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*Title Page

Drivers of carbon stocks in forest edges across Europe

Camille Meeussen[a], Sanne Govaert[a], Thomas Vanneste[a], Stef Haesen[b], Koenraad Van Meerbeek[b], Kurt Bollmann[c], Jörg Brunet[d], Kim Calders[e], Sara A. O. Cousins[f], Martin Diekmann[g], Bente J. Graae[h], Giovanni Iacopetti[i], Jonathan Lenoir[j], Anna Orczewska[k], Quentin Ponette[l], Jan Plue[f], Federico Selvi[i], Fabien Spicher[j], Mia Vedel-Sørensen[h], Hans Verbeeck[e], Pieter Vermeir[m], Kris Verheyen[a], Pieter Vangansbeke[a] and Pieter De Frenne[a]

[a]Forest & Nature Lab, Department of Environment, Faculty of Bioscience Engineering, Ghent University, Geraardsbergsesteenweg 267, 9090 Melle-Gontrode, Belgium

[b]Department of Earth and Environmental Sciences, KU Leuven, Celestijnenlaan 200E, 3001, Leuven, Belgium

[c]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

[d]Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Box 49, 230 53 Alnarp, Sweden

[e]CAVElab – Computational and Applied Vegetation Ecology, Department of Environment, Faculty of Bioscience Engineering, Ghent University, Coupure Links 653, 9000 Ghent, Belgium

[f]Biogeography and Geomatics, Department of Physical Geography, Stockholm University, Svante Arrhenius väg 8, 106 91 Stockholm, Sweden

[g]Vegetation Ecology and Conservation Biology, Institute of Ecology, FB2, University of Bremen, Leobener Str. 5, 28359 Bremen, Germany

[h]Department of Biology, Norwegian University of Science and Technology, Høgskoleringen 5, 7491 Trondheim, Norway

[i]Department of Agriculture, Food, Environment and Forestry, University of Florence, P. le Cascine 28, 50144 Florence, Italy

[j]UR « Ecologie et Dynamique des Systèmes Anthropisés » (EDYSAN, UMR 7058 CNRS-UPJV), Université de Picardie Jules Verne, 1 Rue des Louvels, 80037 Amiens, France

[k]Institute of Biology, Biotechnology and Environmental Protection, Faculty of Natural Sciences, University of Silesia, Bankowa 9, 40-007 Katowice, Poland

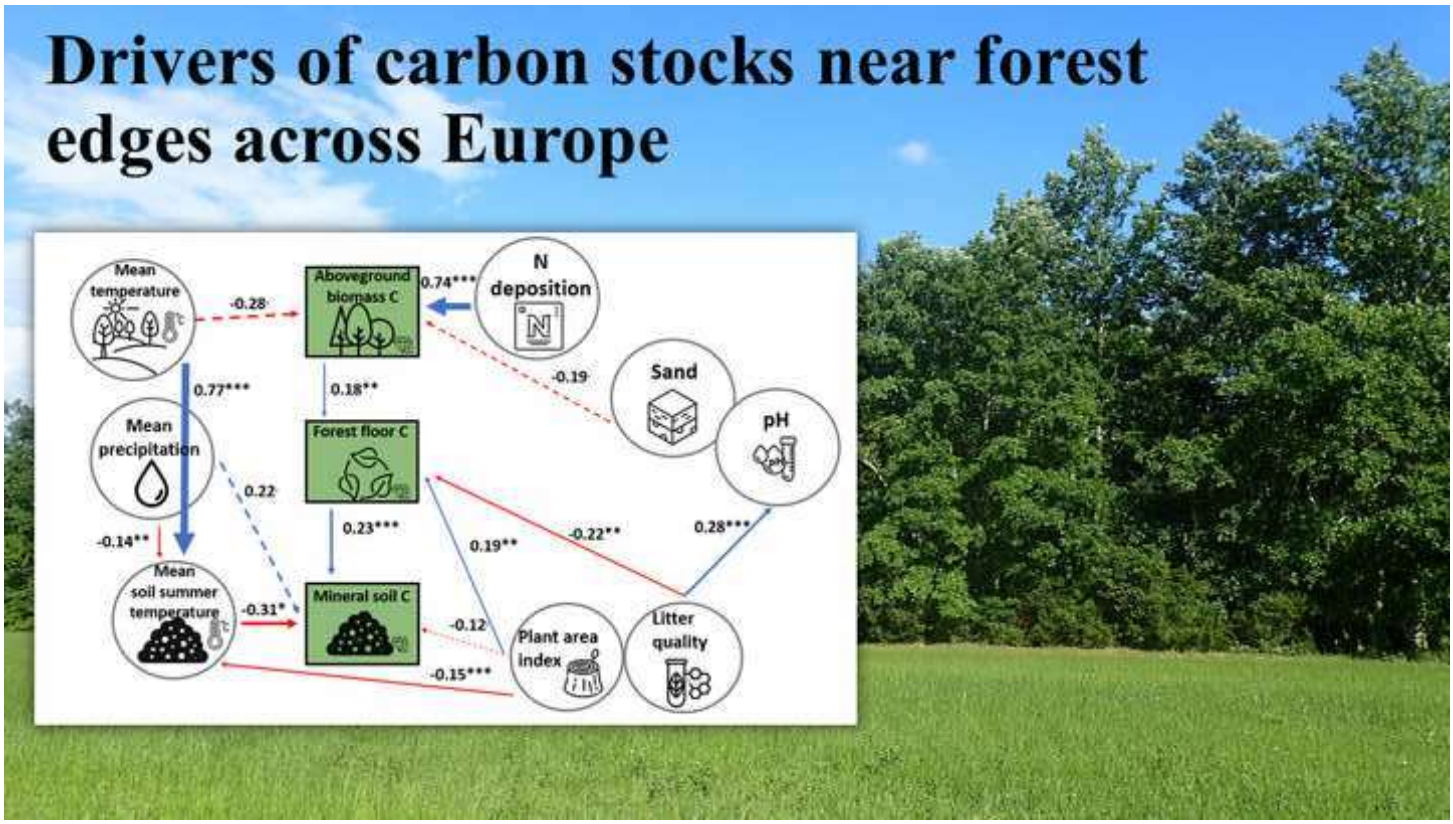
[l]Earth and Life Institute, Université catholique de Louvain, Croix de Sud 2, 1348 Louvain-la-Neuve, Belgium

[m]Laboratory for Chemical Analysis (LCA), Department of Green Chemistry and Technology, Faculty of Bioscience Engineering, Voskenslaan 270, 9000 Ghent, Belgium

Corresponding author:

Camille Meeussen
Ghent University
Camille.meeussen@ugent.be

*Graphical Abstract



***Highlights (for review : 3 to 5 bullet points (maximum 85 characters including spaces per bullet point)**

Highlights

- Carbon stocks were studied in temperate deciduous forest edges across Europe
- Total and aboveground biomass C-stocks were higher near forest edges
- Nitrogen deposition was an important driver of the increase in C near the edge
- The additional C stored in deciduous forest edges across Europe amounts to 183 Tg C
- Small forest patches and natural forest edges should be preserved

*Manuscript (double-spaced and continuously LINE and PAGE numbered)-for final publication
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[a]Forest & Nature Lab, Department of Environment, Faculty of Bioscience Engineering, Ghent University, Geraardsbergsesteenweg 267, 9090 Melle-Gontrode, Belgium

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[g]Vegetation Ecology and Conservation Biology, Institute of Ecology, FB2, University of Bremen, Leobener Str. 5, 28359 Bremen, Germany

[h]Department of Biology, Norwegian University of Science and Technology, Høgskoleringen 5, 7491 Trondheim, Norway

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[k]Institute of Biology, Biotechnology and Environmental Protection, Faculty of Natural Sciences, University of Silesia, Bankowa 9, 40-007 Katowice, Poland

[l]Earth and Life Institute, Université catholique de Louvain, Croix de Sud 2, 1348 Louvain-la-Neuve, Belgium

[m]Laboratory for Chemical Analysis (LCA), Department of Green Chemistry and Technology, Faculty of Bioscience Engineering, Voskenslaan 270, 9000 Ghent, Belgium

Corresponding author:

Camille Meeussen
Ghent University
Camille.meeussen@ugent.be

Abstract

Forests play a key role in global carbon cycling and sequestration. However, the potential for carbon drawdown is affected by forest fragmentation and resulting changes in microclimate, nutrient inputs, disturbance and productivity near edges. Up to 20% of the global forested area lies within 100 m of an edge and, even in temperate forests, knowledge on how edge conditions affect carbon stocks and how far this influence penetrates in forest interiors is scarce. Here we studied carbon stocks in the aboveground biomass, forest floor and the mineral topsoil in 225 plots in deciduous forest edges across Europe and tested the impact of macroclimate, nitrogen deposition and smaller-grained drivers (e.g. microclimate) on these stocks. Total carbon and the carbon in the aboveground biomass stock were on average 39% and 95% higher close to the forest edge than in the interior. The increase in the aboveground biomass stock close to the edge was mainly related to enhanced nitrogen deposition. No edge influence was found for stocks in the mineral topsoil. Edge-to-interior gradients in forest floor carbon changed across latitudes: carbon stocks in the forest floor were higher near the edge in southern Europe. Forest floor carbon decreased with increasing litter quality (i.e. high decomposition rate) and decreasing plant area index, whereas higher soil temperatures negatively affected the mineral topsoil carbon. Based on high-resolution forest fragmentation maps, we estimate that the additional carbon stored in deciduous forest edges across Europe amounts to not less than 183 Tg C, which is equivalent to the aboveground and belowground storage capacity of 1 million ha of additional forest. This study underpins the importance of including edge influences when quantifying the carbon stocks in temperate forests and stresses the importance of preserving small forest patches with a high edge-to-core surface area, and natural forest edges.

