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Drivers of carbon stocks in forest edges across Europe

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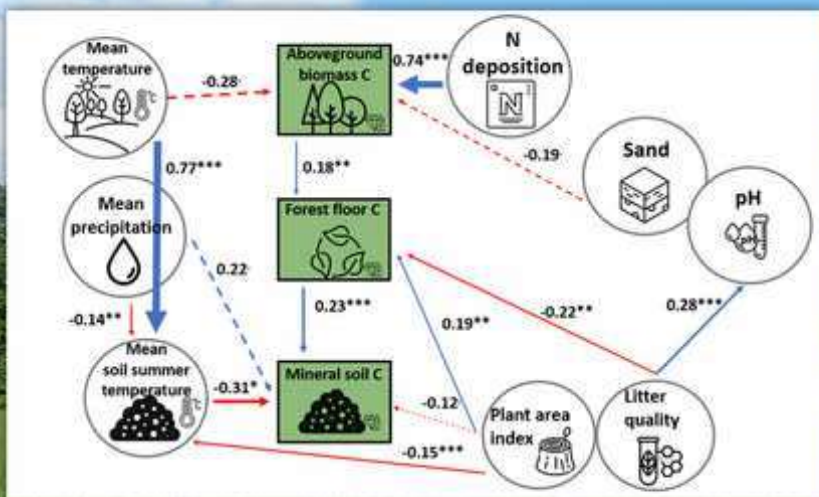
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Drivers of carbon stocks near forest edges across Europe



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

1 Drivers of carbon stocks in forest edges 2 across Europe 3

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41 Abstract

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

63 Keywords

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

66 1. Introduction

67 Forests play a key role in the carbon (C) cycle as they store large quantities of C in the living
68 aboveground biomass (stems, branches and leaves), forest soil, roots, dead wood and the litter layer
69 (Fahey et al., 2010). By storing roughly 30% of the anthropogenic C-emissions during the last
70 decades (Pan et al., 2011), forests serve as an important C-sink and regulator of the global climate
71 system. However, C-storage is strongly determined by the environment. Across large spatial extents
72 (i.e. latitude and elevation), C-storage is impacted by the climate (Jobbágy and Jackson, 2000; Pan
73 et al., 2011; Dieleman et al., 2013; Tashi et al., 2016) as temperature and humidity drive primary
74 production, decomposition and respiration (Luysaert et al., 2007; Smith et al., 2019). For instance,
75 high belowground C-stocks are found in the soil in cold biomes at higher latitudes and elevations
76 and high C-stocks in the aboveground biomass are found in the tropics (Pan et al., 2011; Dieleman
77 et al., 2013; Tashi et al., 2016), resulting in latitudinal and elevational trade-offs in distribution
78 between above- and belowground C-stocks. Tree species composition, soil characteristics and
79 management are major drivers of C-stocks as well (Schulp et al., 2008; Vesterdal et al., 2013; De
80 Vos et al., 2015; Mayer et al., 2020). Forest management does not only reduce the aboveground
81 stock by removal of tree stems, but can also influence the input rate of organic matter and the
82 release rate of C from the soil (Jandl et al., 2007; Schulp et al., 2008; Naudts et al., 2016; Mayer et
83 al., 2020). Forest management and fragmentation also have an impact on forest microclimates
84 (Matlack, 1993; Chen et al., 1999; Kovács et al., 2017), further affecting C-storage (Cahoon et al.,
85 2012; Smith et al., 2019). Finally, also nitrogen (N) deposition seems to play an important role in C-
86 storage processes, via an enhanced tree growth or changes in litter decomposition (i.e. suppressed or
87 increased enzyme activity), affecting the C-storage potential (Magnani et al., 2007; Manning et al.,
88 2008; Mayer et al., 2020).

