Drivers of carbon stocks in forest edges across Europe

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HIGHLIGHTS

- Carbon stocks were studied in temperate deciduous forest edges across Europe.
- Total and aboveground biomass C-stocks were higher near forest edges.
- N-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.

GRAPHICAL ABSTRACT
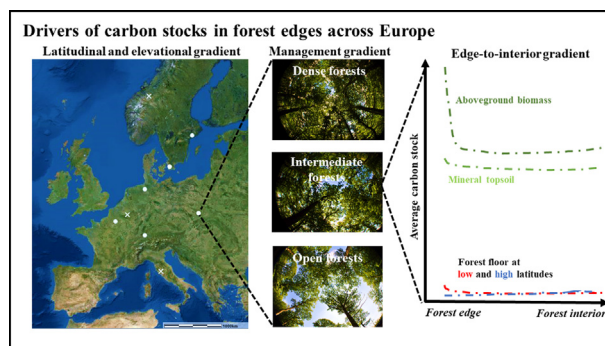
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ABSTRACT

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 into 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 carbon in the aboveground biomass stock were on average 39% and 95% higher at the forest edge than 100 m into 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

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latitude: 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 carbon, which is equivalent to the 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 natural forest edges and small forest patches with a high edge-to-interior surface area.

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). During the last decades, forests sequestered roughly 30% of the anthropogenic C-emissions (Pan et al., 2011), and they therefore 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. suppressed 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. On the one hand, 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). Lastly, 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 C in the aboveground biomass (i.e. woody biomass and foliage), forest floor and mineral topsoil layer in 45 temperate forest edges across Europe. The edges were subject to different management regimes and situated along a latitudinal gradient from Italy to Norway. Additionally, we tested the combined impact of large-scale drivers (e.g. macroclimate) and several local drivers (e.g. microclimate) on the C-stocks. Finally, we quantify the consequences of edge influences for estimates of C-stocks in Europe 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? And 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

As the macroclimate is an important driver of C-stocks (Pan et al., 2011), we studied deciduous forests along a 2300 km wide latitudinal gradient from central Italy (42° N) to central Norway (63° N) (mean annual temperature difference ≈ 13 °C), crossing the temperate forest biome and including forests at the transition zones with the sub-Mediterranean and boreo-nemoral forest system. 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 to capture climatic variation resulting from elevational differences (elevation range: 21–908 m above sea level, expected temperature difference ≈ 5.76 °C (ICAO, 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, as management might strongly impact C-storage (Mayer et al., 2020). 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 a matrix of agricultural land. In each transect, five circular plots with a 9 m radius were established to sample the C-stocks ($n = 225$). All plots were 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 (Fig. 1). The last plot, situated at 99.5 m from the forest edge, was considered as representative of the forest's interior. An interior distance of c. 100 m was selected as it is in line with other studies finding edge influences both in C-stocks as well as in the microclimate to dissipate within such a distance (Ziter et al., 2014; Remy et al., 2016; Reinmann and Hutyra, 2017; Schmidt et al., 2019; Smith et al., 2019).

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 (i.e. five measurement points per transect). 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.

