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Key Points:
- National Forest Inventory data of South Korea were assimilated into a biogeochemical model to estimate carbon and nitrogen turnover times
- The nitrogen turnover time (376–499 years) was ~45 times longer than the carbon turnover time (9–10 years)
- The carbon and nitrogen turnover times decreased with temperature and increased with stand age and carbon:nitrogen ratio

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Carbon and Nitrogen Turnover Times of South Korean Forests Estimated via Data-Model Fusion

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Abstract Biogeochemical models use estimates of carbon (C) and nitrogen (N) turnover times for the future projection of global forest C and N stocks, but unexplained variation in the C and N turnover times is causing considerable uncertainty. This study aimed to estimate C and N turnover times of South Korean forests and explain their variation with forest type, temperature, precipitation, stand age, and ecosystem C:N ratio. We used the balance method and data-model fusion to estimate the C and N turnover times. Data-model fusion was used to integrate the National Forest Inventory data (2011–2020) with a biogeochemical model, Forest Biomass and Dead organic matter Carbon and Nitrogen (FBD-CAN). The N turnover time (376–499 years) was ~45 times longer than the C turnover time (9–10 years). Forest type had no substantial effects on the C and N turnover times. However, the C and N turnover times were positively correlated with stand age and ecosystem C:N ratio, and negatively correlated with temperature. Overall, ecosystem C:N ratio, stand age, temperature, and precipitation explained 45%, 15%, 12%, and 3%, respectively, of the total variation of the C and N turnover times. These results contribute to the understanding and prediction of forest C and N changes in a changing world and highlight the importance of considering C:N ratio for reliable estimation of the C and N turnover times.

Plain Language Summary Forests are major sinks of carbon and nitrogen that can cause global warming when present in gaseous forms. Turnover times, referring to the time an element remains in an ecosystem, are measures of the long-term stability of carbon and nitrogen. Models use estimates of turnover times for future projections of carbon and nitrogen cycles, but limited knowledge in turnover times and model uncertainty are causing trouble. Data-model fusion is a technic that combines data and model's output to decrease model uncertainty. We used data-model fusion to estimate carbon and nitrogen turnover times with a model and field-measured carbon and nitrogen data in the South Korean forests. We then explained how forest type, temperature, precipitation, forest age, and carbon:nitrogen ratio affect carbon and nitrogen turnover times. The results indicated that nitrogen turnover time is ~45 times longer than carbon turnover time. Forest type had no substantial effect on carbon and nitrogen turnover times. Increasing temperature decreased carbon and nitrogen turnover times, while forest age and carbon:nitrogen ratio increased them. The carbon:nitrogen ratio was a key factor affecting carbon and nitrogen turnover times. Future efforts to estimate turnover times should take the impact of the carbon:nitrogen ratio into account.

1. Introduction

Carbon (C) and nitrogen (N) are fundamental elements that support forest life. The assessment of C and N stocks has been a core focus since the inception of biogeochemistry in terms of the implications of C sequestration and N losses (Högberg et al., 2017; Howarth et al., 2006; Pan et al., 2011). At the ecosystem level, C and N stocks are the balance between (a) input fluxes to forests including photosynthesis, N deposition, and biological N fixation, (b) internal fluxes in forests such as litterfall, N mineralization, and N retranslocation, and (c) output fluxes from forests through respiration, N leaching, and denitrification (Agren & Andersson, 2012; Gundersen, 1991). This balance can be interpreted by turnover time, which represents the average time elapsed between the input of an element to forests and its output from forests in an autonomous

system at the steady state (i.e., mean transit time; Barrett, 2002; Sierra et al., 2017). The turnover time of an element is longer when the element remains in forests for a longer period of time through internal fluxes rather than leaving through output fluxes. Forests with a long turnover time for C and N are long-term sinks for these elements (Schlesinger, 2009). However, a recent study demonstrated that the long-term C sink capacity of forests would be constrained under the future climate because of the pervasive decrease in C turnover time of woody biomass as a result of increased tree mortality (Yu et al., 2019). Hence, the goal now should be to improve understanding of the forest C and N turnover and the controlling biotic and abiotic factors in order to sustain forest ability to act as C and N sinks.

It is crucial to precisely estimate the C and N turnover times as these dominate uncertainty in future projections of global forest C and N stocks of biogeochemical models (Friend et al., 2014; Ge et al., 2019; Johnson et al., 2016; Thurner et al., 2017). A field measurement-based study estimated that the average C turnover times of vegetation and soil in northeastern Asia, covering tropical, temperate, and boreal forests, were 7.6 and 17.7 years, respectively (Wang et al., 2018). A data-model fusion study estimated that the average C turnover time of evergreen coniferous forests in North America was 85.9 years (Zhou et al., 2012). The Coupled Model Intercomparison Project Phase 5 (CMIP5) estimated that the global averages of C turnover times of tropical, temperate, and boreal forests were 14.2, 23.5, and 53.3 years, respectively (Carvalhais et al., 2014). Meanwhile, other studies have estimated the N turnover times. A replicated chronosequence study found that the N turnover time of the forest floor in lodgepole pine forests in North America was 26.6 years (Smithwick et al., 2009). A biogeochemical model estimated that the global averages of the N turnover time of plant biomass, litter, and soil were 6.1, 1.0, and 116.7 years, respectively (Wang et al., 2010). A global data synthesis study showed that the global average of N turnover times of a terrestrial ecosystem was ~500 years (Galloway et al., 2004; Gruber & Galloway, 2008).

At the global terrestrial ecosystem scale, the C turnover time varies from years to decades in wood, months to years in litter, and decades to centuries in stabilized dead organic matter (DOM; Sierra et al., 2017). The large variations in the C turnover times of wood, litter, and DOM can cause greater variation in the C turnover time at the whole ecosystem level. Several studies have identified controlling factors of the C turnover times to better understand their variation. Evergreen forests have shorter C turnover times than deciduous forests, while coniferous forests have longer C turnover times than broad-leaved forests (Wang et al., 2018; Zhou et al., 2010). The C turnover time is shorter in stands with higher temperature and precipitation because these accelerate the respiration of vegetation and soil microbes (Cai et al., 2020; Ge et al., 2019). The C turnover time of soil organic C showed a decreasing trend with increasing temperature and precipitation, from the 1980s to the 2010s under climate change (Chen et al., 2020). The C turnover times of vegetation and soil are longer in older stands because these have smaller C output fluxes relative to C stocks (Wang et al., 2018).

However, the large variation in the C and N turnover times remains unexplained, resulting in uncertainty in their estimations. Wang et al. (2018) used a number of factors, including forest type, climate, and stand age, to explain variations in the C turnover times of vegetation and soil in northeastern Asian forests, but the explained variations were only 27% and 44%, respectively. Moreover, although various abiotic and biotic factors affect the C cycles in forests, such as tree species composition, biogeochemical composition of DOM, and soil pH, texture, and microbial community, only a few have been used to explain the variation in the C turnover times (Cai et al., 2020; Carvalhais et al., 2014). In particular, the explanatory power of the C:N ratio for the variation in the C turnover time has not yet been quantified, to our knowledge, through a regional or broader scale study, although it has reportedly played a key role in the interactions between the C and N cycles (Gruber & Galloway, 2008).

In addition, estimation methods and their assumptions may enlarge uncertainty in the estimation of turnover times. The turnover time of an element is usually calculated with the "balance method," whereby the stock of the element is divided by its output flux (Schwartz, 1979; Sierra et al., 2017). However, measurement of the stocks and output fluxes of C and N at a broad spatial range is challenging, especially for N output fluxes such as N leaching and denitrification, resulting in the dearth of long-term empirical data for an accurate estimation of turnover times (Addiscott, 1996). The latter triggered the use of biogeochemical models for estimating turnover times (Carvalhais et al., 2014; Derrien & Amelung, 2011). However, biogeochemical models also have uncertainty in their estimations because of the inadequate representation

of the phenological processes accruing within forest ecosystems and the lack of fit of model parameters (Carvalhais et al., 2014; Pugh et al., 2020; Wang et al., 2010). In this regard, Pugh et al. (2020) reported that the estimated global C turnover times by six biogeochemical models varied from 12.2 to 23.5 years because of differences in model structures and parameters, which determine resource allocation, turnover rate, and the interaction between the C and N cycles. Other studies have also related model uncertainty to the use of either the steady or nonsteady-state assumptions in the estimation of turnover times (e.g., Carvalhais et al., 2008). For example, using steady-state assumption underestimated the C turnover time by 29%, which resulted in the underestimation (five times lower) of the net ecosystem productivity (Ge et al., 2019).

Meanwhile, studies estimating the N turnover times are relatively limited compared to those of the C turnover times. In particular, prior knowledge regarding the variation of the N turnover times over a regional or broader scale and their controlling factors is significantly limited. Since this limited knowledge can cause uncertainties in biogeochemical models for future projections of global forest C and N stocks (Zhou et al., 2012), there is a need to improve the understanding of the C and N turnover times.

Recent studies have adopted data-model fusion to diminish the uncertainties residing in biogeochemical models (Ge et al., 2019; Zhou et al., 2012). Data-model fusion is a tool that assimilates observation data with a biogeochemical model to provide reliable simulation results (Nyström et al., 2015). This tool has been used to adjust model parameters to reduce uncertainties in the simulation of forest C stock and flux (Xu et al., 2006), to inform a model structure that better explains soil incubation data (Liang et al., 2015), and to analyze uncertainty factors in an ecosystem C cycle model (Weng et al., 2011). However, there have been, to our knowledge, no studies that have used data-model fusion to reduce uncertainty in the estimation of both C and N turnover times and to explain their variation.

The present study aimed to estimate the C and N turnover times in forests. The study forests were the entire South Korean forests, temperate forests located in northeastern Asia characterized by their monsoon climate. They are young forests that were regenerated in the 1970s and thus are not in a steady state considering their fast growth. Consequently, we used the balance method to calculate the C and N turnover times rather than the "traceable scheme" which assumes the steady state (Luo et al., 2017; Xia et al., 2013). The required stocks and output fluxes of C and N for the balance method were calculated via data-model fusion. The National Forest Inventory (NFI) data of South Korea were used as a data set for the data-model fusion. This data set included the C and N stocks of various pools in the forest, such as wood, woody debris, and mineral soil, which had been measured twice with a 5-year interval. A biogeochemical model that simulates forest C and N cycles, Forest Biomass and Dead organic matter Carbon and Nitrogen (FBD-CAN; Kim et al., 2019), was chosen for data-model fusion because of its proven applicability to South Korean forests and few calculation requirements (Kim et al., 2019; Lee et al., 2014). We expected that the N turnover times would be longer than the C turnover times because limited resources (e.g., N) usually have longer turnover times than those that are not limited (e.g., C; Aerts & de Caluwe, 1995; Eckstein et al., 1999). Additionally, variations in the C and N turnover times throughout South Korean forests would be explained by forest type, mean annual temperature, annual precipitation, stand age, and ecosystem C:N ratio (i.e., the ratio of the total C to N stock in the ecosystem). Since the C:N ratio is one of the main factors that regulates the C and N output fluxes (Li et al., 2017; Pei et al., 2019; Reich et al., 2005), we expected that it would explain as much of the variation in the C and N turnover times as other abiotic and biotic factors have in previous studies.

2. Materials and Methods

2.1. Study Forest

South Korean forests are in northeastern Asia. The climate is a temperate monsoon climate, in which ~70% of mean annual precipitation occurs in the summer (Korea Meteorological Administration [KMA], 2020). The mean annual temperature and precipitation from 2011 to 2020 were ~13.0°C and 1264.2 mm, respectively (KMA, 2020). The average stand age ranges from mid-30 to mid-40 years (Korea Forest Service (KFS), 2020), which is relatively young compared to those of other temperate forests located at similar latitudes (33°–39°N; Martin et al., 2016; Pan et al., 2011). This is because the devastated forests after the Korean war were restored in the 1970–1980s through National Forest Rehabilitation Plans (Food and Agriculture

Organization [FAO], 2016). The three main forest types found here are evergreen coniferous forests (EC), deciduous broad-leaved forests (DB), and mixed forests (Mix; combination of both evergreen coniferous and deciduous broad-leaved species), accounting for 36.9%, 32.0%, and 26.9% of the total forest area, respectively (KFS, 2020). The main soil type is Inceptisol, followed by Ultisol and Entisol based on USDA soil taxonomy (Song et al., 2019).

Here, we selected 64 permanent forest plots surveyed twice through the sixth (2011–2015) and the seventh (2016–2020) NFI covering the three main forest types in South Korea (Figure S1). All 64 permanent forest plots were well preserved between the two repeated measurements, and there were no records of forest management, such as tending, thinning, and harvesting, in the NFI data. Detailed information, including the history, sampling design, and data collection methods of the NFI, can be found in Vidal et al. (2016).