Keywords

Aboveground biomass carbon, Edge influence, Habitat fragmentation, Latitudinal gradient, Microclimate, Temperate deciduous forests

1. Introduction

Forests play a key role in the carbon (C) cycle as they store large quantities of C in the living aboveground biomass (stems, branches and leaves), forest soil, roots, dead wood and the litter layer (Fahey et al., 2010). By storing roughly 30% of the anthropogenic C-emissions during the last decades (Pan et al., 2011), forests serve as an important C-sink and regulator of the global climate system. However, C-storage is strongly determined by the environment. Across large spatial extents (i.e. latitude and elevation), C-storage is impacted by the climate (Jobbágy and Jackson, 2000; Pan et al., 2011; Dieleman et al., 2013; Tashi et al., 2016) as temperature and humidity drive primary production, decomposition and respiration (Luyssaert et al., 2007; Smith et al., 2019). For instance, high belowground C-stocks are found in the soil in cold biomes at higher latitudes and elevations and high C-stocks in the aboveground biomass are found in the tropics (Pan et al., 2011; Dieleman et al., 2013; Tashi et al., 2016), resulting in latitudinal and elevational trade-offs in distribution between above- and belowground C-stocks. Tree species composition, soil characteristics and management are major drivers of C-stocks as well (Schulp et al., 2008; Vesterdal et al., 2013; De Vos et al., 2015; Mayer et al., 2020). Forest management does not only reduce the aboveground stock by removal of tree stems, but can also influence the input rate of organic matter and the release rate of C from the soil (Jandl et al., 2007; Schulp et al., 2008; Naudts et al., 2016; Mayer et al., 2020). Forest management and fragmentation also have an impact on forest microclimates (Matlack, 1993; Chen et al., 1999; Kovács et al., 2017), further affecting C-storage (Cahoon et al., 2012; Smith et al., 2019). Finally, also nitrogen (N) deposition seems to play an important role in C-storage processes, via an enhanced tree growth or changes in litter decomposition (i.e. supressed or increased enzyme activity), affecting the C-storage potential (Magnani et al., 2007; Manning et al., 2008; Mayer et al., 2020).

So far, the majority of data on C-storage in forests is derived from intact forests and forest interiors, while forest edges are largely understudied (Smith et al., 2018). However, up to 20% of the global forested area lies within 100 m of a forest edge (Haddad et al., 2015) and is subject to strong edge

influences that penetrate far towards the interior (Schmidt et al., 2017). Forest edges differ in vegetation structure and composition, compared to interiors (Harper et al., 2005; Meeussen et al., 2020). Furthermore, due to the strong differences in structure between forest edges and adjacent lands, edges further receive higher levels of atmospheric N deposition (Weathers et al., 2001; Devlaeminck et al., 2005; De Schrijver et al., 2007; Wuyts et al., 2008). Finally, the forest edge microclimate will substantially differ from the microclimate in both open areas and forest interiors, due to changes in air-mixing, solar radiation and humidity (Matlack, 1993; Chen et al., 1999; Schmidt et al., 2017). Such edge influences can consequently affect productivity, decomposition and C-storage.

Especially in temperate deciduous forests that are overall strongly fragmented (Haddad et al., 2015), the question on how above- and belowground C-stocks are impacted by edge influences is currently unresolved (Ziter et al., 2014). The few studies focussing on C-storage and -cycling near edges in temperate forests often gave contrasting results. Ziter et al. (2014) for instance, found no change in edge-to-interior aboveground C-storage whereas Reinmann and Hutyra (2017) and Remy et al. (2016) found an increased C-stock in the aboveground biomass in the proximity of an edge. They attributed this increase to an enhanced productivity and/or higher stem density in forest edges, the result of improved light conditions and elevated N inputs (Remy et al., 2016; Reinmann and Hutyra, 2017). Contrasting patterns in forest floor C-stocks were found as well. Faster decomposition of litter in the forest interior, leading to lower forest floor stocks, might be caused by a higher soil moisture content because a large part of the incoming solar radiation is captured and reflected by the canopy (Riutta et al., 2012). On the other hand, higher forest floor C-stocks in the interior were found by Remy et al. (2016), likely impacted by faster decomposition near the edge due to a complex interplay of specific edge conditions (i.e. decomposer macrofauna community, soil pH, microclimate and atmospheric deposition) (Remy et al., 2016, 2018). Finally, also the mineral topsoil layer will be affected by fragmentation and edge conditions; Remy et al. (2016) found evidence for an elevated C-concentration and -storage in the mineral topsoil at the edge of the

forest. A higher N deposition or input from adjacent land uses (e.g. fertilizers), as is common in forest transition zones (Wuyts et al., 2008), might affect the C-cycling by reducing soil respiration (Janssens et al., 2010), though also an increased soil respiration near temperate forest edges has been found (Smith et al., 2019). It is clear that C-dynamics are very sensitive to changes in local climates, vegetation and soil characteristics. Therefore, edge influences need to be taken into account for accurate estimations of C-stocks in temperate forest systems (Smith et al., 2018).

Here we quantify above- and belowground C-stocks in 225 plots in 45 edge-to-interior transects in deciduous temperate forests across Europe. The transects were subject to different management regimes and situated along a latitudinal gradient from Italy to Norway, crossing the temperate forest biome and including transects at the transition zones with the sub-Mediterranean and boreo-nemoral forest system. We assessed C in the aboveground biomass (i.e. woody biomass and foliage), forest floor and mineral topsoil layer (0-20 cm). Additionally, we tested the combined impact of macroclimate and N deposition (i.e. large-scale drivers) and several local drivers (i.e. forest management, species composition, microclimate and soil characteristics) on the C-stocks. Finally, we quantify the consequences of this edge influence for estimates of C stocks in European forests based on high-resolution forest edge and fragmentation maps. We specifically addressed the following questions: (1) How do edge-to-interior gradients affect C-stocks in forests? Are these edge-to-interior patterns spatially consistent throughout Europe? (2) What is the relative importance of driving factors of C-stocks across macro- and microclimatic gradients in European deciduous forests?

2. Materials and Methods

2.1 Study design and area

We studied forests along a 2300 km wide latitudinal gradient from central Italy (42 °N) to central Norway (63 °N) (Δ mean annual temperature ≈ 13 °C). Along this south-north gradient, nine regions were selected: Central Italy, Northern Switzerland, Northern France, Belgium, Southern Poland, Northern Germany, Southern Sweden, Central Sweden and Central Norway. In three regions, i.e. Norway, Belgium and Italy, an elevational gradient was established as well covering low, intermediate and high elevational sites. This to include the climatic variation resulting from elevational differences (21 - 908 m above sea level (m a.s.l.) Δ temperature ≈ 5.76 °C (ICAV, 1993))(**Fig. 1**).

In all 15 sites (i.e. nine lowland, three intermediate and three high-elevational sites), we collected data in three forest stands with a distinct management type. The first type, hereafter referred to as 'dense forests', was always a dense and vertically complex forest stand with a well-developed shrub layer, since it had not been managed for more than ten years and in general not thinned for at least three decades. A second type, 'intermediate forests', comprised stands with a lower basal area and canopy cover, resulting from regular thinning events (last time approximately five to ten years ago). The third management type represented 'open forests' with a simple structure and no shrub and subdominant tree layer. These forests were intensively thinned in the recent past (one to four years before sampling).

In each of the 45 forest stands, we studied a 100 m-long edge-to-interior gradient. The studied edges were all south-oriented and bordered by arable land, open grassland or very large clearings inside a forest. Each transect encompassed five plots (quadrat of 3 by 3 m; n = 225), all at a fixed distance perpendicular to the edge according to an exponential pattern. The centre of the first plot was located at a distance of 1.5 m from the outermost line of tree trunks towards the interior, followed by plots centred at 4.5 m, 12.5 m, 36.5 m and 99.5 m.