2.2.1.1. 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 the circular 9 m radius plot. 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, clustered within four transects) 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 with an average DBH to all individual stems of the multi-stemmed tree. Subsequently, the aboveground biomass (AGB, including foliage) was calculated for every tree based on its DBH via a multi-species biomass equation (Eq. (1), with β_0 and β_1 group-specific parameters (see Table A2) and
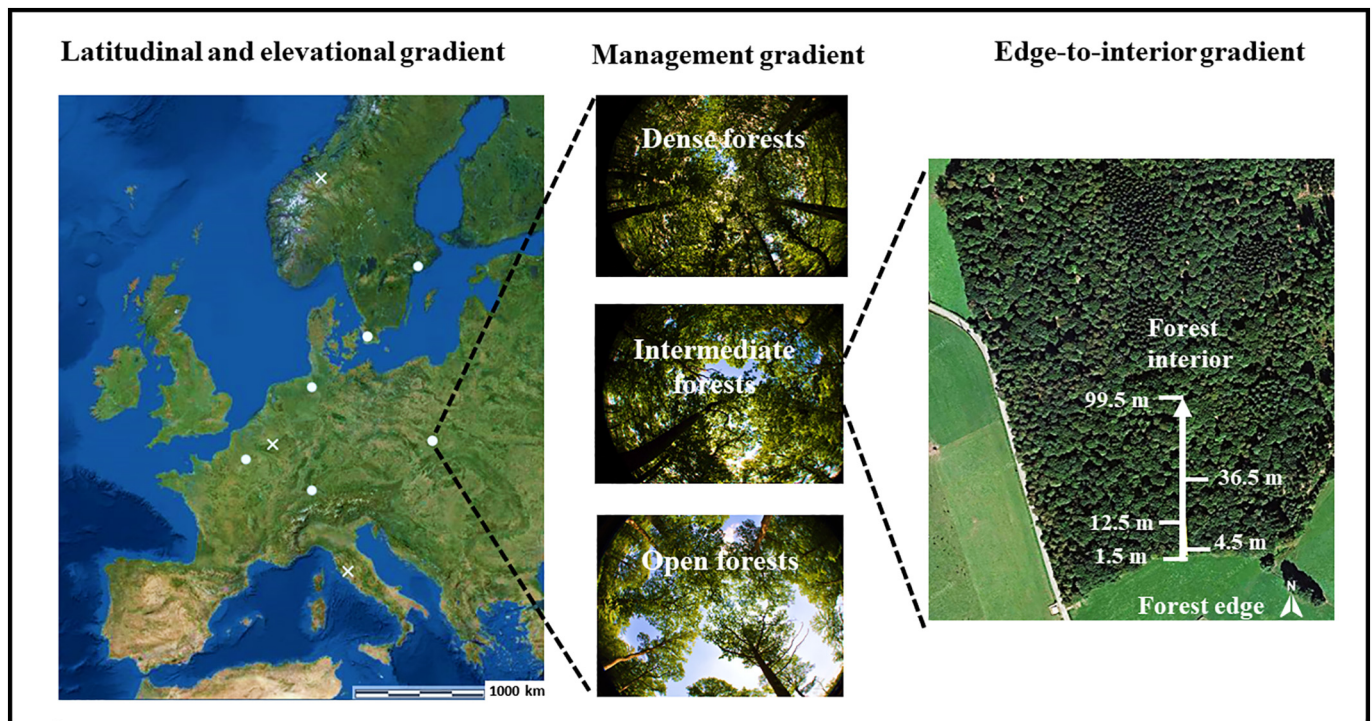
Fig. 1. Study design with the four design variables (latitude, elevation, management and distance to the edge). Left: The nine regions along a latitudinal gradient, including three elevational gradients (white crosses on the map). Background map from: http://databasin.org. Middle: The three forest management 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.

DBH the diameter at breast height in cm, 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.

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

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 more than 40 tree species, making it practically 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, however no comparison against destructive sampling in Europe was done. To further justify 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.

2.2.1.2. 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. To be sure that the sample was representative for the selected distances, we sampled in a smaller quadrat (3 by 3 m) in the centre of the larger circular 9 m radius plot. The litter, fragmentation and humus layer were sampled and weighted after drying to constant weight for 48 h 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)).

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

2.2.1.3. Mineral topsoil carbon. For the C-stock in the mineral topsoil layers, five subsamples were taken in each plot, more specifically within the smaller 3 by 3 m quadrats. Sampling occurred 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 h. 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.

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

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

2.2.1.4. 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 C-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. Drivers were mainly selected based on the literature, suggesting that the local and regional climate, N-deposition, soil characteristics and forest management are important factors affecting the different C-stocks (Pan et al., 2011; Vesterdal et al., 2013; Smith et al., 2019; Mayer et al., 2020).

2.2.2.1. 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.

Modeled 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).

2.2.2.2. 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. More technical details on the terrestrial laser scanning campaign and data processing 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).

2.2.2.3. 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–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 5 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 by 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, 2020). 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). For distance to the edge, as well as for latitude and elevation continuous variables were used in the models. 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 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).

