1 Methods and materials

1.1 Data selection for this study

We compiled a comprehensive database (see §1.2) on carbon fluxes, ecosystem properties and stand characteristics of forest stands[29]. For this study, the database was queried for biometric-based NPP, chamber-based Rh, eddy-covariance or biometric-based NEP, their uncertainties and ecosystem attributes such as aboveground biomass, stand age, stand height and stand density. The quality of the data set used in this study was enhanced by excluding model-based flux estimates and flux estimates for fertilized and irrigated experimental treatments. Data from a total of 519 temperate and boreal forests that reported one or more of the variables were used in this study.

1.2 The database

A comprehensive relational database structure was designed to store information on carbon fluxes, ecosystem properties, and site information of forest stands. Data entries originated from peer-reviewed literature, established databases e.g.[30,31] and personal communications with research groups involved in regional networks (AmeriFlux, AsiaFlux, CarboEurope-IP, ChinaFlux, Fluxnet-Canada, NECC, TCOS-Siberia, USCCC), and the Fluxnet project[32]. The high quality of the database is ensured by several features: (i) referential integrity is ensured by the structure of the database, (ii) literature and databases are browsed without discrimination for sites, regions, biomes or climate zones; data selection is only based on strict methodological criteria, (ii) consistency of the NPP data is ensured by a hierarchical framework, (iv) uncertainty of the fluxes are estimated in a consistent manner accounting for the methodological approach and the length of the time series, (v) the uncertainty of aggregated fluxes is estimated, and (vi) a variety of observed and/or modelled meta-data is included in the database.

Structure of the database

The database is structured by site. A site is a forest or a stand with a known geographical location, biome (USA Department of Agriculture biome classification[33]), tree species composition and management regime. Hence, different treatments within an experimental forest or different aged stands that form a chronosequence were recorded as different sites. Each site in the database is linked to at least one carbon balance component and each component is further linked to the methodology that was used to estimate it. Due to its structure, the database can contain multiple estimates of the same flux for the same year (i.e. if these estimates were reported in different studies or estimated with different measurement techniques). Because data from different sources or references are stored as different entries, the structure of the database thus ensures referential integrity.

Selection criteria

NPP estimates were included in the database when they were based on direct measurements of the main components of NPP[34] if these achieved these criteria: the net annual production of leaves or needles was determined by collecting leaf/needle fall throughout the year; annual stem and branch increment were determined using species- and region-specific allometric equations relating aboveground woody biomass increment to the change in basal area of individual trees in the plot; and coarse-root production was determined through species- and region-specific allometric equations relating root mass to basal area and fine-root production was determined by repeated soil coring, isotopic estimates of fine-root turnover combined with biomass measurements, upscaled root-length production observed in minirhizotrons or the soil respiration and litterfall constraint formulated by Raich and Nadelhoffer (1989)[35]. Furthermore, to be included in the database, foliage, stem, branch, coarse and fine root biomass increment had to be corrected for the annual litterfall of these components.

Direct measurements of annual and multiple-year NEP were included in the database when based on continuous measurements with a tower-based eddy covariance system. NEP estimates were accepted when data gaps due to system failure, stable atmospheric conditions or data rejection were filled by means of standardized methods[36,37] to provide complete datasets. These data, however, do not include corrections for possible effects of advection, which may lead to a biased night time respiration even at high turbulence.

Biometric NEP estimates were included in our database when they were based on the difference between biomass production and heterotrophic respiration e.g. see[38] or repeated biomass inventories and soil respiration measurements e.g. see[39].

Estimates of heterotrophic respiration Rh were included in the database when based on subtracting chamber measurements from undisturbed plots from measured and up-scaled root respiration[40] or chamber measurements after trenching or girdling.