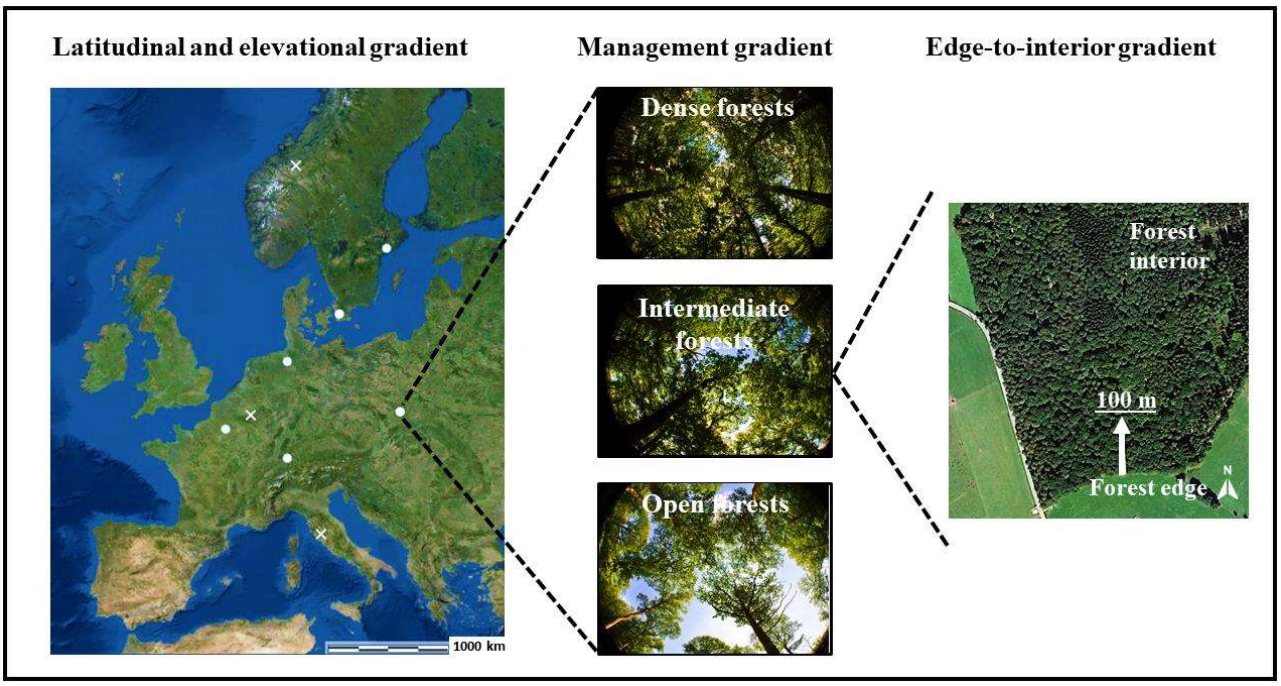


Figure 1: Study design with the four design variables (latitude, elevation, management and distance to the edge). Left: The nine regions along a latitudinal gradient, including three elevational gradients (white crosses on the map). Background map from: http://databasin.org. Middle: The three forest management types. Right: A 100-m long gradient (arrow) from the edge towards the interior was established in each forest. Picture of one of the Belgian transects from Google Earth.

We focused on mesic deciduous forests, in general dominated by oaks (*Quercus robur, Q. petraea* or *Q. cerris)*. Other important tree species were *Fagus sylvatica*, *Betula pubescens*, *Populus tremula*, *Ulmus glabra*, *Alnus incana* and *Carpinus betulus*. All forests were larger than four hectare and ancient (i.e. continuously forested since the oldest available land use maps, which is typically at least 150-300 years ago). For further details regarding the study design, forest structure and site selection see Govaert et al. (2020) and Meeussen et al. (2020).

2.2 Data collection

2.2.1 Carbon stocks

Carbon stocks were assessed between May and July 2018 in all plots. Four different C-stocks were studied: aboveground biomass C (AGBC), forest floor C, mineral topsoil C and total C by pooling together the three previous stocks.

Aboveground biomass carbon

For the calculation of the AGBC, we measured the diameter at breast height (DBH, 1.3 m) of all standing trees (both alive and dead, n = 3891) within a circular 9-m radius plot, with the same centre as the 3 by 3 m plots. To determine the plot dimensions, an ultrasound hypsometer (Vertex IV, Haglöf, Sweden) was used. The DBH was measured for all trees with a DBH ≥ 7.5 cm with a caliper via two DBH measurements per stem, perpendicular to each other. For multi-stemmed trees, all individual stems (DBH ≥ 7.5 cm) were measured and treated as separate individuals in the calculations. However, in a very limited number of plots (n = 5 in Norway and n = 7 in Italy) in coppiced forests, due to the presence of a very high number of multi-stemmed trees, we counted the number of stems per tree and assigned the DBH of a visually representative stem to all individual stems of the multi-stemmed tree. Subsequently, the aboveground biomass (AGB, including foliage) was calculated for every tree based on their DBH via a multi-species biomass equation (**eq. 1**, Jenkins et al., 2003). All tree species were assigned to one of the ten different multi-species biomass groups developed by Jenkins et al. (2003), each represented by a unique diameter-based aboveground biomass regression equation. The classification in the groups was based on literature and expert knowledge (**Table A1**). Five stems, left unidentified, were allocated to the dominant tree species at plot level and classified accordingly.

$$Total\ AGB\ (kg\ dry\ weight) = exp(\beta_0 + \beta_1 \times ln(DBH)) \quad (1)$$

With β_0 and β_1 group-specific parameters (**see Table A2**) and DBH the diameter at breast height in cm.

To avoid outliers in the AGB-estimations of trees whose DBH exceeded the range of values used to build the equations (n = 34 stems), their DBH was lowered in the allometric equation to the maximum DBH used to establish that equation (i.e. no extrapolation was allowed). Although originally applied in North-America, the biomass groups are based on a large dataset and therefore an invaluable alternative when species-specific and local equations are not available and the tree species pool is large (e.g. our dataset contains nine regions at the continental scale with > 40 tree species, making it impossible to use local species-specific equations). Moreover, in the study of

Bartholomée et al. (2018) the multi-species biomass equations rendered comparable results for European species-specific equations (mainly Zianis et al. (2005)), even though no comparison against destructive sampling in Europe was done. To further verify the use of these multi-species biomass equations, we calculated the AGB for the Belgian plots using precise local and species-specific equations (i.e. the allometric equations for stem volume by Dagnelie et al. (1999) and the biomass expansion factors of Vande Walle et al. (2005)). Both the local equations and the multi-species biomass equation rendered virtually indistinguishable AGB-values for the Belgian plots (R^2 = 0.98, see **Appendix A1** and **Fig. A1**). As a final step, we then determined the total AGB per plot by dividing the total AGB of a given plot by its forested area, as for the two outermost 9-m radius plots a fraction of the circle fell beyond the forest edge, and converted the units to Mg or ton per ha. Finally, the C-stock at plot level (Mg ha^{-1}) was calculated by multiplying the AGB with a C content value of 47 %, a factor suggested by the IPPC (2006) for temperate trees.

Forest floor carbon

In each plot, one random sample of the forest floor, the organic material (i.e. O-horizon) on top of the mineral topsoil, was taken in a 20 by 20 cm square frame after removal of understorey vegetation. The litter, fragmentation and humus layer were sampled and weighted after drying to constant weight for 48 hours at 65 °C. Afterwards, the samples were pooled, milled and analysed for total C-concentration. Samples were combusted at 1200 °C and the gases were measured by a thermal conductivity detector in a CNS elemental analyser (vario Macro Cube, Elementar, Germany). The C-stock in the forest floor was calculated based on the biomass of the samples and the C-concentration (**eq. 2**).

$$Forest\ floor\ C\ stock\left(\frac{Mg}{ha}\right) = C\ concentration\ \left(\frac{g}{g}\right) \times biomass\ of\ the\ organic\ layer\ \left(\frac{Mg}{ha}\right) \quad (2)$$

Mineral topsoil carbon

For the C-stock in the mineral topsoil layers, five subsamples were taken in each plot with a soil corer after removal of the organic layers. We sampled the mineral topsoil at a depth of 0-10 cm and 10-20 cm. We here neglect soil layers deeper than 20 cm as in European forests approximately half

of the C-stock up to 1-m depth is stored in that 20-cm topsoil layer (De Vos et al., 2015) and as we expect the highest edge influences to occur in the topsoil. Subsamples were pooled per layer and dried to constant weight at 40 °C for 48 hours. Subsequently, samples were ground, sieved over a 2-mm mesh, and analysed for the total concentration of C, via the same method as for the forest floor. As only C concentrations were available, we estimated the soil bulk density for each layer based on C-concentration values making use of the regression equation of Wang and Huang (2020)(**eq. 3**). Finally, we obtained the C-stock per layer by multiplying the C-concentrations with the estimated soil bulk density and soil depth (**eq. 4**). The C-stock in the mineral topsoil was defined as the sum of the stocks in the 0-10 cm and 10-20 cm layers.

$$Bulk\ density = 1.5607 - 0.2721 \times C\ concentration \left(\frac{g}{100\,g}\right)^{0.5} \quad (3)$$

$$Mineral\ soil\ C\ stock \left(\frac{Mg}{ha}\right) = C\ concentration \left(\frac{g}{100g}\right) \times bulk\ density \left(\frac{g}{cm^3}\right) \times soil\ depth\ (cm) \quad (4)$$

Total carbon stock

The total C-stock per plot (Mg ha^{-1}) was determined as the sum of the C in the AGBC-stock and the C-stocks in the forest floor and mineral topsoil. We only focused on these major carbon pools but acknowledge that this is an underestimation of the total C present at plot level as part of the aboveground stock (i.e. the stock in the understorey or in the downed dead woody biomass) and the belowground stock (i.e. root biomass and the soil organic C stored deeper than 20 cm) were not considered here.

