RESEARCH ARTICLE

Key Points:
- Consistent harmonized observations on carbon and nutrients in litterfall are available from 320 plots across European forests
- Litterfall of broadleaves contributes more carbon and nutrients to the forest floor than conifers
- Models can predict observed litterfall on average and can be improved by recalibrating based on foliage biomass and/or stand density

Supporting Information:
- Supporting Information S1
- Data Set S1

Correspondence to:
M. Neumann,
mathias.neumann@boku.ac.at

Quantifying Carbon and Nutrient Input From Litterfall in European Forests Using Field Observations and Modeling

Mathias Neumann[1] [iD], Liisa Ukonmaanaho[2], James Johnson[3] [iD], Sue Benham[4], Lars Vesterdal[5] [iD], Radek Novotný[6], Arne Verstraeten[7], Lars Lundin[8] [iD], Anne Thimonier[9] [iD], Panagiotis Michopoulos[10], and Hubert Hasenauer[1]

[1]Institute of Silviculture, Department of Forest and Soil Sciences, University of Natural Resources and Life Sciences, Vienna, Austria, [2]Natural Resources Institute Finland, Helsinki, Finland, [3]School of Agriculture and Food Science, University College Dublin, Dublin, Ireland, [4]Forest Research, Alice Holt Lodge, Farnham, UK, [5]Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark, [6]Forestry and Game Management Research Institute, Praha, Czech Republic, [7]Research Institute for Nature and Forest, Brussels, Belgium, [8]Swedish University of Agricultural Sciences, Uppsala, Sweden, [9]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland, [10]Forest Research Institute of Athens, Athens, Greece

Abstract Litterfall is a major, yet poorly studied, process within forest ecosystems globally. It is important for carbon dynamics, edaphic communities, and maintaining site fertility. Reliable information on the carbon and nutrient input from litterfall, provided by litter traps, is relevant to a wide audience including policy makers and soil scientists. We used litterfall observations of 320 plots from the pan-European forest monitoring network of the "International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests" to quantify litterfall fluxes. Eight litterfall models were evaluated (four using climate information and four using biomass abundance). We scaled up our results to the total European forest area and quantified the contribution of litterfall to the forest carbon cycle using net primary production aggregated by bioregions (north, central, and south) and by forest types (conifers and broadleaves). The 1,604 analyzed annual litterfall observations indicated an average carbon input of 224 g C $\cdot$ m^{-2} $\cdot$ year^{-1} (annual nutrient inputs 4.49 g N, 0.32 g P, and 1.05 g K $\cdot$ m^{-2}), representing a substantial percentage of net primary production from 36% in north Europe to 32% in central Europe. The annual turnover of carbon and nutrient in broadleaf canopies was larger than for conifers. The evaluated models provide large-scale litterfall predictions with a bias less than 10%. Each year litterfall in European forests transfers 351 Tg C, 8.2 Tg N, 0.6 Tg P, and 1.9 Tg K to the forest floor. The performance of litterfall models may be improved by including foliage biomass and proxies for forest management.

Plain Language Summary All plants shed parts of their biomass periodically. This litterfall is important for transferring carbon and nutrients from the canopy back to the soil. Every year in European forests about one third of carbon produced via photosynthesis falls to the forest floor as litterfall. Broadleaved trees shed more carbon and nutrients than conifers. Models can be used to quantify the average flux across Europe, but need improvement to be applicable at fine scales.

1. Introduction

Plants shed parts of their biomass (litterfall) periodically, which is a key biogeochemical process within ecosystems and links above and belowground pools (Bray & Gorham, 1964; Chave et al., 2010; Liu et al., 2004). Litterfall is important for forest nutrient cycling (Vitousek, 1984); the input of cations (i.e., nitrogen, phosphorus, and sulfur) by litterfall is much more important than other sources such as environmental deposition (Likens, 2013). Litterfall is also central to the global carbon (C) cycle. In forests, litterfall transfers about one third of the annual C uptake (about 18 Pg C $\cdot$ year^{-1}) to the soil surface (Grace, 2004; Malhi et al., 2011; Zhao & Running, 2010). Within soils, the interaction of C input by litterfall and C output due to decomposition results in highly variable forest floor and soil C stocks. The importance of forest litterfall for the global macroecology (Sayer, 2006) is highlighted by the fact that the forest floor accounts for about 9.0%, and soil for 54.1%, of the total European forest C stocks (Forest Europe, 2015). This translates to an average C density of 22.1 Mg C $\cdot$ ha^{-1} for the European forest floor (De Vos et al., 2015).

Litter is decomposed and/or incorporated into the soil by fungi, bacteria, and invertebrates (Couteaux et al., 1995). The efficiency of litter decomposition influences the formation of forest floor pools, humus layers, and the mobilization of stored nutrients through the decomposition rate (i.e., mass loss per unit of time) and rate of mineralization, which are regulated by climate, soil type, and litter quality (Cornelissen et al., 2007). Leaf litter from broadleaves and grasses has the highest decomposition rates, while the decomposition of components with a high lignin content (e.g., wood, bark, or coniferous needles) takes much longer (Zhang et al., 2008). These differences in decomposition rates control the forest floor C stocks, which may range from about $6 \, Mg \, C \cdot ha^{-1}$ for broadleaf forests to more than $12 \, Mg \, C \cdot ha^{-1}$ in conifer forests (Domke et al., 2016). This large variation in forest floor biomass influences forest succession, since the thickness of the litter on the forest floor controls germination and seedling establishment and thus future plant species mixtures (Ganade & Brown, 2002). Species change due to forest management or climate change (Kelly & Goulden, 2008) will likely alter the quality and timing of litterfall as well as forest productivity and C stocks (Sayer, 2006). This suggests that enhancing our understanding of litterfall and decomposition processes is not only beneficial for understanding the global C cycle but is also important for soil quality, biodiversity, and evaluating effects of forest management. An up-to-date harmonized database on litterfall and relevant metadata would facilitate such activities.

Information on European forest C is available from repeated measurements in national forest inventories (Tomppo et al., 2010). Most countries have no systematic monitoring of litterfall and its C input to the forest floor, since litterfall is difficult to collect, is not obligatory for greenhouse gas reporting, and exhibits high variability in space and time. In addition, data collection is limited by the fast decomposition rate of shed biomass and the high costs of field measurements and the associated lab analysis (Bray & Gorham, 1964).

Numerous studies have examined regional drivers of litterfall (e.g., Berg & Meentemeyer, 2001; Solberg et al., 2015; Ťupek et al., 2015; Vesterdal et al., 2008). However, few have analyzed litterfall across continental scales (Liu et al., 2004, Eurasia; Chave et al., 2010, South America; and Bray & Gorham, 1964; globally). These studies have used statistical modeling to identify the key drivers of litterfall. The results showed that tree species and climate are the main drivers of litterfall in Eurasia (Liu et al., 2004), while soil type was reported as the most important factor in tropical South America (Chave et al., 2010). The importance of temperature and precipitation has been supported by regional studies (Berg & Meentemeyer, 2001; Solberg et al., 2015; Ťupek et al., 2015). Climate influences soil fertility, which affects biomass production and consequently litterfall quantity (Vitousek, 1984).

In arid regions or heavily degraded forests, the relationship between litterfall and climate (Liu et al., 2004) may be obscured by other factors limiting plant growth and/or low vegetation cover (Sisay et al., 2017). Therefore, some studies estimate litterfall as a ratio of biomass abundance (i.e., tree biomass fractions that can be shed such as leaves and needles) based on productivity and/or leaf area index (LAI; He et al., 2012; Malhi et al., 2011). Currently used and tested only in Scandinavia (Solberg et al., 2015; Ťupek et al., 2015), European litterfall models based on foliage biomass could be an alternative to models which use climate information (Liu et al., 2004). Using biomass abundance may result in more realistic litterfall estimates, since vegetation quantity is the basic driving and limiting factor for litterfall. Regression models using climate information imply that litterfall correlates with temperature and precipitation. The models assume an equilibrium of actual local biomass abundance and the potential that can be reached under the local climate conditions (Liu et al., 2004). In addition, biomass abundance is more widely available than litterfall, for instance, from forest inventory data in combination with biomass functions (Neumann, Moreno, Mues, et al., 2016; Tomppo et al., 2010) or from remote sensing technologies (Yang et al., 2006).

Field measurements of litterfall mainly come from litter traps commonly located in long-term forest research plots. Laboratory analyses following the litter collection are carried out to determine the chemical composition including C and nutrient information. Liu et al. (2004) collated more than 400 plots with litterfall information across Eurasia, yet did not report element content. Their data covered the second half of the twentieth century (1950 to 1997), and 100 of the 400 plots were located in Europe, mainly in Great Britain and Scandinavia (Liu et al., 2004).

In 1985 a pan-European forest-monitoring network was launched by the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (called ICP Forests) under the UNECE Convention on Long-Range Transboundary Air Pollution to monitor forest damage observed in

some parts of Europe at that time. This program includes the collection of litterfall and its elemental properties, as an indicator for nutrient flux to forest soils (Ferretti et al., 2010). Litterfall measurements have been collected at 320 intensive monitoring plots (Level II) across Europe since 1985, following a standardized manual since 2002 and using standardized analytical methods to determine elemental concentrations (Ukonmaanaho et al., 2016). This long-term and large-scale data set represents consistent C and nutrient information for litterfall in Europe and as such will likely stimulate follow-up studies that enhance our understanding of forest litterfall and its spatio-temporal importance in the C cycle (Grace, 2004).