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

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 models, with the AGBC, the C-stock in the forest floor and the C-stock in the mineral topsoil, are similarly structured. The component model for the AGBC consisted of seven predictor variables: the three regional variables (N-deposition,
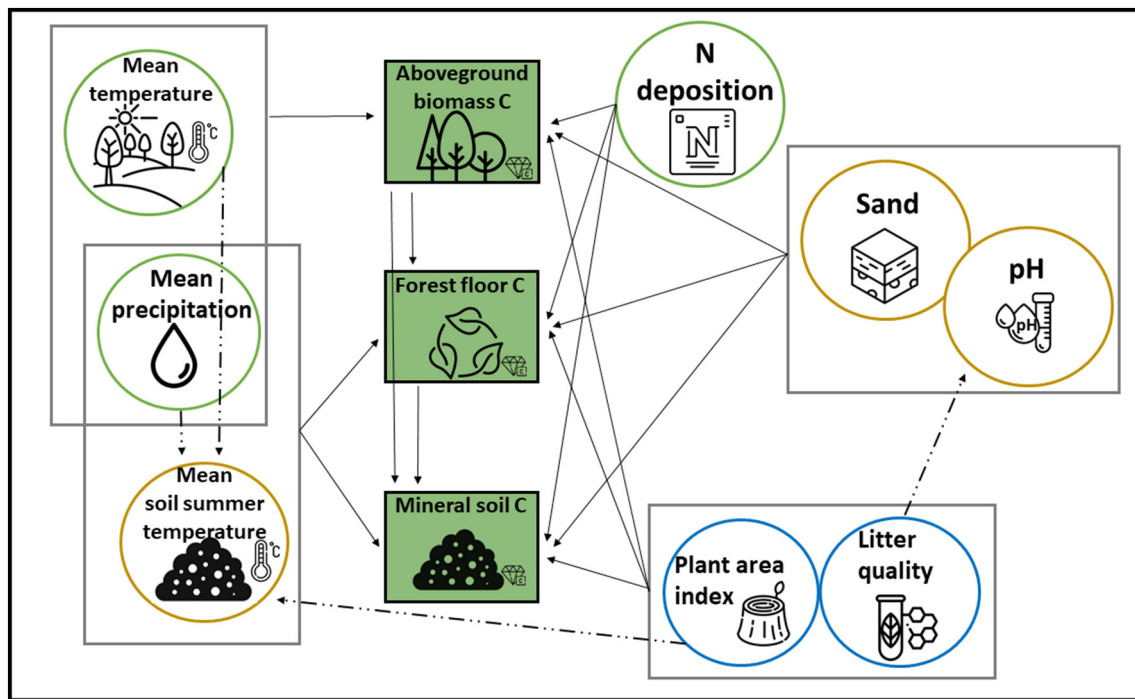
Fig. 2. Full piecewise SEM of the determinants of carbon (C) stocks in the aboveground biomass (AGB, Mg C ha^{-1}), the forest floor (Mg C ha^{-1}) and the mineral topsoil (Mg C ha^{-1}) in deciduous forest edges across Europe. We tested the impact of three large-scale drivers, indicated by green circles (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 among 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.

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

The model fit was assessed via Shipley's test of directed separation, which is a test for conditional independence, meaning that no missing relationships can be detected in the model. If the *p*-value 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).

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). The average percentual increase in total C-storage from the interior (plot 5, at 99.5 m from the edge) to the edge (plot 1, at 1.5 m from the edge) amounted to 39%.