Consistency of the flux data

Although NPP data are more widely available than other carbon-flux estimates, there are considerable problems of consistency among NPP studies. Reported NPP values can range from the net primary production of a single component (e.g. foliage NPP) to the complete NPP of the ecosystem. In this study we accounted for these inconsistencies by combining 6 components and 4 aggregation levels of NPP in a hierarchical framework. For more details see Fig. 1 in[29]. At the lowest hierarchical level, stem and foliage NPP were used to calculate aboveground NPP ($ANPP_1$; foliage + stem NPP). The next hierarchical level included branch NPP. If branch NPP was measured, wood NPP (stem + branch NPP) and $ANPP_2$ (foliage + stem + branch NPP or foliage + wood NPP) were calculated. Coarse and fine root NPP were recorded as separate components and summed to obtain the below ground NPP ($BNPP_1$; coarse + fine roots NPP). If all required low level components were available, the total NPP ($TNPP_1$) was calculated as $ANPP_2$ + $BNPP_1$. The framework was considered hierarchical because a certain level of NPP was calculated only when all underlying components were measured.

Given this careful processing and quality evaluation of data for each site, the NPP data are consistent when a single level of NPP data is used. It should be noted that minor inconsistencies remain within an individual component (i.e. the use of different cut-off diameters between coarse and fine roots). However, the variation due to these inconsistencies is expected to disappear when NPP estimates of a higher level are used (i.e. the variation due to different cut-off diameters are expected to disappear when total belowground NPP ($BNPP_1$) is used).

Uncertainty of the measured CO_2-fluxes

Our flux data span multiple biomes and the data come from diverse sources. Different biomes have different sources of uncertainty[41,42]. Although recently efforts have been made to quantify the uncertainties of eddy covariance measurements[43-47], uncertainty of CO_2-flux estimates are only rarely reported in the literature and when reported it is often unclear whether the given value denotes instrumental, spatial, temporal and/or other sources of variability. Therefore, we did not use the reported uncertainty and instead estimated the total uncertainty for every component flux contained in the database. The uncertainty was estimated in a uniform way based on expert judgment[48]. We could not identify prior information that could constrain the absolute range of the estimated NEP. Without measurements or prior information, experts agreed that the NEP of a forest most likely ranges from -100 to 600 g C m^{-2} yr^{-1}. The absolute range of the NEP estimate is thus ± 350 g C m^{-2} yr^{-1} ([29]). However, all methodological approaches contained in the database used site-specific observations and are therefore expected to reduce the uncertainty surrounding the NEP estimates. Hence, the uncertainty was reduced with a method-specific factor. When NEP was determined by eddy covariance measurements the method-specific factor was set to 0.3 or 30% of 350 g C m^{-2} yr^{-1} to reproduce the uncertainty estimate of 105 g C m^{-2} yr^{-1} presented by[49-51]. The other method-specific reduction factors were then set between 0.2 and 1.0 and selected by expert judgment. The applied method-specific reduction factors (i.e. 30% for eddy covariance), are tabulated in[29]. When a flux was a multiple-year mean value, its value is less prone to inter-annual variability and therefore its uncertainty (s_{ij}) was further reduced by accounting for the length of the time series. Thus:

$$s_{ijl} = \left(p_i \times RF_j\right) \Big/ \sqrt{l_{ijl}} \qquad (1)$$

Where p_i is the initial uncertainty for site i in the absence of measurements (see Table 2 in[29]) and RF_j is the reduction factor for method j according to Luyssaert et al.[29] and l_{ij} is the length of the time series (in years) for site i for which the fluxes where estimated with method j in year l. Our uncertainty framework resulted in 95% confidence intervals (based on s_{ijl}) ranging between 105 and 350 g C m^{-2} yr^{-1} for NEP.