The key objectives were as follows:

1. to quantify annual C and nutrient fluxes across Europe using consistent observations,
2. to evaluate and improve existing litterfall estimation models, and
3. to estimate the total litterfall contribution to C and nutrient cycling in European forests addressing regional- and species-specific differences, and temporal trends.

2. Materials and Methods

2.1. Litterfall Data

The litterfall observations were taken from the ongoing ICP Forests Level II network, a pan-European forest monitoring program covering the full geographical range of European forests (Ferretti et al., 2010). After eliminating plots with missing values, 320 plots with observations between 2002 and 2012 were used (Figure 1). ICP Forests Level II plots have a size of at least 0.25 ha with six or more litter traps. The minimum trap size is 0.18 m^2, and the opening is placed at 1 to 1.3 m above ground for collecting litterfall information every second to fourth week. The collected litter is sorted and dried at a maximum temperature of 80 °C to avoid loss of volatile fractions prior to the elemental analysis. After applying the moisture correction using a subsample dried at 105 °C to account for residual water, dry litterfall amounts in $g \cdot m^{-2}$ are reported to the ICP Forests database (Ukonmaanaho et al., 2016).

2.2. Litterfall Models

Litterfall models have been developed to generalize litterfall data spatially (from point to landscape scale) and temporally (across different years). Such models can be distinguished into (1) statistical regression models requiring climate information (Liu et al., 2004) and (2) models using the biomass abundance approach (He et al., 2012; Malhi et al., 2011). Here we outline differences in the conceptual approaches for estimating foliar litterfall. For further details we refer readers to the supporting information.

We obtained four different litterfall regression models from the Eurasian study of Liu et al. (2004) that use temperature and precipitation as predictors (equations (1a)–(4)),

$$\text{broadleaves}: \quad \text{foliar LF} = \exp(3.235 + 0.563 \times \log(T + 10) + 0.125 \times \log(P)) \tag{1a}$$

$$\text{conifers}: \quad \text{foliar LF} = \exp(2.131 + 0.399 \times \log(T + 10) + 0.316 \times \log(P)) \tag{1b}$$

$$\text{broadleaves}: \quad \text{foliar LF} = \exp(3.732 + 0.687 \times \log(T + 10)) \tag{2a}$$

$$\text{conifers}: \quad \text{foliar LF} = \exp(3.472 + 0.683 \times \log(T + 10)) \tag{2b}$$

$$\text{all}: \quad \text{foliar LF} = \exp(2.241 + 0.650 \times \log(T + 10) + 0.211 \times \log(P)) \tag{3}$$

$$\text{all}: \quad \text{foliar LF} = \exp(3.102 + 0.853 \times \log(T + 10)) \tag{4}$$

where foliar LF is the dry foliar litterfall rate ($g \cdot m^{-2} \cdot year^{-1}$), T (°C) is the average annual temperature, and P (mm) is the total annual precipitation (Liu et al., 2004).

The biomass abundance approach estimates litterfall using data on tree biomass that can be shed (e.g., leaves and needles) and is a process-oriented approach, commonly used within biogeochemical modeling (Pietsch & Hasenauer, 2006; White et al., 2000). Foliar biomass or leaf area are important measures for biomass abundance (He et al., 2012) and can be obtained either "top-down" from satellite data or "bottom-up" using allometric biomass functions. Satellite data provide continuous LAI information according to the biome type (Friedl et al., 2010; Yang et al., 2006). We compiled two top-down models using specific leaf area (SLA) and annual foliar turnover rates from the standard BIOME-BGC parameterization (White et al., 2000) and local central European parameters (Pietsch et al., 2005). Seven forestry relevant land cover types were selected (for details see Table S1). Examples of the two top-down models predicting foliar C flux ($g\ C \cdot m^{-2} \cdot year^{-1}$)
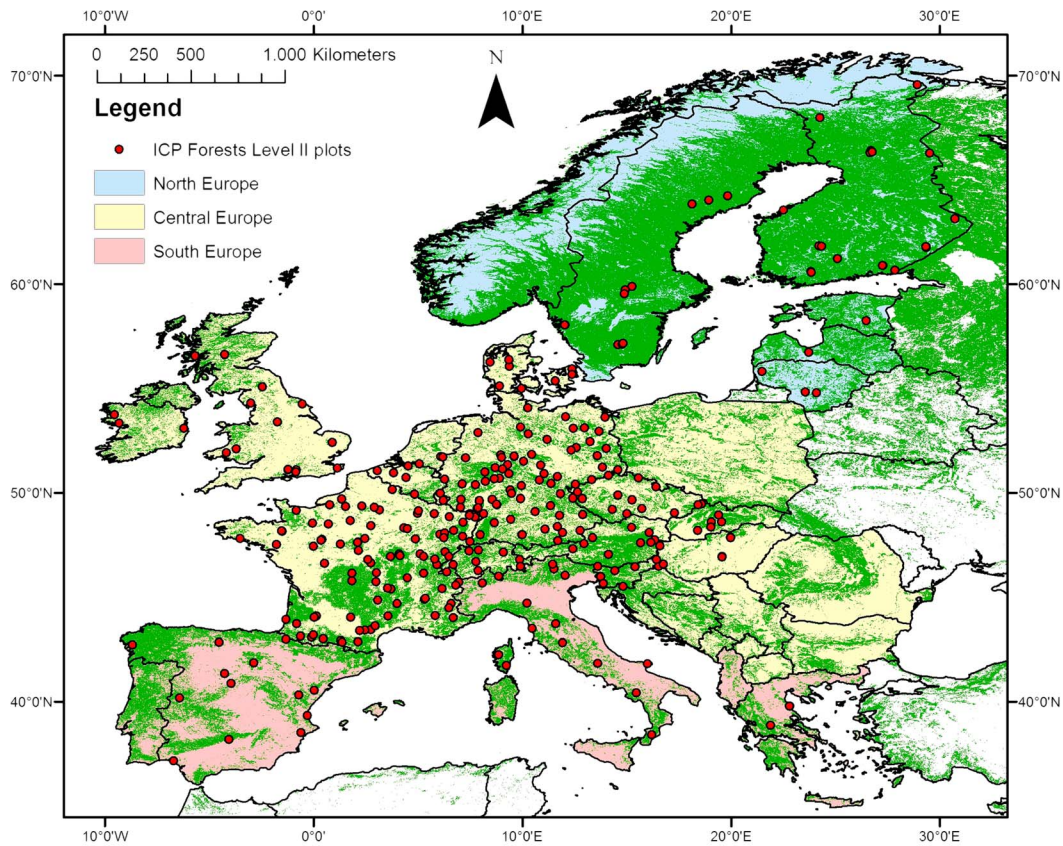
Figure 1. Locations of the 320 ICP Forests Level II plots with litterfall observations from 2002 to 2012 http://icp-forests.net/page/level-ii across the three bioregions. Forest areas represent land cover types 1–5 (closed forests) and 8 and 9 (woodlands) of MODIS Land Cover MCD12Q1 (Friedl et al., 2010).

in evergreen coniferous forests are given below. Equation (5) is the model that uses standard parameters, while equation (6) uses central European parameters,

$$\text{foliar LF carbon} = \text{LAI}/8.2 \times 0.260 \qquad + 6 \text{ models} \qquad (5)$$

$$\text{foliar LF carbon} = \text{LAI}/10.2 \times 0.195 \qquad + 6 \text{ models} \qquad (6)$$

where 8.2 and 10.2 are the SLAs in $m^2 \cdot kg^{-1}$ C (LAI divided by SLA is equal to foliar C) and 0.260 and 0.195 are the annual turnover rates (TO; $year^{-1}$; Pietsch et al., 2005; White et al., 2000). SLA and TO for other land cover types are provided in Table S1.

We also compiled bottom-up biomass abundance using tree diameter measurements and biomass functions for three forest types (*Pinus* sp., other conifers and broadleaves) from Neumann, Moreno, Mues, et al. (2016). In equation (7) we show an example for the bottom-up litterfall model for *Pinus* sp.,

$$\text{foliar LF} = \text{Fol.Biomass} \times 0.383 \qquad + 2 \text{ models} \qquad (7)$$

where foliar LF is the foliar litterfall rate ($g \cdot m^{-2} \cdot year^{-1}$), Fol. Biomass is tree foliage biomass ($g \cdot m^{-2}$), and 0.383 is the TO ($year^{-1}$) for *Pinus* sp. (all coefficients and biomass functions provided in Table S2).

The final model (equation (8)) uses net primary production (NPP) as a measure for biomass abundance to estimate litterfall. Climate and LAI influence NPP, the amount of biomass produced by photosynthesis. Thus litterfall correlates well with NPP (Malhi et al., 2011) and is considered as a constant fraction of NPP independent of tree species,

$$\text{foliar LF carbon} = \text{NPP} \times 0.34 \qquad (8)$$

where NPP is net primary production ($g \, C \cdot m^{-2} \cdot year^{-1}$) and 0.34 is the litterfall fraction suggested by Malhi et al. (2011).

AGU
100
ADVANCING EARTH
AND SPACE SCIENCE

Global Biogeochemical Cycles

10.1029/2017GB005825

Since the models based on LAI and NPP (equations (5), (6), and (8)) predict litterfall C, we divided the model output by the average carbon fraction (CF) of a specific plot (equation (9)) to get litterfall rate, which is comparable to the ICP Forests Level II observations and other model outputs (equations (1a)–(4) and (7)). When no elemental plot-level information was available, we used average region-specific CF (Table 2). We calculated root-mean-square error, mean absolute error, mean bias error, and coefficient of determination (R^2) to evaluate the models as described in Willmott and Matsuura (2006).