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

92 influences that penetrate far towards the interior (Schmidt et al., 2017). Forest edges differ in
93 vegetation structure and composition, compared to interiors (Harper et al., 2005; Meeussen et al.,
94 2020). Furthermore, due to the strong differences in structure between forest edges and adjacent
95 lands, edges further receive higher levels of atmospheric N deposition (Weathers et al., 2001;
96 Devlaeminck et al., 2005; De Schrijver et al., 2007; Wuyts et al., 2008). Finally, the forest edge
97 microclimate will substantially differ from the microclimate in both open areas and forest interiors,
98 due to changes in air-mixing, solar radiation and humidity (Matlack, 1993; Chen et al., 1999;
99 Schmidt et al., 2017). Such edge influences can consequently affect productivity, decomposition
100 and C-storage.

101 Especially in temperate deciduous forests that are overall strongly fragmented (Haddad et al., 2015),
102 the question on how above- and belowground C-stocks are impacted by edge influences is currently
103 unresolved (Ziter et al., 2014). The few studies focussing on C-storage and -cycling near edges in
104 temperate forests often gave contrasting results. Ziter et al. (2014) for instance, found no change in
105 edge-to-interior aboveground C-storage whereas Reinmann and Hutrya (2017) and Remy et al.
106 (2016) found an increased C-stock in the aboveground biomass in the proximity of an edge. They
107 attributed this increase to an enhanced productivity and/or higher stem density in forest edges, the
108 result of improved light conditions and elevated N inputs (Remy et al., 2016; Reinmann and Hutrya,
109 2017). Contrasting patterns in forest floor C-stocks were found as well. Faster decomposition of
110 litter in the forest interior, leading to lower forest floor stocks, might be caused by a higher soil
111 moisture content because a large part of the incoming solar radiation is captured and reflected by
112 the canopy (Riutta et al., 2012). On the other hand, higher forest floor C-stocks in the interior were
113 found by Remy et al. (2016), likely impacted by faster decomposition near the edge due to a
114 complex interplay of specific edge conditions (i.e. decomposer macrofauna community, soil pH,
115 microclimate and atmospheric deposition) (Remy et al., 2016, 2018). Finally, also the mineral
116 topsoil layer will be affected by fragmentation and edge conditions; Remy et al. (2016) found
117 evidence for an elevated C-concentration and -storage in the mineral topsoil at the edge of the