2.2.2 Environmental drivers

To be able to test the impact of spatial scale, both large-scale (i.e. regional) drivers and local (i.e. plot) characteristics were selected for further analyses.

Regional drivers: macroclimate and N deposition

Macroclimatic characteristics and N deposition were used to reflect regional drivers. Macroclimatic data were obtained from CHELSA (version 1.2, average climatic conditions over the period 1979-2013 at a spatial resolution of 30 arc sec, Karger et al., 2017). For each site, the mean annual temperature (MAT, °C) and the mean total annual precipitation (MAP, mm $year^{-1}$) were extracted.

Modelled atmospheric N deposition data were downloaded from the European Monitoring and Evaluation Program (EMEP) for the year 2016 at a resolution of 50 by 50 km. For each site, the total atmospheric N deposition rate was estimated as the sum of both dry and wet deposition of reduced and oxidized nitrogen. Due to the steep transition in vegetation height and altered wind patterns, forest edges are hotspots for N deposition, with sometimes up to four times higher atmospheric deposition values measured near edges compared to the interior (Weathers et al., 2001; De Schrijver et al., 2007; Wuyts et al., 2008). To account for such elevated edge depositions, the deposition rates were corrected using a decreasing exponential curve, which was fitted based on actual measured throughfall data of NH_4^+ and NO_3^- in oak-dominated forest edges by Wuyts et al. (2008) (see **Appendix A2** and **Fig. A2**).

Local characteristics of the forest structure and tree community

Subsequently, two local stand characteristics were used, i.e. litter quality and plant area index. The litter quality serves as a proxy for the effect of the tree community on litter and topsoil C-stocks while the plant area index is a metric for stand structure. Both variables enable us to study the effect of forest community and structural variation due to management and edge-to-interior gradients on C-stocks.

The litter quality is a tree species-specific index ranging between one and five, which describes the quality of the litter and thus the rate of leaf litter decomposition. If the litter quality is very low (scores close to one), decomposition rates are slow and litter will accumulate on the forest floor. High values (scores close to five) denote a relatively high decomposition rate. The litter quality is determined by the surrounding tree and shrub species and was calculated at plot level as the average of the cover-weighted values for all present shrubs (1-7 m) and trees (> 7 m) in the 9-m radius plot survey (*sensu* Verheyen et al., 2012; Maes et al., 2019; Vanneste et al., 2020). Scores for individual tree and shrub species can be found in the appendix (**Table A3**).

The plant area index is the total of the one-sided area of woody (e.g. branches and stems) and non-woody biomass (i.e. leaves) per unit of surface area and can be interpreted as a metric for forest

density. The plant area index was determined (May and July 2018, leaf-on conditions) with a RIEGL VZ-400 terrestrial laser scanner and was calculated as the integral of the plant area per volume density (m^2 m^{-3}) over the canopy height. A detailed description of the sampling campaign can be found in Meeussen et al. (2020). During the growing season, the plant area index is mainly determined by the amount of foliage biomass; typical ratios of the woody to total plant area are less than 0.4 (Gower et al., 1999; Kalácska et al., 2005).

Local soil characteristics

In addition, three more local drivers were extracted, reflecting the soil characteristics.

1. The upper part of the mineral topsoil (0-10 cm) was used for the extraction of soil pH-values. The pH-H_2O was determined by shaking a 1:5 ratio soil/H_2O mixture for 5 min at 300 r.p.m. and measuring with an Orion 920A pH meter with a Ross sure-flow 8172 BNWP pH electrode model (Thermo Scientific Orion, USA).
2. We selected the percentage sand as proxy for soil texture. Soil texture (percentage silt, clay and sand) was determined on the pooled 10-20 cm depth samples. These samples were analysed for texture via sedimentation with a Robinson–Köhnpipette according to ISO 11277 (2009).
3. We measured soil temperature as proxy for the microclimate, since respiration and the decomposition of organic matter are stimulated under higher temperatures (Nadelhoffer et al., 1991; Cahoon et al., 2012; Wiesmeier et al., 2019). An increased C-mineralisation rate was previously observed for temperatures above 10 °C while below 10 °C the mineralisation rates were not triggered by temperature increases (Nadelhoffer et al., 1991). Cold temperatures will thus limit C-mineralisation, whereas the majority of soil C-cycling will occur during the summer. Therefore, the mean soil temperature during the summer (June-July-August 2018) was selected as our metric for soil microclimate temperature. Soil temperatures were recorded at hourly intervals, in the centre of each plot, using a lascar temperature logger (EasyLog EL-USB-1, accuracy at -35 to +80 °C: ± 0.5 °C). The loggers

were buried in the ground in a protective plastic tube at a depth of five cm. Missing or incorrect data, due to for instance logger malfunctioning or the uprooting of loggers, were replaced with the data of the most nearby sensor. Errors were detected in 44 plots but could always be corrected with measurements from the nearest plot within the same forest.

2.3 High-resolution forest maps and estimates of carbon storage in deciduous forest edges across Europe

To estimate the impact of forest edge influences on C-stocks we calculated the total area of deciduous forests and their edge area across Europe. Europe was defined as all 27 EU countries, plus Albania, Bosnia and Herzegovina, Kosovo, Liechtenstein, Montenegro, North Macedonia, Norway, Serbia and Switzerland. The Canary Islands and Azores, as well as Europe's overseas territories were excluded from the analysis. Calculations were based on the Copernicus Forest Type map of 2015 at a resolution of 20 m × 20 m (FTY 2015, https://land.copernicus.eu/). Based on this map, the total area of broadleaved forests was determined as well as the total edge perimeter, i.e. the sum of all cells' edges of deciduous forest bordering a non-forest cell. Subsequently, the total edge area of deciduous forest was estimated by multiplying the edge perimeter length with a depth of edge influence of 4.5 m, as we found a significant difference between C-stocks up to this depth (based on a post hoc Tukey Multiple Comparisons Test; see Results). Finally, the total C-stock in deciduous forests across Europe was calculated without edge influences (i.e. all forested area had an average C-stock which was the same as the average total C-stock in the interior of our forest). Then, a second calculation took into account the edge influences, in which we divided the forest into three regions: the outer edge (the forested area along the forest edge up to 3 m towards the interior), intermediate region (the area between 3 m and 4.5 m from the edge) and interior. We subsequently took the average C-stock at 1.5 m as the C-stock for the outer edge, the C-stock at 3.5 m for the intermediate region and the C-stock for the interior as in the first calculation to calculate the total C-stock in deciduous forest across Europe with edge influences.

2.4 Data analysis

Data analyses were executed in R (R Core Team, 2019). For the exploration of edge influences on C-stocks, four linear mixed-effects models were established (i.e. one for each of our C-stocks), making use of the R-package 'nlme' (Pinheiro et al., 2020). Two random intercept terms, region and transect (nested within region), were used in all our models to account for the nested design (plots nested in transects, nested in regions) and potential autocorrelation effects. The fixed structure of the model was composed of the four design variables (i.e. latitude, elevation, management type and distance to the edge). Moreover, we included a two-way interaction term between each predictor variable and distance to the edge to study spatial variation in edge-to-interior patterns in C-stocks (**eq. 5**). Since the distribution of our plots follows an exponential pattern, distance to the edge was log-transformed prior to the analyses. Two plots (outliers) were removed from the analysis as they biased the results due to the presence of multiple large beech trees (*Fagus sylvatica*) near the forest edge. All continuous predictor variables were standardized (z-transformation) to allow for a better comparison of model coefficients. If distance to the edge was a significant driver, a post hoc (Tukey Multiple Comparisons) test was executed using the 'glht' function ('multcomp' R-package) to explore how the five different edge distances (here as factor) influenced the C-stocks (significance level $p < 0.05$) (Hothorn et al., 2008).

$$y \sim latitude + elevation + management\ type + distance\ to\ the\ edge + distance\ to\ the\ edge\ x\ latitude + distance\ to\ the\ edge\ x\ elevation + distance\ to\ the\ edge\ x\ management\ type + (1 \mid region/transect) \quad (5)$$