We also tested new multiple linear regression models to identify drivers for litterfall and examined the potential for improving existing litterfall models. The selection of the predictor variables or covariates was based on an information criterion framework controlling for autocorrelation (Akaike, 1974; K. Burnham & Anderson, 2004). The tested covariates were temperature, precipitation, LAI (each of current year and year before), elevation, stand density index (Reineke, 1933), and the quadratic mean diameter of forest plots. Stand density index was used to account for intertree competition, and the quadratic mean diameter was used as a continuous surrogate for tree age effects on litterfall (stand age is only available in classes/categories).

2.3. Forest Structural Data

Every five years for each tree within the plot with a diameter at breast height >5 cm (measured 1.3 m above the ground) the species and the diameter at breast height were recorded (Dobbertin & Neumann, 2016). Tree height was recorded on a subsample of trees within the plot. These data were used to compute forest characteristics, for example, basal area, stand age, quadratic mean diameter, stem number, and stand density index (Reineke, 1933).

Live foliage biomass stocks needed for equation (7) were derived from European allometric biomass functions (Burger, 1942, 1949; Diéguez-Aranda et al., 2009; Lexer & Hönninger, 2001) compiled in Neumann, Moreno, Mues, et al. (2016) and described in Table S2. Previous research has reported significant differences by species in litterfall (Liu et al., 2004) and CF (Lamlom & Savidge, 2003), and thus, the plots were assigned a forest type (conifers or broadleaves) based on basal area. The most common coniferous species were Norway spruce (*Picea abies* [L.] H. Karst), Scots pine (*Pinus sylvestris* L.), and silver fir (*Abies alba* Mill.), while the most common broadleaved species were European beech (*Fagus sylvatica* L.), sessile oak (*Quercus petraea* [Matt.] Liebl.), and pedunculate oak (*Q. robur* L.), all of which were deciduous. Only four plots were dominated by evergreen broadleaf species (three plots with *Q. ilex* L., one plot with *Q. suber* L.), and we decided against separating the broadleaf species into evergreen and deciduous.

2.4. Additional Data and Analysis

The eight litterfall models (equations (1a)–(8)) require average annual temperature and annual precipitation sum, land cover, LAI, and NPP as input information. Average annual temperature and annual precipitation sum were obtained from European daily climate data available at a 1 by 1 km resolution (Moreno & Hasenauer, 2016), after evaluation against global climate data (Hijmans et al., 2005). The Moderate Resolution Imaging Spectroradiometer (MODIS) satellite-based land cover product, MOD12Q1 Version 4 Type 2, provided land cover information at the same spatial resolution (Friedl et al., 2010), and gridded LAI information for eight-day periods came from MODIS LAI Collection 5 (Yang et al., 2006). For our analysis we retrieved the highest LAI for each pixel for 2002 to 2012 (in total 11 European LAI maps).

We obtained an NPP data set resulting from a combination of the MOD17 algorithm and European high-resolution daily climate data validated with forest inventory information (Moreno & Hasenauer, 2016; Neumann, Moreno, Thurnher, et al., 2016). All data sources were available at a 1 by 1 km resolution and for the years 2002 to 2012 (30 arc sec or 0.0083° at the equator). Summary statistics are given in Table 1. All statistical analysis and visualizations were produced using the R language and environment (R Development Core Team, 2016).

The recorded litterfall data span different time periods (Table 1). We aggregated the data by year and combined values from individual compartments—(1) foliage, (2) branches with diameter <2 cm, and (3)

Table 1

Summary Statistics (Mean, Minimum, and Maximum in Parenthesis) for All Plots With Litterfall Observations

Variable	All	Broadleaves	Conifers
Plots (*n*)	320	150	170
Reported litterfall values (*n*)	43686	19313	23855
Litterfall amount ($g \cdot m^{-2}$)	22.0 (0.0–1292.0)	24.0 (0.0–1102.0)	19.4 (0.0–1292.0)
Elevation (m)	496 (2–1970)	414 (18–1659)	564 (2–1970)
Average temperature (℃)	9.4 (−1.2–19.4)	10.3 (−0.4–17.3)	8.8 (−1.2–19.4)
Precipitation sum (mm)	806 (250–2122)	789 (253–2122)	820 (250–2193)
LAI ($m^2 \cdot m^{-2}$)	5.4 (1.0–6.9)	5.9 (1.4–6.9)	5.1 (1.0–6.9)
NPP ($g \cdot C \cdot m^{-2} \cdot year^{-1}$)	660 (166–1271)	671 (346–1025)	652 (166–1271)
Basal area ($m^2 \cdot ha^{-1}$)	32.8 (3.1–134.6)	29.4 (7.0–56.1)	35.7 (3.1–134.6)
Age (year-year)	60–80 (0–20–>140)	80–100 (20–40–>140)	60–80 (0–20–>140)
Mean diameter (cm)	32.1 (6.7–57.7)	32.1 (13.7–57.7)	32.1 (6.7–48.9)
Foliage biomass ($kg \cdot ha^{-1}$)	5204 (599–17433)	2973 (927–8350)	7155 (599–17433)
Stem number (ha^{-1})	485 (85–2904)	472 (85–1948)	497 (96–2904)
Stand density index (−)	609 (97–2773)	552 (137–1006)	660 (97–2773)

Note. Temperature and precipitation from Moreno and Hasenauer (2016), leaf area index (LAI) after Yang et al. (2006), and net primary production (NPP) from Neumann, Moreno, Thurnher, et al. (2016).

other biomass—to get the total annual litterfall. This was multiplied by the C concentration in litter biomass, the CF to get the litterfall C flux (equation (9)).

$$\text{LF carbon} = (\text{foliar LF} + \text{branch LF} + \text{other LF}) \times \text{CF} \qquad (9)$$

We calculated a weighted CF for all plots with elemental information (195 plots with a total of 862 annual observations) by multiplying the CF for each compartment (foliar, branch, and other) by the mass of the pool. Similarly, we calculated the fraction of the main nutrients—(1) nitrogen, (2) phosphorus, and (3) potassium. A classification of litterfall beyond the three compartments (equation (9)) was not feasible due to inconsistencies and changes in the litterfall data collection. Further details of the calculation procedure are given in the supporting information.

The number of plots with litterfall data and forest cover differed across Europe (Figure 1). Furthermore, bioclimatic differences across Europe may influence litterfall. Thus, we split the data in three bioregions: (1) northern Europe (mainly boreal forests), (2) central Europe (temperate-Atlantic forests), and (3) southern Europe (Mediterranean forests). We quantified interannual variability by calculating standard deviation for regions and by forest types and by computing the average standard deviation of all 320 plots (i.e., mean of the plots annual variation).

Table 2

Observed Annual Litterfall Rates ($g \cdot m^{-2} \cdot year^{-1}$, Compartments and Total Sum), Elemental Percentages (Carbon, Nitrogen, Phosphorus, and Potassium), and Number of Observations for Europe and by Bioregion and Forest Type Showing Mean ± Standard Deviation

Variable	Europe All	North Conifers	North Broadleaves	Central Conifers	Central Broadleaves	South Conifers	South Broadleaves
n (litterfall)	1604	118	6	678	647	80	75
Foliar litterfall	260 ± 119	177 ± 93	192 ± 74	234 ± 121	296 ± 108	268 ± 116	294 ± 107
Branch litterfall	70 ± 55	-	-	59 ± 46	87 ± 60	50 ± 46	69 ± 59
Other litterfall	105 ± 95	-	-	81 ± 66	132 ± 113	140 ± 96	76 ± 66
Total litterfall	433 ± 213	322 ± 201	276 ± 127	373 ± 176	514 ± 227	465 ± 202	434 ± 160
n (elemental)	862	99	37	299	281	75	71
C fraction	51.7 ± 2.0	52.9 ± 1.9	54.2 ± 0.9	51.9 ± 1.6	50.4 ± 1.6	53.0 ± 1.8	51.3 ± 1.5
N fraction	1.037 ± 0.323	0.810 ± 0.203	0.988 ± 0.189	0.985 ± 0.240	1.230 ± 0.330	0.716 ± 0.228	1.121 ± 0.251
P fraction	0.073 ± 0.038	0.078 ± 0.027	0.158 ± 0.054	0.070 ± 0.024	0.084 ± 0.038	0.051 ± 0.023	0.076 ± 0.035
K fraction	0.242 ± 0.154	0.168 ± 0.057	0.318 ± 0.101	0.196 ± 0.064	0.429 ± 0.138	0.202 ± 0.066	0.336 ± 0.121

