereas NPP increases compared with the standard version of LPJ; younger stands see their NPP boosted by the introduction of height-dependent NPP relationship. In ORCHIDEE-FM, however, both NPP and HR are reduced compared with the standard version of ORCHIDEE, but HR is reduced to a larger extent than NPP. HR reduction is due to reduced mortality in younger stands and wood exports in older ones, both processes that reduce the soil and litter carbon pools available for respiration. In fact, reduced size of soil and litter carbon pools is also modelled by LPI_d, otherwise HR would exactly follow the NPP increase. Hence, the observed model-dependent changes are largely due to differences in the 'standard versions' of LPJ and ORCHIDEE: the lower NPP in 'standard' LPJ corresponds to older forests, whereas the higher NPP in 'standard' ORCHIDEE corresponds to younger forests. The introduction of age structure therefore makes LPJ_d and ORCHIDEE-FM converge from opposite initial parameterizations.

The key issue of age reconstruction. Our results show that three different age reconstruction methods are all sensible lead to different trends in carbon stocks (Fig. 4) and NEP (Fig. 7). Even the more advanced method that reproduced both harvest and 1990 age distribution, FM_{cr} underestimates the increase in carbon stocks by a factor of two. The quality of forest age distribution and wood statistics driving these algorithms is a key issue for age reconstruction. Forest inventories do not consistently report the areas of 'exploited forests', 'unexploited forests', 'forests unavailable for wood supply' and 'other wooded lands', the classification used by the FAO when reporting the harvest statistics. Only 'exploited forests' should be affected by the age resetting of reconstruction algorithms, but it is often not clear from FAO statistics which area of the forest really contributes to wood supply. In addition, estimating wood harvest is always challenging. Local consumption (e.g. wood given away to supply residents with fuel wood) and processing losses are seldom reliably reported, and their estimation is another source of uncertainty in FAO statistics.

Beside the uncertainty in area and wood demand statistics, two processes driving the stock increase between 1950 and 2000 have not been quantified, and could therefore explain the twofold underestimate of the increase in carbon stocks even in the 'best' scenario *FMc_clim_co2*:

- Many coppices have been converted into high forests (standards) in several European countries over the last 50 years (e.g. France, Italy) whereas all forests are assumed to have always been high forests in OR-CHIDEE-FM.
- The change in the share of forest area covered by each PFT is not reported in FAO statistics, and therefore assumed to be constant over time in our reconstruction algorithms. This assumption ignores the probable increase in the proportion of faster growing conifers due to a political and economic context favouring their introduction.

If these processes were included in the model and if, as a result, ORCHIDEE-FM was able to correctly reproduce the observed increase in carbon stocks, the impact attributed to age structure in NEP change would probably increase relative to $[CO_2]$ and climate.

To our knowledge, only two studies simulating age structure have taken a historical perspective on the carbon budget of European forests, and therefore had to deal with this reconstruction issue. Both use a reconstruction algorithm based on demand, similar to our FM_d and FM_c algorithms, but with different initial conditions. Nabuurs et al. (2000) is restricted to Finland. Their reconstruction algorithm - built in the EFISCEN model benefits from inventory data for the initial age structure from an inventory campaign of 1923. With few modifications to the algorithm to address specificities in the history of Finnish forest management, they manage to reproduce the evolution of age structure through time. In Zaehle et al. (2006), the initial age structure over Europe in 1940 is deduced from a 'standard rotation length' that sets productivity and harvest at equilibrium in 1940. However, the relevance of the algorithm and initial conditions is not evaluated against historical data. This comparison reinforces our choice of the FM_c simulation as a 'best available estimate'.

Local specificities vs. general modelling assumptions

The explicit modelling of age structure and management in ORCHIDEE-FM removes a large bias from the ORCHIDEE simulations when compared against observed NEP. This characteristic has already been observed at site scale (Bellassen et al., 2011a) and for other GVMs fitted with age-structure parameterizations (Zaehle et al., 2006; Desai et al., 2007). Our map of above-ground biomass per grid point across Europe (Fig. 5d) is similar, although with a lower resolution, to the recent biomass map produced by Gallaun et al. (2010). There is also reasonably good agreement between simulated values and inventory-derived estimates of volume increment and above-ground biomass at country level (Fig. 3). Nevertheless, a considerable amount of variation remains to be explained at this smaller-scale level. Part of this variation is due to the uniform representation of management in the largescale ORCHIDEE-FM simulations presented in this study. A single idealized management type is indeed applied: even-aged forests with intermediate thinning intensity and thinning from above. A better heed of local management practices may in some cases reduce the RMSE. Switzerland, for example, has a long tradition of continuous forest cover, 'plenterwald', a type of management which leads to higher biomass levels and could explain the large mismatch with the simulations (Thurig & Schelhaas, 2006). ORCHIDEE-FM has been designed to simulate various management types such as unthinned stands (Wolf et al., in press) or coppices (Liberloo et al., 2010). Hence, our modelling framework is able to account for local management practices, but requires a currently unavailable input layer on management type and intensity. When available, assimilating such data into the modelling framework may substantially reduce the current variability seen in Fig. 3.