Subsequently, two piecewise structural equation models (SEM, R-package 'piecewiseSEM', Lefcheck, 2016) were constructed to gain more insight into the mechanisms affecting forest C-stocks directly and indirectly (**Fig. 2**). Piecewise SEM was selected, as this method allows for the fitting of hierarchical data and thus random effects via a set of separate linear mixed-effect models. Again, region and transect nested within region were used as random intercept terms in all subsequent component models. A set of three linear mixed-effect component models was fitted to investigate the impact of regional and local determinants on the C-stocks. The three component

362 models, with the AGBC, the C-stock in the forest floor and the C-stock in the mineral topsoil, are
363 similarly structured. The component model for the AGBC consisted of seven predictor variables:
364 the three regional variables (N deposition, MAP and MAT), two local predictors (litter quality and
365 plant area index) and two of the three soil variables (pH and sand). The component models for the
366 C-stock in the forest floor and mineral topsoil contained the same predictors as mentioned in the
367 previous model, except for the MAT, which was substituted by the soil temperature. We avoided
368 the use of MAT and soil temperature in the same component model, because of their strong positive
369 correlation (R^2 = 0.89, **Fig. A3**). In addition, also the AGBC-stock was used as predictor for the
370 stock in the forest floor while both the AGBC and the forest floor C served as possible predictors
371 for the mineral topsoil C-stock (**Fig. 2**). Finally, a second SEM was established, very similar to the
372 SEM explained above but taking into account additional relationships between predictor variables.
373 Therefore, the set of three linear mixed-effect component models was extended with two more
374 mixed-effects component models. For these two final component models studying the relationships
375 amongst predictors, we have firstly a model exploring the influence of litter quality on topsoil pH
376 and secondly a model analysing the impact of MAT, MAP and plant area index on the soil
377 temperature (**Fig. 2**). These extra relationships were added based on previous research showing that
378 the litter quality can strongly affect topsoil conditions (Maes et al., 2019). Soil temperature, on the
379 other hand, is strongly correlated with the MAT but is also buffered in forests (De Frenne et al.,
380 2019). This buffering capacity of forests increases among others with increasing density or biomass
381 (Frey et al., 2016; Jucker et al., 2018). Finally, soil temperature can be impacted by water
382 availability, because sites with a higher moisture availability are more buffered against temperature
383 fluctuations and high temperatures (Ashcroft and Gollan, 2013; Greiser et al., 2018). Therefore,
384 litter quality, MAT, MAP and plant area index could also indirectly affect C-stocks.

385 The model fit was assessed via Shipley's test of directed separation, which is a test for conditional
386 independence, meaning that no missing relationships can be detected in the model. If the *p*-value
387 exceeds the threshold for significance ($p > 0.05$), then the hypothesized relationships are consistent

with the data (Shipley, 2009). Post hoc inspection of the test of directed separation revealed a nonsensical claim, between N deposition and the soil temperature in the second SEM, as we did not expect a direct influence of N deposition on the soil temperature. Therefore this path was omitted from the evaluation of the goodness-of-fit by adding them as correlated errors (*mean soil summer temperature %~~% N deposition in R*) (Lefcheck, 2016). No problems were detected for the first SEM without additional relationships between predictor variables. The fit of the individual component models is displayed as the proportion of variance explained by the fixed effects (marginal R^2) and the proportion of the variance explained by both fixed and random effects (conditional R^2) (Nakagawa and Schielzeth, 2013).

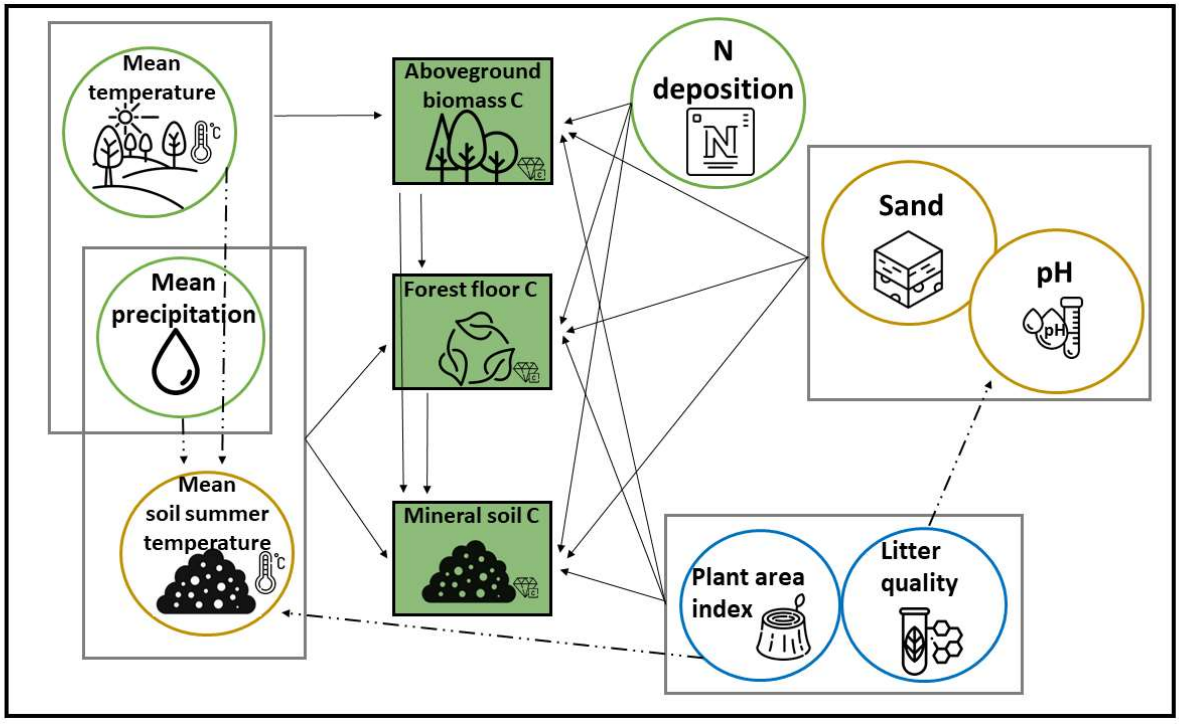


Figure 2: Full piecewise SEM of the determinants of carbon (C) stocks in the aboveground biomass (AGB, Mg C ha^{-1}), the forest floor (Mg C ha^{-1}) and the mineral topsoil (Mg C ha^{-1}) in deciduous forests edges across Europe. We tested the impact of three large-scale drivers, indicated by green circles (mean annual temperature in °C, mean annual precipitation in mm $yr.^{-1}$ and the nitrogen (N) deposition in kg ha^{-1} $yr.^{-1}$), two local stand characteristics visualized in the blue circles (the plant area index and litter quality) and three local soil characteristics, shown in the brown circles (sand, pH and the mean soil summer temperature in °C). The pathways amongst predictor variables, additional pathways of the second model, are displayed as dashed-dotted lines. For ease of presenting, parts of the figure were boxed as to avoid a multitude of arrows relating to the variables inside.

3. Results

3.1 Variation in carbon stocks

Strong differences in the C-stocks were observed between the regions (**Table B1**). The total stocks were highest in Northern Switzerland, Northern Germany and Southern Sweden whereas Central Sweden and Central Italy had the lowest stocks. No impact of latitude, elevation or management were detected on the total C-stock (**Table B2**), though the total stock was significantly higher near the forest edge ($p < 0.001$, **Fig 3a**) up to a distance of approximately 4.5 m from the edge (**Table B2**). Total C-storage was on average 39% higher at the edge (= 1.5 m) than in the forest interior (= 99.5 m).

The AGBC ranged between 7 and 373 Mg C ha^{-1} with an average of 103 Mg C ha^{-1}. Similar as for the total C-stock, we found a significant impact of distance to the forest edge on the AGBC, with an enhanced AGBC near the edge up to a distance of 4.5 m ($p < 0.001$) (**Fig. 3b, Table B2**). Here, on average, the stock was 95% at the edge. AGBC-stocks did not significantly differ across management types ($p = 0.12$, **Table B2**). In the forest floor, the C-stock ranged between 0.2 and 44 Mg C ha^{-1} with an average of 5 Mg C ha^{-1} across all sites and management types. We found a significant positive interaction between distance to the edge and latitude ($p = 0.03$, **Table B2**), indicating that C-stocks in the forest floor near the edge are higher in the southern regions (**Fig. 3c**). Finally, the average C-stock in the mineral topsoil layer amounted to 81 Mg C ha^{-1} whereas the minimum and maximum values were 34 and 152 Mg C ha^{-1} respectively. Carbon stocks in the mineral topsoil did not significantly differ between the plots (**Fig. 3d**). We did find a positive impact of elevation on the mineral C-stocks ($p = 0.01$, **Table B2**).