2.2. Data

2.2.1. Carbon and Nitrogen Stocks

The data set for the data-model fusion included the C (Mg C ha^{-1}) and N (Mg N ha^{-1}) stocks in eight C and N pools of each plot for the sixth and seventh NFI (Table S1). The eight C and N pools were wood, foliage, fine root, woody debris, litter layer (L layer), combined fermentation and humus layer (F + H layer), dead fine root, and mineral soil (0–30 cm). The wood included stem, branch, and coarse root, and the woody debris included logs, snags, coarse root debris, and dead branch (Harmon & Sexton, 1996; Yan et al., 2006). The stem volume was estimated using allometric equations with the measured diameter at breast height (Korea Forest Research Institute [KFRI] (2014); Lee et al., 2014). The stem volume was used to calculate the C and N stocks in wood, foliage, and fine root with species-specific coefficients, as per the following Equations 1–7, Kim et al. (2019), Lee et al. (2014):

$$\text{SM} = V_s \cdot p_w \tag{1}$$

$$\text{WC} = \text{SM} \cdot \text{BCF}_w \cdot \text{C}_w \tag{2}$$

$$\text{WN} = \text{SM} \cdot \text{BCF}_w \cdot \text{N}_w \tag{3}$$

$$\text{FC} = \text{SM} \cdot \text{BCF}_f \cdot \text{C}_f \tag{4}$$

$$\text{FN} = \text{SM} \cdot \text{BCF}_f \cdot \text{N}_f \tag{5}$$

$$\text{FRC} = \text{SM} \cdot \text{BCF}_{\text{fr}} \cdot \text{C}_{\text{fr}} \tag{6}$$

$$\text{FRN} = \text{SM} \cdot \text{BCF}_{\text{fr}} \cdot \text{N}_{\text{fr}} \tag{7}$$

where SM denotes stem biomass; WC and WN are the C and N stocks in wood; FC and FN are the C and N stocks in foliage; FRC and FRN are the C and N stocks in fine root; V_s is stem volume; p_w is stem wood density; BCF$_w$ is the biomass conversion factor to account for not only the stem volume, but also for the volume of branch and coarse root; BCF$_f$ and BCF$_{\text{fr}}$ are biomass conversion factors to convert stem biomass into foliage and fine root biomass, respectively; C$_w$, C$_f$, and C$_{\text{fr}}$ are C concentrations (%) of wood, foliage, and fine root, respectively; N$_w$, N$_f$, and N$_{\text{fr}}$ are N concentrations (%) of wood, foliage, and fine root, respectively.

The C and N stocks in woody debris were calculated from the measured volume of logs and snags per hectare as per the following Equations 8 and 9:

$$\text{WDC} = V_{\text{ls}} \cdot p_s \cdot \text{BCF}_{\text{wd}} \cdot \text{C}_s \tag{8}$$

$$\text{WDN} = V_{\text{ls}} \cdot p_s \cdot \text{BCF}_{\text{wd}} \cdot \text{N}_s \tag{9}$$

where WDC and WDN denote the C and N stocks in woody debris, respectively; V_{ls} is the measured volume of logs and snags per hectare (m^3 ha^{-1}); p_s is the wood density (g cm^{-3}) of snags; BCF$_{\text{wd}}$ is the biomass conversion factor to account for not only the volume of logs and snags but also the volume of coarse root debris and dead branch; and the C$_s$ and N$_s$ are the C and N concentrations (%) of snags, respectively. The p_s, C$_s$,

Table 1
General Characteristics of the 64 Permanent Forest Plots

Characteristics	Evergreen coniferous forest ($n = 15$)				Deciduous broad-leaved forest ($n = 20$)				Mixed forest ($n = 29$)			
	Mean	Std	Min	Max	Mean	Std	Min	Max	Mean	Std	Min	Max
Mean annual temperature (°C)	11.76	0.83	10.54	12.87	10.88	1.84	6.70	13.26	11.57	1.22	9.06	13.87
Annual precipitation (mm)	1,285	103	1,100	1,479	1,284	102	1,102	1,449	1,259	84	1,122	1,464
Stand age (years)	38.67	8.06	30.00	60.00	36.67	8.37	20.00	60.00	34.68	4.81	30.00	40.00

Note. n is the number of permanent forest plots of each forest types used in the present study, and std, min, and max indicate standard deviation, minimum, and maximum, respectively.

and N_s were obtained from results of a nation-wide snag survey. The C and N stocks in dead fine root were calculated using the measured C and N stocks in L layer as per the following Equations 10 and 11:

$$\text{DFRC} = \text{LC} \cdot R_{\text{L,DFR}} \tag{10}$$

$$\text{DFRN} = \text{LN} \cdot R_{\text{L,DFR}} \tag{11}$$

where DFRC and DFRN denote the C and N stocks in dead fine root, respectively; LC and LN are the C and N stocks in the L layer, respectively; and the $R_{\text{L,DFR}}$ is the ratio between the dry mass per hectare (Mg ha^{-1}) of the L layer and dead fine root, which was obtained from a previous modeling study conducted for forests in South Korea (Lee et al., 2014). The C and N stocks in the L layer, F + H layer, and mineral soil were directly taken from the NFI data as the Korea Forest Service provided them, without additional calculations (Kim et al., 2016; J. Lee et al., 2018).

2.2.2. Input Data

Input data, such as mean annual temperature (°C), annual precipitation (mm year^{-1}), annual N deposition (kg N ha^{-1} year^{-1}), solar radiation (W m^{-2}), and stand age (years), were used to conduct data-model fusion. The mean annual temperature and precipitation data were downloaded from the WorldClim database (Table 1; http://www.worldclim.com/version2). The N deposition data were extracted from the global N deposition map generated by a chemical transport model, called the European Monitoring and Evaluation Programme developed at the Meteorological Synthesizing Centre (Schwede et al., 2018; https://thredds.met.no/). The solar radiation data were calculated using the latitude and digital elevation model with the Area Solar Radiation tool in ArcGis Pro 2.6. Data regarding the stand age was obtained from the NFI data (Table 1).

2.3. Model

FBD-CAN was adopted to conduct the data-model fusion and was developed by integrating a forest C model, Forest Biomass and Dead organic matter Carbon (FBDC), with a newly designed N module (Kim et al., 2018, 2019; Lee et al., 2014; Yi et al., 2013). The FBDC has previously been applied in temperate, tropical, and alpine regions where input data availability is limited (Lee et al., 2014, 2016, 2017, S. J. Lee et al., 2018; Yi et al., 2013), and the reliability of FBD-CAN has been validated by a pilot study conducted in a *Pinus densiflora* Siebold & Zucc. forest in central Korea (Kim et al., 2019). The FBD-CAN is composed of multiple C and N pools, which are connected with C and N flux modules (Figure 1). This model has three compartments; tree biomass (including wood, foliage, and fine root pools), primary DOM (including woody debris, L layer, F + H layer, and dead fine root pools), and mineral soil (including active soil organic matter, slow soil organic matter, passive soil organic matter,
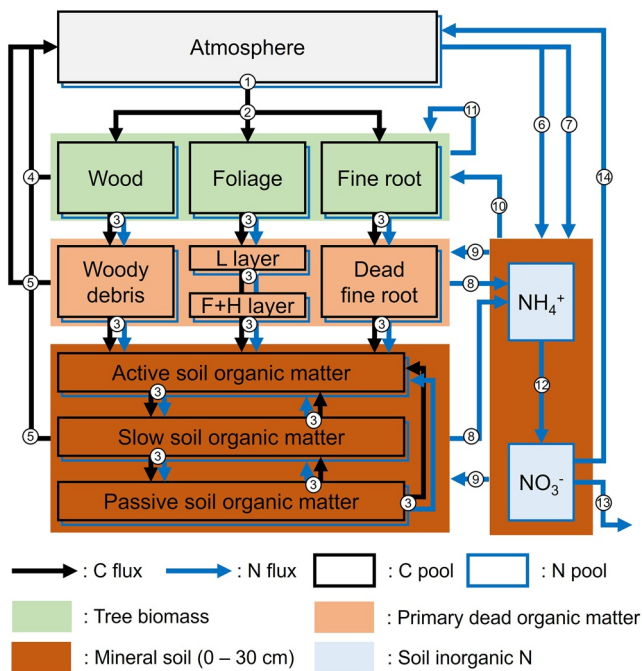

Figure 1. Theoretical representation of the pools and fluxes in the carbon (C) and nitrogen (N) cycles within the Forest Biomass and Dead organic matter Carbon and Nitrogen (FBD-CAN; ① photosynthesis; ② C allocation; ③ turnover; ④ autotrophic respiration; ⑤ heterotrophic respiration; ⑥ N deposition; ⑦ biological N fixation; ⑧ N mineralization; ⑨ N immobilization; ⑩ tree N uptake; ⑪ N resorption at turnover of foliage and fine root; ⑫ nitrification; ⑬ N leaching; and ⑭ denitrification). L, litter layer; F + H layer, combined fermentation and humus layer.

and soil inorganic N pools). The FBD-CAN includes C and N flux modules, such as photosynthesis, C allocation, turnover, autotrophic respiration (R_a) from tree biomass, heterotrophic respiration (R_h) from primary DOM and mineral soil, N deposition, biological N fixation, N mineralization, N immobilization, tree N uptake, N resorption at turnover of foliage and fine root, nitrification, N leaching, and denitrification. The FBD-CAN considers (a) the limitations on photosynthesis when soil inorganic N content is smaller than the required N for tree growth and N immobilization and (b) the limitations on N mineralization when the C:N ratio of primary DOM or mineral soil is higher than the critical C:N ratio that determines whether N is immobilized or mineralized.

The FBD-CAN was upgraded from the previous version in Kim et al. (2019). First, a simple canopy photosynthesis module based on Farquhar et al. (1980) was integrated into the FBD-CAN (Bonan, 2019). This module calculates gross primary production, R_a from tree biomass, and net primary production with four input data (i.e., atmospheric CO_2 concentration, solar radiation, temperature, and relative humidity), two parameters (i.e., specific leaf area [m^2 kg^{-1}] and C use efficiency [%]), and the C and N stocks in foliage. Second, the FBD-CAN was upgraded to simulate the C and N cycles of EC, DB, and Mix by using the adjusted model parameters for each forest type, which were estimated by the data-model fusion. Lastly, the structure of FBD-CAN was mathematically represented for more efficient computation in the data-model fusion (Luo et al., 2017) as per the following Equations 12 and 13:

$$\frac{dX(t)_C}{dt} = B_C \cdot I(t)_C - A_C \cdot \tau_C \cdot K_C \cdot X(t)_C \tag{12}$$

$$\frac{dX(t)_N}{dt} = B_N \cdot I(t)_N - A_N \cdot \tau_N \cdot K_N \cdot X(t)_N \tag{13}$$

where $X(t)_{C \text{ or } N}$ denotes a vector of the C or N stocks of each C or N pool at a time t, respectively; $B_{C \text{ or } N}$ is a vector representing the partitioning fraction of the C or N input to each C or N pool, respectively; $I(t)_{C \text{ or } N}$ is the C or N input at a time t, respectively; $A_{C \text{ or } N}$ is a square matrix of transfer parameters quantifying C or N fluxes among C or N pools, respectively; $\tau_{C \text{ or } N}$ is a diagonal matrix of scalar quantifying responses of C or N turnover rates from each C or N pool to climatic variables, respectively; and $K_{C \text{ or } N}$ is a diagonal matrix of C or N turnover rates of each C or N pool, respectively.