Not all variability is caused by local management practices. Some of the observed anomalies could disappear following the use of finer input data. In the case of Italy and Spain, age structure is only known at country level. As these countries also have very strong climate gradients, the low spatial resolution of the age structure is probably the basis for a poor match between observations and simulations, as the relationship between age and aboveground biomass is much steeper in regions with favourable growth conditions. This could partly explain the mismatch between simulated and observed aboveground biomass in Italy. Alternatively, the high proportion of evergreen broadleaves may also in part explain this mismatch, as the management rules of ORCHIDEE-FM have not been validated for this PFT.

Model and data errors

In addition to local specificities (see Local specificities vs. general modelling assumptions), structural errors in ORCHIDEE-FM also cause some of the model-data mismatch. This is the case for Nordic countries, where the age-related decline in productivity simulated by ORCHIDEE-FM is probably too intense for the slow-growing conifers in this region. Allometry also explains a minor part of this mismatch (Jalkanen *et al.*, 2005).

Similarly, extreme climate events, such as fires or storms, are not directly accounted for in our modelling framework. Although their impact is generally negligible at large scale (Schelhaas *et al.*, 2003), disturbances may strongly impact the results of a given inventory at country level. In Mediterranean countries, in particular, fire and drought-related mortality may partly explain the variability unexplained by ORCHIDEE-FM (Fig. 3).

The set-up of our modelling experiment may also induce errors in the attribution of the NEP trend due to ill-prescribed initial values of soil and biomass carbon. The small downward trend with time of aboveground biomass simulated in the STD_clim_co2 scenario for broadleaves (Fig. 4) represents an equilibration from initial values being twice as high as the inventoryderived estimates. The positive NEP trend with time of the STD scenario that is used as a baseline to derive the effect of climate, [CO₂] and age structure from other scenarios also comes from an ongoing equilibration from preindustrial conditions to the conditions of the 1950s. Although these equilibration effects are unlikely to exist for biomass in the ORCHIDEE-FM simulations, provided the age reconstruction is correct, they may still exist for soil carbon due to the approximation made for its initial conditions (see Initial conditions). A more satisfying solution could be to initialize soil carbon from a data-derived map with specific values for each land-use type and/or forest type. The recently published maps by Jones et al. (2010) are a first step in that direction.

Moreover, we used net area changes instead of gross reforestation and deforestation area changes, which may result in an underestimation of changes in soil carbon: the deforested lands would move out of the forest category, and only the gains in soil carbon in reforested lands would be accounted for. In this context, a separation of the budget of forests remaining forests from that of forests moving in or out of the forest category would be most proper (Schulze *et al.*, 2010). Although not compatible with the current version of the model, this separation could be introduced in the future.

Other instances of data/model miss-match may result from the inaccuracy of inventory-derived estimates. The case of NPP is the clearest example, as only wood increment is measured *in situ*. Inventoryderived NPP is the result of three successive extrapolations: first from wood increment to woody NPP, using assumptions on wood density and BEF for branches; second from woody NPP to total NPP, applying a constant woody NPP to total NPP ratio; and third, this total NPP is corrected for litterfall, based on biomass stocks and turnover rates. Ciais *et al.* (2008) stressed that the trend between NPP and biomass is more robust than the estimated values of NPP. This explains the discrepancy between simulated and inventory-derived estimates in NPP, especially as simulated values are closer than inventory-derived estimates to other measurement-derived estimates such as extrapolated site studies (Fig. 6).

The mismatch between observations and simulations for Nordic broadleaves (Fig. 3) is also largely due to erroneous inventory-derived estimates. Birch often occurs in small proportion in Scandinavian coniferous stands. Therefore, when the total stock and increment of broadleaves, which includes the contribution of birches from mixed stands, is divided by the smaller area of pure broadleaf stands, the result is a large overestimate. This source of error is being corrected for in recent inventories.