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, the stock almost doubled (+95%) from the interior to
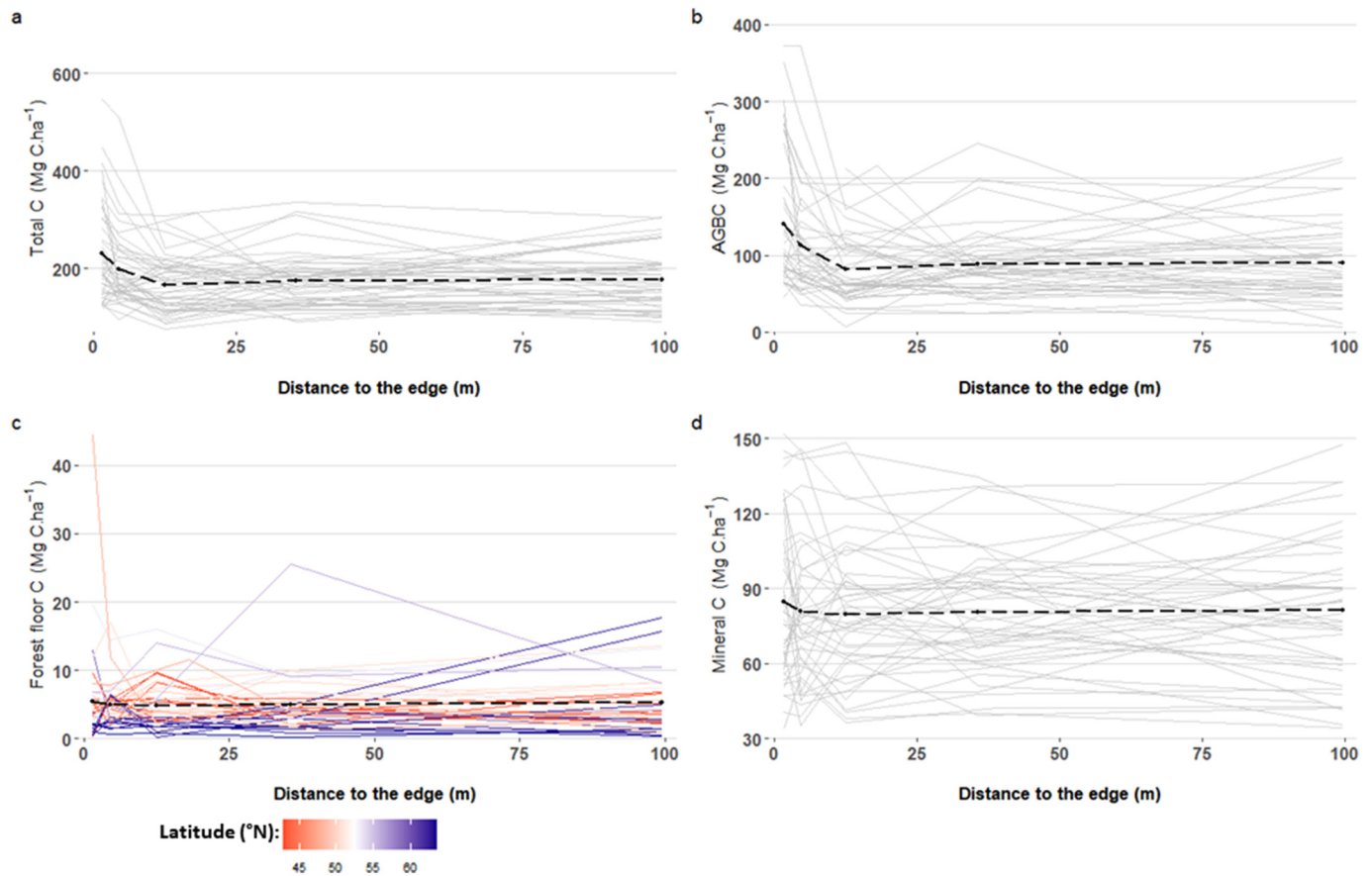
Fig. 3. Edge-to-interior patterns of a) the total carbon (C) stock (Mg C ha^{-1}), b) aboveground biomass C-stock (AGBC, Mg C ha^{-1}), c) forest floor C-stock (Mg C ha^{-1}) and d) mineral topsoil C-stock (Mg C ha^{-1}). The black dashed lines indicate the average stock across sites and management types 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.

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).

3.2. Piecewise structural equation models: drivers of carbon storage

Our piecewise SEM, without relationships among 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. In the forest floor, C-stocks 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.