2.4. Data-Model Fusion

Data-model fusion, also called data assimilation, is a statistical approach to identifying model parameters that minimize deviations between data and a model, thereby producing more reliable simulation results (Ge et al., 2019; Minunno et al., 2019). The target model parameters for the data-model fusion are listed in Table S2. The probabilistic inversion approach was used to conduct the data-model fusion as described by Xu et al. (2006) and Liang et al. (2015). This approach is based on Bayes' theorem as per the following Equation 14:

$$P(\theta|Z) \propto P(Z|\theta) \cdot P(\theta) \tag{14}$$

where $P(\theta|Z)$ denotes the posterior probability density function (PDF) of the model parameters (θ); $P(Z|\theta)$ is a likelihood function integrating the information in the observed data and the modeled values, "Data" and "Model" in data-model fusion; and $P(\theta)$ is the prior knowledge of model parameters (θ). The posterior PDFs of the model parameters were separately generated for EC, DB, and Mix. The prior PDFs of the model parameters were provided as the uniform distribution over specific parameter ranges for each forest type as described in Table S2. The likelihood function was calculated by the following Equation 15 as defined in Liang et al. (2015) and Hou et al. (2019)

$$P(Z|\theta) \propto \exp\left\{-\sum_{i=1}^{22}\frac{|Z_i \quad X_i|^2}{2 \cdot \sigma_i^2}\right\} \tag{15}$$

where Z_i denotes the observed C stock (from $i = 1$ to $i = 10$) and N stock (from $i = 11$ to $i = 22$) of each C and N pool for the seventh NFI (Table S1); X_i is the modeled C stock (from $i = 1$ to $i = 10$) and N stock (from $i = 11$ to $i = 22$) for the seventh NFI by the FBD-CAN using the observed C and N stocks for the sixth NFI as the initial data to run the model; and σ_i^2 is the standard deviation of the observed C and N stocks. The

Metropolis-Hastings (MH) algorithm, one of the Markov Chain Monte Carlo techniques (Hastings, 1970; Metropolis et al., 1953), was used to establish the posterior PDFs of the model parameters (θ). The MH algorithm iterates a proposing step and a moving step (Xu et al., 2006). The proposing step generates a new model parameter (θ^{new}) based on the previously accepted model parameter (θ^{old}) with a proposal distribution $P\left(\theta^{\text{old}}\right)$ expressed as per the following Equation 16:

$$\theta^{\text{new}} = \theta^{\text{old}} + \frac{d\left(\theta_{\max} - \theta_{\min}\right)}{D} \tag{16}$$

where $\theta_{\max}$ and $\theta_{\min}$ are the maximum and the minimum values of the prior ranges of the model parameters (Table S2), respectively; d is a random variable, that is, higher than -0.5 and lower than 0.5 with a uniform distribution; and D is the proposing step size, which was set to 20 in the present study. The moving step accepts or rejects the new model parameter (θ^{new}) generated in the proposing step according to the Metropolis criterion (Xu et al., 2006). Since using the first 25% of the accepted model parameters in modeling can cause unacceptable variation and large uncertainty, the first 25% of the accepted model parameters were discarded and only the remainder was used to generate the posterior PDFs (Figure S2).

2.5. Model Simulation

The FBD-CAN estimated the stocks and fluxes of C and N, represented in its model structure (Figure 1), for the 64 permanent forest plots for the seventh NFI by using (a) the observed C and N stocks for the sixth NFI to determine the initial state of the C and N stocks of each plot (Table S1), (b) the input data such as mean annual temperature, annual precipitation, annual N deposition, solar radiation, and stand age, and (c) the maximum likelihood estimates of the posterior PDF of each model parameter in each forest type produced by the data-model fusion (Table S2 and Figure S2). We used these estimated stocks and fluxes of C and N to calculate the C and N turnover times of tree biomass (CTT_{tree} and NTT_{tree}), primary DOM (CTT_{DOM} and NTT_{DOM}), mineral soil (CTT_{soil} and NTT_{soil}), and the ecosystem ($\text{CTT}_{\text{system}}$ and $\text{NTT}_{\text{system}}$; including tree biomass, primary DOM, and mineral soil) of the 64 permanent forest plots for the seventh NFI as per the following Equations 17 and 18; Qubaja et al. (2020); Sierra et al. (2017):

$$\text{CTT}_i = \frac{Cs_i}{Co_i} \tag{17}$$

$$\text{NTT}_i = \frac{Ns_i}{No_i} \tag{18}$$

where CTT_i and NTT_i are the C and N turnover times of compartment , respectively; Cs_i and Ns_i are the estimated C and N stocks of compartment i, respectively; Co_i and No_i are the estimated C and N output fluxes from compartment i, respectively; and i is tree biomass, primary DOM, mineral soil, or ecosystem.

The performance of the FBD-CAN was examined by using the R squared of the linear relationship between the observed and estimated C and N stocks of ecosystem for the seventh NFI. Moreover, the root-mean-square error (RMSE) was calculated to test the reliability of the FBD-CAN as per the following Equation 19:

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^{n}\left(\hat{y}_i - y_i\right)^2}{n}} \tag{19}$$

where n is the number of observations of each forest type; $\hat{y}_i$ is the observed ecosystem C and N stocks of the ith permanent forest plot for the seventh NFI; and y_i is the estimated ecosystem C and N stocks of the ith permanent forest plot for the seventh NFI.

2.6. Statistical Analysis

Analysis of variance (ANOVA) was conducted to evaluate the significance of any differences in the estimated stocks and fluxes of C and N between forest types. Differences in turnover times due to forest type and element type (i.e., C and N) were tested by two-way ANOVA. The relationships of the C and N turnover times with factors, including mean annual temperature, annual precipitation, stand age, and ecosystem C:N ratio, were analyzed using linear regression. We calculated ecosystem C:N ratio by dividing ecosystem C stock to ecosystem N stock. Additionally, redundancy analysis (RDA) and variance partitioning analysis
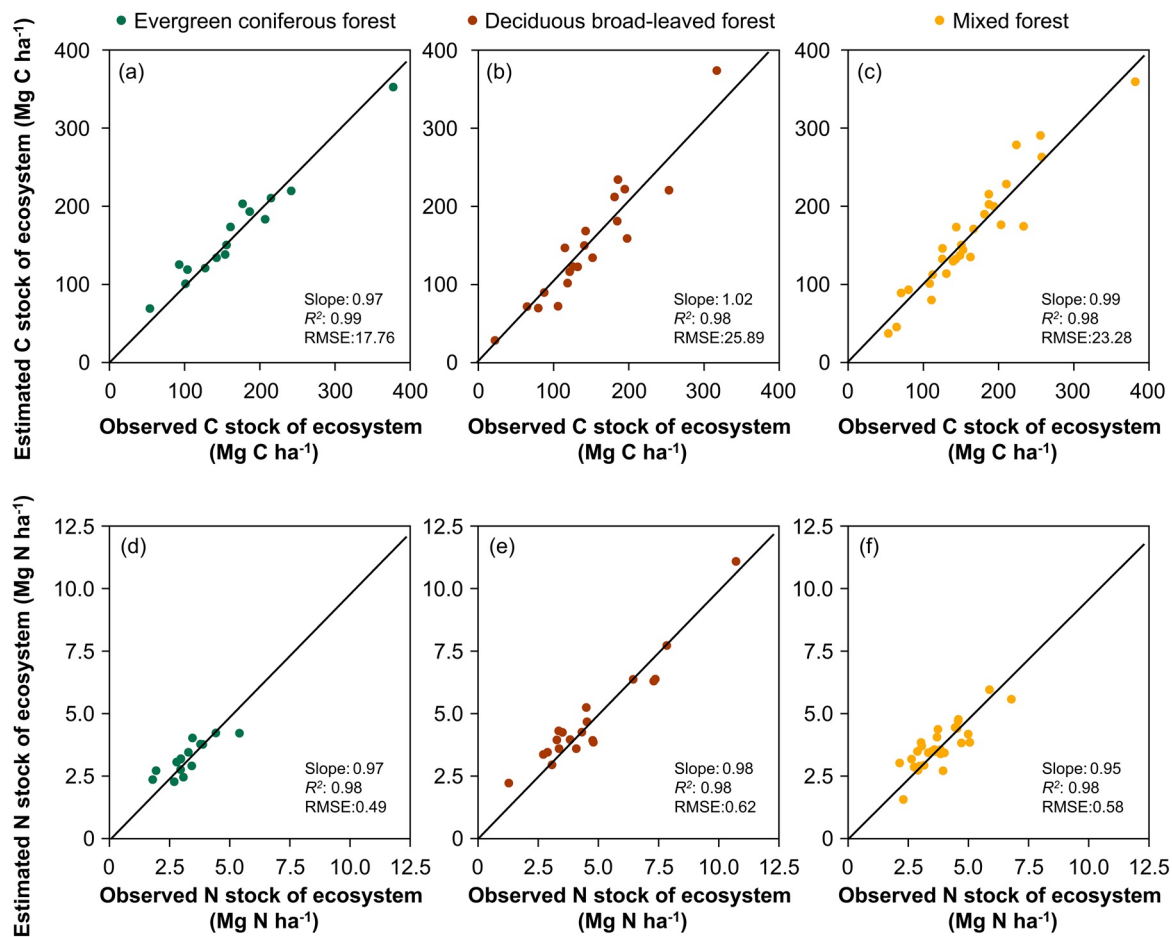
Figure 2. Scatterplots of the estimated and observed ecosystem carbon (C; a–c) and nitrogen (N; d–f) stocks for the 64 permanent forest plots. The solid lines represent the fitted linear regression lines. The slopes and coefficient of determination (R^2) of linear relationships between the estimated and observed values as well as the root-mean-square error (RMSE) are shown.

(VPA) were conducted to extract and summarize the variation of the C and N turnover times that could be explained by the factors. All statistical analyses were conducted with the statistical software R version 4.0.3 (R Core Team, 2020).

3. Results

3.1. Model Validation

The model validation results showed that the estimated and observed values were consistent (Figure 2). The estimated C stocks of ecosystem (mean ± standard deviation) of EC, DB, and Mix were 166.97 ± 65.48, 150.42 ± 76.13, and 162.78 ± 72.28 Mg C ha^{-1}, respectively (Figures 2a–2c). The estimated N stocks of ecosystem of EC, DB, and Mix were 3.13 ± 0.85, 4.59 ± 2.10, and 3.71 ± 1.01 Mg N ha^{-1}, respectively (Figures 2d–2f). The slopes of the linear relationships between the estimated and observed values ranged from 0.95 to 1.02, indicating that the range of underestimation and overestimation was between 2% and 5%. The RMSEs between the estimated and observed ecosystem C stocks of EC, DB, and Mix were 17.76, 25.89, and 23.28 Mg C ha^{-1}, respectively, and these values accounted for 10.6%, 17.2%, and 14.1% of the observed ecosystem C stocks of EC, DB, and Mix, respectively. The RMSEs between the estimated and observed ecosystem N stocks of EC, DB, and Mix were 0.49, 0.62, and 0.58 Mg N ha^{-1}, respectively, and these values accounted for 15.7%, 13.6%, and 15.8% of the observed ecosystem N stocks of EC, DB, and Mix, respectively.
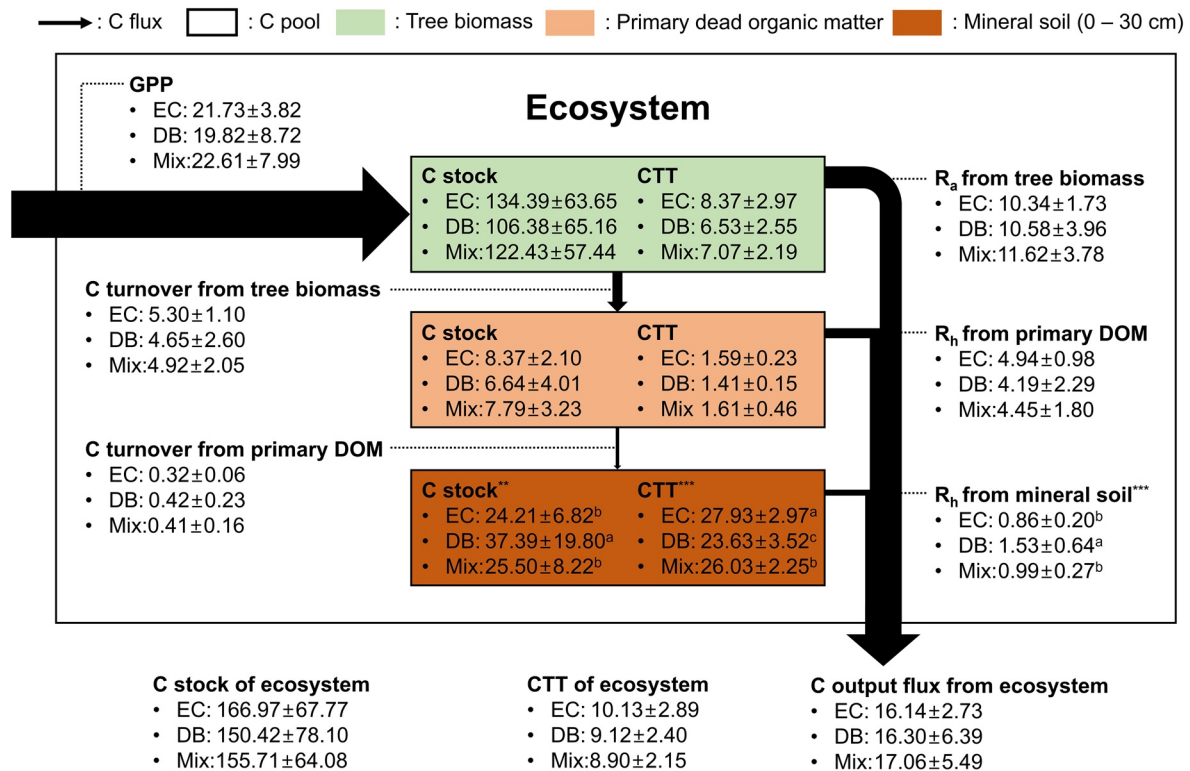
Figure 3. Estimated carbon (C) stocks (Mg C ha^{-1}), C fluxes (Mg C ha^{-1} year^{-1}), and C turnover times (CTTs; years) for the seventh National Forest Inventory. Values represent the mean ± standard deviation. The asterisks next to the bold letters and different subscript letters next to the numbers indicate significant differences between forest types ($^{**}P < 0.01$; $^{***}P < 0.001$). Arrows indicate the direction of the C fluxes. Arrow width is proportional to the size of the C flux. EC, evergreen coniferous forest; DB, deciduous broad-leaved forest; Mix, mixed forest; R_a, autotrophic respiration; R_h, heterotrophic respiration; GPP, gross primary production; DOM, dead organic matter.