Note. In north Europe we could not separate branch and other litterfall, since these compartments are often aggregated. The numbers of elemental observations differ from those for litterfall, since not all plots provided elemental data and we calculated elemental fractions separately for conifers and broadleaves.
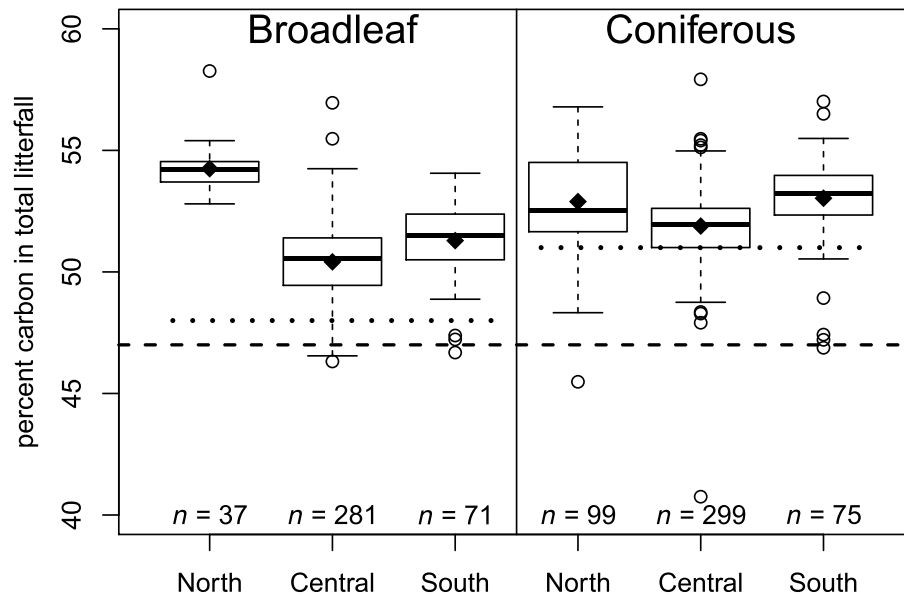
Figure 2. Observed carbon fractions in total litterfall by forest type and bioregion compared with literature values. The dashed horizontal line represents the default IPCC carbon fraction of 47% (IPCC, 2006; McGroddy et al., 2004), and the dotted lines represent the values 48% and 51% for broadleaf and coniferous species, respectively (IPCC, 2006; Lamlom & Savidge, 2003). Results from this study are shown as box and whisker plots. The box represents the median and the 25th and 75th percentiles, the diamond represents the arithmetic mean, the whiskers extend to 1.5 of the interquartile range, and the values outside this range are indicated by circles. The number of observations ($n = \ldots$) varies since elemental information is available only for some plots (in total 862 annual observations).

3. Results

3.1. Observed European Litterfall, Carbon, and Nutrient Fluxes

We used data from 320 plots with 1,604 consistent observations of annual litterfall rate and 862 observations of elemental composition for the years 2002 to 2012; thus, each plot had on average litterfall observations for about 5 years (Table 2). The mean and standard deviation of total litterfall was $433 \pm 213 \, \mathrm{g \cdot m^{-2} \cdot year^{-1}}$ and for foliar litterfall $260 \pm 119 \, \mathrm{g \cdot m^{-2} \cdot year^{-1}}$. Average interannual variability was $121 \, \mathrm{g \cdot m^{-2} \cdot year^{-1}}$ for total and $64 \, \mathrm{g \cdot m^{-2} \cdot year^{-1}}$ for foliar litterfall. We compared the observed CF with values from the literature (Intergovernmental Panel on Climate Change (IPCC), 2006; Lamlom & Savidge, 2003) by species and region (Figure 2). The default CF literature value for temperate and boreal forest biomass was 47%, and the CF values were 48% and 51% for broadleaf and coniferous forests (IPCC, 2006; Lamlom & Savidge, 2003). Table 2 provides a summary of the litterfall, C, and nutrient results obtained from the observations of the 320 plots (195 plots also had elemental information; Data Set S1 contains the used data). The CF of the three litterfall compartments is given in Table S6.

3.2. Evaluation of Existing Litterfall Models

We compared predicted versus observed litterfall information and evaluated the performance of the eight models (Table 3). Results for the most accurate total litterfall model based on (1) climate, (2) top-down LAI, (3) bottom-up biomass, and (4) NPP are shown in Figures 3 and 4. Results for foliar litterfall are shown in Table S7 and Figures S3–S5. The performance of foliar litterfall models was better than models predicting total litterfall, in particular for the bottom-up biomass models (Tables 3 and S7).

3.3. Development of New Litterfall Models

With multiple linear regression analysis we explored the drivers of litterfall and whether we could improve existing models. The models were fitted for total and foliage litterfall separately as well as by bioregion and forest type. We show the results for total litterfall

Table 3
Error Analysis of Models for Estimating Total Litterfall Rate ($g \cdot m^{-2} \cdot year^{-1}$)

Eq. #	Model	RMSE	MAE	MBE	R^2
1	Liu T + P spec.	214.6	149.8	+65.3	0.081
2	Liu T spec.	208.7	145.0	+46.8	0.089
3	Liu T + P	218.3	152.7	+59.9	0.030
4	Liu T	212.4	149.4	+37.0	0.040
5	White LAI	246.2	196.7	−95.6	0.033
6	Pietsch LAI	223.3	159.1	+55.5	0.040
7	Fol. Biomass	237.4	169.9	+50.0	0.090
8	Malhi NPP	224.5	166.1	+3.0	0.010

Note. The models are described in the text under equations (1a)–(8). Evaluation parameters are as follows: root-mean-square error (RMSE), mean absolute error (MAE), mean bias error (MBE), and coefficient of determination (R^2; Willmott & Matsuura, 2006).
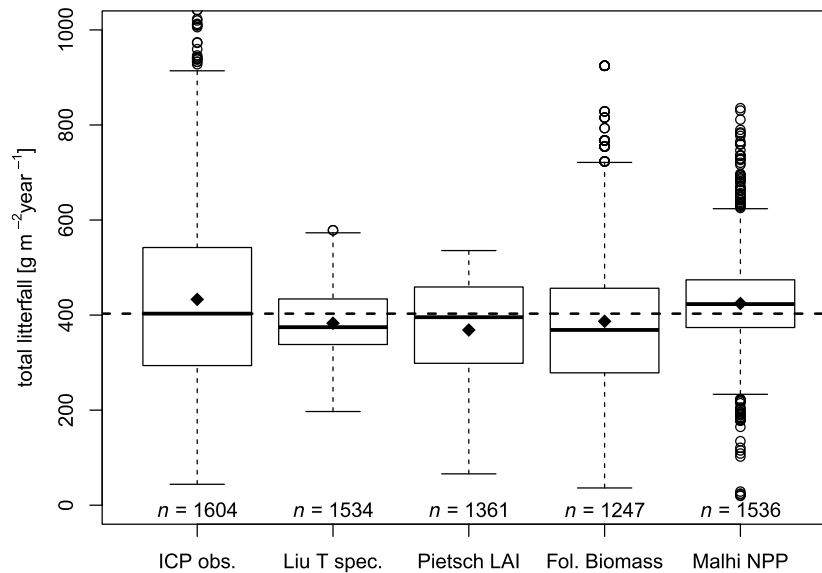
Figure 3. Europe-wide comparison of observed total litterfall rates with outputs from selected models. From left to right we show the observations on the ICP Forests Level II plots "ICP obs." (the dashed line extends the observed median), output of the species-specific model using temperature "Liu T spec.," estimates based on leaf area index and central European parameters "Pietsch LAI," estimates using foliage biomass "Fol. Biomass," and finally assuming that litterfall is a constant fraction of net primary production ("Malhi NPP"). The number of observations varies since some input information was missing for certain locations. For description of box and whiskers plots see Figure 2.

here and provide all other results in Tables S4 and S5. The best model for total litterfall based on an information criterion framework is given in equation (10).

$$LF = 83.330 + \mathbf{0.146}\ SDI - 0.786\ LAI + 26.465\ LAI\_lag + \mathbf{17.762}\ T - 0.047\ P\_lag \qquad R^2 = 0.123 \qquad (10)$$

LF is the annual total litterfall ($g \cdot m^{-2} \cdot year^{-1}$), SDI is the stand density index (Reineke, 1933), LAI is the leaf area index ($m^2 \cdot m^{-2}$), LAI_lag is the LAI of the previous year, T is the current mean annual temperature (°C), and P_lag is the precipitation sum (mm) of the previous year. The bold font indicates significance at $p < 0.001$, and we provide the coefficient of determination R^2 to assess the model performance. Since information of a previous year is often difficult to obtain, we simplified the model from equation (10) using only input information from the current year (equation (11)),

$$LF = 109.532 + \mathbf{0.153}\ SDI + \mathbf{19.922}\ LAI + \mathbf{18.296}\ T - 0.054\ P \qquad R^2 = 0.113 \qquad (11)$$

where P is the precipitation sum of the current year, and all other parameters are as previously defined. Models were also tested by fitting previous conditions and periodic means, but using information from the current year showed the best performance. Note that the R^2 was similar to that for equation (10) and SDI, a measure of forest management impacts, was again highly significant.