A similar approach was followed to estimate the uncertainty of NPP and Rh. However, for these fluxes the latitude of the site contained prior information regarding their absolute range (i.e. NPP at a boreal site is likely lower than the NPP at a temperate site [29]). Consequently, the absolute range for NPP in the absence of measurements depends on the latitude. For each site contained in the database the latitude was known and as such, the absolute range in the absence of measurements (p_i) could be estimated. This initial uncertainty was then reduced by the method-specific factor and further adjusted for the length of the time series. Our uncertainty framework resulted in 95% confidence intervals ranging between 110 and 545 g C m^{-2} yr^{-1} for NPP. This range compares to uncertainties reported for a single forest[34,52]. The 95% confidence intervals of Rh ranged between and 95 and 295 g C m^{-2} yr^{-1}.We are not aware of observation-based studies that report the uncertainty of Rh observations. Therefore, the spatial variability of Rh in the database (250 g C m^{-2} yr^{-1}) was used to validate the expert-based assessment.

Aggregated fluxes and their uncertainty

According to the analyses presented in this study the data had first to be aggregated by year and then by site. For a given site (i), a single weighted mean flux estimate (F) was produced for each available year l. When the flux component was determined with k different methods j in year l, the flux determined by method j for site i was then given as F_{ijl}. The average flux across methods (F_{il}) was calculated as the weighted mean:

$$F_{il} = \sum_{j=1}^{k} \left(w_{ijl} \times F_{ijl} \bigg/ \sum_{j=1}^{k} w_{ijl} \right) \qquad (2)$$

Where, $w_{ijl} = 1 / s_{ijl}^2$. The uncertainty of the weighted mean was estimated by means of error propagation:

$$s_{il} = \sqrt{\sum_{j=1}^{k} s_{ijl}^4 \times w_{ijl}} \qquad (3)$$

Following, the weighted mean flux component was calculated across years:

$$F_i = \sum_{l=1}^{m} \left(w_{il} \times F_{il} \bigg/ \sum_{l=1}^{m} w_{il} \right) \qquad (4)$$

Where, $w_{il} = 1 / s_{il}^2$, m the number of years for which flux estimates are available for site i. The uncertainty of the weighted mean was estimated by means of error propagation:

$$s_i = \sqrt{\sum_{l=1}^{m} s_{il}^4 \times w_{il}} \qquad (5)$$

Site description data

Additional site information related to stand characteristics, standing biomass, leaf area index and growing environment were added to the database as separate tables. Stand characteristics such as basal area, mean tree diameter, mean tree height, mean tree density and mean stand age are available for many sites. Also the observed standing biomass and its major components, the maximal observed leaf area index, and some methodological details of the leaf area measurement technique were available and stored in the database for many sites.

Availability of the database

The database its manual and appendices can be downloaded from ftp://ftp.bgc-jena.mpg.de/pub/outgoing/mjung/CfluxDB_Luyssaert/ and http://www.ua.ac.be/main.aspx?c=sebastiaan.luyssaert&n=35884

1.3 Self-thinning and data modeling

Self-thinning is the process of density-dependent mortality. For even-aged, single species stands Yoda *et al*.[23] proposed an empirical summary of this process:

$$W = c \cdot n^{\gamma - 1} \quad (4)$$

where W is the mean biomass of an individual tree (g tree^{-1}), n the decreasing stand density (tree m^{-2}), and c a stand-specific constant (g m$^{2(\gamma-1)}$ tree$^{-\gamma}$) that dependents on species, light regime and nutrition status. The exponent γ (dimensionless) has been derived from tree geometry (i.e. height and ground area)[23]. The biomass per unit area (*B*; g m^{-2}) equals the product of *W* and *n*, therefore, the self thinning law for stands is derived by multiplying Eq. 4 by *n*:

$$B = c \cdot n^{\gamma} \tag{5}$$

Taking the logarithm of this equation yields a linear relationship:

$$\log(B) = \log(c) - \gamma \cdot \log(n) \tag{6}$$

For even-aged single-species stands *γ* was estimated at -0.5 ([23]) In Fig. 2 we used the functional relationship of Eq. 6 and estimated *c* and γ at the biome-level. During the life-time of a forest its density decreases from n_{start} to n_{end}, n_{end} -n_{start} individual trees will be lost. The biomass of each tree is given by Eq. 4 and the total loss of biomass (L) during the life-time of the forest is given by:

$$L = \sum_{nstart}^{nend} c \cdot n^{\gamma-1} \tag{7}$$

At the same time the standing biomass increased according to Eq. 5:

$$G = c \cdot (n_{end} - n_{start})^{\gamma} \tag{8}$$

Self-thinning theory was originally developed and validated for even-aged single-species stands. Since it was first published, it has been shown to be equally valid for uneven-aged multi-species plant communities[53,54]. Applying Eqs. 4 to 8 to uneven-aged forests requires that the biomass of recruitment is negligible. In the old growth beech forest of Hainich[11] the upper canopy layer accounted for 91% of the biomass, the 2nd canopy for 9% and recruitment for less than 1%. Consequently, ignoring recruitment most likely will result in only small errors in G and L. There are no theoretical grounds for not being able to apply self-thinning estimates to multi-species plant communities because the primary driver of self-thinning is similarity in resource use[55]; the trade-off between density and size will be compensated among species[56]. Consistent with this, we observed that all boreal and temperate forests (Fig. 2), including the sub set of unmanaged boreal and temperate forests (not shown), followed the self-thinning theory with γ approaching -0.5. We interpreted this as a negligible effect of recruitment and species interactions on biomass and, therefore, used the observed relationship between biomass and density data to calculate a proxy for NPP and Rh components of flux-computed NEP. Nevertheless, these proxies were only used for interpretation of the primary results. Thus, all green and orange symbols (Figs 1, 2, S2, S3 and S4) are field-observations.

In this study, self-thinning theory was only applied to: (1) estimate the expected ratio between Rh and NPP across densities and (2) estimate the importance of woody biomass production in NEP of old forests. First, the gross biomass production (B_{gross}) (including branches, stem and coarse roots) is thus G+L. G, L and B_{gross} can be calculated for tree-by-tree changes in density from n_{start} to n_{end} (Fig. S5a). Following a change in density, the sequestered carbon is then given by the difference of B_{gross} before and just after tree mortality occurred. The carbon released through decomposition of woody debris is given by *L* (Fig. S5b). Assuming foliage and fine root NPP and their decomposition offset each other, allows us to apply ΔL:$\Delta Bgross$ as a proxy for Rh:NPP (Fig. S5c). It should, however, be noted that legacy woody debris that existed prior to stand establishment is not included in our estimate of *L*. With a decomposition rate of 1 to 3% yr^{-1} [57], ΔL is likely to underestimate Rh for the first 30 to 100 years. Second, $\Delta Bgross$ (and ΔL) are expressed on a per tree basis (gC m^{-2} lost $tree^{-1}$) but need to be converted on a per year basis to obtain woody NPP (gC m^{-2} yr^{-1}). The observed maximum and minimum density for stands older than 200 years was used as n_{start} to n_{end} and the observed age range was used to determine the time required to realize this density decrease (lost tree yr^{-1}). $\Delta Bgross$, Δn and Δt were combined to estimate woody NPP (gC m^{-2} yr^{-1}) for forests of 200 years and older.

1.4 Odum's hypothesis as an implicit assumption in ecosystem models

The mathematical equation which governs NEP in models is $dM/dt = NPP - k \cdot M$ where, *M* is the carbon stock (g C m^{-2}), *k* is a decay rate describing the biomass mortality and soil carbon decomposition and *NPP* (g C m^{-2} yr^{-1}) is the net primary production. When the modeled leaf area index (LAI), atmospheric CO_2 concentration and climate are constant, NPP is also constant. During a spin-up, which is required to reach steady state, LAI, atmospheric CO_2 concentration and climate are constant. Hence, M approaches NPP/k and thus dM/dt (or NEP) is zero. In addition, modeled forests are usually mature but of unknown age. Consequently, in the absence of disturbances, ecosystem models predict that mature forests are carbon neutral and thus reflect Odum's hypothesis.