3.2. Stocks and Fluxes of Carbon and Nitrogen

Figure 3 summarizes the estimated C stocks and fluxes of tree biomass, primary DOM, mineral soil, and the ecosystem for EC, DB, and Mix. The C stocks of ecosystem (mean ± standard deviation) for EC, DB, and Mix were 166.97 ± 65.48, 150.42 ± 76.13, and 162.78 ± 72.28 Mg C ha^{-1}, respectively, and there was no significant difference between the forest types ($P > 0.05$). Tree biomass was the major C compartment, storing >70% of the C stock of the ecosystem, followed by mineral soil and primary DOM. The C output fluxes from the ecosystem for EC, DB, and Mix were 16.14 ± 2.73, 16.30 ± 6.39, and 17.06 ± 5.49 Mg C ha^{-1} year^{-1}, respectively, showing no significant difference between the forest types ($P > 0.05$). R_a from tree biomass was the major C output flux from the ecosystem accounting for >60% of the total C output flux, followed by R_h from primary DOM and R_h from mineral soil.

The estimated N stocks and fluxes of tree biomass, primary DOM, mineral soil, and the ecosystem for EC, DB, and Mix are presented in Figure 4. The N stocks of the ecosystem (mean ± standard deviation) for EC, DB, and Mix were 3.13 ± 0.85, 4.59 ± 2.10, and 3.71 ± 1.01 Mg N ha^{-1}, respectively, and the N stock of the ecosystem for DB was significantly larger than those for EC and Mix ($P < 0.05$). Mineral soil contributed >60% to the N stock of the ecosystem, followed by tree biomass and primary DOM. DB had the largest N output flux from the ecosystem of 20.55 ± 25.36 kg N ha^{-1} year^{-1} ($P < 0.05$), followed by 6.47 ± 1.48 and 11.07 ± 9.50 kg N ha^{-1} year^{-1} for EC and Mix, respectively.

3.3. Carbon and Nitrogen Turnover Times

The CTT$_{tree}$ values (mean ± standard deviation) for EC, DB, and Mix were 8.37 ± 2.97, 6.53 ± 2.55, and 7.07 ± 2.19 years, respectively, while the NTT$_{tree}$ values for EC, DB, and Mix were 27.71 ± 10.40, 25.36 ± 8.53, and 28.22 ± 6.81 years, respectively (Figure 5a). Across the three different forest types, the average NTT$_{tree}$
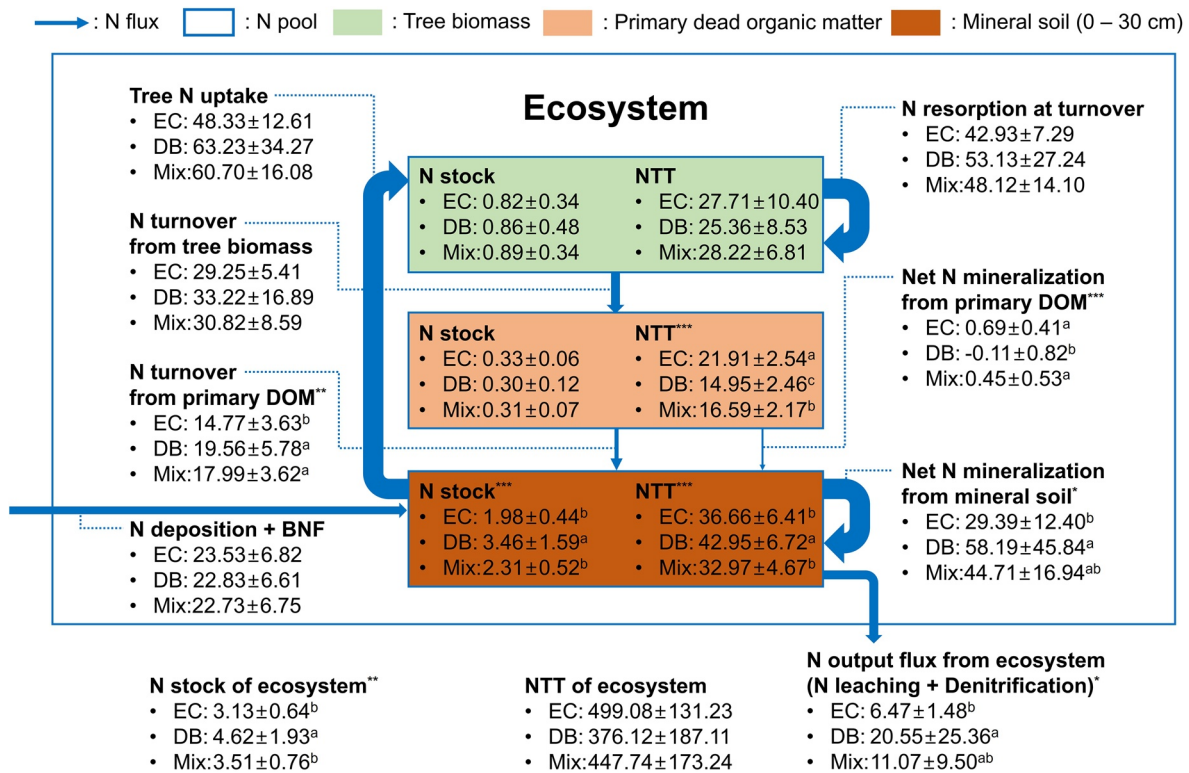
Figure 4. Estimated nitrogen (N) stocks (Mg N ha^{-1}), N fluxes (kg N ha^{-1} year^{-1}), and N turnover times (NTTs; years) for the seventh National Forest Inventory. Values represent the mean ± standard deviation. The asterisks next to the bold letters and different superscript letters next to the numbers indicate significant differences between forest types ($^{**}P < 0.01$; $^{***}P < 0.001$). Arrows indicate the direction of the N fluxes. Arrow width is proportional to the size of the N flux. The negative value for the net N mineralization from primary dead organic matter (DOM) indicates that the N immobilization was greater than the N mineralization in primary DOM. BNF, biological N fixation.

was approximately three times longer than the average CTT$_{tree}$, but there was no significant difference in CTT$_{tree}$ and NTT$_{tree}$ between forest types.

The CTT$_{DOM}$ values for EC, DB, and Mix were 1.59 ± 0.23, 1.41 ± 0.15, and 1.61 ± 0.46 years, respectively, whereas the NTT$_{DOM}$ for EC, DB, and Mix were 21.91 ± 2.54, 14.95 ± 2.46, and 16.59 ± 2.17 years, respectively (Figure 5b). Across the three different forest types, the average NTT$_{DOM}$ was ~10 times longer than the
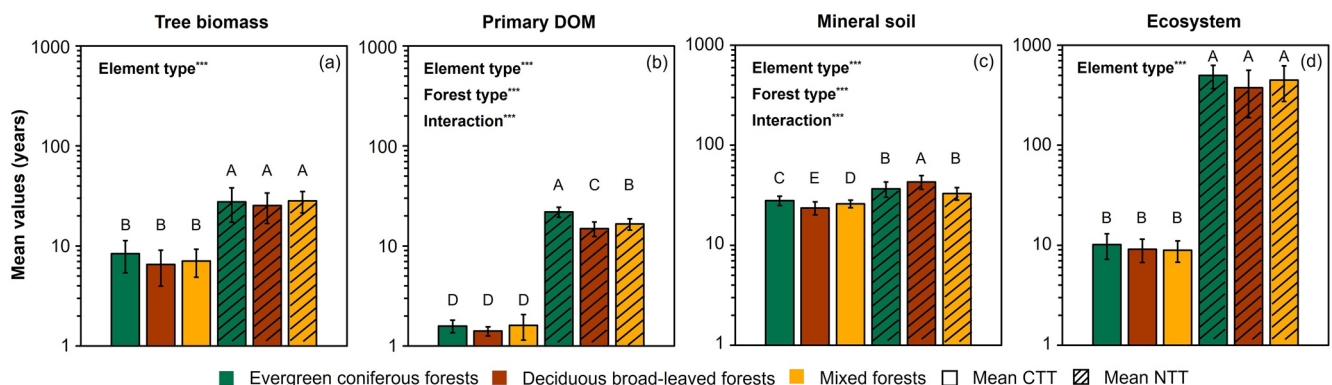

Figure 5. Mean carbon turnover times and nitrogen turnover time (years) of tree biomass (a), primary dead organic matter (DOM; b), mineral soil (c), and the ecosystem (d). Vertical lines through the colored bars represent ±standard deviation. The bold letters in the boxes denote the significance of differences in turnover times between forest and element types as well as the significance of interaction effects between forest and element types on turnover times ($P < 0.001$). The different letters above the colored bars indicate significant differences among turnover times at the significance level of 0.001 determined by Tukey's post hoc test. Table S3 shows the statistical results.
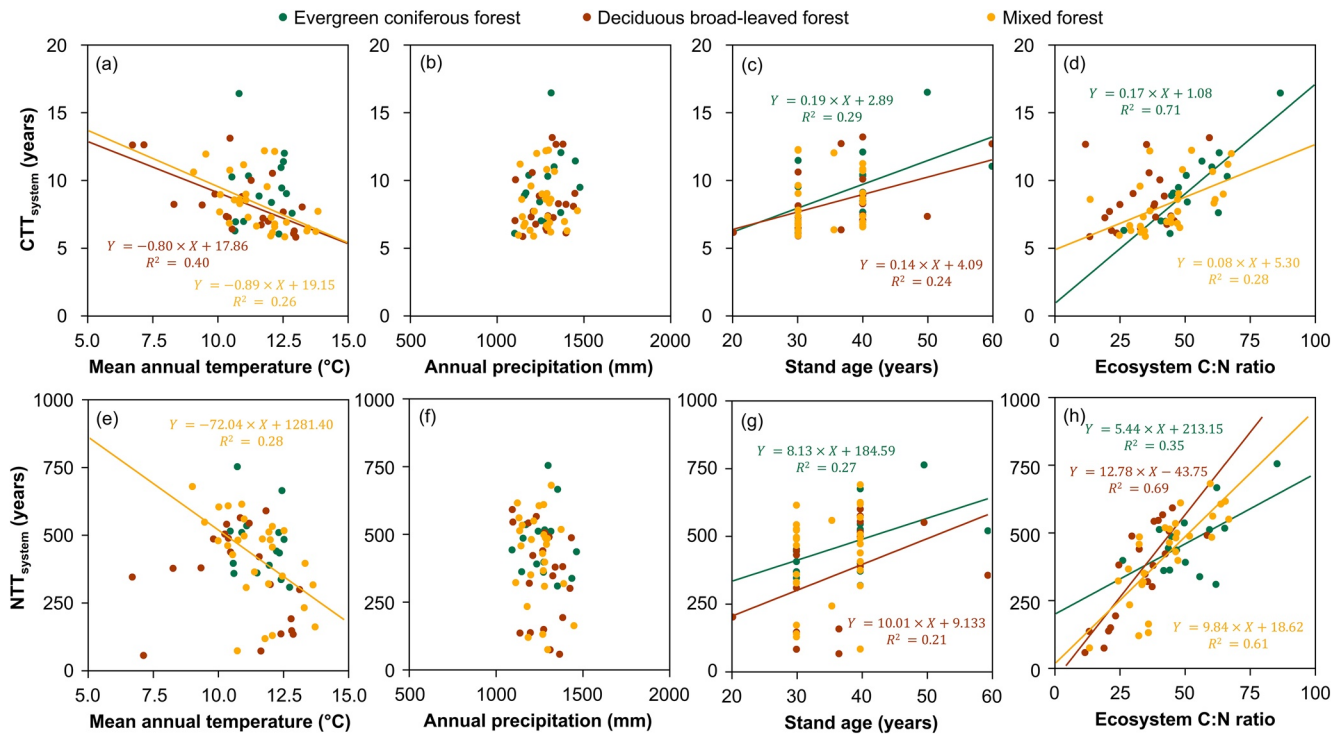
Figure 6. Bivariate relationships between both carbon (C) turnover times of the ecosystem (CTT_{system}; years; a–d) and nitrogen (N) turnover times of the ecosystem (NTT_{system}; years; e–h) and mean annual temperature (°C), annual precipitation (mm), stand age (years), and ecosystem C:N ratio for each forest type. Linear fitted lines and equations are only shown for significant ($P < 0.05$) bivariate relationships.

average CTT_{DOM}. Tukey's post hoc test revealed that the NTT_{DOM} for EC was longer than that for Mix, and that for Mix was longer than that for DB. However, there was no significant difference in CTT_{DOM} between forest types (Table S3).