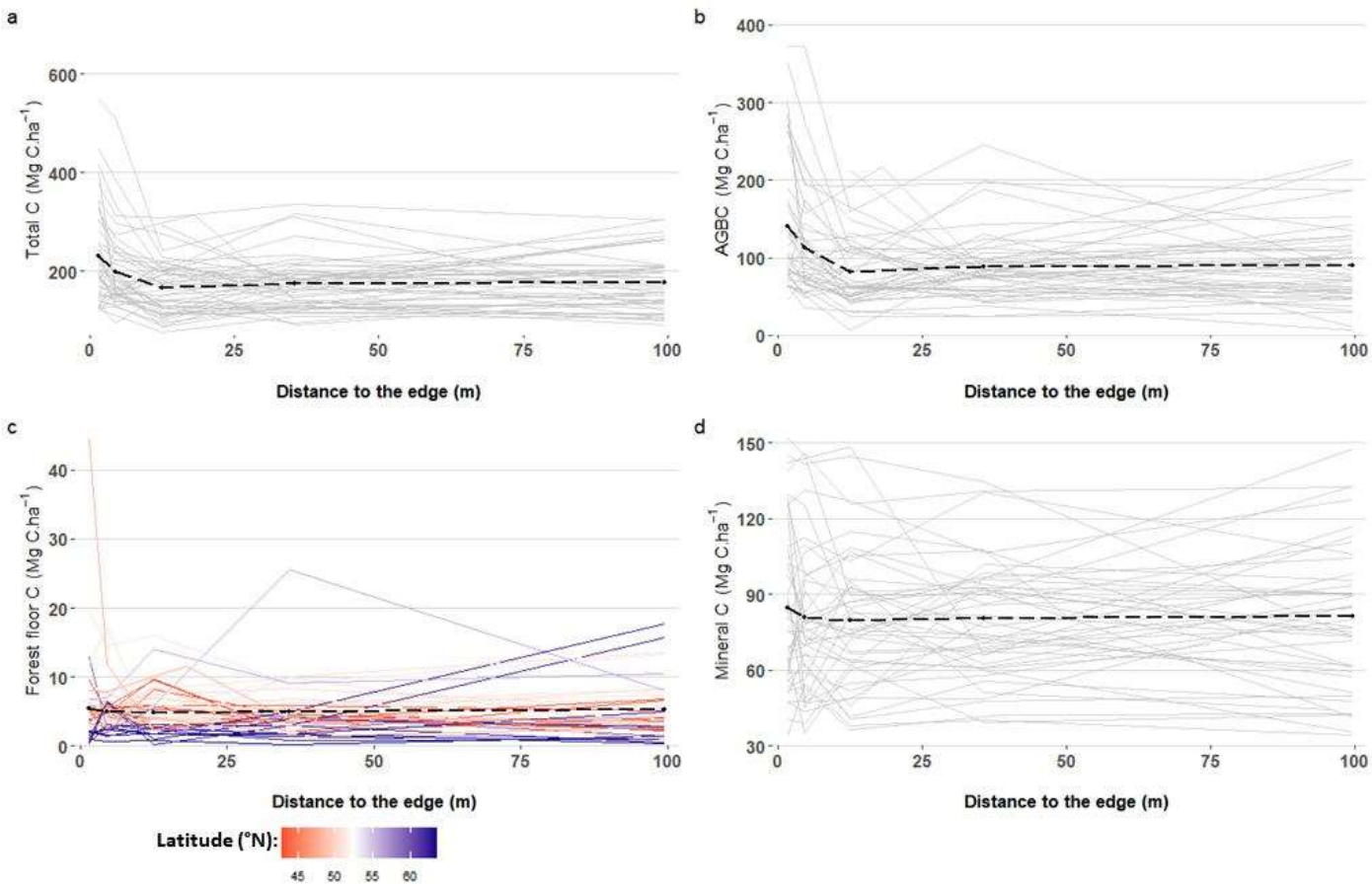


Figure 3: Edge-to-interior patterns of a) the total carbon (C) stock (Mg C ha^{-1}), b) aboveground biomass C-stock (AGBC, Mg C ha^{-}1), c) forest floor C-stock (Mg C ha^{-}1) and d) mineral topsoil C-stock (Mg C ha^{-}1). The black dashed lines indicate the average stock across sites and management types whereas the solid grey lines show the observed stocks in each of the transects and plots. Colours in panel c demonstrate the effect of the latitude; red colours represent southern latitudes and blue colours indicate northern latitudes. Latitude was only displayed for the forest floor C-stocks because it had a significant interaction effect with distance to the edge whereas this effect was absent for the other stocks.

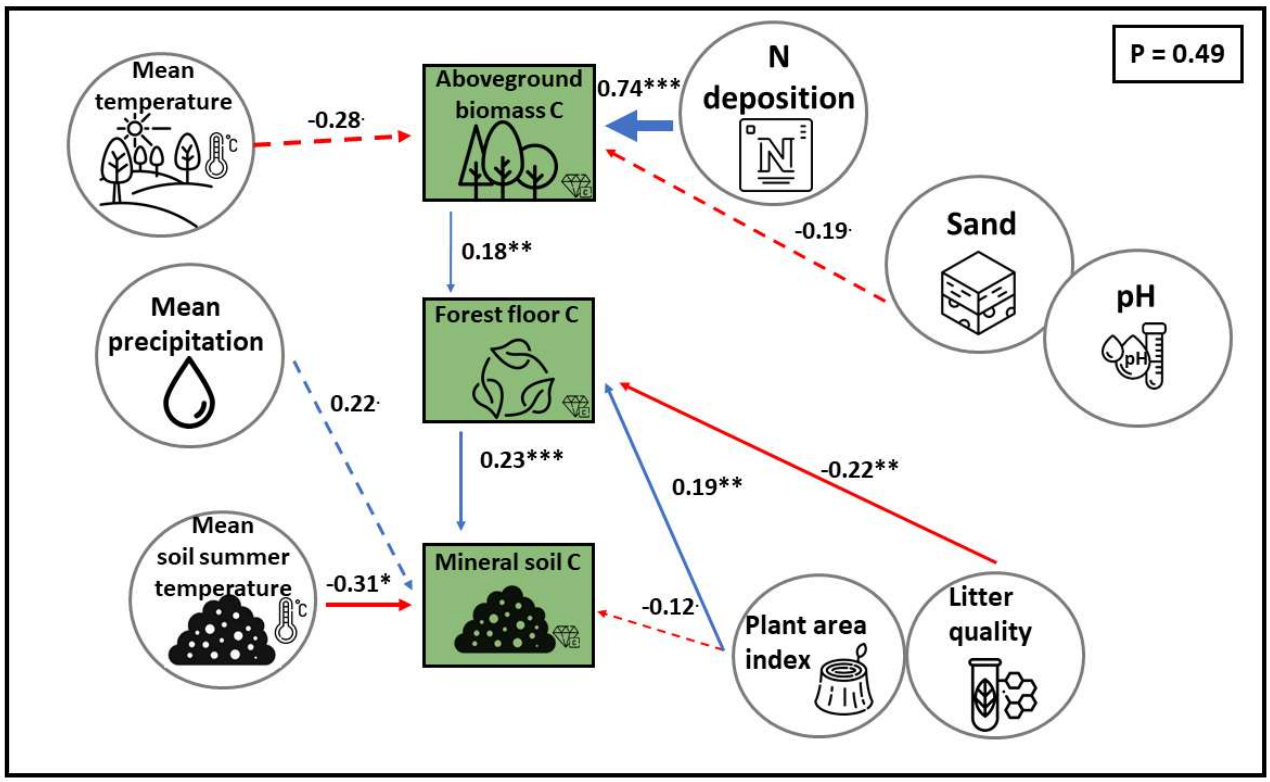
3.2 Piecewise structural equation models: drivers of carbon storage

Our piecewise SEM, without relationships amongst predictors, reproduced the data well (p = 0.49, AIC = 77) (**Fig. 4**). We found a significant impact of regional drivers and local (soil) characteristics on the C-stocks. The AGBC-Stock increased with elevated N deposition (p < 0.001) whereas a sandy soil texture (p = 0.08) and high MAT (p = 0.06) had a close to significant negative impact. We could not find an impact of N deposition on the C-stocks in the forest floor and mineral soil. Carbon stocks in the forest floor were affected by the AGBC, litter quality and the plant area index.

Hence, the forest floor stock was lowest in forests with a high litter quality (p = 0.005) and a low plant area index (p = 0.009). We also found a positive effect of AGBC on the forest floor C-stock (p = 0.009). Further, the stock in the forest floor itself had a significant positive impact on the C-stock in the mineral topsoil (p < 0.001). The MAP and the soil temperature were two additional determinants of the mineral C-stock. The stock was higher in colder soils (p = 0.01) and a higher precipitation had a marginally positive impact on the mineral C-stock as well (p = 0.08).