SDI requires information on forest structure that can be derived from forest inventory plots. Such information may be missing for large-scale applications and so we also calibrated models ignoring potential stand density effects. We ran regressions using all available European data (equation (12)) and after splitting the data by bioregion (equations (13)–(15)) with the following results:

Europe :	$LF = \mathbf{217.001} + \mathbf{19.310}\ LAI + \mathbf{13.751}\ T - 0.030\ P$	$R^2 = 0.067$	(12)
North :	$LF = 104.674 + 24.411\ LAI + 30.244\ T - 0.012\ P$	$R^2 = 0.364$	(13)
Central :	$LF = \mathbf{374.018} + 13.373\ LAI + 6.223\ T - \mathbf{0.092}\ P$	$R^2 = 0.035$	(14)
South :	$LF = 125.562 + 19.888\ LAI + 12.160\ T + 0.115\ P$	$R^2 = 0.100$	(15)

3.4. Total Carbon and Nutrient Input by Litterfall Within European Forests

An important but difficult step within C modeling is the assessment of C input through litterfall for large forest areas. We calculated the total annual C litterfall flux for European forests (Tg C · year^{-1}) by applying
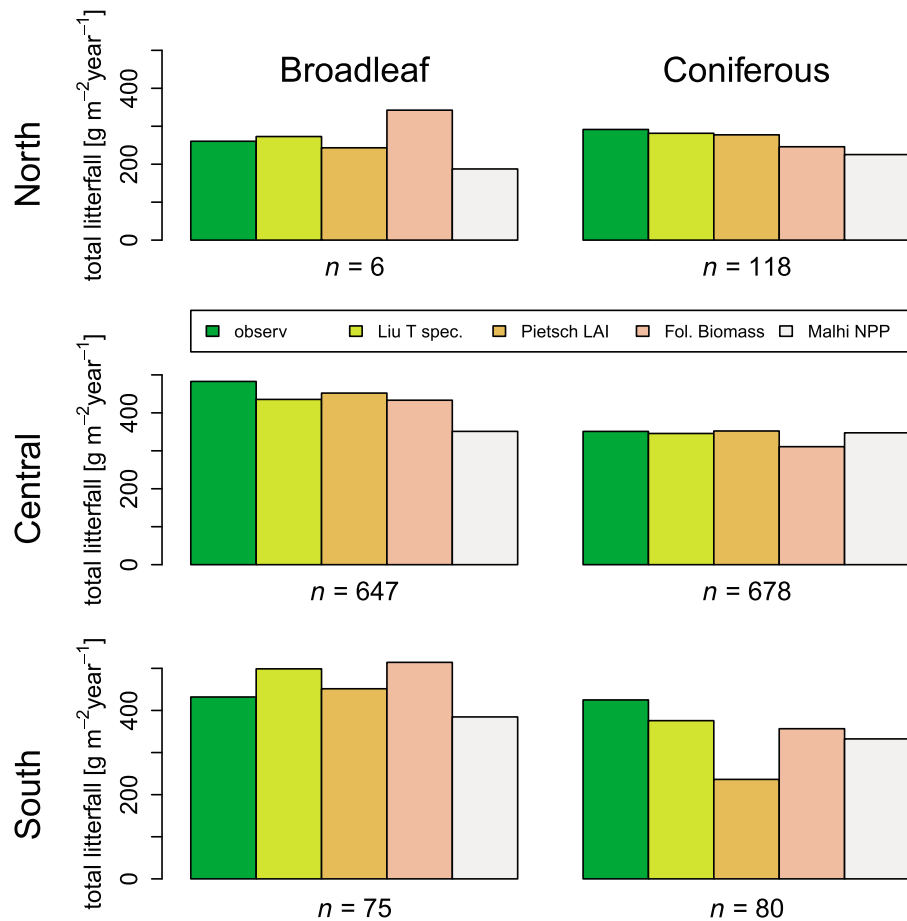
Figure 4. Comparison of median litterfall observations and output from selected models (see Figure 3 for details) grouped by forest types and bioregions. We show the median to accommodate the skewness in the results. At the bottom is the number of observations in each bioregion (n = …).

equation (12) on a 1 by 1 km raster. We chose equation (12), because it requires standard input data, and thus, the model can be applied to any forest pixel in Europe. We multiplied the predicted mean litterfall and its standard deviation of 4,293,495 pixels (masking nonforest pixels) by forest area and CF (Table 2). The propagated standard deviation provides a measure for uncertainty. We computed the C litterfall rate and its variation for Europe as a whole, and for northern Europe (Fennoscandia and Baltic states), central Europe (all countries except north and south), and southern Europe (Spain, Italy and Greece). The forest area came from official forest statistics (Forest Europe, 2015), the gridded LAI from MODIS LAI Collection 5 (Yang et al., 2006), and annual mean temperature and precipitation sum from Moreno and Hasenauer (2016). An example for 2010 is shown in Figure S15. Next we calculated total C in litterfall following a slightly different procedure by multiplying forest area by the observed mean C litterfall from the plots (n = 1604; Table 2). We also computed nutrient fluxes based on the observations using the same approach. Results are given in Tg · year^{-1} for Europe and separately for north Europe, central Europe, and south Europe (Table 4).

The results in Table 4 allow for a comparison of litterfall input with current forest C stocks; a snapshot of forest conditions derived from forest inventory data (Moreno et al., 2017). Litterfall represents a substantial proportion of C uptake each year (Malhi et al., 2011), so we quantified C allocation to litterfall by comparing litterfall C with NPP, thus providing a temporal comparison of litterfall with consistent NPP information available since 2000 over all Europe on a 1 by 1 km resolution (Neumann, Moreno, Thurnher, et al., 2016). We grouped our data by bioregion and forest type (in total six groups) and calculated mean litterfall C and mean NPP for each group and each year between 2002 and 2012 (e.g., mean litterfall of broadleaves in southern Europe in year 2005 is 192 g C · m^{-2} · year^{-1}). Figure 5 provides NPP for all plots over 11 years to have a comparable consistent sample size. The number of litterfall observations varies each year (Figure S17). We also calculated the linear trend of litterfall C and NPP to examine regional change over time (Table 4).

Table 4
Modeled and Observed Carbon (C) and Nutrient Litterfall Fluxes in Europe and the Bioregions

	Forest area (1000 km^2)	Forest carbon (Tg C)	n pixels	Carbon litterfall, equation (12) (Tg C · year^{-1})	n observ.	Observed carbon and nutrient flux				Linear trend	
						(Tg C · year^{-1})	(Tg N · year^{-1})	(Tg P · year^{-1})	(Tg K · year^{-1})	NPP	LF
Europe	1818	12,275	4,293,495	351 ± 73	1,604	375	8.161	0.575	1.905	−5.0	+1.3
North	702	3,202	2,133,756	113 ± 19	124	120	1.956	0.204	0.406	−27.6	−7.3
Central	768	7,604	1,536,895	160 ± 21	1,325	174	3.764	0.248	0.876	−3.8	+2.3
South	348	1,469	622,844	79 ± 12	155	82	1.361	0.096	0.410	−18.0	−1.4

Note. We show forest area from Forest Europe (2015), total live forest C stocks (Moreno et al., 2017), number of forested pixels (Figure 1) used for applying equation (12), and the resulting total C flux in litterfall. Next, we provide the number of litterfall observations available in this study (Table 2) and the upscaled C and nutrient fluxes based only on observations. Finally, we show the results of the linear trend analysis for 2002 to 2012 for net primary production (NPP) and litterfall (LF), both in g C · m^{-2} · year^{-1}.

4. Discussion

Litterfall is an important, relatively constant annual C and nutrient input to the forest floor across Europe (Table 2 and Figure 5). Although the litter CF of conifers is larger than that of broadleaves (52.3% versus 50.9%; Figure 2), the C flux in broadleaf forests (255 g C · m^{-2} · year^{-1}) remains larger than in coniferous
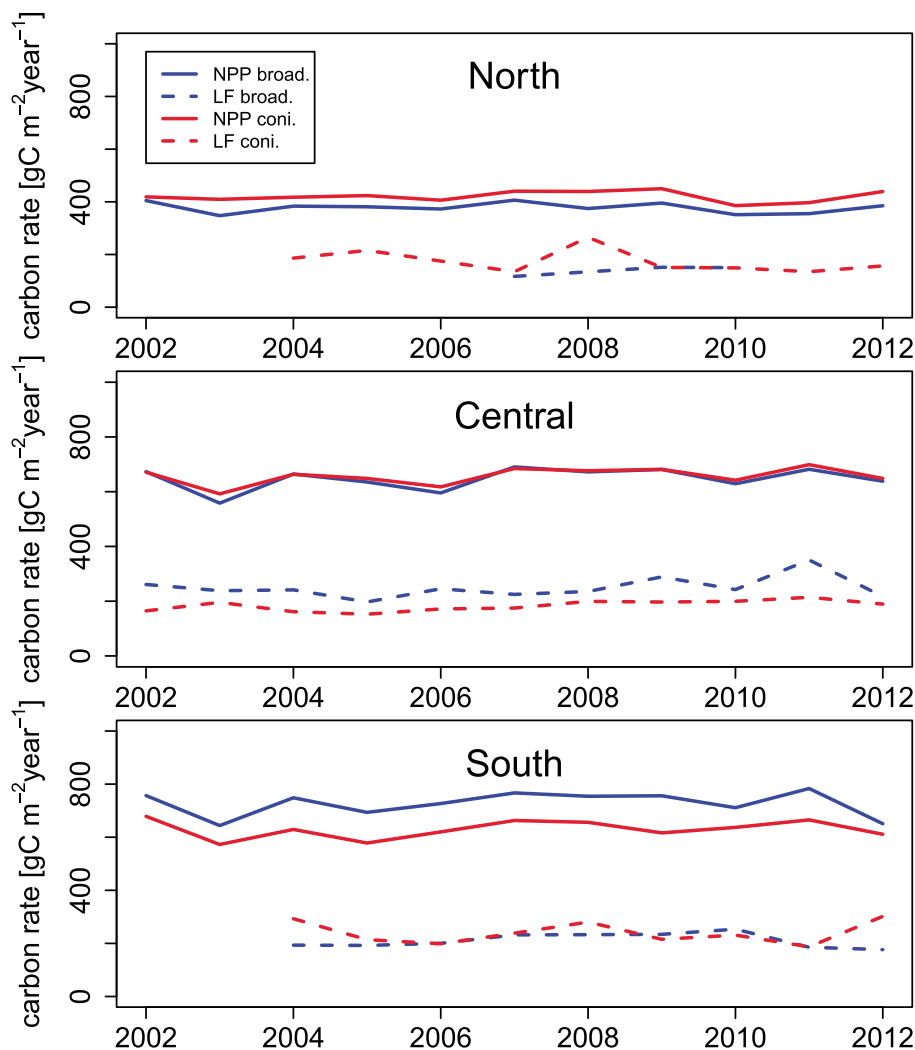

Figure 5. Median observed carbon litterfall rates (LF, dashed lines) and net primary production (NPP, solid lines) from 2002 to 2012 annually in the three regions and for broadleaf (blue) and coniferous forest types (red). We use median litterfall and NPP to accommodate the skewness.

forests (191 g C · m^{-2} · year^{-1}) due to their higher annual litterfall amount (Table 2). This confirms previous findings by Liu et al. (2004). Higher litterfall rates in southern European forests (Table 2) compensate for their lower forest cover (19% of European forest area, 12% of European C stocks) contributing 23% (79 Tg C · year^{-1}) to total C input to soil from litterfall in Europe (351 Tg C · year^{-1}; Table 4). Central Europe contributes 46% or 160 Tg C · year^{-1} and north Europe 32% or 113 Tg C · year^{-1}. These estimates are based on observations (equation (12)) and gridded pan-European data at a 1 by 1 km resolution.