1.5 Data processing

The total uncertainty (s_i) for the flux contained in the data set were estimated using a framework based on expert judgment (See §1.2). The uncertainty framework was designed to account for differences in data quality between sites due to length of time series, methodology and conceptual difficulties (i.e. gap filling). The uncertainties were propagated throughout the analyses by means of random realizations based on Monte Carlo principles[58].

The 95% uncertainty interval for biomass, age and density was set to 20% of the observed values and the uncertainties for NPP, wNPP, Rh and NEP were extracted from the database. One thousand realizations of the dataset were simulated by adding a normally distributed uncertainty to the observed estimates for both the dependent and independent variable. The normally distributed uncertainties were calculated by multiplying the total uncertainty of the flux (s_i) by a normally distributed random number with a mean equal to zero and a variance equal to one. Following, each relationship or test between a dependent and independent variable was estimated a thousand times, once for each random realization.

For the relationships between age, NEP, Rh/NPP and NPP, the moving weighted mean was calculated for a moving window of 15 observations. For a given age we then plotted the mean value for all 1000 simulations (i.e. black line) and the 95% confidence interval of the mean value (i.e. gray area around the black line). For a given age, the confidence interval was estimated as the 2.5 and 97.5 percentile of the mean values of the 1000 simulations. Also for a given age, the 2.5 and 97.5 percentile of all 1000 random realizations for the individual sites within a window of 15 observations was used as the uncertainty to estimate the probability that an individual forest is a source rather than a sink.

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Supplementary figures

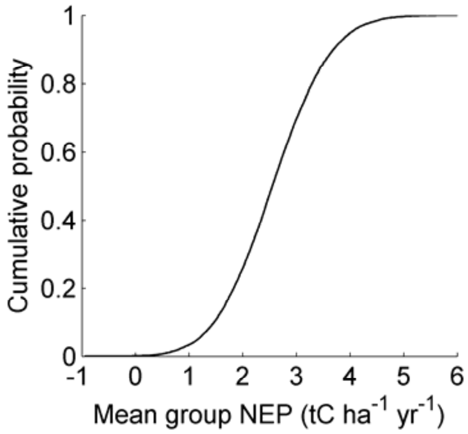
Figure S1. Cumulative probability of finding a given mean NEP for a group of 10 randomly selected forests older than 200 years. The minimal group NEP for forests older than 100 years was -0.5 tC ha^{-1} yr^{-1} with a probability of 0.0012 (negative value indicates a source), -1.1 tC ha^{-1} yr^{-1} for forests older than 200 years (p = 0.0008) and -0.9 tC ha^{-1} yr^{-1} for forests older than 300 years (p = 0.0007). Overlapping cumulative distribution functions (not shown) suggested that the results did not depend on the selected age threshold when set to 100, 200 or 300 years. The group probabilities were calculated by simulating 1000 possible realizations of the NEP data and their uncertainties.

Figure S2. Changes in net primary production (NPP) as a function of forest age (a) Relationships of observed NPP vs. age where green shows the temperate and orange the boreal forests. The thick black line shows the weighted mean within a moving window of 15 observations. The black lines above and below the weighted mean show the weighted mean NPP for temperate and boreal forests, respectively. The outer thin black line shows the 95% confidence interval of the individual flux observations. It appears that temperate and boreal forests each show a pattern of declining NPP. Only when the two data sets are combined is the late-successional increase apparent. This reflects the lack of data from boreal forests older than 300 years, considering that boreal NPP is usually lower than temperate NPP. The apparent increase in NPP is likely because the available estimates for the oldest forests are dominated by data from temperate regions that have higher average NPP; (b) Relationship between observed NPP and age where green shows the unmanaged and brown the managed forests. The thick black line shows the weighted mean within a moving window of 15 observations. The black lines above and below the weighted mean show the weighted mean NPP for managed and unmanaged forests, respectively. The outer thin black line shows the 95% confidence interval of the individual flux observations. NPP in unmanaged forests appears to be independent of age which could be due to differences in disturbance history.