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

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

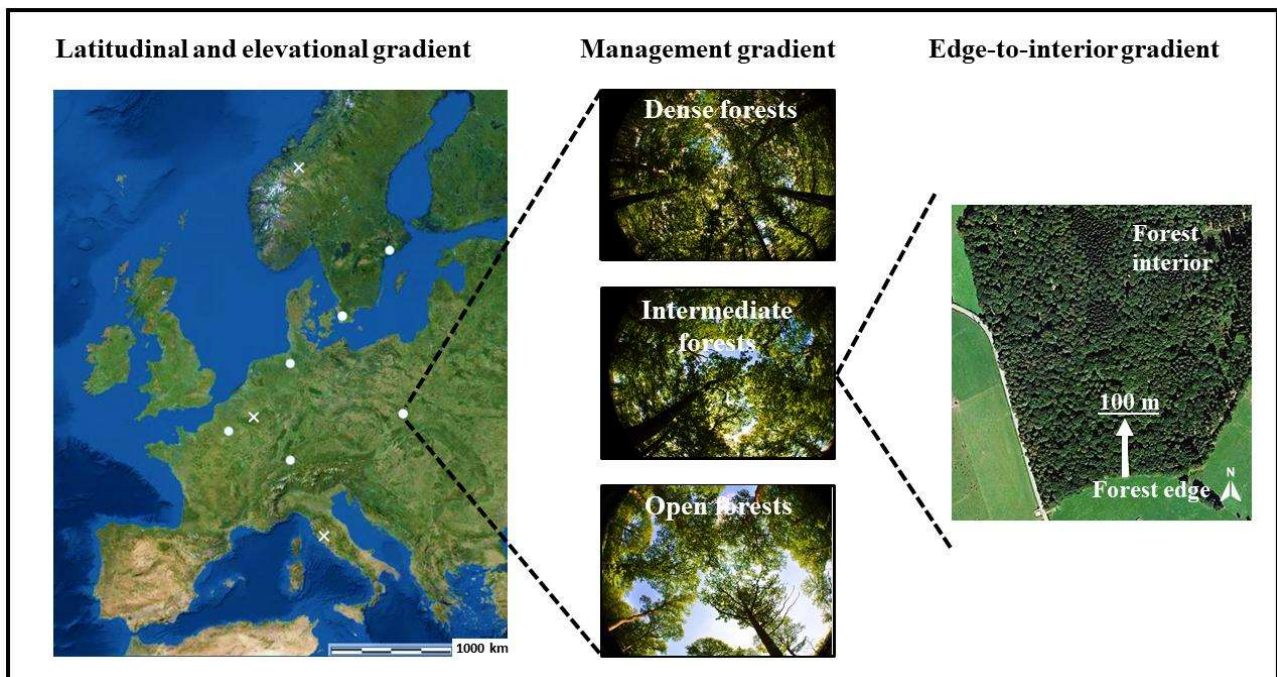
138 2. Materials and Methods

139 2.1 Study design and area

140 We studied forests along a 2300 km wide latitudinal gradient from central Italy (42 °N) to central
141 Norway (63 °N) (Δ mean annual temperature \approx 13 °C). Along this south-north gradient, nine
142 regions were selected: Central Italy, Northern Switzerland, Northern France, Belgium, Southern
143 Poland, Northern Germany, Southern Sweden, Central Sweden and Central Norway. In three
144 regions, i.e. Norway, Belgium and Italy, an elevational gradient was established as well covering
145 low, intermediate and high elevational sites. This to include the climatic variation resulting from
146 elevational differences (21 - 908 m above sea level (m a.s.l.) Δ temperature \approx 5.76 °C (ICAV,
147 1993))(Fig. 1).

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

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



163
 164 **Figure 1:** Study design with the four design variables (latitude, elevation, management and distance to the edge). Left:
 165 The nine regions along a latitudinal gradient, including three elevational gradients (white crosses on the map).
 166 Background map from: <http://databasin.org>. Middle: The three forest management types. Right: A 100-m long gradient
 167 (arrow) from the edge towards the interior was established in each forest. Picture of one of the Belgian transects from
 168 Google Earth.

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

175 *2.2 Data collection*

176 *2.2.1 Carbon stocks*

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

180 *Aboveground biomass carbon*

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

$$197 \quad \text{Total AGB (kg dry weight)} = \exp(\beta_0 + \beta_1 \times \ln(DBH)) \quad (1)$$

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

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

207 Bartholomée et al. (2018) the multi-species biomass equations rendered comparable results for
208 European species-specific equations (mainly Zianis et al. (2005)), even though no comparison
209 against destructive sampling in Europe was done. To further verify the use of these multi-species
210 biomass equations, we calculated the AGB for the Belgian plots using precise local and species-
211 specific equations (i.e. the allometric equations for stem volume by Dagnelie et al. (1999) and the
212 biomass expansion factors of Vande Walle et al. (2005)). Both the local equations and the multi-
213 species biomass equation rendered virtually indistinguishable AGB-values for the Belgian plots (R^2
214 = 0.98, see **Appendix A1** and **Fig. A1**). As a final step, we then determined the total AGB per plot
215 by dividing the total AGB of a given plot by its forested area, as for the two outermost 9-m radius
216 plots a fraction of the circle fell beyond the forest edge, and converted the units to Mg or ton per ha.
217 Finally, the C-stock at plot level (Mg ha^{-1}) was calculated by multiplying the AGB with a C content
218 value of 47 %, a factor suggested by the IPPC (2006) for temperate trees.