Conclusion

This study puts forward a new figure, i.e. 175 ± 52 g $C m^{-2} yr^{-1}$ for the carbon sink (NEP) of European forests in the 1990s. To the best of our knowledge, this study presents the second estimate of the European carbon balance based on a GVM that fully integrates forest management in its model formulation. Our study clearly demonstrates the need of accounting for forest age structure in GVMs if the simulations aim at reproducing NEP and biomass of managed forest. By comparing three reconstructions of forest age distribution between 1950 and 2000, we show that age reconstruction is not trivial and that different justifiable approaches lead to widely different estimates of carbon stocks, not all consistent with historical data. Our estimate for the change in NEP is 1 ± 0.5 g C m⁻² yr⁻² between 1950 and 2000. This estimate is based on simulations with the age reconstruction that mimics both harvest volume and age distribution in 1990. Sixty one per cent of the change in NEP was attributed to changes in [CO₂], 26% to changes in climate and 13% to changes in forest age structure. The spatially homogeneous increase in the NPP, due to a homogeneous increase in [CO₂], contributes more to increase in NEP than the spatially heterogeneous changes in HR.

The scale considered for attribution of drivers is paramount: the local, heterogeneous, patterns in NEP change are largely driven by the similarly heterogeneous changes in HR. Moreover, climate and age structure can contribute much more than $[CO_2]$ to changes in carbon fluxes at the local scale. The NEP of countries or regions with ageing forests tends to be decreasing. If the current high NEP needs to be maintained, the intensity of the disturbances, i.e. harvest, would need to be increased. However, increased disturbances would diminish or even halt the ongoing increase in standing biomass and thus may lower NBP. Obtaining high, but sustainable levels of NEP and NBP to optimize the forest sink both within the ecosystem and globally requires tuning of harvest levels.

Acknowledgements

This work was funded by the French Ministry for Research. It benefited from data generated by GHG-Europe ('Greenhouse gas management in European land use systems', grant No. 244122). The study was supported by the EU-FP7 project Carbones ('30-year re-analysis of carbon fluxes and pools over Europe and the Globe', grant No. 242316) and by ANR project Autrement (ANR-06-PADD-002). Sebastiaan Luyssaert is funded by the ERC starting grant 242564.

References

- Ball J, Woodrow T, Berry J (1987) A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. Progress in Photosynthesis, 4, 221–224.
- Bellassen V, Le Maire G, Dhote JF, Viovy N, Ciais P (2010) Modeling forest management within a global vegetation model – Part 1: model structure and general behaviour. *Ecological Modelling*, 221, 2458–2474.
- Bellassen V, Delbart N, Le Maire G, Viovy N, Luyssaert S, Ciais P (2011a) Potential knowledge gain in large-scale simulations of carbon fluxes from remotely sensed biomass and height. *Forest Ecology and Management*, **261**, 515–530.
- Bellassen V, Le Maire G, Guin O, Dhote JF, Viovy N, Ciais P (2011b) Modeling forest management within a global vegetation model – Part 2: model validation from tree to continental scale. *Ecological Modelling*, **222**, 57–75.
- Botta A, Viovy N, Ciais P, Friedlingstein P, Monfray P (2000) A global prognostic scheme of leaf onset using satellite data. Global Change Biology, 6, 709–725.
- Bottcher H, Kurz WA, Freibauer A (2008) Accounting of forest carbon sinks and sources under a future climate protocol-factoring out past disturbance and management effects on age-class structure. *Environmental Science & Policy*, **11**, 669–686.
- Buchroithner MF, Buttner G, Steenmans C, Bossard M, Feranec J, Kolar J (2000) Land Cover – Land use mapping within the European CORINE programme. In: *Remote* Sensing for Environmental Data in Albania: A Strategy for Integrated Management, (ed Buchroithner MF), pp. 89–100. Springer-Verlag New York, LLC.
- Churkina G, Zaehle S, Hughes J et al. (2010) Interactions between nitrogen deposition, land cover conversion, and climate change determine the contemporary carbon balance of Europe. *Biogeosciences*, 7, 2749–2764.
- Ciais P, Schelhaas MJ, Zaehle S et al. (2008) Carbon accumulation in European forests. Nature Geoscience, 1, 425–429.
- Ciais P, Piao SL, Cadule P, Friedlingstein P, Chedin A (2009) Variability and recent trends in the African terrestrial carbon balance. *Biogeosciences*, **6**, 1935–1948.
- Collatz GJ, Ribas-Carbo M, Berry JA (1992) coupled photosynthesis-stomatal conductance model for leaves of C4 plants. *Australian Journal of Plant Physiology*, 19, 519–538.
- Davi H, Dufrene E, Francois C et al. (2006) Sensitivity of water and carbon fluxes to climate changes from 1960 to 2100 in European forest ecosystems. Agricultural and Forest Meteorology, 141, 35–56.
- Deheza M, Bellassen V (2010) Getting Carbon Value out of the Forestry and Wood Sector in Annex I Countries: The French Example. Climate Report, CDC Climat Research, Paris, France.