3.3. Additional carbon storage in forest edges across Europe

Based on the high-resolution forest Copernicus map, we found that broadleaved forests cover an area of approximately 118 million ha across Europa and their edge perimeter amounts to approximately 9.4 billion m. When not considering edge influences, European deciduous forest store approximately 20,757 Tg C. However, if edge influences in broadleaved forests were taken into account, an additional 183 Tg C was stored (Table 1).
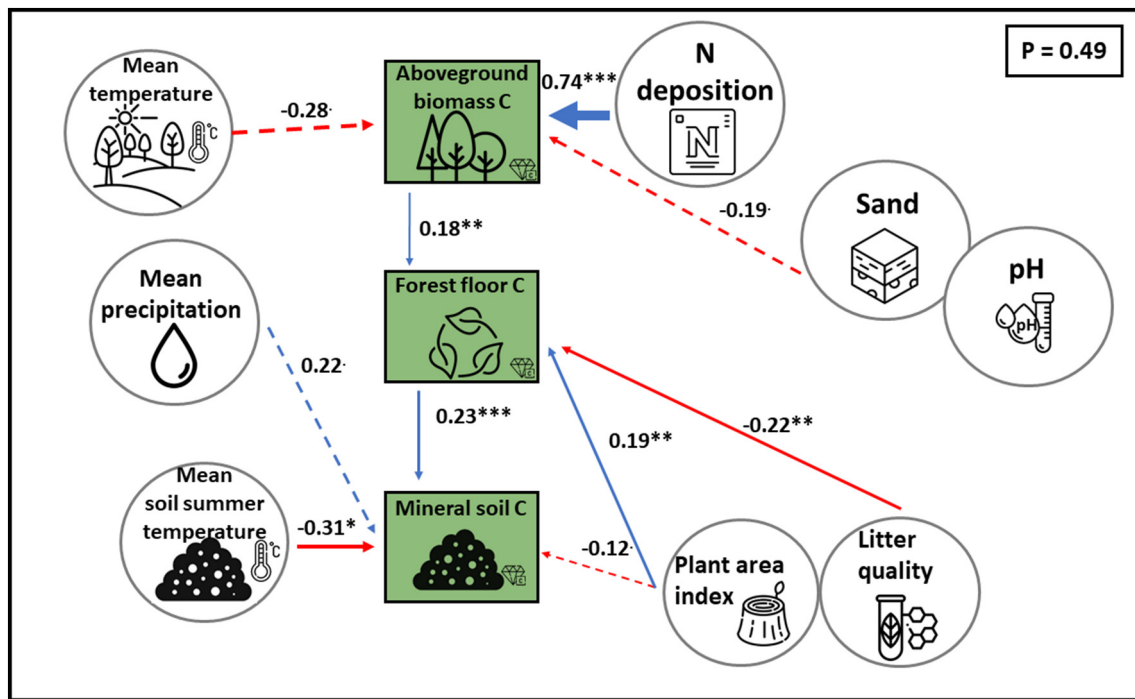
Fig. 4. Basic piecewise SEM of the determinants of carbon stocks in the aboveground biomass (AGBC), the forest floor and the mineral topsoil in deciduous forests edges across Europe. Solid arrows indicate significant pathways ($p < 0.05$) while marginally significant paths ($p < 0.1$) are represented by dashed arrows. All other non-significant paths were omitted from the fig. A negative impact is visualized in red, whereas blue indicates a positive relationship. The thickness of arrows corresponds to the effect size. Standard estimates of path coefficients and their p-values ($p < 0.001 = $ ***, $p < 0.01 = $ **, $p < 0.05 = $ *, $p < 0.1 = $.) are mentioned above each arrow. The marginal R^2 and conditional R^2 are 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-stock in the mineral topsoil.

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 (average percentual increase), 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), but might also be influenced by the presence of large trees (Ziter et al., 2014; Lutz et al., 2018; Saeed et al., 2019). In our transects, stem diameters did not show clear edge-to-interior patterns, whereas we did find an increased stem density near the forest edge (Meeussen et al., 2020). Therefore, we assume that the enhanced C-stocks in the proximity of the edge can likely be attributed to a higher basal area resulting from a higher stem density rather than the presence of large trees.