Broadleaves have a lower CF and higher fraction of nutrients than conifers except in north Europe (Figures 2 and S7–S9). This could be due to the higher lignin content of conifers needles, as CF correlates with lignin content (Lamlom & Savidge, 2003). ICP Forests determines the C content by drying the biomass to a maximum of 80 °C and corrects for the residual moisture (Ukonmaanaho et al., 2016). This approach retains volatile components and results in a higher C content versus drying with temperatures greater than 100 °C used for deriving CF in greenhouse gas reporting (Lamlom & Savidge, 2003). Based on our results, we can support the use of forest type-specific CF suggested by IPCC (2006), since CF differs significantly between conifers and broadleaves across Europe ($p < 0.001$) and the forest type-specific values better agree with observed CF values (Figure 2). The default IPCC CF of 47% (IPCC, 2006; McGroddy et al., 2004) provides conservative estimates, which are about 9% lower than estimates based on observed litterfall CF (Table S6).

Although the compiled data set is from plots across Europe, most plots are located at low elevations and in central-western Europe (Figure 1). Furthermore, the site conditions of broadleaves and conifers differ and European broadleaf forests more frequent occur at lower elevations with warmer and drier conditions (Table 1). Thus, estimation models were applied to address this variation and to extrapolate the collected litterfall information to areas with few or no observations. Models based on climate or on biomass abundance estimate litterfall rates with a bias from 1 to 10%, R^2 values were low ranging from 0.03 to 0.09, and models for foliar litterfall perform slightly better than for total litterfall (Tables 3 and S7). Better performance of foliar litterfall models may be due to higher variability of nonfoliar litterfall. The evaluated models can predict average litterfall with low biases but fail in capturing fine-scale variation. Our results also confirm that climate is a key driver for litterfall (Berg & Meentemeyer, 2001; Liu et al., 2004). Based on our results, temperature appears more strongly correlated with litterfall across Europe than precipitation, since models using only temperature perform better than models which also use precipitation (Table 3). In addition, fitting new models revealed insignificant effect of precipitation (equations (10)–(15)). We provide empirical evidence for the importance of biomass abundance on litterfall and the associated litterfall estimations. Both top-down LAI with European coefficients ("Pietsch LAI") or bottom-up foliage biomass ("Fol. biomass") provide estimates with an error comparable to estimates based on climate (Table 3) and reproduce observed latitudinal gradients in central and north Europe (Figure 4). We note that we used broad biomass functions that might not represent species- and country-specific conditions sufficiently (Table S2) and the performance of estimates based on biomass abundance is better for foliar litterfall (Figures S3–S5 and Table S7).

Consequently, there are prospects to advance litterfall estimates, despite previous research which indicated difficulties in predicting litterfall at finer spatial resolutions (Bray & Gorham, 1964; Liu et al., 2004). Comparing foliar biomass with foliar litterfall by species (Figure S18) suggests that species-specific parameters instead of the averaged European parameters and/or biomass functions (Tables S1 and S2) may help to express the observed local variation (Figure 4). SLA and TO, the parameters to convert biomass abundance into litterfall, were assumed constant in our study, while climate-dependent parameters might better capture natural conditions (Laanaia et al., 2016; Vaz et al., 2011). Our results indicate that recalibrating models for species and/or regions using climate, LAI, and stand density, in particular for foliar litterfall, can enhance the model performance with R^2 values of more than 0.5 (equation (13)–(15) and Tables S4 and S5). Stand density index, a site- and age-independent tree competition measure (Hasenauer et al., 1994; Reineke, 1933), strongly depends on forest management and disturbances, both of which have shaped European forests (Forest Europe, 2015). Stand density is positively related to litterfall rates as greater competition for light results in higher foliar and branch mortality (Hennessey et al., 1992). Including stand density in our litterfall models (equations (10)–(12)) improved the R^2 values from 0.067 to 0.123. Thus, accounting for stand density may also improve litterfall rate estimates in other regions affected by forest management. The mean age of trees in a forest (using average diameter as a proxy)—another indicator for management—did not influence total or foliar litterfall (Tables S4 and S5). This seems to contradict studies that identified stand age as driving

litterfall (Chen et al., 2002; Huang et al., 2017). Another interpretation could be that the underlying driver was actually stand density, which is often correlated with stand age.

In this study we examined temporal litterfall patterns from 2002 to 2012 across Europe for the first time (Figure 5). No litterfall anomalies related to drought years or increased natural disturbance activity within the period were observed (Senf & Seidl, 2017; Spinoni et al., 2015). The litterfall represents a substantial and rather constant proportion (33.9%) of NPP (Tables 1 and 2). The C in litterfall is mostly released to the atmosphere after decay, which makes the litter pool important for understanding greenhouse gas emissions from the forest floor (Leitner et al., 2016). It appears that litterfall rates have increased since 2002 at an annual rate of 1.3 $g \cdot C \cdot m^{-2} \cdot year^{-1}$ and NPP decreased by 5.0 $g \, C \, m^{-2} \cdot year^{-1}$, although trends were not statistically significant (Table 4). A similar study in tropical forests indicated that litterfall accounts for 34% of NPP (Malhi et al., 2011), suggesting that C allocation patterns are similar within forests even across climatic zones; however, regional differences may exist. In central Europe litterfall accounts for 32.2% of NPP (a litterfall trend of +2.3 $g \, C \cdot m^{-2} \cdot year^{-1}$ and an NPP trend of −3.8 $g \, C \cdot m^{-2} \cdot year^{-1}$). In northern and southern Europe the contribution of litterfall is slightly larger and we observed a decreasing trend in litterfall (north 36.3% of NPP, −7.3 $g \, C \cdot m^{-2} \cdot year^{-1}$, south 33.5% and −1.4 $g \, C \cdot m^{-2} \cdot year^{-1}$; Table 4 and Figure 5), although trends were not statistically significant.

Continued monitoring of litterfall will help to validate and explain these patterns. The large annual variation, in particular for tree species with masting behavior such as *Fagus sylvatica* (Nussbaumer et al., 2016), and only 11 years of observations may have obscured or over emphasized actual patterns (Table 2 and Figure S16). Potential drivers may include aging of forests, changing stand density (equations (10)–(12)), increasing forest growth (Pretzsch et al., 2014), more frequent disturbances and pathogen attacks (Seidl et al., 2014), or elevated CO_2 concentration and nitrogen deposition (Norby et al., 2010). So far there are no indications that increasing temperature, precipitation, or LAI (cf. Liu et al., 2004) have led to higher litterfall rates (Figure S6). Apart from the continuation of ongoing monitoring our knowledge of litterfall could be improved by increasing sampling in currently poorly covered regions (Figure 1), keeping the sampling and analytical designs consistent (Ukonmaanaho et al., 2016) and collecting consistent data on soil and litter pools (De Vos et al., 2015).

The importance of litterfall inputs for C dynamics and estimating greenhouse gas emissions from soil pools is widely recognized. Combining litter input with decomposition models (Liski et al., 2005; Zhang et al., 2008) or forest floor and soil C stocks (Hansen et al., 2009) could further enhance our understanding of C inputs, C stocks in the forest floor, and the effect of tree species. This may help to disentangle effects of species, site conditions, and feedback between species and site fertility, for instance, due to promoting establishment of conifers on poor sites through historic forest management practices in Europe (Augusto et al., 2015; Vose & Lee Allen, 1991). The transformation of forests from conifer to broadleaf species due to climate change or forest management (Kelly & Goulden, 2008) may result in higher inputs of litter with a lower residence time due to faster decay rates and thus more rapid nutrient cycling (Zhang et al., 2008). Anticipated increase of broadleaves in European forests (Hanewinkel et al., 2012) may in turn enhance forest growth due to improved nutrient supply by faster mobilization of litter layers. However, this requires empirical data on litter stocks and considering the inherent differences between tree species such as wood density and growth rates (Hansen et al., 2009).