RECONSTRUCTION AND ATTRIBUTION OF EUROPEAN FOREST SINK 3291

- Deleuze C, Pain O, Dhote JF, Herve JC (2004) A flexible radial increment model for individual trees in pure even-aged stands. Annals of Forest Science, 61, 327–335.
- Desai AR, Moorcroft PR, Bolstad PV, Davis KJ (2007) Regional carbon fluxes from an observationally constrained dynamic ecosystem model: impacts of disturbance, CO₂ fertilization, and heterogeneous land cover. *Journal of Geophysical Research-Biogeosciences*, **112**, G01017.
- Dhôte J-F, Hervé J-C (2000) Changements de productivité dans quatre forêts de chênes sessiles depuis 1930: une approche au niveau du peuplement. Annals of Forest Science, 57, 651–680.
- Eggers J, Lindner M, Zudin S, Zaehle S, Lisk J (2008) Impact of changing wood demand, climate and land use on European forest resources and carbon stocks during the 21st century. *Global Change Biology*, 14, 2288–2303.
- FAO (2006) Global Forest Assessment Report 2005. FAO Forestry Paper, FAO, Rome.
- FAO (2010) FAOSTAT, statistical database of the Food and Agriculture Organisation (FAO). Available at: http://faostat.fao.org/ (accessed 1 March 2010).
- Farquhar GD, Caemmerer SV, Berry JA (1980) A biochemical-model of photosynthetic CO₂ assimilation in leaves of C-3 species. *Planta*, 149, 78–90.
- Friedlingstein P, Joel G, Field CB, Fung IY (1999) Toward an allocation scheme for global terrestrial carbon models. *Global Change Biology*, 5, 755–770.
- Friedlingstein P, Cox P, Betts R et al. (2006) Climate-carbon cycle feedback analysis: results from the (CMIP)-M-4 model intercomparison. *Journal of Climate*, 19, 3337– 3353.
- Gallaun H, Zanchi G, Nabuurs GJ, Hengeveld G, Schardt M, Verkerk PJ (2010) EUwide maps of growing stock and above-ground biomass in forests based on remote sensing and field measurements. *Forest Ecology and Management*, 260, 252–261.
- Gervois S, Ciais P, De Noblet-Ducoudre N, Brisson N, Vuichard N, Viovy N (2008) Carbon and water balance of European croplands throughout the 20th century. *Global Biogeochemical Cycles*, 22.
- Gloor M, Phillips OL, Lloyd JJ et al. (2009) Does the disturbance hypothesis explain the biomass increase in basin-wide Amazon forest plot data? Global Change Biology, 15, 2418–2430.
- Gold S (2003) The Development of European Forest Resources, 1950 to 2000: A Better Information Base. Geneva Forest and Timber discussion paper, UNECE-FAO, Geneva, Switzerland.
- Harrison RG, Jones CD, Hughes JK (2008) Competing roles of rising CO₂ and climate change in the contemporary European carbon balance. *Biogeosciences*, 5, 1–10.
- Hungate BA, Dukes JS, Shaw MR, Luo YQ, Field CB (2003) Nitrogen and climate change. *Science*, **302**, 1512–1513.
- Jalkanen A, Makipaa R, Stahl G, Lehtonen A, Petersson H (2005) Estimation of the biomass stock of trees in Sweden: comparison of biomass equations and agedependent biomass expansion factors. *Annals of Forest Science*, 62, 845–851.
- Janssens IA, Dieleman W, Luyssaert S et al. (2010) Reduction of forest soil respiration in response to nitrogen deposition. *Nature Geoscience*, **3**, 315–322.
- Jones A, Montanarella L, Jones R (2010) Soil Atlas of Europe. Joint Research Centre, Ispra, Italy.
- Jung M, Vetter M, Herold M et al. (2007) Uncertainties of modeling gross primary productivity over Europe: a systematic study on the effects of using different drivers and terrestrial biosphere models. *Global Biogeochemical Cycles*, 21.
- Kalnay E, Kanamitsu M, Kistler R et al. (1996) The NCEP/NCAR 40-year reanalysis project. Bulletin of the American Meteorological Society, 77, 437–471.
- Karjalainen T, Pussinen A, Liski J, Nabuurs GJ, Eggers T, Lapvetelainen T, Kaipainen T (2003) Scenario analysis of the impacts of forest management and climate change on the European forest sector carbon budget. *Forest Policy and Economics*, 5, 141–155.
- Krinner G, Viovy N, De Noblet-Ducoudre N et al. (2005) A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. Global Biogeochemical Cycles, 19, 44.
- Kurz WA, Apps MJ (1999) A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecological Applications*, 9, 526–547.
- Kuusela K (1994) Forest Resources in Europe/Kullervo Kuusela. Cambridge University Press, Cambridge, UK.
- Le Quere C, Raupach MR, Canadell JG *et al.* (2009) Trends in the sources and sinks of carbon dioxide. *Nature Geoscience*, **2**, 831–836.
- Liberloo M, Luyssaert S, Bellassen V et al. (2010) Bio-energy retains its mitigation potential under elevated CO₂. PLOS-one, **5**, e1–e1648.
- Lindner M, Lucht W, Bouriaud O, Green T, Janssens I (2004) Specific Study on Forest Greenhouse Gas Budget. CarboEurope-GHG, Jena.
- Luo YQ, Gerten D, Le Maire G et al. (2008) Modeled interactive effects of precipitation, temperature, and CO₂ on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology*, **14**, 1986–1999.
- Luyssaert S, Schulze ED, Borner A *et al.* (2008) Old-growth forests as global carbon sinks. *Nature*, **455**, 213–215.