These patterns strongly contrast with recent findings from the subtropics (Saeed et al., 2019) and tropics (Smith et al., 2018; Silva Junior et al., 2020). 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 broadleaved tree species seem to have a higher resilience against increased wind speeds and could profit from the improved light conditions near edges (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 adjust to the changed environmental conditions and 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

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

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

[a] See Section '2.3 High-resolution forest maps and estimates of carbon storage in deciduous forest edges across Europe'.

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. This could be the result of changes in soil characteristics and a decreased microbial activity, as decreasing temperatures slow down decomposition (Dieleman et al., 2013; Tashi et al., 2016). 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. One possible explanation could be that the effect of management becomes only visible after a longer period, especially in the mineral topsoil. Or, alternatively, that moderate canopy thinning practices, typical for our study sites, might quickly be compensated by enhanced growth and productivity of the remaining trees (Juodvalkis et al., 2005; Smith et al., 2018; Mayer et al., 2020). Large forest clearings or intense management activities, however, although creating new forest edges, might easily offset the surplus C stored in these newly created edges and therefore decrease the C-stock. Also natural disturbances (e.g. damage by wind, insects and forest fires), which are likely to increase in coming decades (Seidl et al., 2014), can further weaken the forest C-sink by creating large canopy openings, too vast to be compensated by additional C-storage in forest edges.

4.2. Impacts for European forest C-stocks

We observed that edge characteristics have a positive impact on C-stocks in the temperate forest biome (Smith et al., 2018). Due to the fact that this biome is heavily fragmented (Haddad et al., 2015), C-uptake could be higher than previously thought for temperate forests. Based on high-resolution forest maps, we estimate that the length of deciduous forest edges across Europe amounts to 9.4 billion metres, implying that not less than 183 Tg of additional C is stored in deciduous forest edges across Europe. This would result in an approximately 1.8% increase of the C-stock in Europe, which currently amounts to circa 9900 Tg C (this estimate takes into account the above- and belowground forest biomass in the EU27 while our numbers include aboveground biomass, forest floor and topsoil C-stocks and are based on more countries than only the EU27) (MCPFE, 2011). In addition, 183 Tg C is equivalent to the C-drawdown potential of an additional 1 million ha of forests (the size of a third of a country such as Belgium). Note that for these area extrapolations, the cumulated length of edges throughout Europe was assumed to remain constant, and edge influences were not taken into account. This is, however, a conservative estimate because our modeled forest edges are straight, the borders of squared 20 by 20 m cells, and thus lack natural variability. On the other hand, as our studied forests are ancient forests and south-oriented edges (with higher light levels and a high atmospheric deposition because the prevailing wind direction in Western Europe is (south-) west), we might overestimate the C-stocks at young and northern forest edges. C-stocks might further be impacted by edge-to-interior gradients as edge trees tend to differ in architecture by, for instance, investing more in lateral crown development (Mourelle et al., 2001). However, current allometric

models for predicting aboveground biomass do not consider such edge influences, leading to possible over- or underestimations of C-stocks near forest edges.

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

4.3. Drivers of carbon stocks and their implications

4.3.1. Nitrogen deposition

We found a strong positive effect of N-deposition on the AGBC. An increased atmospheric deposition in forest transition zones could therefore be a significant driver of elevated AGBC-stocks near forest edges. An increase in N-availability could promote growth and biomass production (Hyvönen et al., 2008; Thomas et al., 2010) and thus enhance C-storage in the aboveground biomass. Moreover, in additional analyses we found a significant negative interaction effect between N-deposition and edge distance. This could indicate that edge influences are stronger in regions where available N is not limiting. Although, this interaction effect might also be strengthened by other edge related gradients such as edge influences in humidity, light or wind. For the forest floor and mineral topsoil, we could not find a direct impact of N-deposition, contrasting previous studies. Indeed, there is growing evidence that N-fertilisation could affect the C-stocks in the forest floor and mineral topsoil due to increased plant growth, input of organic matter and an altered decomposition (Johnson and Curtis, 2001; Manning et al., 2008; Lovett et al., 2013; Mayer et al., 2020).