Greenhouse gas assessments would benefit from reliable litterfall information, since currently forest inventory systems (Tomppo et al., 2010) do not provide such data. While forest inventories provide robust large-scale information on tree biomass (about 37% of total forest C, Forest Europe, 2015), integrating litterfall measurements with soil C models may help to better quantify C dynamics. Forest inventories using local biomass functions often provide foliage biomass, which can be converted into litterfall C as shown in this study. In this study we provided two European estimates for C input from litterfall across the same forest area (Forest Europe, 2015): (1) based on average C flux from observations ($n = 1604$; 375 Tg $C \cdot year^{-1}$) and (2) by applying equation (12) on a 1 by 1 km resolution for entire Europe with climate and LAI information ($n = 4,293,495$; 351 Tg $C \cdot year^{-1}$). The annual C input from litterfall represents about 3% of the live forest C stocks of 12,275 Tg C (Table 4), and thus, within three decades, the total live forest C stock is transferred to the forest floor. Litterfall also transfers large amounts of nutrients to the soil (4.49 g N $\cdot m^{-2} \cdot year^{-1}$, 0.32 g P $\cdot m^{-2} \cdot year^{-1}$, and 1.05 g K $\cdot m^{-2} \cdot year^{-1}$; Table 2). The nutrient input of forest litterfall is thus

equivalent to applying about 80 kg of NPK fertilizer with 16% N, 4% P, and 8% K per hectare each year. Litterfall is thus both ecologically and economically important for nutrient recycling and site fertility. Consequently, it is not only essential for quantifying and understanding C dynamics but also for sustaining ecosystem functioning and ecosystem health.

Data accessibility

The original data used here (Version ALFDB.LII.2015.0) is accessible from the ICP Forests Programme Coordination Centre hosted by the Thünen Institute in Eberswalde (www.icp-forests.net) as specified in the ICP Forests Manual (2017) Part I. Processed results used in this study are provided as Data Set S1.

References

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*(6), 716–723. https://doi.org/10.1109/TAC.1974.1100705

Augusto, L., De Schrijver, A., Vesterdal, L., Smolander, A., Prescott, C., & Ranger, J. (2015). Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests. *Biological Reviews*, *90*(2), 444–466. https://doi.org/10.1111/brv.12119

Berg, B., & Meentemeyer, V. (2001). Litter fall in some European coniferous forests as dependent on climate: A synthesis. *Canadian Journal of Forest Research*, *31*(2), 292–301. https://doi.org/10.1139/x00-172

Bray, J. R., & Gorham, E. (1964). Litter production in forests of the world. *Advances in Ecological Research*, *2*, 101–157. https://doi.org/10.1016/S0065-2504(08)60331-1

Burger, H. (1942). Holz, Blattmenge und Zuwachs. V. Mitteilung. Fichten und Föhren verschiedener Herkunft auf verschiedenen Kulturorten. *Mitteilungen Der Schweizerischen Anstalt Für Forstliches Versuchswesen*, *22*, 10–62.

Burger, H. (1949). Holz, Blattmenge und Zuwachs. X. Mitteilung. Die Buche. *Mitteilungen Der Schweizerischen Anstalt Für Forstliches Versuchswesen*, *26*, 419–468.

Burnham, K., & Anderson, D. (2004). In K. P. Burnham & D. R. Anderson (Eds.), *Model selection and multimodel inference*. New York, NY: Springer. https://doi.org/10.1007/b97636

Chave, J., Navarrete, D., Almeida, S., Álvarez, E., Aragão, L. E. O. C., Bonal, D., et al. (2010). Regional and seasonal patterns of litterfall in tropical South America. *Biogeosciences*, *7*(1), 43–55. https://doi.org/10.5194/bg-7-43-2010

Chen, W., Chen, J. M., Price, D. T., & Cihlar, J. (2002). Effects of stand age on net primary productivity of boreal black spruce forests in Ontario, Canada. *Canadian Journal of Forest Research*, *32*(5), 833–842. https://doi.org/10.1139/x01-165

Cornelissen, J. H. C., Van Bodegom, P. M., Aerts, R., Callaghan, T. V., Van Logtestijn, R. S. P., Alatalo, J., et al. (2007). Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecology Letters*, *10*(7), 619–627. https://doi.org/10.1111/j.1461-0248.2007.01051.x

Couteaux, M. M., Bottner, P., & Berg, B. (1995). Litter decomposition, climate and litter quality. *Trends in Ecology & Evolution*, *10*(2), 63–66. https://doi.org/10.1016/S0169-5347(00)88978-8

De Vos, B., Cools, N., Ilvesniemi, H., Vesterdal, L., Vanguelova, E., & Carnicelli, S. (2015). Benchmark values for forest soil carbon stocks in Europe: Results from a large scale forest soil survey. *Geoderma*, *251–252*, 33–46. https://doi.org/10.1016/j.geoderma.2015.03.008

Diéguez-Aranda, U., Rojo Alboreca, A., Castedo-Dorado, F., Álvarez González, J., Barrio-Anta, M., Crecente-Campo, F., et al. (2009). *Herramientas selvícolas para la gestión forestal sostenible en Galicia*. Xunta de Galicia: Dirección Xeral de Montes, Consellería do Medio Rural. Retrieved from http://www.usc.es/uxfs/IMG/Herramientas_selvicolas_para_la_gestion_forestal_sostenible_en_galicia.pdf

Dobbertin, M., & Neumann, M. (2016). Part V: Tree growth. In *UNECE ICP Forests, Programme Coordinating Centre (ed.): Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests* (p. 28). Eberswalde, Germany: Thünen Institute of Forest Ecosystems. http://icp-forests.net/page/icp-forests-manual

Domke, G. M., Perry, C. H., Walters, B. F., Woodall, C. W., Russell, M. B., & Smith, J. E. (2016). Estimating litter carbon stocks on forest land in the United States. *Science of the Total Environment*, *557–558*, 469–478. https://doi.org/10.1016/j.scitotenv.2016.03.090

Ferretti, M., Fischer, R., Mues, V., Granke, O., & Lorenz, M. (2010). Basic design principles for the ICP Forests Monitoring Networks. Manual Part II. In *Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests* (p. 22). Hamburg, Germany, http://icp-forests.net/page/icp-forests-manual: UNECE ICP Forests Programme Co-ordinating Centre. https://doi.org/10.1007/s13157-010-0025-y

Forest Europe (2015). State of Europe's Forests 2015. Ministerial Conference on the Protection of Forests in Europe FOREST EUROPE Liaison Unit Madrid, Spain. Retrieved from http://foresteurope.org/state-europes-forests-2015-report/

Friedl, M., Sulla-Menashe, D., Tan, B., Schneider, A., Ramankutty, N., Sibley, A., & Huang, X. (2010). MODIS Collection 5 global land cover: Algorithm refinements and characterization of new datasets. *Remote Sensing of Environment*, *114*(1), 168–182. https://doi.org/10.1016/j.rse.2009.08.016

Ganade, G., & Brown, V. K. (2002). Succession in old pastures of central Amazonia: Role of soil fertility and plant litter. *Ecology*, *83*(3), 743–754. https://doi.org/10.1890/0012-9658(2002)083%5B0743:SIOPOC%5D2.0.CO;2

Grace, J. (2004). Understanding and managing the global carbon cycle. *Journal of Ecology*, *92*(2), 189–202. https://doi.org/10.1111/j.0022-0477.2004.00874.x

Hanewinkel, M., Cullmann, D. A., Schelhaas, M.-J., Nabuurs, G.-J., & Zimmermann, N. E. (2012). Climate change may cause severe loss in the economic value of European forest land. *Nature Climate Change*, *3*(3), 203–207. https://doi.org/10.1038/nclimate1687

Hansen, K., Vesterdal, L., Schmidt, I. K., Gundersen, P., Sevel, L., Bastrup-Birk, A., et al. (2009). Litterfall and nutrient return in five tree species in a common garden experiment. *Forest Ecology and Management*, *257*(10), 2133–2144. https://doi.org/10.1016/j.foreco.2009.02.021

Hasenauer, H., Burkhart, H., & Sterba, H. (1994). Variation in potential volume yield of loblolly pine plantations. *Forest Science*, *40*(1), 162–176.

He, L., Chen, J. M., Pan, Y., Birdsey, R., & Kattge, J. (2012). Relationships between net primary productivity and forest stand age in U.S. forests. *Global Biogeochemical Cycles*, *26*, GB3009. https://doi.org/10.1029/2010GB003942

Hennessey, T. C., Dougherty, P. M., Cregg, B. M., & Wittwer, R. F. (1992). Annual variation in needle fall of a loblolly pine stand in relation to climate and stand density. *Forest Ecology and Management*, *51*(4), 329–338. https://doi.org/10.1016/0378-1127(92)90332-4

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*(15), 1965–1978. https://doi.org/10.1002/joc.1276

Huang, Y., Ma, Y., Zhao, K., Niklaus, P., Schmid, B., & He, J. (2017). Positive effects of biodiversity on litterfall quantity and quality along a chronosequence in a subtropical forest. *Journal of Plant Ecology*, *10*, 28–35. https://doi.org/10.1093/jpe/rtw115

IPCC (2006). In H. S. Eggleston, et al. (Eds.), *2006 IPCC Guidelines for National Greenhouse Gas Inventories, Volume 4: Agriculture, Forestry and Other Land Use* (p. 83). Prepared by the National Greenhouse Gas Inventories Programme). Japan: IGES. http://www.ipcc-nggip.iges.or.jp/public/2006gl/index.html

Kelly, A. E., & Goulden, M. L. (2008). Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(33), 11,823–11,826. https://doi.org/10.1073/pnas.0802891105