The CTT_{soil} values for EC, DB, and Mix were 27.93 ± 2.97, 23.63 ± 3.52, and 26.03 ± 2.25 years, respectively, while the NTT_{soil} values for EC, DB, and Mix were 36.66 ± 6.41, 42.95 ± 6.72, and 32.97 ± 4.67 years, respectively (Figure 5c). Across the three different forest types, the average NTT_{soil} was approximately one-and-a-half times longer than the average CTT_{soil}. The NTT_{soil} for DB was longer than those for EC and Mix, but the CTT_{soil} for DB was the shortest.

The CTT_{system} values for EC, DB, and Mix were 10.13 ± 2.89, 9.12 ± 2.40, and 8.90 ± 2.15 years, respectively, while the NTT_{system} values for EC, DB, and Mix were 499.08 ± 131.23, 376.12 ± 187.11, and 447.74 ± 173.24 years, respectively (Figure 5d). Across three different forest types, the average NTT_{system} was ~45 times longer than the average CTT_{system}, but there was no significant difference in CTT_{system} and NTT_{system} between forest types. Additionally, the NTT_{system} was larger than the sum of NTT_{tree}, NTT_{DOM}, and NTT_{soil}, while the CTT_{system} was smaller than the sum of CTT_{tree}, CTT_{DOM}, and CTT_{soil}.

3.4. Controlling Factors of Carbon and Nitrogen Turnover Times

The CTT_{system} values for DB and Mix decreased with an increase in mean annual temperature, whereas the CTT_{system} for EC had no linear relationship with mean annual temperature (Figure 6a). There was no significant response of the CTT_{system} to the change in annual precipitation for EC, DB, and Mix (Figure 6b). The CTT_{system} for EC and DB increased with stand age, while there was no linear relationship between the CTT_{system} and stand age for Mix (Figure 6c). The CTT_{system} values for EC and Mix increased with an increase in ecosystem C:N ratio, while the CTT_{system} for DB showed no linear relationship with ecosystem C:N ratio (Figure 6d).
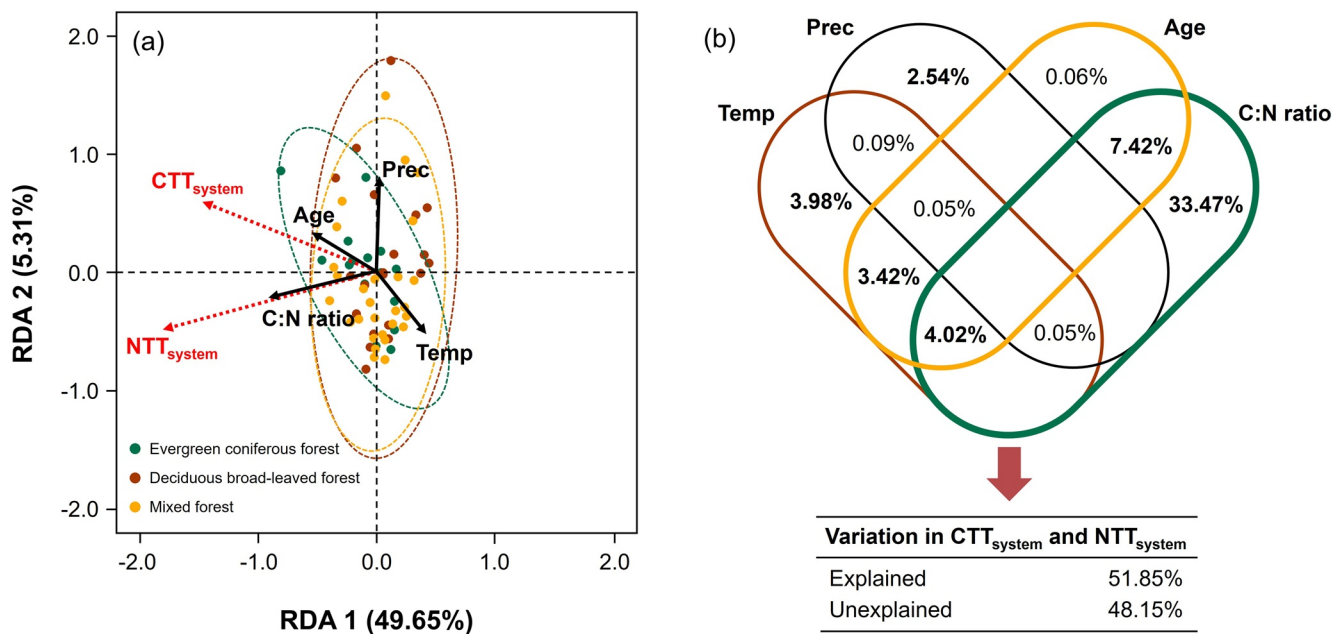
Figure 7. Redundancy analysis (RDA) displaying the variance in the carbon (C) turnover times of the ecosystem (CTT_{system}; years) and nitrogen (N) turnover times of the ecosystem (NTT_{system}; years) explained by mean annual temperature (°C; Temp), annual precipitation (mm; Prec), stand age (years; Age), and ecosystem C:N ratio (C:N ratio) at the significance level of 0.05 (a). Variance partitioning analysis map of the explanatory powers of Temp, Prec, Age, and C:N ratio to the variance of the CTT_{system} and NTT_{system} (b). The explanatory power below zero is not represented.

The NTT_{system} for Mix decreased with an increase in mean annual temperature, but such linear relationships were not significant for EC and DB (Figure 6e). Annual precipitation had no significant control over NTT_{system} values for EC, DB, and Mix (Figure 6f). The NTT_{system} values of EC and DB increased with an increase in stand age, but there was no linear relationship between the NTT_{system} and stand age for Mix (Figure 6g). The NTT_{system} increased with an increase in ecosystem C:N ratio for the three forest types (Figure 6h).

The results of the RDA showed that RDA 1 and RDA 2 axes explained 50% and 5% of the variations in CTT_{system} and NTT_{system}, respectively (Figure 7a). The CTT_{system} was positively related to ecosystem C:N ratio, and stand age in order of explanatory power, but it was negatively related to mean annual temperature. Following the order of explanatory power, the NTT_{system} was positively related to ecosystem C:N ratio and stand age, while it was negatively related to mean annual temperature.

The VPA showed that ~52% of the variation in the CTT_{system} and NTT_{system} was explained by mean annual temperature, annual precipitation, stand age, and C:N ratio (Figure 7b). C:N ratio, stand age, mean annual temperature, and annual precipitation explained 45%, 15%, 12%, and 3%, respectively, of the variation in the CTT_{system} and NTT_{system}. The shared variation of the CTT_{system} and NTT_{system} was explained by both ecosystem C:N ratio and stand age and both the stand age and mean annual temperature were ~11% and 8%, respectively.

4. Discussion

4.1. Carbon and Nitrogen Turnover Times

The range of CTT_{system} values (8.90–10.13 years) estimated for the three forest types is close to that found by Yan et al. (2017), who estimated that the CTT_{system} for South Korean forests to be ~10 years. However, Carvalhais et al. (2014) and Yan et al. (2017) reported that the global mean CTT_{system} values for temperate forests were 23.5 and 25.0 years, respectively. The shorter CTT_{system} in the South Korean forests compared to that in the global temperate forests might be due to their young stand age (mid-30 to mid-40 years), considering that much shorter C turnover times of vegetation and soil have been observed when stand age is young (Wang et al., 2018). This was also evidenced in the present study by an increase in CTT_{system} with an

increase in stand age (Figure 6). This trend is likely due to the increase in ecosystem C stocks with stand age (Mao et al., 2010; Noh et al., 2010; Wang et al., 2019), as reported by previous studies assessing the trends in C turnover times in temperate forests of northeastern Asia (Ge et al., 2019; Wang et al., 2018).

The largest NTT_{system} observed in our study was as long as 500 years. A study conducted in the Hubbard Brook Experimental Forest (HBEF) similarly reported a long N turnover time of over 1,000 years (Yanai et al., 2013). In contrast, Wang et al. (2010) reported a much shorter N turnover time of 124 years than those in this study and in the HBEF study. This difference is likely due to the difference in the calculation methods and assumptions of the N turnover time. Wang et al. (2010) calculated the N turnover time of the ecosystem by summing up all the N turnover times of plant biomass, litter, and soil under the steady-state assumption, while this study used the balance method by dividing the ecosystem N stock by the N output flux. If Wang et al. (2010) used the balance method, the N turnover time of the ecosystem would be 459.18 years, which is similar estimate to the result of this study. This further shows how the calculation methods and assumptions can affect the estimates of the N turnover times.

The longer CTT_{soil} compared to CTT_{tree} and CTT_{DOM} indicates that mineral soil is particularly important for assessing the C storage efficiency in forests, though tree biomass had most C stock stored in the ecosystem. Similarly, the longer NTT_{soil} compared to NTT_{tree} and NTT_{DOM} indicates that mineral soil is not only a compartment where major N input and output fluxes occur in an ecosystem, but also has greater capabilities for retaining N in forests than tree biomass and primary DOM. We also found that the NTT_{system} was longer than sum of the NTT_{tree}, NTT_{DOM}, and NTT_{soil}, while the CTT_{system} was shorter than sum of CTT_{tree}, CTT_{DOM}, and CTT_{soil}. This indicates that once N enters the ecosystem, it transits through tree biomass, primary DOM, and mineral soil several times before exiting the ecosystem, while C can easily exit from the ecosystem without passing through these compartments several times. These results show that the turnover time of the ecosystem is not just the sum of the turnover times of various compartments and that the relationship between the turnover time of the ecosystem and those of various compartments depends on the type of element and the fluxes associated with the element. Thus, it is necessary to understand the C and N turnover times at the whole ecosystem scale with consideration of the various compartments in ecosystems for reliable estimations of the C and N turnover times and future projection of global forest C and N stocks using biogeochemical models.

4.2. Comparison of the Carbon and Nitrogen Turnover Times

Consistent with our expectations, the results of this study indicated that N turnover time was longer than C turnover time for tree biomass, primary DOM, mineral soil, and the ecosystem. In particular, the NTT_{system} was ~45 times longer than the CTT_{system}. This result may be attributed to the dominance of internal N fluxes in the N cycle (Figure 4), whereas output C fluxes dominated the C cycle (Figure 3; Kreutzer et al., 2009; Wang et al., 2018; Yanai et al., 2013). This result is consistent with those of previous studies. For example, Wang et al. (2010) highlighted the dominant role of internal N fluxes in the N cycle and demonstrated that the N turnover time was >10 times longer than the C turnover time at the whole ecosystem level in the terrestrial biosphere. Hirose and Oikawa (2012) reported that the N turnover time of foliage was longer than the C turnover time of foliage in a temperate forest due to N resorption at turnover of foliage. The longer N turnover time compared to C turnover time was also found for the forest floor (Schulte-Bisping & Beese, 2016) and litter (Dincher et al., 2020). Likewise, there is an evidence that C release rates are faster than N release rates in litter (Torreta & Takeda, 1999), woody debris (Chen et al., 2001; Noh et al., 2017), and dead fine root (Tong et al., 2012). Considering that limited resources in forests usually have long turnover times (Aerts & de Caluwe, 1995; Eckstein et al., 1999), the much longer NTT_{system} than CTT_{system} observed in the present study supports that N is a primary growth-limiting resource in temperate forests (McGroddy et al., 2004; Reich & Oleksyn, 2004).