219 *Forest floor carbon*

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

$$228 \text{ Forest floor C stock } \left(\frac{\text{Mg}}{\text{ha}} \right) = \text{C concentration } \left(\frac{\text{g}}{\text{g}} \right) \times \text{biomass of the organic layer } \left(\frac{\text{Mg}}{\text{ha}} \right) \quad (2)$$

229 *Mineral topsoil carbon*

230 For the C-stock in the mineral topsoil layers, five subsamples were taken in each plot with a soil
231 corer after removal of the organic layers. We sampled the mineral topsoil at a depth of 0-10 cm and
232 10-20 cm. We here neglect soil layers deeper than 20 cm as in European forests approximately half

233 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
234 expect the highest edge influences to occur in the topsoil. Subsamples were pooled per layer and
235 dried to constant weight at 40 °C for 48 hours. Subsequently, samples were ground, sieved over a 2-
236 mm mesh, and analysed for the total concentration of C, via the same method as for the forest floor.
237 As only C concentrations were available, we estimated the soil bulk density for each layer based on
238 C-concentration values making use of the regression equation of Wang and Huang (2020)(eq. 3).
239 Finally, we obtained the C-stock per layer by multiplying the C-concentrations with the estimated
240 soil bulk density and soil depth (eq. 4). The C-stock in the mineral topsoil was defined as the sum
241 of the stocks in the 0-10 cm and 10-20 cm layers.

$$242 \text{ Bulk density} = 1.5607 - 0.2721 \times C \text{ concentration} \left(\frac{g}{100g} \right)^{0.5} \quad (3)$$

$$243 \text{ Mineral soil C stock} \left(\frac{Mg}{ha} \right) = C \text{ concentration} \left(\frac{g}{100g} \right) \times \text{bulk density} \left(\frac{g}{cm^3} \right) \times \text{soil depth (cm)} \quad (4)$$

244 *Total carbon stock*

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

251 *2.2.2 Environmental drivers*

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

254 *Regional drivers: macroclimate and N deposition*

255 Macroclimatic characteristics and N deposition were used to reflect regional drivers. Macroclimatic
256 data were obtained from CHELSA (version 1.2, average climatic conditions over the period 1979-
257 2013 at a spatial resolution of 30 arc sec, Karger et al., 2017). For each site, the mean annual
258 temperature (MAT, °C) and the mean total annual precipitation (MAP, $mm \text{ year}^{-1}$) were extracted.

259 Modelled atmospheric N deposition data were downloaded from the European Monitoring and
260 Evaluation Program (EMEP) for the year 2016 at a resolution of 50 by 50 km. For each site, the
261 total atmospheric N deposition rate was estimated as the sum of both dry and wet deposition of
262 reduced and oxidized nitrogen. Due to the steep transition in vegetation height and altered wind
263 patterns, forest edges are hotspots for N deposition, with sometimes up to four times higher
264 atmospheric deposition values measured near edges compared to the interior (Weathers et al., 2001;
265 De Schrijver et al., 2007; Wuyts et al., 2008). To account for such elevated edge depositions, the
266 deposition rates were corrected using a decreasing exponential curve, which was fitted based on
267 actual measured throughfall data of NH_4^+ and NO_3^- in oak-dominated forest edges by Wuyts et al.
268 (2008) (see **Appendix A2** and **Fig. A2**).