Figure S3. Biomass accumulation as a function of stand age, shown as the relationship between aboveground biomass and the logarithm of stand age. The thick black line shows the weighted mean within a moving window of 15 observations. The grey area around this line shows the 95% confidence interval of the median. Each data point represents a forest stand (green is temperate, and orange is boreal), many of which have different growing conditions and species composition.

Figure S4. Productivity and productivity indexes derived from the self-thinning theory fitted to the observed biomass and density data. (a) Biomass losses (L; blue line), net biomass stock (B, red line) and gross biomass stock (B_{gross}, green line) as a function of stand density. (b) Changes in gross biomass and biomass losses expressed per tree lost as a function of stand density. (c) $\Delta L{:}\Delta Bgross$ (dotted line and dark confidence intervals) as a proxy of Rh:NPP. $\Delta L{:}\Delta Bgross$ which was obtained from the self-thinning plot (Fig. 2) is in reasonable agreement with the observed Rh:NPP (full line and light gray confidence intervals).

Figure S5. The reporting and accounting of carbon stocks under the UNFCCC is confined to national borders, because nations are the signing parties. Art. 2 of the UNFCCC calls for stabilization of greenhouse gas concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system[59]. Art. 4.2(a) clarifies that this should be achieved by national policies and taking corresponding measures on the mitigation of climate change, by limiting its anthropogenic emissions of greenhouse gases and protecting and enhancing its greenhouse gas sinks and reservoirs. However, unmanaged systems (red area) are traditionally considered to be carbon-neutral and therefore only managed ecosystems are considered within the Framework (cyan area). Nations have to report their carbon-stocks according to the rules set by the IPCC Good Practice Guidance which includes land-use types of Cropland, Grassland, Forest, Wetlands and Settlements (light and dark cyan area). Under the Kyoto Protocol the accounting of changes in carbon-stock by afforestation, reforestation and deforestation (ARD) is mandatory (Art. 3.3). In addition, Nations can select to account for changes of carbon-stocks in cropland, grassland, forest and revegetation projects (dark cyan area) or exclude certain regions (i.e. USA-Alaska). Most European countries have selected to include only forestry into their accounting system and thus not account for carbon-stock changes in agriculture. In addition, flexible mechanisms allow trading of carbon credits between countries. Nations can also receive credits from land-use projects funded in other industrial countries via the Joint Implementation (JI) mechanism. So far, the land-use sector is excluded from the European carbon trade. Also, afforestation projects funded in non-annex I countries may be added to the national carbon-balance via the Clean Development Mechanism (CDM), but this amount will be negligible until 2012.


Cumulative probability
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0.8
0.6
0.4
0.2
0
-1 0 1 2 3 4 5 6
Mean group NEP (tC ha^-1 yr^-1)