- Luyssaert S, Ciais P, Piao SL et al. (2010) The European carbon balance. Part 3: forests. Global Change Biology, **16**, 1429–1450.
- Milne R, Van Oijen M (2005) A comparison of two modelling studies of environmental effects on forest carbon stocks across Europe. Annals of Forest Science, 62, 911–923.
- Nabuurs GJ, Schelhaas MJ, Pussinen A(2000) Validation of the European Forest Information Scenario Model (EFISCEN) and a projection of Finnish forests. *Silva Fennica*, 34, 167–179.
- Nabuurs GJ, Pussinen A, Karjalainen T, Erhard M, Kramer K (2002) Stemwood volume increment changes in European forests due to climate change – a simulation study with the EFISCEN model. *Global Change Biology*, **8**, 304–316.
- Norby RJ, Warren JM, Iversen CM, Medlyn BE, Mcmurtrie RE (2010) CO₂ enhancement of forest productivity constrained by limited nitrogen availability. Proceedings of the National Academy of Sciences of the United States of America, 107, 19368–19373.
- Piao SL, Friedlingstein P, Ciais P, Zhou LM, Chen AP (2006) Effect of climate and CO₂ changes on the greening of the Northern Hemisphere over the past two decades. *Geophysical Research Letters*, 33.
- Pongratz J, Reick CH, Raddatz T, Claussen M (2009) Effects of anthropogenic land cover change on the carbon cycle of the last millennium. *Global Biogeochemical Cycles*, 23, 13.
- Pussinen A, Nabuurs GJ, Wieggers HJJ et al. (2009) Modelling long-term impacts of environmental change on mid- and high-latitude European forests and options for adaptive forest management. Forest Ecology and Management, 258, 1806–1813.
- Reineke LH (1933) Perfecting a stand-density index for even-aged forests. Journal of Agricultural Research, 46, 627–638.
- Schelhaas MJ (2010). Personal Communication.
- Schelhaas MJ, Nabuurs GJ, Schuck A (2003) Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology*, 9, 1620–1633.
- Schelhaas MJ, Varis S, Schuck A, Nabuurs GJ (2006) EFISCEN Inventory Database. Available at: http://www.efi.int/portal/virtual_library/databases/efiscen/ (accessed 1 March 2010).
- Schulp CJE, Nabuurs GJ, Verburg PH (2008) Future carbon sequestration in Europe effects of land use change. Agriculture Ecosystems & Environment, 127, 251–264.
- Schulze ED, Ciais P, Luyssaert S et al. (2010) The European carbon balance. Part 4: integration of carbon and other trace-gas fluxes. Global Change Biology, 16, 1451– 1469.
- Shevliakova E, Pacala SW, Malyshev S et al. (2009) Carbon cycling under 300 years of land use change: importance of the secondary vegetation sink. Global Biogeochemical Cycles, 23.
- Swedish National Forest Inventory (2010). Available at: http://www-nfi.slu.se/ (accessed 1 March 2010).
- Thurig E, Schelhaas MJ (2006) Evaluation of a large-scale forest scenario model in heterogeneous forests: a case study for Switzerland. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 36, 671–683.
- UNFCCC, 2010. Documentation to facilitate negotiations among Parties. FCCC/KP/ AWG/2010/6/Add.2.
- Vetter M, Wirth C, Bottcher H, Churkina G, Schulze ED, Wutzler T, Weber G (2005) Partitioning direct and indirect human-induced effects on carbon sequestration of managed coniferous forests using model simulations and forest inventories. *Global Change Biology*, **11**, 810–827.
- Vetter M, Churkina G, Jung M et al. (2008) Analyzing the causes and spatial pattern of the European 2003 carbon flux anomaly using seven models. *Biogeosciences*, **5**, 561–583.
- Wolf A, Ciais P, Bellassen V, Delbart N, Field CB, Berry JA (in press) Forest biomass allometry in global land surface models. *Global Biogeochemical Cycles*.
- Zaehle S, Friend AD (2010) Carbon and nitrogen cycle dynamics in the O-CN land surface model: 1. Model description, site-scale evaluation, and sensitivity to parameter estimates. *Global Biogeochemical Cycles*, 24.
- Zaehle S, Sitch S, Smith B, Hatterman F (2005) Effects of parameter uncertainties on the modeling of terrestrial biosphere dynamics. *Global Biogeochemical Cycles*, **19**.
- Zaehle S, Sitch S, Prentice IC et al. (2006) The importance of age-related decline in forest NPP for modeling regional carbon balances. Ecological Applications, 16, 1555–1574.
- Zaehle S, Bondeau A, Carter TR et al. (2007) Projected changes in terrestrial carbon storage in Europe under climate and land-use change, 1990-2100. Ecosystems, 10, 380–401.
- Zaehle S, Friend AD, Friedlingstein P, Dentener F, Peylin P, Schulz M (2010) Carbon and nitrogen cycle dynamics in the O-CN land surface model: 2. Role of the nitrogen cycle in the historical terrestrial carbon balance. *Global Biogeochemical Cycles*, 24.
- Zhao M, Running SW, Nemani RR (2006) Sensitivity of Moderate Resolution Imaging Spectroradiometer (MODIS) terrestrial primary production to the accuracy of meteorological reanalyses. *Journal of Geophysical Research-Biogeosciences*, **111**.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Proportion of broadleaves (a) and needleleaves (b) in the modelling framework.