As expected, similar results were detected in the piecewise SEM in which more relationships between the predictors (e.g. between MAT and soil temperature: see the dashed-dotted lines in **Fig. 2**) were included (p = 0.14 and AIC = 125) (**Fig. B1**). Marginal and conditional R^2 of all the component models for both SEMs are shown in **Table B3**.

Due to the strong impact of N deposition on the AGBC, we tested the additional impact of N, distance to the edge and their interaction in a simple linear mixed-effect model (similar as those described in the materials and methods section). We found a significant negative impact of their interaction (p = 0.04) on the AGBC.



457 ***Figure 4:*** Basic piecewise SEM of the determinants of carbon stocks in the aboveground biomass (AGBC), the forest
458 floor and the mineral topsoil in deciduous forests edges across Europe. Solid arrows indicate significant pathways ($p <$
459 0.05) while marginally significant paths ($p < 0.1$) are represented by dashed arrows. All other non-significant paths
460 were omitted from the figure. A negative impact is visualized in red, whereas blue indicates a positive relationship. The
461 thickness of arrows corresponds to the effect size. Standard estimates of path coefficients and their p-values ($p < 0.001$
462 = ***, $p < 0.01$ = **, $p < 0.05$ = *, $p < 0.1$ = ·) are mentioned above each arrow. The marginal R^2 and conditional R^2 are
463 respectively 0.30 and 0.53 for the AGBC, 0.21 and 0.29 for the C-stock in the forest floor and 0.20 and 0.59 for the C-
464 stock in the mineral topsoil.

465 *3.3 Additional carbon storage in forest edges across Europe*

466 Based on the high-resolution forest Copernicus map, we found that broadleaved forests cover an
467 area of approximately 118 million ha across Europa and their edge perimeter amounts to
468 approximately 9.4 billion m. When not taking into account edge effects, European deciduous forest
469 store approximately 20,757 Tg C. However, if edge influences in broadleaved forests were taken
470 into account, an additional 183 Tg C was stored (**Table 1**).

471 ***Table 1:*** Estimates of carbon storage with and without edge influences in deciduous forests across Europe.

		Forest area (ha)	Average total C stock (Mg ha^{-1})	C-stock (Tg)	Total C-stock (Tg)
Estimates without edge influences		117,803,139	176.2	20,757	20,757
Estimates with edge influences	**Edge (up to 3m from the edge)**	2,816,899	229.9	647	20,940
	Edge (between 3 and 4.5 m)	1,408,450	199.2	281	
	Interior	113,577,790	176.2	20,012	

472

4. Discussion

4.1 Gradients in carbon storage

We detected strong edge-to-interior trends in the total C-stock and the C-stock in the aboveground biomass (AGBC). These stocks were 39 and 95% higher, respectively, at the edge than in the forest interior. On average, both stocks were elevated up to a distance of 4.5 m from the edge, whereas from this point we did no longer detect significant changes in the average stocks towards the interior. These trends are similar to those found by Remy et al. (2016) reporting that the total C-stock and the aboveground C-stock were respectively, 43% and 56% higher at the forest edge compared to the forest interior. The increase is likely due to the a higher biomass and/or increased productivity near temperate forest edges (Remy et al., 2016; Reinmann and Hutyra, 2017). In our transects, enhanced C-stocks in the proximity of an edge can likely be attributed to an increased stem density and basal area near the edge as DBH did not show clear edge-to-interior patterns (Meeussen et al., 2020).

These patterns strongly contrast with recent findings from the tropics (Smith et al., 2018). In the tropical forest biome, after edge creation, the C-stock in the remaining forest patches is negatively affected due to altered microclimate conditions (i.e. higher wind speed and reduced moisture availability), leading to an increased tree mortality and a change in species composition near edges (i.e. more pioneer species with a lower C-storage potential) (Laurance et al., 1997; Chaplin-Kramer et al., 2015; Brinck et al., 2017; Ordway and Asner, 2020). On the contrary, most temperate broadleaf tree species seem to have a higher resilience against increased wind speeds and could profit from the improved light conditions near edges (*reviewed by* Smith et al., 2018). Contrasting trends in tropical and temperate forest biomes are probably not only caused by species identity effects, but might depend on forest age, soil characteristics and management as well. Our studied edges were embedded in an agricultural landscape and subject to management interventions (e.g. to avoid storm damage to nearby crops or to promote wood quality). Furthermore, the majority of our edges were old forest edges, which have had more time to develop a dense vegetation structure.

Several processes such as edge sealing or expansion might alter edge influences in older forest edges in comparison to young ones (Harper et al., 2005). Both management and forest age might therefore be important factors explaining the differences found between tropical and temperate forests.

For the forest floor, we also found an impact of distance to the edge, though latitude influenced this trend. With decreasing latitude, C-stocks in the forest floor were higher near the edge. A higher stock near the edge in southern regions might be due to a lower decomposition driven by a limiting moisture availability (Riutta et al., 2012). A higher forest floor accumulation near forest edges might also be related to higher disturbances caused by wind, increasing the input but also redistributing the litter (Feeley, 2004; Vasconcelos and Luizão, 2004). Contrary to Remy et al. (2016), no edge-to-interior trends were detected for the mineral C-stock; this might be due to the high spatial variability of this stock potentially masking small-scale variability (e.g. Fahey et al., 2010).

Looking at the other design gradients, we only found a positive impact of elevation on the C-stock in the mineral topsoil. Dieleman et al. (2013) and Tashi et al. (2016) also detected an elevated stock with increasing elevation. They attributed their results to changes in soil characteristics and a decreased microbial activity, as decreasing temperatures slow down decomposition. Although, one might expect to find a reduced C-storage in managed forests, due to the removal of stems, a decrease in litter input and increases in disturbance, we did not find an impact of management type on any of the stocks. Similarly, no impact of management was found in the reviews by Johnson and Curtis (2001) and Mayer et al. (2020). Possible explanations could be that moderate canopy thinning practices, typical for our study sites, might quickly be compensated by enhanced growth, and productivity of the remaining trees or changes in C-storage (especially in the mineral topsoil) or that the effect might only be visible after a longer period (Juodvalkis et al., 2005; Smith et al., 2018; Mayer et al., 2020). Forest clearings or intense management activities, however, creating additional non-forested area, might easily offset the surplus C stored in newly created edges and therefore

525 decrease the C-stock. Natural disturbances (i.e. damage by wind, insects and forest fires) are also
526 likely to increase in coming decades, further weakening the forest C-sink (Seidl et al., 2014).

527 Given the high species diversity and extended design of the study, we needed to apply a generic
528 allometric biomass model (Jenkins et al., 2003), taking into account only the tree species and DBH.
529 Height, for instance, might also affect the biomass, though for simplicity and as these measurements
530 might be subject to large uncertainties (Zianis, 2008) , we chose not to include this parameter.
531 Besides, Bartholmée et al. (2018) applied the multi-species biomass equations successfully in
532 Europe and our comparison with local biomass equations rendered excellent results as well.
533 Furthermore, the magnitude of our stocks is comparable to previous studies in temperate Europe.
534 So, we found similar ranges of C-stocks in the aboveground biomass (7 - 373 Mg ha^{-1}) as found by
535 Remy et al. (2016) in the woody biomass (22 - 400 Mg ha^{-1}) at forest edges in Belgium and
536 Denmark. With values ranging between 34 and 152 Mg C ha^{-1}, we assessed similar quantities of C
537 stored in the mineral topsoil as in Remy et al. (2016) (32 - 202 Mg C ha^{-1}) and Schulp et al. (2008)
538 (53.3 - 97.1 Mg C ha^{-1}, in the Netherlands). Average C-stocks in the forest floor were relatively low
539 (5 Mg ha^{-1}) in comparison to Schulp et al. (2008) (11 - 29 Mg ha^{-1}) and De Vos et al. (2015) (22 Mg
540 ha^{-1}, across 22 European countries). However, we mainly focused on oak-dominated forests with an
541 intermediate litter quality whereas C-stocks in the forest floor are expected to be higher under
542 conifers and beech trees (Vesterdal et al., 2013).