Figure S1

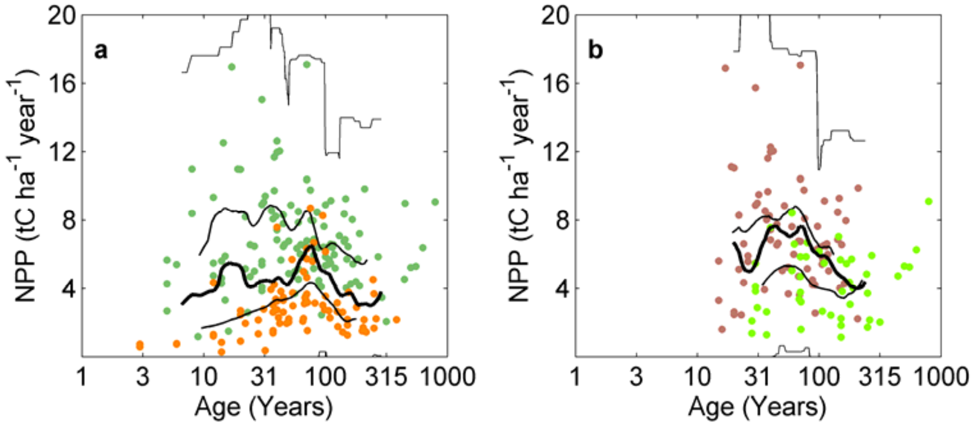

Figure S2

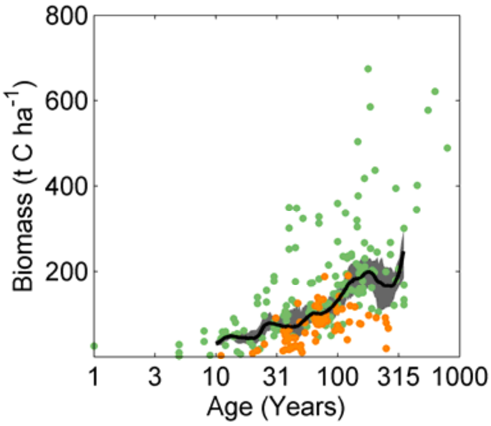

Figure S3

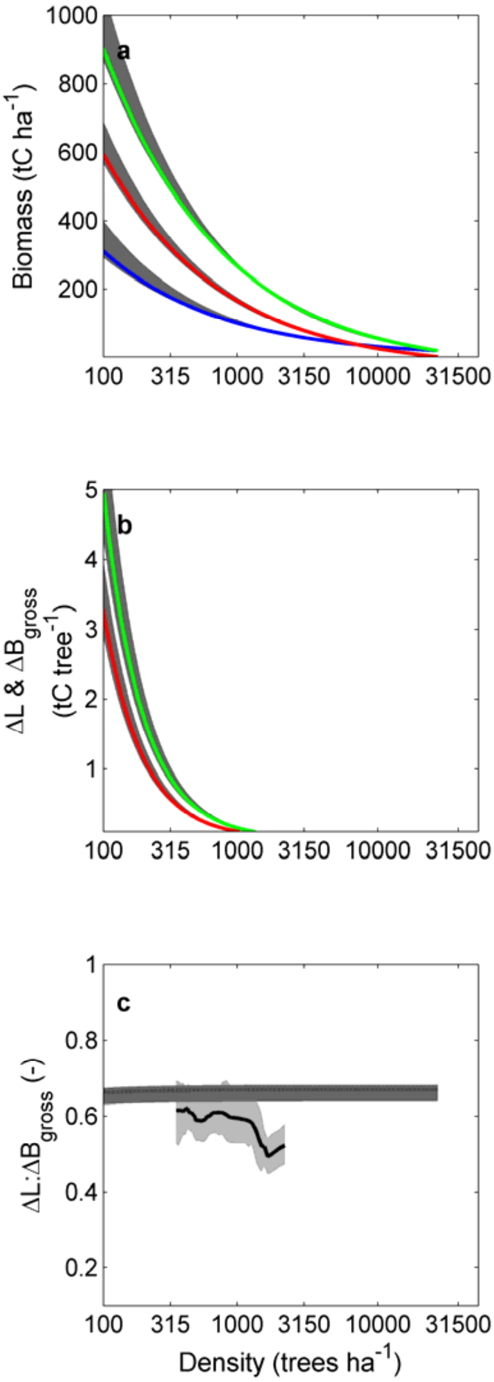
a
Biomass (tC ha-1)
1000
800
600
400
200
100
315
1000
3150
10000
31500
b
ΔL & ΔBgross (tC tree-1)
5
4
3
2
1
c
ΔL:ΔBgross (-)
1
0.8
0.6
0.4
0.2
Density (trees ha-1)