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

4.3.2. Macro- and microclimate

We detected a marginally significant negative impact of the MAT on the AGBC, though this might be the result of a correlation between stem density and latitude (Meeussen et al., 2020). Besides macroclimate, it is likely that the microclimate and an increased light availability will contribute to changes in productivity near forest edges (Remy et al., 2016; Reinmann and Hutyra, 2017; Smith et al., 2018). Near forest edges, the combination of a favourable microclimate and N-enrichment could thus promote a higher standing stock. Furthermore, we found a negative impact of soil temperature on the mineral topsoil C-stock. This indicates that with increasing soil temperature, less C is stored in the mineral topsoil. Temperature is generally acknowledged as a global driver of soil C-stocks, with large stocks in high-latitudinal and -elevational regions (Jobbágy and Jackson, 2000; Pan et al., 2011; Dieleman et al., 2013; Tashi et al., 2016), though our results show that the local microclimatic conditions might also play a crucial role. Future temperature rises could lead to a more beneficial soil microclimate for microbial respiration and C-mineralisation in colder regions (Nadelhoffer et al., 1991; Smith et al., 2019; Mayer et al., 2020). The stimulating effect of climate warming is shown by our additional

analyses as well; we found a strong positive effect of MAT on soil temperature, which has a negative effect on C-stock in the mineral topsoil layers. In water-stressed areas, the temperature feedback could be even stronger (shown by a negative impact of the MAP on the soil temperature) as these sites are more sensitive to temperature changes (Von Arx et al., 2013). Besides, there is a marginally significant direct positive influence of the MAP on C-stock in the mineral topsoil. Humid conditions can promote net primary production or cause a reduced decomposition by affecting soil chemical properties (e.g. formation of stabilizing components, leaching of basic cations, increased weathering, higher soil acidity) (Jobbágy and Jackson, 2000; Meier and Leuschner, 2010; Doetterl et al., 2015). We could not find a direct link between mean annual precipitation and the stock in the AGB or forest floor. Yet, as suggested earlier, small-spatial gradients in humidity near forest edges could be responsible for the increased forest floor C-stock in southern regions.

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

4.3.3. Management and species selection

Plant area index and litter quality were two drivers of C-stocks in the forest floor. Forests with a high plant area index, which is mainly driven by foliage biomass (Kalácska et al., 2005), have a high litter production, positively affecting the forest floor biomass and C-stock. A high plant area index can be the result of a reduced management but is also related to species composition. Certain species create denser forest canopies because of a higher branching density or leaf biomass (Mourelle et al., 2001; Niinemets, 2010). Also mixing different tree species can 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 (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 litter 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 (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.

4.4. Limitations and opportunities for future research

As we currently lack information on how C-stocks are impacted by edge influences in Europe, we focused in this study on edge-to-interior gradients in three of the major C-pools (the aboveground biomass, forest floor and topsoil C-stock) along a latitudinal gradient. For feasibility reasons across 225 European forest plots, we did not consider other stocks such as the belowground living biomass stock (roots) or the stock in understorey herbs and very small shrubs and trees with a DBH below 7.5 m. These stocks, although they generally only represent less than 10% of C-stocks in forests (Vande Walle et al., 2001; Lal and Lorenz, 2012; Landuyt et al., 2019) might also be influenced by environmental changes near forest edges (Remy et al., 2016; Saeed et al., 2019). Considering these stocks in future research could nevertheless further contribute to filling this knowledge gap and improve our predictions on C-stocks near forest edges.