543 *4.2 Impacts for European forest C-stocks*

544 We observed that edge characteristics have a positive impact on C-stocks in the temperate forest
545 biome (Smith et al., 2018). Due to the fact that this biome is heavily fragmented (Haddad et al.,
546 2015), C-uptake could be higher than previously thought for temperate forests. Based on high-
547 resolution 20 × 20 m forest maps, we estimate that the additional C-storage in the 9.4 billion m of
548 deciduous forest edges across Europe amounts to not less than 183 Tg C. This would mean an
549 approximately 1.8 % increase of the C-stock in Europe, which currently amounts to circa 9,900 Tg
550 C (this estimate only takes into account the above- and belowground forest biomass in the EU27

551 while our numbers include forest floor and topsoil C-stocks and are based on more countries than
552 only the EU27) (MCPFE, 2011). In addition, 183 Tg C is equivalent to the C-drawdown potential of
553 an additional 1 million ha of forests (the size of a third of a country such as Belgium). Note that for
554 these area extrapolations, the cumulated length of edges throughout Europe was assumed to remain
555 constant, and edge influences were not taken into account. This is a conservative estimate because
556 our modeled forest edges are straight, the borders of squared 20 × 20 m cells, and thus lack natural
557 variability. Moreover, as our studied forests are ancient forests and south-oriented edges (with
558 higher light levels and a high atmospheric deposition because the prevailing wind direction in
559 Western Europe is (south-) west), we might overestimate the C-stocks at young and northern forest
560 edges. C-stocks might further be impacted by edge-to-interior gradients as edge trees tend to differ
561 in architecture by, for instance, investing more in lateral crown development (Mourelle et al., 2001).
562 However, current allometric models do not take into account such edge influences.

563 With these estimations, we underpin the importance of forest edges for C-sequestration and climate
564 regulation. This study gives support to take into account edge influences when quantifying C-
565 stocks. Moreover, it stresses the need to maintain old forest edges intact, without intensive
566 management, and indicates that also small forests, with a large share of edges, could contribute
567 highly to climate change mitigation (Ziter et al., 2014; Valdés et al., 2020). We do not recommend
568 splitting large forests into smaller pieces but rather highlight that forest managers and policy makers
569 should value smaller forest patches, specifically old ones due to their additional benefits for C-
570 storage. Moreover, creating more natural forest edges, with frayed instead of straight borders
571 between adjacent lands, could increase the proportion of edges.

572 *4.3 Drivers of carbon stocks and their implications*

573 *Nitrogen deposition*

574 We found a strong positive effect of N deposition on the AGBC. An increased atmospheric
575 deposition in forest transition zones could therefore be a significant driver of elevated AGBC-stocks
576 near forest edges. An increase in N availability could promote growth and biomass production

577 (Hyvönen et al., 2008; Thomas et al., 2010) and thus enhance C-storage in the aboveground
578 biomass. Moreover, in additional analyses we found a significant negative interaction effect
579 between N deposition and edge distance, which could indicate that edge influences are strongest in
580 regions where available N is not limiting. However, edge influences in humidity, light or wind
581 might also affect this pattern. Despite the growing evidence that N fertilisation could also affect the
582 C-stock in the forest floor and mineral topsoil due to increased plant growth, input of organic matter
583 and an altered decomposition (Johnson and Curtis, 2001; Manning et al., 2008; Lovett et al., 2013;
584 Mayer et al., 2020), we could not find a direct link between N deposition and these C-stocks in our
585 SEM.

586 In general, high N input levels might thus benefit C-storage, especially when N is limiting the plant
587 growth; however, excessive N can lead to severe environmental damage such as eutrophication and
588 soil acidification causing biodiversity loss and compositional homogenisation (Gao et al., 2015;
589 Gilliam, 2019; Staude et al., 2020). Besides, a reduction in N input does not necessarily decrease
590 the C-storage as this *per se* does not mean a reduction in plant available N (Wamelink et al., 2009).

591 *Macro- and microclimate*

592 We detected a marginally significant negative impact of the MAT on the AGBC, though this might
593 be the result of a correlation between stem density and latitude (Meeussen et al., 2020). Besides
594 macroclimate, it is likely that the microclimate and an increased light availability will contribute to
595 changes in productivity near forest edges (Remy et al., 2016; Reinmann and Hutyra, 2017; Smith et
596 al., 2018). Near forest edges, the combination of a favourable microclimate and N enrichment could
597 thus promote a higher standing stock. Furthermore, we found a negative impact of soil temperature
598 on the mineral topsoil C-stock. This indicates that with increasing soil temperature, less C is stored
599 in the mineral topsoil. Temperature is generally acknowledged as a global driver of soil C-stocks,
600 with large stocks in high-latitudinal and -elevational regions (Jobbágy and Jackson, 2000; Pan et al.,
601 2011; Dieleman et al., 2013; Tashi et al., 2016), though our results show that the local
602 microclimatic conditions might also play a crucial role. Future temperature rises could lead to a

603 more beneficial soil microclimate for microbial respiration and C-mineralisation in colder regions
604 (Nadelhoffer et al., 1991; Smith et al., 2019; Mayer et al., 2020). The stimulating effect of climate
605 warming is shown by our additional analyses as well; we found a strong positive effect of MAT on
606 soil temperature, which has a negative effect on C-stock in the mineral topsoil layers. In water-
607 stressed areas, the temperature feedback could be even stronger (shown by a negative impact of the
608 MAP on the soil temperature) as these sites are more sensitive to temperature changes (von Arx et
609 al., 2013). Besides, there is a marginally significant direct positive influence of the MAP on C-stock
610 in the mineral topsoil. Humid conditions can promote net primary production or cause a reduced
611 decomposition by affecting soil chemical properties (e.g. formation of stabilizing components,
612 leaching of basic cations, increased weathering, higher soil acidity) (Jobbágy and Jackson, 2000;
613 Meier and Leuschner, 2010; Doetterl et al., 2015).

614 Our results suggest that changes in temperature and precipitation could both have impacts on C-
615 stocks near forest edges. They add to the growing evidence that soil C losses will increase when
616 global temperatures keep on rising, further catalysing climate change (Crowther et al., 2016). As
617 warming rates are higher in high-latitude ecosystems (*synthesized by* Serreze and Barry, 2011),
618 where soil C-stocks are generally larger (Pan et al., 2011), especially so in the deep soil layers of
619 the permafrost, soil warming is likely to further amplify climate change throughout a positive
620 feedback loop.

621 *Management and species selection*

622 Plant area index and litter quality were two drivers of C-stocks in the forest floor. Forests with a
623 high plant area index, which is mainly driven by foliage biomass (Kalácska et al., 2005), have a
624 high litter production, positively affecting the forest floor biomass and subsequently C-stock. A
625 high plant area index can be the result of a reduced management but is also related to species
626 composition. Certain species create denser forest canopies because of a higher branching density or
627 leaf biomass (Mourelle et al., 2001; Niinemets, 2010). Also mixing different tree species can
628 generate a well-filled forest canopy (Jucker et al., 2015). However, not only the quantity of organic

matter input is of importance, but also the quality (Schulp et al., 2008; Vesterdal et al., 2013). Previous research showed that tree species, and more specifically the chemical composition of their litter, strongly affect the rate of decomposition (*synthesised by* Vesterdal et al., 2013). This is demonstrated by the negative relationship between litter quality and the C-stock in the forest floor in our model. Selecting species with a low litter quality (*e.g. Fagus sylvatica*) can thus benefit forest floor accretion, albeit a low quality can affect soil acidity as shown by the positive impact of litter quality on pH in our additional analyses. Soil acidification causes alterations in nutrient cycling and can subsequently influence understorey growth and diversity, negatively affect soil organisms or eventually lead to a decline in tree species (Sverdrup et al., 1994; Joner et al., 2005; Houle et al., 2007; Bowman et al., 2008; Selvi et al., 2016).

Tree species composition and forest management do not only affect the C-stock in the forest floor via their impact on litter quantity and quality but can also affect the C-stock in the mineral topsoil. One way is indirectly via the microclimate, revealed by the negative impact of plant area index on soil temperature. Keeping forests dense with a high biomass and complex structure, could impede forest microclimates from reaching extreme temperatures (Frey et al., 2016; Kovács et al., 2017). Harvests, on the other hand, reduce canopy cover and increase the solar radiation on the forest floor, enhancing soil warming (*reviewed by* Mayer et al., 2020). Therefore, the impact of climate (change) on C-stocks will be determined by its interaction with forest structure. Managers should thus keep forests divers and heterogeneous enough to temporarily mitigate soil warming and to safeguard C-stocks in the mineral topsoil.

5. Conclusion

Despite forest edges constitute a large part of fragmented landscapes, only few studies focussed on edge-to-interior gradients in C-stocks in temperate forests. We found that C-stocks in temperate forests edges are higher than in forest interiors, especially due to an elevated C-stock in the aboveground biomass, representing the equivalent of the carbon stocks of an additional 1 million ha of forests. This is likely the outcome of elevated N deposition, increased light availability and

altered microclimate conditions in the proximity of edges. However, the aboveground biomass is a dynamic and sensitive C-pool and C-storage in temperate forests is still under threat as it is likely that climate change will negatively affect C-stocks in forests. Management and species selection, for instance choosing for a high plant area index, could temporarily mitigate the effect of climate change inside forests and increase C-stocking in the forest floor and mineral topsoil. Moreover, small forest patches should be preserved and edges without sharp boundaries implemented where possible. Our study provides continental-scale evidence of elevated C-stocks near temperate forest edges, showing the importance of small forest fragments and stressing that edge dynamics cannot be neglected when estimating the C-storage in temperate forests.

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