4.3. Explaining the Variation of the Carbon and Nitrogen Turnover Times

There was no difference in the C and N turnover times of the ecosystem between forest types. This result is inconsistent with those of previous studies, wherein forest types affected the C and N turnover times (Quichimbo et al., 2020; Wang et al., 2018; Zhang et al., 2010; Zhou et al., 2010). These studies found that

the C and N turnover times changed with forest type because forest types determine leaf lifespan (Reich et al., 1992), C use efficiency (Kwon & Larsen, 2013), and decomposition rate (Noh et al., 2017). The discrepancy between the results of the present study and those of previous studies may be due to the confounding effects of temperature, precipitation, stand age, and C:N ratio on the C and N turnover times. Similarly, Wang et al. (2018) demonstrated that the explained variation of the C turnover times by forest types was only ~1%, and they noted that the impact of forest type on C turnover times can be minor if other abiotic and biotic factors dominantly control the variation of the C turnover times. Moreover, evergreen forests have shorter C turnover times than deciduous forests, while coniferous forests have longer C turnover times than broad-leaved forests (Wang et al., 2018; Zhou et al., 2010). This contrasting effect between leaf senescence timing (i.e., deciduous versus evergreen) and leaf type (i.e., broad-leaved versus coniferous) on the turnover time might obscure the difference in the C and N turnover times between forest types.

When assessing the effects of abiotic and biotic factors, we found that the CTT_{system} and NTT_{system} were negatively associated with mean annual temperature, but positively related to stand age and C:N ratio (Figures 6 and 7). The decrease in CTT_{system} with increasing mean annual temperature has also been reported in previous studies for C turnover times (Carvalhais et al., 2014; Wang et al., 2018; Yan et al., 2017; Cai et al., 2020; Yang et al., 2020). This result can be explained by the dependence of the decomposition rate and microbial activity on temperature (Quan et al., 2014). The negative relationship between NTT_{system} and mean annual temperature might be due to increased substrate supply (Liski et al., 2003), enhanced microbial activity (Lellei-Kovács et al., 2016), and accelerated N mineralization (Dan et al., 2019) with increasing temperature, which can lead to an increase in N leaching and decrease in N turnover times (Jabloun et al., 2015). The decrease in CTT_{system} and NTT_{system} with the increase in temperature indicates that global warming would constrain the long-term capacity of forests to store C and N. Moreover, a shortened C and N turnover times as a consequence of increased temperature will result in greater CO_2 and N_2O emissions from forests into the atmosphere, and thereby exacerbating the greenhouse effect (Bonan, 2008). Meanwhile, considering that global warming is also expected to increase tree mortality (Yu et al., 2019), the negative impact of a future increase in temperature on the C and N turnover times could be larger than reported in our study because the FBD-CAN does not account for the impact of temperature on tree mortality.

The positive relationships between CTT_{system} and NTT_{system} and ecosystem C:N ratio were because the FBD-CAN was designed to consider the decrease in decomposition and N mineralization rate with the increase in C:N ratio and the decrease N leaching when inorganic N content is low (Kim et al., 2019), as reported in the previous experimental studies. For example, a high C:N ratio can decelerate the decomposition and N mineralization rate in litter, thereby lengthening the C and N turnover times (Li et al., 2017; Reich et al., 2005). The N immobilization rate is rapid when the C:N ratio is high, making N remain longer in the ecosystem in organic forms (Pei et al., 2019). N leaching in forests decreases with an increase in the C:N ratio (Gundersen et al., 1998). While previous studies have reported that temperature, precipitation, or stand age is the main factor controlling the variation of the C and N turnover times (Chen et al., 2013; Wang et al., 2018; Yan et al., 2017), we found that the C:N ratio was the most important factor, explaining ~34% of the variation in CTT_{system} and NTT_{system} that could not be explained by other factors (Figure 7b). Considering that the dominant factor determining the C and N turnover times can differ with latitude and range of climatic variables (Carvalhais et al., 2014), our results indicate that the C:N ratio can play an important role when explaining the variation of the C and N turnover times in the South Korean forest. Moreover, these results emphasize that biogeochemical models need to consider the effects of the C:N ratio on the C and N turnover times for reliable future projections of global forest C and N stocks.

Annual precipitation had no significant relationship with CTT_{system} and NTT_{system}, while previous studies have reported the decrease of the C and N turnover times with an increase in annual precipitation (Cai et al., 2020; Carvalhais et al., 2014; Chen et al., 2013; Ge et al., 2019; Wang et al., 2018; Yan et al., 2017) due to accelerated soil respiration (Deng et al., 2012; Knapp et al., 2008; Miao et al., 2017) and N leaching (Donner et al., 2004; Howarth et al., 2006; Kong et al., 2013; Ye et al., 2016). These discrepancies in the responses of CTT_{system} and NTT_{system} to annual precipitation might be due to the following three reasons. First, annual precipitation may not be an adequate indicator of soil moisture that directly affects the soil respiration and N leaching because it does not account for the temporal or seasonal distribution of precipitation within a year (Sanderman et al., 2003). Especially, this tendency is apparent in South Korean forests, in which ~70%

of mean annual precipitation occurs in the summer. Second, the narrower range of annual precipitation in this study (1,100–1,479 mm) compared to others (100–2,400 mm; Ge et al., 2019; Wang et al., 2018; Yan et al., 2017) might hinder its potential effects on CTT_{system} and NTT_{system} because it would not create significant differences in soil moisture between the 64 permanent forest plots, thereby resulting in insignificant responses of soil respiration and N leaching to annual precipitation. Third, the effects of annual precipitation on ecosystem C and N stocks might obscure the responses of CTT_{system} and NTT_{system} to the increasing soil respiration and N leaching as a result of increasing annual precipitation. This is because CTT_{system} and NTT_{system} are not only determined by C and N output fluxes, such as soil respiration and N leaching, but also by ecosystem C and N stocks, which reportedly change along precipitation gradient (Han et al., 2019; Hobley et al., 2015; Khan et al., 2019; Lie et al., 2018). This might hide the effects of annual precipitation on soil respiration and N leaching.

4.4. Limitations of the Study

Our estimates on the C and N turnover times are different from mean transit time because South Korean forests are not in a steady state (Lu et al., 2018; Sierra et al., 2017), which is evidenced by the greater total input fluxes than total output fluxes of C and N. Considering that forests usually come close to the steady state when the stand is old and that the C and N turnover times increase with the increase in stand age, the CTT_{system} and NTT_{system} from the present study might be shorter than the estimates under the steady state. However, it would be meaningful to compare our estimates with mean transit time in future studies because most ecosystems are not in steady state due to their C and N cycles varying with time (Ge et al., 2019; Lu et al., 2018). This would broaden our knowledge of the changes of C and N turnover times over time.

The explained variation of the CTT_{system} and NTT_{system} was only ~50%, though this value was larger than that in a previous study (Wang et al., 2018). The unexplained variation might result from the limited range of mean annual temperature, annual precipitation, and stand age (Table 1) and the missing factors that can affect the C and N turnover times, such as species composition, biogeochemical composition of DOM, soil pH, soil texture, and soil microbial community. Clarifying the unexplained variation in the C and N turnover times in future studies would increase the reliability of future projections using biogeochemical models.

Although the data-model fusion can reduce the uncertainty in simulations based on the unfitted model parameters, it has other sources of uncertainty including the input data and model structure. In terms of data uncertainty, we used the estimates of the C and N stocks of foliage and fine roots (Equations 4–7), which are known to have some degree of uncertainty (Yang et al., 2021). The uncertainty in these estimates can lead to unreliable estimation of the C and N turnover times. This is because foliage and fine root are major compartments determining the C and N turnover times of forests through their higher turnover rate, decomposition rate, and N concentration compared to that of the woody compartments (Negrón-Juárez et al., 2015; Yan et al., 2017). In terms of the model structure, the FBD-CAN does not consider the impact of abiotic and biotic factors, such as lignin content, labile C content, soil pH, and soil texture, on decomposition and microbial activities as well as the life-cycle of soil microbes. Moreover, C and N allocation within trees and competition between roots and microbes for available N are not yet well represented in the FBD-CAN (Kim et al., 2019).

5. Conclusions

This study provides estimates of the C and N turnover times, which can be used for the future projection of forest C and N stocks in temperate forests. Our findings will improve our understanding of the C and N turnover times in temperate forests and their relationships with abiotic and biotic factors by providing novel insights into how the C and N turnover times may vary with climatic conditions, time, and the changes in N deposition. We suggest that biogeochemical models need to include the effects of the C:N ratio when estimating the C and N turnover times for a more accurate projection of the forest C and N stocks. Our study is one of the leading studies to estimate the N turnover time and explain its variation with abiotic and biotic factors at the regional scale. Thus, this regional-scale study can serve as basis for further studies aiming to use a biogeochemical modeling approach to estimate the C and N turnover times at a regional or national

scale (e.g., continental and global scales) in a changing world. Future studies should also account for the structural and empirical limitations associated with the use of biogeochemical models.

Data Availability Statement

The MATLAB codes for the FBD-CAN and data-model fusion are available by contacting Hyung-Sub Kim, the first author of this article and the model developer. Data sets for this study come from public sources (all listed in the Section 2), Korea Forest Service, and Korea Forestry Promotion Institute. These data sets were uploaded via Dryad (https://datadryad.org/stash/share/xiVYFReK_poHpdLQn0JN4MT87QPKFHhulPoFSb0GBV0).

References

Addiscott, T. M. (1996). Measuring and modelling nitrogen leaching: Parallel problems. *Plant and Soil*, *181*(1), 1–6. https://doi.org/10.1007/BF00011284

Aerts, R., & de Caluwe, H. (1995). Interspecific and intraspecific differences in shoot and leaf lifespan of four *Carex* species which differ in maximum dry matter production. *Oecologia*, *102*(4), 467–477. https://doi.org/10.1007/BF00341359

Agren, G. I., & Andersson, F. O. (2012). *Terrestrial ecosystem ecology. Principles and applications*. Cambridge University Press.

Barrett, D. (2002). Steady state turnover time of carbon in the Australian terrestrial biosphere. *Global Biogeochemical Cycles*, *16*(4), 1108. https://doi.org/10.1029/2002GB001860

Bonan, G. B. (2008). Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science*, *320*(5882), 1444–1449. https://doi.org/10.1126/science.1155121

Bonan, G. B. (2019). *Climate change and terrestrial ecosystem modeling*. Cambridge University Press. https://doi.org/10.1017/9781107339217

Cai, A., Chang, N., Zhang, W., Liang, G., Zhang, X., Hou, E., et al. (2020). The spatial patterns of litter turnover time in Chinese terrestrial ecosystems. *European Journal of Soil Science*, *71*(5), 856–867. https://doi.org/10.1111/ejss.12922

Carvalhais, N., Forkel, M., Khomik, M., Bellarby, J., Jung, M., Migliavacca, M., et al. (2014). Global covariation of carbon turnover times with climate in terrestrial ecosystems. *Nature*, *514*(7521), 213–217. https://doi.org/10.1038/nature13731

Carvalhais, N., Reichstein, M., Seixas, J., Collatz, G. J., Pereira, J. S., Berbigier, P., et al. (2008). Implications of the carbon cycle steady state assumption for biogeochemical modeling performance and inverse parameter retrieval. *Global Biogeochemical Cycles*, *22*, GB2007. https://doi.org/10.1029/2007GB003033

Chen, H., Harmon, M. E., & Griffiths, R. P. (2001). Decomposition and nitrogen release from decomposing woody roots in coniferous forests of the Pacific Northwest: A chronosequence approach. *Canadian Journal of Forest Research*, *31*(2), 246–260. https://doi.org/10.1139/cjfr-31-2-246

Chen, S., Huang, Y., Zou, J., & Shi, Y. (2013). Mean residence time of global topsoil organic carbon depends on temperature, precipitation and soil nitrogen. *Global and Planetary Change*, *100*, 99–108. https://doi.org/10.1016/j.gloplacha.2012.10.006

Chen, S., Zou, J., Hu, Z., & Lu, Y. (2020). Temporal and spatial variations in the mean residence time of soil organic carbon and their relationship with climatic, soil and vegetation drivers. *Global and Planetary Change*, *195*, 103359.