269 *Local characteristics of the forest structure and tree community*

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

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

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

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

291 *Local soil characteristics*

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

- 293 1. The upper part of the mineral topsoil (0-10 cm) was used for the extraction of soil pH-
294 values. The pH-H₂O was determined by shaking a 1:5 ratio soil/H₂O mixture for 5 min at
295 300 r.p.m. and measuring with an Orion 920A pH meter with a Ross sure-flow 8172 BNWP
296 pH electrode model (Thermo Scientific Orion, USA).
- 297 2. We selected the percentage sand as proxy for soil texture. Soil texture (percentage silt, clay
298 and sand) was determined on the pooled 10-20 cm depth samples. These samples were
299 analysed for texture via sedimentation with a Robinson–Köhnpipette according to ISO
300 11277 (2009).
- 301 3. We measured soil temperature as proxy for the microclimate, since respiration and the
302 decomposition of organic matter are stimulated under higher temperatures (Nadelhoffer et
303 al., 1991; Cahoon et al., 2012; Wiesmeier et al., 2019). An increased C-mineralisation rate
304 was previously observed for temperatures above 10 °C while below 10 °C the mineralisation
305 rates were not triggered by temperature increases (Nadelhoffer et al., 1991). Cold
306 temperatures will thus limit C-mineralisation, whereas the majority of soil C-cycling will
307 occur during the summer. Therefore, the mean soil temperature during the summer (June-
308 July-August 2018) was selected as our metric for soil microclimate temperature. Soil
309 temperatures were recorded at hourly intervals, in the centre of each plot, using a lascar
310 temperature logger (EasyLog EL-USB-1, accuracy at -35 to +80 °C: ± 0.5 °C). The loggers

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

315 *2.3 High-resolution forest maps and estimates of carbon storage in deciduous forest edges across Europe*

316 To estimate the impact of forest edge influences on C-stocks we calculated the total area of
317 deciduous forests and their edge area across Europe. Europe was defined as all 27 EU countries,
318 plus Albania, Bosnia and Herzegovina, Kosovo, Liechtenstein, Montenegro, North Macedonia,
319 Norway, Serbia and Switzerland. The Canary Islands and Azores, as well as Europe's overseas
320 territories were excluded from the analysis. Calculations were based on the Copernicus Forest Type
321 map of 2015 at a resolution of 20 m × 20 m (FTY 2015, <https://land.copernicus.eu/>). Based on this
322 map, the total area of broadleaved forests was determined as well as the total edge perimeter, i.e. the
323 sum of all cells' edges of deciduous forest bordering a non-forest cell. Subsequently, the total edge
324 area of deciduous forest was estimated by multiplying the edge perimeter length with a depth of
325 edge influence of 4.5 m, as we found a significant difference between C-stocks up to this depth
326 (based on a post hoc Tukey Multiple Comparisons Test; see Results). Finally, the total C-stock in
327 deciduous forests across Europe was calculated without edge influences (i.e. all forested area had an
328 average C-stock which was the same as the average total C-stock in the interior of our forest). Then,
329 a second calculation took into account the edge influences, in which we divided the forest into three
330 regions: the outer edge (the forested area along the forest edge up to 3 m towards the interior),
331 intermediate region (the area between 3 m and 4.5 m from the edge) and interior. We subsequently
332 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
333 intermediate region and the C-stock for the interior as in the first calculation to calculate the total C-
334 stock in deciduous forest across Europe with edge influences.