Figure S2. Maps of simulated GPP over Europe.

Figure S3. Maps of simulated NPP over Europe.

Figure S4. Maps of simulated HR over Europe.

Figure S5. Maps of simulated NEP over Europe.

Figure S6. Maps of simulated volume increment (V_{inc}) over Europe.

Figure S7. Maps of simulated above-ground biomass (AGB) over Europe.

Figure S8. Maps of simulated soil organic carbon (SOC, litter + soil carbon) over Europe.

Figure S9. Maps of simulated average (a, b) and dominant (c, d) height over Europe.

Figure S10. Maps of simulated average stand age over Europe.

Figure S11. Disaggregated impact of changing climate, [CO₂] and age structure on the NPP change between 1950 and 2000.

Figure S12. Disaggregated impact of changing climate, [CO₂] and age structure on the HR change between 1950 and 2000.

Figure S13. Dominant factors explaining the changes in carbon fluxes of European forests change between 1950 and 2000.

Figure S14. Carbon balance of European forests in the 1990s.

Figure S15. Climate drivers.

Figure S16. Simulated age structure, wood harvest and volume increment for each European country (*FMc_clim_co2 simulation*).

Appendix S1. Carbon balance of European countries in the 1990s.

Appendix S2. List of abbreviations.

Appendix S3. Attribution of NPP (a) and HR (b) change between 1950 and 2000 to different factors.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.