Laanaia, N., Carrer, D., Calvet, J.-C., & Pagé, C. (2016). How will climate change affect the vegetation cycle over France? A generic modeling approach. *Climate Risk Management*, *13*, 31–42. https://doi.org/10.1016/j.crm.2016.06.001

Lamlom, S. H., & Savidge, R. A. (2003). A reassessment of carbon content in wood: Variation within and between 41 North American species. *Biomass and Bioenergy*, *25*(4), 381–388. https://doi.org/10.1016/S0961-9534(03)00033-3

Leitner, S., Sae-Tun, O., Kranzinger, L., Zechmeister-Boltenstern, S., & Zimmermann, M. (2016). Contribution of litter layer to soil greenhouse gas emissions in a temperate beech forest. *Plant and Soil*, *403*(1–2), 455–469. https://doi.org/10.1007/s11104-015-2771-3

Lexer, M. J., & Hönninger, K. (2001). A modified 3D-patch model for spatially explicit simulation of vegetation composition in heterogeneous landscapes. *Forest Ecology and Management*, *144*(1–3), 43–65. https://doi.org/10.1016/S0378-1127(00)00386-8

Likens, G. E. (2013). *Biogeochemistry of a forested ecosystem* (3rd ed.). New York, NY: Springer. https://doi.org/10.1007/978-1-4614-7810-2

Liski, J., Palosuo, T., Peltoniemi, M., & Sievänen, R. (2005). Carbon and decomposition model Yasso for forest soils. *Ecological Modelling*, *189*(1–2), 168–182. https://doi.org/10.1016/j.ecolmodel.2005.03.005

Liu, C., Westman, C. J., Berg, B., Kutsch, W., Wang, G. Z., Man, R., & Ilvesniemi, H. (2004). Variation in litterfall-climate relationships between coniferous and broadleaf forests in Eurasia. *Global Ecology and Biogeography*, *13*(2), 105–114. https://doi.org/10.1111/j.1466-882X.2004.00072.x

McGroddy, M., Daufresne, T., & Hedin, L. (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

Malhi, Y., Doughty, C., & Galbraith, D. (2011). The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *366*(1582), 3225–3245. https://doi.org/10.1098/rstb.2011.0062

Moreno, A., & Hasenauer, H. (2016). Spatial downscaling of European climate data. *International Journal of Climatology*, *36*(3), 1444–1458. https://doi.org/10.1002/joc.4436

Moreno, A., Neumann, M., & Hasenauer, H. (2017). Forest structures across Europe. *Geoscience Data Journal*, *4*(1), 17–28. https://doi.org/10.1002/gdj3.45

Neumann, M., Moreno, A., Mues, V., Härkönen, S., Mura, M., Bouriaud, O., et al. (2016). Comparison of carbon estimation methods for European forests. *Forest Ecology and Management*, *361*, 397–420. https://doi.org/10.1016/j.foreco.2015.11.016

Neumann, M., Moreno, A., Thurnher, C., Mues, V., Härkönen, S., Mura, M., et al. (2016). Creating a regional MODIS satellite-driven net primary production dataset for European forests. *Remote Sensing*, *8*(554), 1–18. https://doi.org/10.3390/rs8070554

Norby, R. J., Warren, J. M., Iversen, C. M., Medlyn, B. E., & McMurtrie, R. E. (2010). CO_2 enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(45), 19,368–19,373. https://doi.org/10.1073/pnas.1006463107

Nussbaumer, A., Waldner, P., Etzold, S., Gessler, A., Benham, S., Thomsen, I. M., et al. (2016). Patterns of mast fruiting of common beech, sessile and common oak, Norway spruce and Scots pine in Central and Northern Europe. *Forest Ecology and Management*, *363*, 237–251. https://doi.org/10.1016/j.foreco.2015.12.033

Pietsch, S. A., & Hasenauer, H. (2006). Evaluating the self-initialization procedure for large-scale ecosystem models. *Global Change Biology*, *12*(9), 1658–1669. https://doi.org/10.1111/j.1365-2486.2006.01211.x

Pietsch, S. A., Hasenauer, H., & Thornton, P. E. (2005). BGC-model parameters for tree species growing in central European forests. *Forest Ecology and Management*, *211*(3), 264–295. https://doi.org/10.1016/j.foreco.2005.02.046

Pretzsch, H., Biber, P., Schütze, G., Uhl, E., & Rötzer, T. (2014). Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nature Communications*, *5*, 4967. https://doi.org/10.1038/ncomms5967

R Development Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.r-project.org/

Reineke, L. (1933). Perfecting a stand-density index for even-aged forests. *Journal of Agricultural Research*, *46*(7), 627–638.

Sayer, E. J. (2006). Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biological Reviews*, *81*(1), 1–31. https://doi.org/10.1017/S1464793105006846

Seidl, R., Schelhaas, M.-J., Rammer, W., & Verkerk, P. J. (2014). Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Climate Change*, *4*, 806–810. https://doi.org/10.1038/nclimate2318

Senf, C., & Seidl, R. (2017). Natural disturbances are spatially diverse but temporally synchronized across temperate forest landscapes in Europe. *Global Change Biology*, *24*(3), 1201–1211. https://doi.org/10.1111/gcb.13897

Sisay, K., Thurnher, C., Belay, B., Lindner, G., & Hasenauer, H. (2017). Volume and carbon estimates for the forest area of the Amhara region in northwestern Ethiopia. *Forests*, *8*(4). https://doi.org/10.3390/f8040122

Solberg, S., Aamlid, D., Tveito, O., & Lystad, S. (2015). Increased needlefall and defoliation in Norway spruce induced by warm and dry weather. *Boreal Environment Research*, *20*, 335–349. Retrieved from https://helda.helsinki.fi/bitstream/handle/10138/228211/ber20-3-335.pdf?sequence=1

Spinoni, J., Naumann, G., Vogt, J. V., & Barbosa, P. (2015). The biggest drought events in Europe from 1950 to 2012. *Journal of Hydrology: Regional Studies*, *3*, 509–524. https://doi.org/10.1016/j.ejrh.2015.01.001

Tomppo, E., Gschwantner, T., Lawrence, M., & McRoberts, R. (2010). *National forest inventories: Pathways for common reporting*. Berlin, Germany: Springer. https://doi.org/10.1007/978-90-481-3233-1

Ťupek, B., Mäkipää, R., Heikkinen, J., Peltoniemi, M., Ukonmaanaho, L., Hokkanen, T., et al. (2015). Foliar turnover rates in Finland—Comparing estimates from needle-cohort and litterfall-biomass methods. *Boreal Environment Research*, *20*, 283–304. Retrieved from https://helda.helsinki.fi/bitstream/handle/10138/228149/ber20-2-283.pdf?sequence=1

Ukonmaanaho, L., Pitman, R., Bastrup-Birk, A., Breda, N., & Rautio, P. (2016). Part XIII: Sampling and analysis of litterfall. In UNECE ICP Forests Programme Co-ordinating Centre (Ed.), *Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests* (p. 15). Eberswalde, Germany: Thünen Institute for Forests Ecosystems. http://icp-forests.net/page/icp-forests-manual

Vaz, M., Maroco, J., Ribeiro, N., Gazarini, L. C., Pereira, J. S., & Chaves, M. M. (2011). Leaf-level responses to light in two co-occurring Quercus (Quercus ilex and Quercus suber): Leaf structure, chemical composition and photosynthesis. *Agroforestry Systems*, *82*(2), 173–181. https://doi.org/10.1007/s10457-010-9343-6

Vesterdal, L., Schmidt, I. K., Callesen, I., Nilsson, L. O., & Gundersen, P. (2008). Carbon and nitrogen in forest floor and mineral soil under six common European tree species. *Forest Ecology and Management*, *255*(1), 35–48. https://doi.org/10.1016/j.foreco.2007.08.015

Vitousek, P. M. (1984). Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology*, *65*(1), 285–298. https://doi.org/10.2307/1939481

Vose, J. M., & Lee Allen, H. (1991). Quantity and timing of needlefall in N and P fertilized loblolly pine stands. *Forest Ecology and Management*, *41*(3–4), 205–219. https://doi.org/10.1016/0378-1127(91)90104-4

White, M. A., Thornton, P. E., Running, S. W., & Nemani, R. R. (2000). Parameterization and sensitivity analysis of the BIOME–BGC terrestrial ecosystem model: Net primary production controls. *Earth Interactions*, *4*(3), 1–85. https://doi.org/10.1175/1087-3562(2000)004%3C0003:PASAOT%3E2.0.CO;2

Willmott, C. J., & Matsuura, K. (2006). On the use of dimensioned measures of error to evaluate the performance of spatial interpolators. *International Journal of Geographical Information Science*, *20*(1), 89–102. https://doi.org/10.1080/13658810500286976

Yang, W., Huang, D., Tan, B., Stroeve, J. C., Shabanov, N. V., Knyazikhin, Y., et al. (2006). Analysis of leaf area index and fraction of PAR absorbed by vegetation products from the Terra MODIS sensor: 2000–2005. *IEEE Transactions on Geoscience and Remote Sensing*, *44*(7), 1829–1842. https://doi.org/10.1109/TGRS.2006.871214

Zhang, D. Q., Hui, D. F., Luo, Y. Q., & Zhou, G. Y. (2008). Rates of litter decomposition in terrestrial ecosystems: Global patterns and controlling factors. *Journal of Plant Ecology-Uk*, *1*(2), 85–93. https://doi.org/10.1093/Jpe/Rtn002

Zhao, M., & Running, S. W. (2010). Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science*, *329*(5994), 940–943. https://doi.org/10.1126/science.1192666