335 *2.4 Data analysis*

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

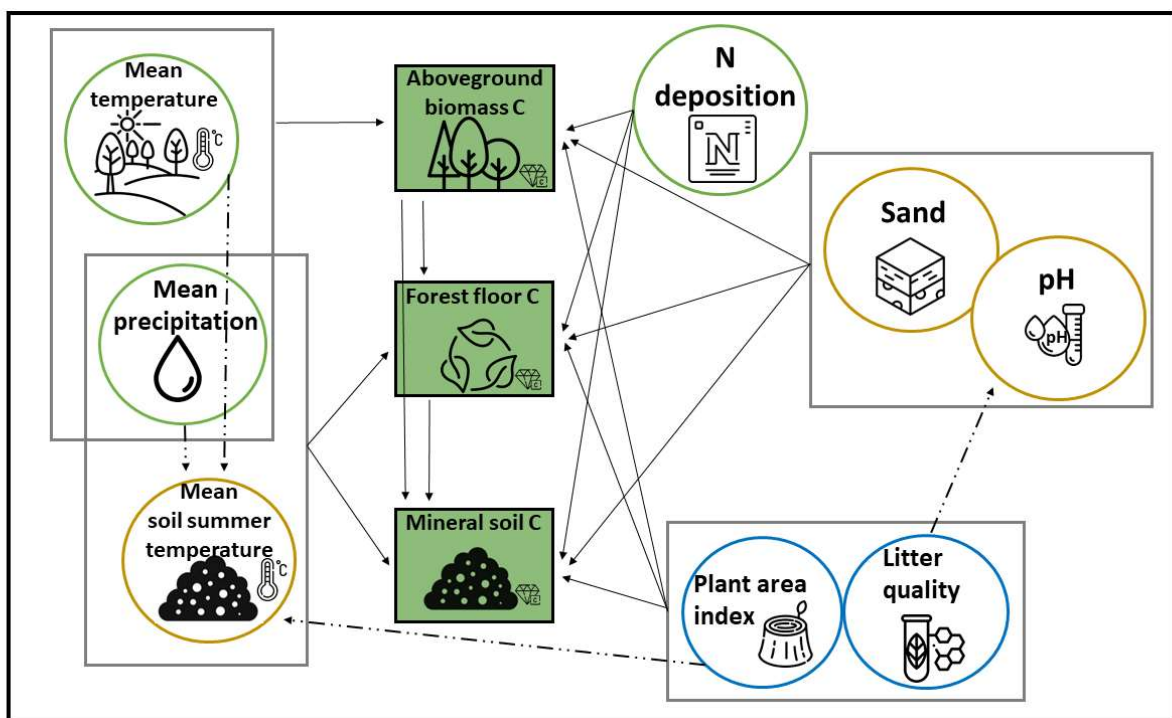
$$\begin{aligned}
 352 \quad y &\sim \textit{latitude} + \textit{elevation} + \textit{management type} + \textit{distance to the edge} + \\
 353 \quad &\textit{distance to the edge} \times \textit{latitude} + \textit{distance to the edge} \times \textit{elevation} + \\
 354 \quad &\textit{distance to the edge} \times \textit{management type} + (1 \mid \textit{region/transect}) \qquad (5)
 \end{aligned}$$

355 Subsequently, two piecewise structural equation models (SEM, R-package ‘piecewiseSEM’,
 356 Lefcheck, 2016) were constructed to gain more insight into the mechanisms affecting forest C-
 357 stocks directly and indirectly (Fig. 2). Piecewise SEM was selected, as this method allows for the
 358 fitting of hierarchical data and thus random effects via a set of separate linear mixed-effect models.
 359 Again, region and transect nested within region were used as random intercept terms in all
 360 subsequent component models. A set of three linear mixed-effect component models was fitted to
 361 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