Dan, X., Chen, Z., Dai, S., He, X., Cai, Z., Zhang, J., & Müller, C. (2019). Effects of changing temperature on gross N transformation rates in acidic subtropical forest soils. *Forests*, *10*(10), 894. https://doi.org/10.3390/f10100894

Deng, Q., Hui, D., Zhang, D., Zhou, G., Liu, J., Liu, S., et al. (2012). Effects of precipitation increase on soil respiration: A three-year field experiment in subtropical forests in China. *PLoS One*, *7*(7), e41493. https://doi.org/10.1371/journal.pone.0041493

Derrien, D., & Amelung, W. (2011). Computing the mean residence time of soil carbon fractions using stable isotopes: Impacts of the model framework. *European Journal of Soil Science*, *62*(2), 237–252. https://doi.org/10.1111/j.1365-2389.2010.01333.x

Dincher, M., Calvaruso, C., & Turpault, M. P. (2020). Major element residence times in humus from a beech forest: The role of element forms and recycling. *Soil Biology and Biochemistry*, *141*, 107674. https://doi.org/10.1016/j.soilbio.2019.107674

Donner, S. D., Kucharik, C. J., & Oppenheimer, M. (2004). The influence of climate on in-stream removal of nitrogen. *Geophysical Research Letters*, *31*, L20509. https://doi.org/10.1029/2004GL020477

Eckstein, R. L., Karlsson, P. S., & Weih, M. (1999). Leaf life span and nutrient resorption as determinants of plant nutrient conservation in temperate-arctic regions. *New Phytologist*, *143*(1), 177–189. https://doi.org/10.1046/j.1469-8137.1999.00429.x

Farquhar, G. D., von Caemmerer, S. V., & Berry, J. A. (1980). A biochemical model of photosynthetic CO_2 assimilation in leaves of C3 species. *Planta*, *149*(1), 78–90. https://doi.org/10.1007/BF00386231

Food and Agriculture Organization (FAO). (2016). *Integrated policy for forests, food security and sustainable livelihoods*. Food and Agriculture Organization.

Friend, A. D., Lucht, W., Rademacher, T. T., Keribin, R., Betts, R., Cadule, P., et al. (2014). Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO_2. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(9), 3280–3285. https://doi.org/10.1073/pnas.1222477110

Galloway, J. N., Dentener, F. J., Capone, D. G., Boyer, E. W., Howarth, R. W., Seitzinger, S. P., et al. (2004). Nitrogen cycles: Past, present, and future. *Biogeochemistry*, *70*(2), 153–226. https://doi.org/10.1007/s10533-004-0370-0

Ge, R., He, H., Ren, X., Zhang, L., Yu, G., Smallman, T. L., et al. (2019). Underestimated ecosystem carbon turnover time and sequestration under the steady state assumption: A perspective from long-term data assimilation. *Global Change Biology*, *25*(3), 938–953. https://doi.org/10.1111/gcb.14547

Gruber, N., & Galloway, J. N. (2008). An Earth-system perspective of the global nitrogen cycle. *Nature*, *451*(7176), 293–296. https://doi.org/10.1038/nature06592

Gundersen, P. (1991). Nitrogen deposition and the forest nitrogen cycle: Role of denitrification. *Forest Ecology and Management*, *44*(1), 15–28. https://doi.org/10.1016/S0269-7491(98)80060-2

Gundersen, P., Callesen, I., & De Vries, W. (1998). Nitrate leaching in forest ecosystems is related to forest floor C:N ratios. *Environmental Pollution*, *102*(1), 403–407. https://doi.org/10.1016/0378-1127(91)90194-Z

Han, X., Gao, G., Li, Z., Chang, R., Jiao, L., & Fu, B. (2019). Effects of plantation age and precipitation gradient on soil carbon and nitrogen changes following afforestation in the Chinese Loess Plateau. *Land Degradation and Development*, *30*(18), 2298–2310. https://doi.org/10.1002/ldr.3422

Harmon, M. E., & Sexton, J. (1996). *Guidelines for measurements of woody detritus in forest ecosystems (Publication No. 20)*. U.S. LTER Network Office, University of Washington.

Hastings, A. W. K. (1970). Monte Carlo sampling methods using Markov Chains and their applications. *Biometrika*, *57*(1), 97–109. https://doi.org/10.1093/biomet/57.1.97

Hirose, T., & Oikawa, S. (2012). Mean residence time of leaf number, area, mass, and nitrogen in canopy photosynthesis. *Oecologia*, *169*(4), 927–937. https://doi.org/10.1007/s00442-012-2266-3

Hobley, E., Wilson, B., Wilkie, A., Gray, J., & Koen, T. (2015). Drivers of soil organic carbon storage and vertical distribution in Eastern Australia. *Plant and Soil*, *390*(1–2), 111–127. https://doi.org/10.1007/s11104-015-2380-1

Högberg, P., Näsholm, T., Franklin, O., & Högberg, M. N. (2017). Tamm review: On the nature of the nitrogen limitation to plant growth in Fennoscandian boreal forests. *Forest Ecology and Management*, *403*, 161–185. https://doi.org/10.1016/j.foreco.2017.04.045

Hou, E., Lu, X., Jiang, L., Wen, D., & Luo, Y. (2019). Quantifying soil phosphorus dynamics: A data assimilation approach. *Journal of Geophysical Research: Biogeosciences*, *124*, 2159–2173. https://doi.org/10.1029/2018JG004903

Howarth, R. W., Swaney, D. P., Boyer, E. W., Marino, R., Jaworski, N., & Goodale, C. (2006). The influence of climate on average nitrogen export from large watersheds in the Northeastern United States. *Biogeochemistry*, *79*(1–2), 163–186. https://doi.org/10.1007/s10533-006-9010-1

Jabloun, M., Schelde, K., Tao, F., & Olesen, J. E. (2015). Effect of temperature and precipitation on nitrate leaching from organic cereal cropping systems in Denmark. *European Journal of Agronomy*, *62*, 55–64. https://doi.org/10.1016/j.eja.2014.09.007

Johnson, M. O., Galbraith, D., Gloor, M., De Deurwaerder, H., Guimberteau, M., Rammig, A., et al. (2016). Variation in stem mortality rates determines patterns of above-ground biomass in Amazonian forests: Implications for dynamic global vegetation models. *Global Change Biology*, *22*(12), 3996–4013. https://doi.org/10.1111/gcb.13315

Khan, D., Muneer, M. A., Nisa, Z. U., Shah, S., Amir, M., Saeed, S., et al. (2019). Effect of climatic factors on stem biomass and carbon stock of *Larix gmelinii* and *Betula platyphylla* in Daxing'anling Mountain of Inner Mongolia, China. *Advances in Meteorology*, *2019*, 1–10. https://doi.org/10.1155/2019/5692574

Kim, D.-H., Lee, S.-H., & Ryu, K.-S. (2016). *National Forest Inventories: Assessment of wood availability and use* (Chap. 35, pp. 655–665). https://doi.org/10.1007/978-3-319-44015-6_35

Kim, H., Kim, S., Lee, J., Chang, H., Roh, Y., An, J., & Son, Y. (2019). Development of a forest carbon and nitrogen model: Pilot application for a *Pinus densiflora* forest in central Korea. *Forest Science and Technology*, *15*(4), 202–209. https://doi.org/10.1080/21580103.2019.1666749

Kim, H., Lee, J., Han, S. H., Kim, S., & Son, Y. (2018). Approaches for developing a forest carbon and nitrogen model through analysis of domestic and overseas models. *Journal of Korean Society of Forest Science*, *107*(2), 140–150. https://doi.org/10.14578/jkfs.2018.107.2.140

Knapp, A. K., Beier, C., Briske, D. D., Classen, A. T., Yiqi, L., Reichstein, M., et al. (2008). Consequences of more extreme precipitation regimes for terrestrial ecosystems. *BioScience*, *58*(9), 811–821. https://doi.org/10.1641/B580908

Kong, D. L., Lü, X. T., Jiang, L. L., Wu, H. F., Miao, Y., & Kardol, P. (2013). Extreme rainfall events can alter inter-annual biomass responses to water and N enrichment. *Biogeosciences*, *10*(12), 8129–8138. https://doi.org/10.5194/bg-10-8129-2013

Korea Forest Research Institute (KFRI). (2014). *Carbon emission factors and biomass allometric equations by species in Korea*. Korea Forest Service.

Korea Forest Service (KFS). (2020). *Statistical yearbook of forestry*. Korea Forest Service.

Korea Meteorological Administration (KMA). (2020). *Climate data open portal*. Korea Meteorological Administration.

Kreutzer, K., Butterbach-Bahl, K., Rennenberg, H., & Papen, H. (2009). The complete nitrogen cycle of an N-saturated spruce forest ecosystem. *Plant Biology*, *11*(5), 643–649. https://doi.org/10.1111/j.1438-8677.2009.00236.x

Kwon, Y., & Larsen, C. P. S. (2013). Effects of forest type and environmental factors on forest carbon use efficiency assessed using MODIS and FIA data across the eastern USA. *International Journal of Remote Sensing*, *34*(23), 8425–8448. https://doi.org/10.1080/01431161.2013.838711

Lee, J., Lee, S., Han, S. H., Kim, S., Roh, Y., Salim, K. A., et al. (2017). Estimating carbon dynamics in an intact lowland mixed dipterocarp forest using a forest carbon model. *Forests*, *8*(4), 114. https://doi.org/10.3390/f8040114

Lee, J., Lim, C. H., Kim, G. S., Markandya, A., Chowdhury, S., Kim, S. J., et al. (2018). Economic viability of the national-scale forestation program: The case of success in the Republic of Korea. *Ecosystem Services*, *29*, 40–46. https://doi.org/10.1016/j.ecoser.2017.11.001

Lee, J., Tolunay, D., Makineci, E., Çömez, A., Son, Y. M., Kim, R., & Son, Y. (2016). Estimating the age-dependent changes in carbon stocks of Scots pine (*Pinus sylvestris* L.) stands in Turkey. *Annals of Forest Science*, *73*(2), 523–531. https://doi.org/10.1007/s13595-016-0546-5

Lee, J., Yoon, T. K., Han, S., Kim, S., Yi, M. J., Park, G. S., et al. (2014). Estimating the carbon dynamics of South Korean forests from 1954 to 2012. *Biogeosciences*, *11*(17), 4637–4650. https://doi.org/10.5194/bg-11-4637-2014

Lee, S. J., Yim, J. S., Son, Y. M., Son, Y., & Kim, R. (2018). Estimation of forest carbon stocks for national greenhouse gas inventory reporting in South Korea. *Forests*, *9*, 625. https://doi.org/10.3390/f9100625

Lellei-Kovács, E., Botta-Dukát, Z., de Dato, G., Estiarte, M., Guidolotti, G., Kopittke, G. R., et al. (2016). Temperature dependence of soil respiration modulated by thresholds in soil water availability across European shrubland ecosystems. *Ecosystems*, *19*(8), 1460–1477. https://doi.org/10.1007/s10021-016-0016-9

Li, W., Bai, Z., Jin, C., Zhang, X., Guan, D., Wang, A., et al. (2017). The influence of tree species on small scale spatial heterogeneity of soil respiration in a temperate mixed forest. *Science of the Total Environment*, *590–591*, 242–248. https://doi.org/10.1016/j.scitotenv.2017.02.229

Liang, J., Li, D., Shi, Z., Tiedje, J. M., Zhou, J., Schuur, E. A. G., et al. (2015). Methods for estimating temperature sensitivity of soil organic matter based on incubation data: A comparative evaluation. *Soil Biology and Biochemistry*, *80*, 127–135. https://doi.org/10.1016/j.soilbio.2014.10.005

Lie, Z., Xue, L., & Jacobs, D. F. (2018). Allocation of forest biomass across broad precipitation gradients in China's forests. *Scientific Reports*, *8*(1), 10536. https://doi.org/10.1038/s41598-018-28899-5

Liski, J., Nissinen, A., Erhard, M., & Taskinen, O. (2003). Climatic effects on litter decomposition from arctic tundra to tropical rainforest. *Global Change Biology*, *9*(4), 575–584. https://doi.org/10.1046/j.1365-2486.2003.00605.x

Lu, X., Wang, Y. P., Luo, Y., & Jiang, L. (2018). Ecosystem carbon transit versus turnover times in response to climate warming and rising atmospheric CO_2 concentration. *Biogeosciences*, *15*(21), 6559–6572. https://doi.org/10.5194/bg-15-6559-2018

Luo, Y., Shi, Z., Lu, X., Xia, J., Liang, J., Jiang, J., et al. (2017). Transient dynamics of terrestrial carbon storage: Mathematical foundation and its applications. *Biogeosciences*, *14*(1), 145–161. https://doi.org/10.5194/bg-14-145-2017

Mao, R., Zeng, D. H., Hu, Y. L., Li, L. J., & Yang, D. (2010). Soil organic carbon and nitrogen stocks in an age-sequence of poplar stands planted on marginal agricultural land in Northeast China. *Plant and Soil*, *332*(1), 277–287. https://doi.org/10.1007/s11104-010-0292-7

Martin, P., Jung, M., Brearley, F. Q., Ribbons, R. R., Lines, E. R., & Jacob, A. L. (2016). Can we set a global threshold age to define mature forests? *PeerJ*, *4*, e1595. https://doi.org/10.7717/peerj.1595

McGroddy, M. E., Daufresne, T., & Hedin, L. O. (2004). Scaling of C:N:P stoichiometry in forests worldwide: Implications of terrestrial Redfield-type ratios. *Ecology*, *85*(9), 2390–2401. https://doi.org/10.1890/03-0351