Figure S4

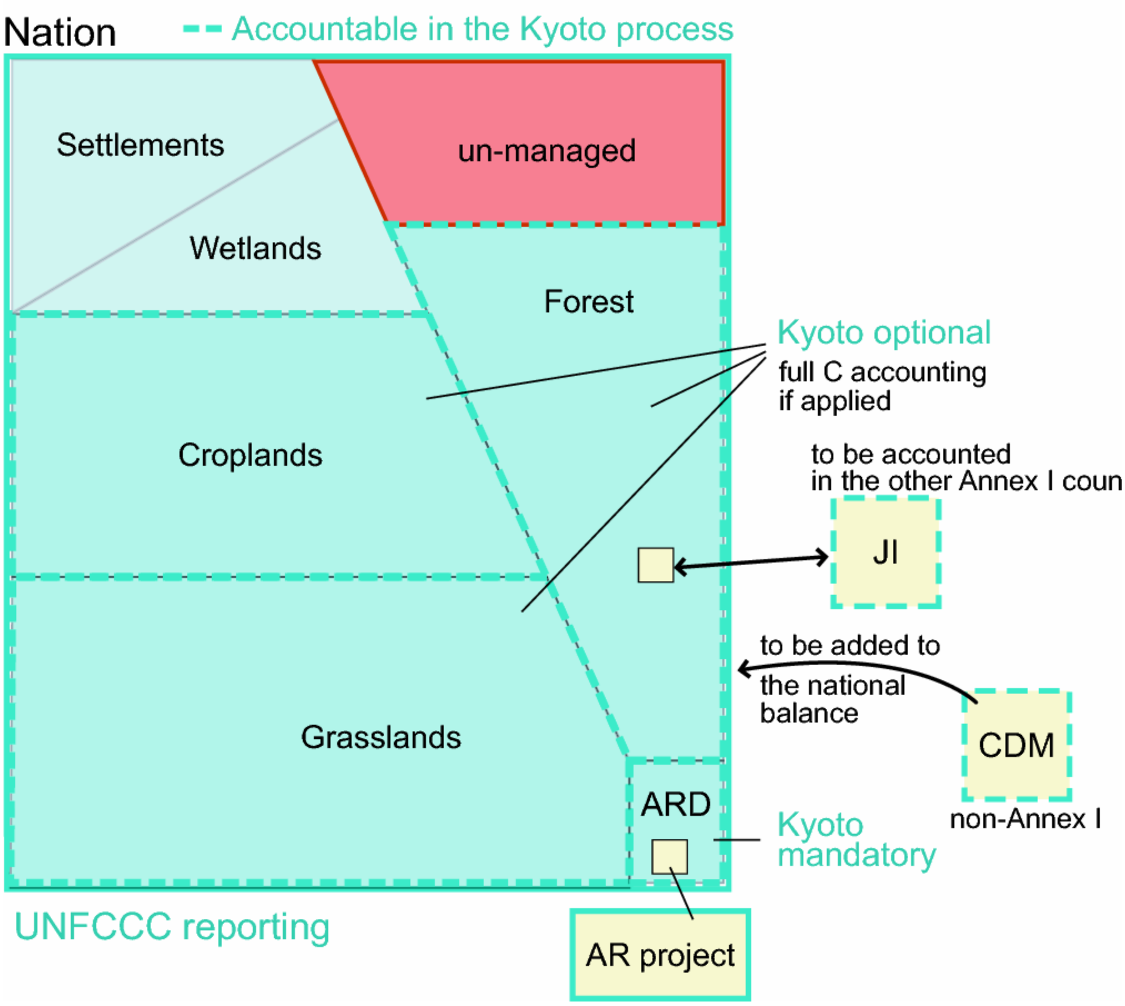
Nation
Accountable in the Kyoto process
Settlements
Wetlands
un-managed
Forest
Croplands
Grasslands
Kyoto optional
full C accounting
if applied
to be accounted
in the other Annex I coun
JI
to be added to
the national
balance
CDM
non-Annex I
ARD
Kyoto
mandatory
UNFCCC reporting
AR project

Figure S5