Moreover, given the high species diversity and extended design of the study, we needed to apply a generic allometric biomass model (Jenkins et al., 2003) taking into account only the tree species and DBH. Height, for instance, might also affect the biomass, though for logistic reasons and as these measurements might be subject to large uncertainties (Zianis, 2008), we chose not to include this variable. Besides, multi-species biomass equations were already successfully applied in Europe (Bartholomée et al., 2018) and our comparison with local biomass equations rendered excellent results as well. Furthermore, the magnitude of our stocks is comparable to previous studies, situated within the same regions of Europe and in the temperate forest biome. So, we found similar ranges of C-stocks in the aboveground biomass (7–373 Mg ha^{-1}) as found by Remy et al. (2016) in the woody biomass (22–400 Mg ha^{-1}) at forest edges in Belgium and Denmark. With values ranging between 34 and 152 Mg C ha^{-1}, we assessed similar quantities of C stored in the mineral topsoil as in Remy et al. (2016) (32–202 Mg C ha^{-1}) and Schulp et al. (2008) (53.3–97.1 Mg C ha^{-1}, in the Netherlands). Average C-stocks in the forest floor were relatively low (5 Mg ha^{-1}) in comparison to Schulp et al. (2008) (11–29 Mg ha^{-1}) and De Vos et al. (2015) (22 Mg ha^{-1}, across 22 European countries). However, under conifers and beech, C-stocks in the forest floor are expected to be higher (Vesterdal et al., 2013) and those are not included here; we mainly focused on oak-dominated forests with an intermediate litter quality.

Comparing C-stocks among different studies is difficult, as contrasting methods are often used to assess each stock. Alternatively, edge effects can also be caused by underlying factors such as land use history, (adjacent) land management or edge age (Schulp et al., 2008; Vesterdal et al., 2013). This makes it harder to compare results on how edge influences affect C-stocks and might be partly responsible for the contrasting results found both within and among forest biomes. A global study assessing C-stocks in forest edges across different forest biomes, following a consistent methodology to collect harmonized, high quality and comparable data would therefore be interesting to understand the current discrepancies.

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. No edge-to-interior trends were found for the mineral topsoil. Edge gradients in the forest floor C-stock were impacted by the latitude, probably resulting from small-scale gradients in humidity. We found however that C-stocks in temperate forests edges are higher than in forest interiors, due to an elevated C-stock in the aboveground biomass, representing the equivalent of the C-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. In sum, both large-scale drivers (e.g. N-deposition) as well as local drivers (e.g. microclimate) should therefore be considered when protecting C-stocks near forest edges. Our study provides continental-scale evidence of elevated C-stocks near temperate forest edges, stressing that edge dynamics cannot be neglected when estimating the C-storage in temperate forests. Hence, small forest patches should be preserved and edges without sharp boundaries implemented where possible.

CRediT authorship contribution statement

Camille Meeussen: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft, Writing - review & editing. **Sanne Govaert:** Conceptualization, Investigation, Writing - review & editing. **Thomas Vanneste:** Investigation, Writing - review & editing. **Stef Haesen:** Formal analysis, Writing - review & editing. **Koenraad Van Meerbeek:** Formal analysis, Writing - review & editing. **Kurt Bollmann:** Investigation, Writing - review & editing. **Jörg Brunet:** Investigation, Writing - review & editing. **Kim Calders:** Formal analysis, Investigation, Writing - review & editing. **Sara A.O. Cousins:** Investigation, Writing - review & editing. **Martin Diekmann:** Investigation, Writing - review & editing. **Bente J. Graae:** Investigation, Writing - review & editing. **Giovanni Iacopetti:** Investigation, Writing - review & editing. **Jonathan Lenoir:** Investigation, Writing - review & editing. **Anna Orczewska:** Investigation, Writing - review & editing. **Quentin Ponette:** Investigation, Writing - review & editing. **Jan Plue:** Investigation, Writing - review & editing. **Federico Selvi:** Investigation, Writing - review & editing. **Fabien Spicher:** Investigation, Writing - review & editing. **Mia Vedel Sørensen:** Investigation, Writing - review & editing. **Hans Verbeeck:** Writing - review & editing. **Pieter Vermeir:** Investigation, Writing - review & editing. **Kris Verheyen:** Conceptualization, Methodology, Investigation, Writing - review & editing. **Pieter Vangansbeke:** Conceptualization, Methodology, Investigation, Writing - review & editing. **Pieter De Frenne:** Conceptualization, Methodology, Investigation, Writing - review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data related to this manuscript are available on Figshare: https://doi. org/10.6084/m9.figshare.13246814.v1.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.scitotenv.2020.143497.

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