Metropolis, N., Rosenbluth, A. W., Rosenbluth, M. N., Teller, A. H., & Teller, E. (1953). Equation of state calculations by fast computing machines. *The Journal of Chemical Physics*, *21*(6), 1087–1092. https://doi.org/10.1063/1.1699114

Miao, Y., Han, H., Du, Y., Zhang, Q., Jiang, L., Hui, D., & Wan, S. (2017). Nonlinear responses of soil respiration to precipitation changes in a semiarid temperate steppe. *Scientific Reports*, *7*(1), 45782. https://doi.org/10.1038/srep45782

Minunno, F., Peltoniemi, M., Härkönen, S., Kalliokoski, T., Makinen, H., & Mäkelä, A. (2019). Bayesian calibration of a carbon balance model PREBAS using data from permanent growth experiments and National Forest Inventory. *Forest Ecology and Management*, *440*, 208–257. https://doi.org/10.1016/j.foreco.2019.02.041

Negrón-Juárez, R. I., Koven, C. D., Riley, W. J., Knox, R. G., & Chambers, J. Q. (2015). Observed allocations of productivity and biomass, and turnover times in tropical forests are not accurately represented in CMIP5 Earth system models. *Environmental Research Letters*, *10*, 064017. https://doi.org/10.1088/1748-9326/10/6/064017

Noh, N. J., Son, Y., Lee, S. K., Seo, K. W., Heo, S. J., Yi, M. J., et al. (2010). Carbon and nitrogen storage in an age-sequence of *Pinus densiflora* stands in Korea. *Science China Life Sciences*, *53*(7), 822–830. https://doi.org/10.1007/s11427-010-4018-0

Noh, N. J., Yoon, T. K., Kim, R. H., Bolton, N. W., Kim, C., & Son, Y. (2017). Carbon and nitrogen accumulation and decomposition from coarse woody debris in a naturally regenerated Korean red pine (*Pinus densiflora* S. et Z.) forest. *Forests*, *8*(6), 12–15. https://doi.org/10.3390/f8060214

Nyström, M., Lindgren, N., Wallerman, J., Grafström, A., Muszta, A., Nyström, K., et al. (2015). Data assimilation in forest inventory: First empirical results. *Forests*, *6*(12), 4540–4557. https://doi.org/10.3390/f6124384

Pan, Y., Chen, J. M., Birdsey, R., McCullough, K., He, L., & Deng, F. (2011). Age structure and disturbance legacy of North American forests. *Biogeosciences*, *8*(3), 715–732. https://doi.org/10.5194/bg-8-715-2011

Pei, G., Liu, J., Peng, B., Gao, D., Wang, C., Dai, W., et al. (2019). Nitrogen, lignin, C/N as important regulators of gross nitrogen release and immobilization during litter decomposition in a temperate forest ecosystem. *Forest Ecology and Management*, *440*, 61–69. https://doi.org/10.1016/j.foreco.2019.03.001

Pugh, T. A. M., Rademacher, T., Shafer, S. L., Steinkamp, J., Barichivich, J., Beckage, B., et al. (2020). Understanding the uncertainty in global forest carbon turnover. *Biogeosciences*, *17*(15), 3961–3989. https://doi.org/10.5194/bg-17-3961-2020

Quan, Q., Wang, C., He, N., Zhang, Z., Wen, X., Su, H., et al. (2014). Forest type affects the coupled relationships of soil C and N mineralization in the temperate forests of northern China. *Scientific Reports*, *4*, 6584. https://doi.org/10.1038/srep06584

Qubaja, R., Grünzweig, J. M., Rotenberg, E., & Yakir, D. (2020). Evidence for large carbon sink and long residence time in semiarid forests based on 15 year flux and inventory records. *Global Change Biology*, *26*(3), 1626–1637. https://doi.org/10.1111/gcb.14927

Quichimbo, P., Jiménez, L., Veintimilla, D., Potthast, K., Tischer, A., Günter, S., et al. (2020). Nutrient dynamics in an Andean Forest Region: A case study of exotic and native species plantations in southern Ecuador. *New Forests*, *51*(2), 313–334. https://doi.org/10.1007/s11056-019-09734-9

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Reich, P. B., & Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(30), 11001–11006. https://doi.org/10.1073/pnas.0403588101

Reich, P. B., Oleksyn, J., Modrzynski, J., Mrozinski, P., Hobbie, S. E., Eissenstat, D. M., et al. (2005). Linking litter calcium, earthworms and soil properties: A common garden test with 14 tree species. *Ecology Letters*, *8*(8), 811–818. https://doi.org/10.1111/j.1461-0248.2005.00779.x

Reich, P. B., Walters, M. B., & Ellsworth, D. S. (1992). Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs*, *62*(3), 365–392. https://doi.org/10.2307/2937116

Sanderman, J., Amundson, R. G., & Baldocchi, D. D. (2003). Application of eddy covariance measurements to the temperature dependence of soil organic matter mean residence time. *Global Biogeochemical Cycles*, *17*(2), 1061. https://doi.org/10.1029/2001GB001833

Schlesinger, W. H. (2009). On the fate of anthropogenic nitrogen. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(1), 203–208. https://doi.org/10.1073/pnas.0810193105

Schulte-Bisping, H., & Beese, F. (2016). N-fluxes and N-turnover in a mixed beech-pine forest under low N-inputs. *European Journal of Forest Research*, *135*(2), 229–241. https://doi.org/10.1007/s10342-015-0931-x

Schwartz, S. E. (1979). Residence times in reservoirs under non-steady-state conditions: Application to atmospheric SO_2 and aerosol sulfate. *Tellus*, *31*(6), 530–547. https://doi.org/10.1111/j.2153-3490.1979.tb00935.x

Schwede, D. B., Simpson, D., Tan, J., Fu, J. S., Dentener, F., Du, E., & deVries, W. (2018). Spatial variation of modelled total, dry and wet nitrogen deposition to forests at global scale. *Environmental Pollution*, *243*, 1287–1301. https://doi.org/10.1016/j.envpol.2018.09.084

Sierra, C. A., Müller, M., Metzler, H., Manzoni, S., & Trumbore, S. E. (2017). The muddle of ages, turnover, transit, and residence times in the carbon cycle. *Global Change Biology*, *23*(5), 1763–1773. https://doi.org/10.1111/gcb.13556

Smithwick, E. A. H., Kashian, D. M., Ryan, M. G., & Turner, M. G. (2009). Long-term nitrogen storage and soil nitrogen availability in postfire lodgepole pine ecosystems. *Ecosystems*, *12*(5), 792–806. https://doi.org/10.1007/s10021-009-9257-1

Song, K.-C., Hyun, B.-K., & Kang, H.-J. (2019). Reclassification of Korean soils according to revised soil taxonomy. *Korean Journal of Soil Science and Fertilizer*, *52*(2), 93–104.

Thurner, M., Beer, C., Ciais, P., Friend, A. D., Ito, A., Kleidon, A., et al. (2017). Evaluation of climate-related carbon turnover processes in global vegetation models for boreal and temperate forests. *Global Change Biology*, *23*(8), 3076–3091. https://doi.org/10.1111/gcb.13660

Tong, J., Xiang, W., Liu, C., Lei, P., Tian, D., Deng, X., & Peng, C. (2012). Tree species effects on fine root decomposition and nitrogen release in subtropical forests in southern China. *Plant Ecology and Diversity*, *5*(3), 323–331. https://doi.org/10.1080/17550874.2012.719937

Torreta, N. K., & Takeda, H. (1999). Carbon and nitrogen dynamics of decomposing leaf litter in a tropical hill evergreen forest. *European Journal of Soil Biology*, *35*(2), 57–63. https://doi.org/10.1016/S1164-5563(99)00111-9

Vidal, C., Alberdi, I., Hernández, L., & Redmond, J. (2016). *National Forest Inventories: Assessment of wood availability and use*. https://doi.org/10.1007/978-3-319-44015-6

Wang, J., Sun, J., Xia, J., He, N., Li, M., & Niu, S. (2018). Soil and vegetation carbon turnover times from tropical to boreal forests. *Functional Ecology*, *32*(1), 71–82. https://doi.org/10.1111/1365-2435.12914

Wang, Y., Liu, L., Yue, F., & Li, D. (2019). Dynamics of carbon and nitrogen storage in two typical plantation ecosystems of different stand ages on the Loess Plateau of China. *PeerJ*, *7*, e7708. https://doi.org/10.7717/peerj.7708

Wang, Y. P., Law, R. M., & Pak, B. (2010). A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere. *Biogeosciences*, *7*(7), 2261–2282. https://doi.org/10.5194/bg-7-2261-2010

Weng, E., Luo, Y., Gao, C., & Oren, R. (2011). Uncertainty analysis of forest carbon sink forecast with varying measurement errors: A data assimilation approach. *Journal of Plant Ecology*, *4*(3), 178–191. https://doi.org/10.1093/jpe/rtr018

Xia, J., Luo, Y., Wang, Y. P., & Hararuk, O. (2013). Traceable components of terrestrial carbon storage capacity in biogeochemical models. *Global Change Biology*, *19*(7), 2104–2116. https://doi.org/10.1111/gcb.12172

Xu, T., White, L., Hui, D., & Luo, Y. (2006). Probabilistic inversion of a terrestrial ecosystem model: Analysis of uncertainty in parameter estimation and model prediction. *Global Biogeochemical Cycles*, *20*, GB2007. https://doi.org/10.1029/2005GB002468

Yan, E., Wang, X., & Huang, J. (2006). Concept and classification of coarse woody debris in forest ecosystems. *Frontiers of Biology in China*, *1*(1), 76–84. https://doi.org/10.1007/s11515-005-0019-y

Yan, Y., Zhou, X., Jiang, L., & Luo, Y. (2017). Effects of carbon turnover time on terrestrial ecosystem carbon storage. *Biogeosciences*, *14*(23), 5441–5454. https://doi.org/10.5194/bg-14-5441-2017

Yanai, R. D., Vadeboncoeur, M. A., Hamburg, S. P., Arthur, M. A., Fuss, C. B., Groffman, P. M., et al. (2013). From missing source to missing sink: Long-term changes in the nitrogen budget of a northern hardwood forest. *Environmental Science and Technology*, *47*(20), 11440–11448. https://doi.org/10.1021/es4025723

Yang, B., Gong, J., Zhang, Z., Li, X., Wang, B., Zhu, C., et al. (2020). Spatial variation of carbon turnover time and carbon uptake in a Chinese desert steppe ecosystem. *Ecological Indicators*, *112*(19), 106120. https://doi.org/10.1016/j.ecolind.2020.106120

Yang, H., Ciais, P., Wang, Y., Huang, Y., Wigneron, J. P., Bastos, A., et al. (2021). Variations of carbon allocation and turnover time across tropical forests. *Global Ecology and Biogeography*, *30*(6), 1271–1285. https://doi.org/10.1111/geb.13302

Ye, J. S., Reynolds, J. F., Maestre, F. T., & Li, F. M. (2016). Hydrological and ecological responses of ecosystems to extreme precipitation regimes: A test of empirical-based hypotheses with an ecosystem model. *Perspectives in Plant Ecology, Evolution and Systematics*, *22*, 36–46. https://doi.org/10.1016/j.ppees.2016.08.001

Yi, K., Park, C. W., Ryu, S. R., Lee, K. H., Yi, M. J., Kim, C., et al. (2013). Simulating the soil carbon dynamics of *Pinus densiflora* forests in central Korea. *Scandinavian Journal of Forest Research*, *28*(3), 241–256. https://doi.org/10.1080/02827581.2012.735698

Yu, K., Smith, W. K., Trugman, A. T., Condit, R., Hubbell, S. P., Sardans, J., et al. (2019). Pervasive decreases in living vegetation carbon turnover time across forest climate zones. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(49), 24662–24667. https://doi.org/10.1073/pnas.1821387116

Zhang, L., Luo, Y., Yu, G., & Zhang, L. (2010). Estimated carbon residence times in three forest ecosystems of eastern China: Applications of probabilistic inversion. *Journal of Geophysical Research*, *115*, G01010. https://doi.org/10.1029/2009JG001004

Zhou, T., Shi, P. J., Jia, G. S., Li, X. J., & Luo, Y. Q. (2010). Spatial patterns of ecosystem carbon residence time in Chinese forests. *Science China Earth Sciences*, *53*(8), 1229–1240. https://doi.org/10.1007/s11430-010-3061-9

Zhou, X., Zhou, T., & Luo, Y. (2012). Uncertainties in carbon residence time and NPP-driven carbon uptake in terrestrial ecosystems of the conterminous USA: A Bayesian approach. *Tellus B: Chemical and Physical Meteorology*, *64*(1), 17223. https://doi.org/10.3402/tellusb.v64i0.17223