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



397

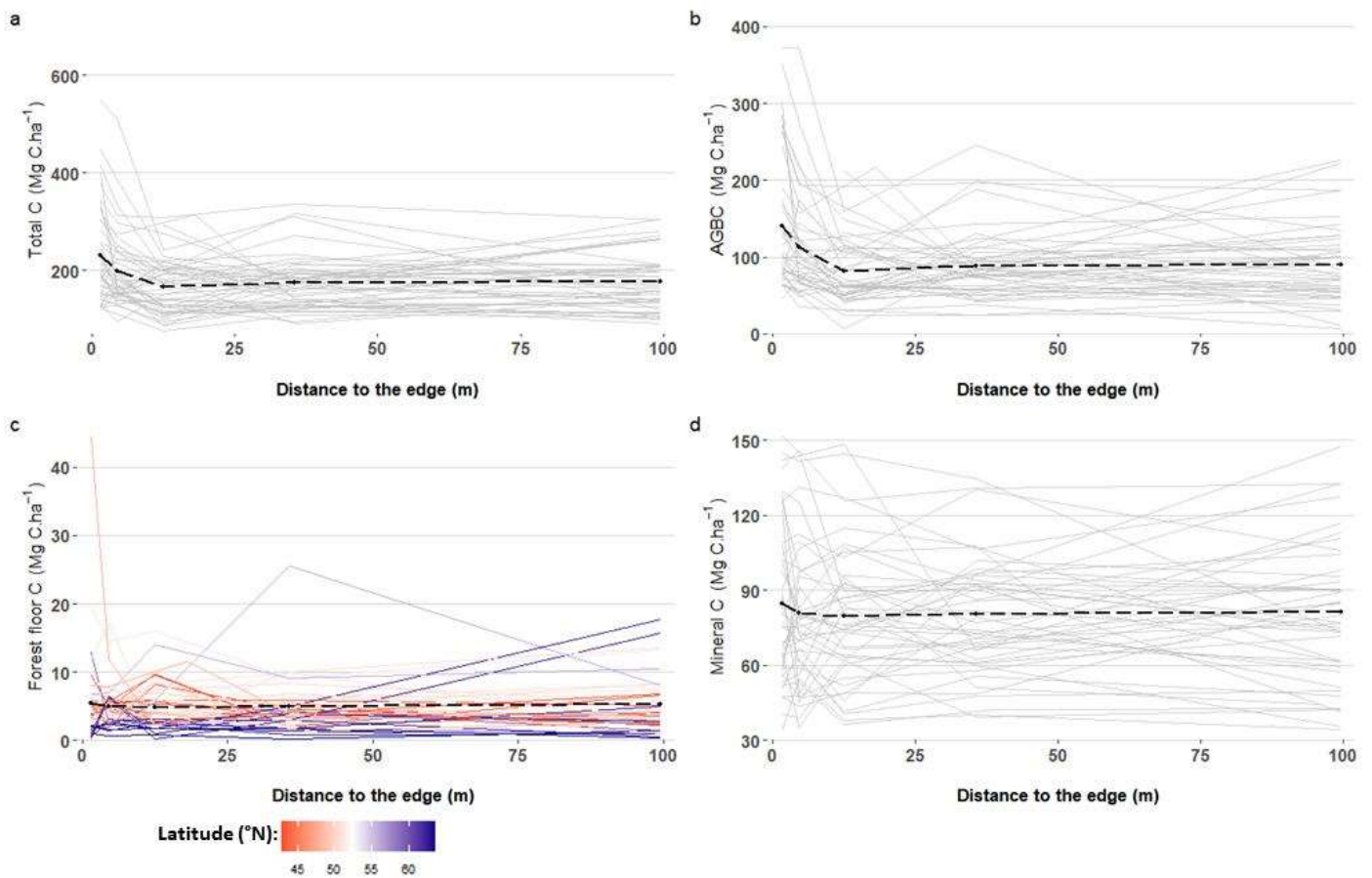
398 **Figure 2:** Full piecewise SEM of the determinants of carbon (C) stocks in the aboveground biomass (AGB, Mg C ha⁻¹),
 399 the forest floor (Mg C ha⁻¹) and the mineral topsoil (Mg C ha⁻¹) in deciduous forests edges across Europe. We tested the
 400 impact of three large-scale drivers, indicated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

406 3. Results

407 3.1 Variation in carbon stocks

408 Strong differences in the C-stocks were observed between the regions (**Table B1**). The total stocks
409 were highest in Northern Switzerland, Northern Germany and Southern Sweden whereas Central
410 Sweden and Central Italy had the lowest stocks. No impact of latitude, elevation or management
411 were detected on the total C-stock (**Table B2**), though the total stock was significantly higher near
412 the forest edge ($p < 0.001$, **Fig 3a**) up to a distance of approximately 4.5 m from the edge (**Table**
413 **B2**). Total C-storage was on average 39% higher at the edge (= 1.5 m) than in the forest interior (=
414 99.5 m).

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



427
 428 **Figure 3:** Edge-to-interior patterns of a) the total carbon (C) stock (Mg C ha^{-1}), b) aboveground biomass C-stock
 429 (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
 430 lines indicate the average stock across sites and management types whereas the solid grey lines show the observed
 431 stocks in each of the transects and plots. Colours in panel c demonstrate the effect of the latitude; red colours represent
 432 southern latitudes and blue colours indicate northern latitudes. Latitude was only displayed for the forest floor C-stocks
 433 because it had a significant interaction effect with distance to the edge whereas this effect was absent for the other
 434 stocks.

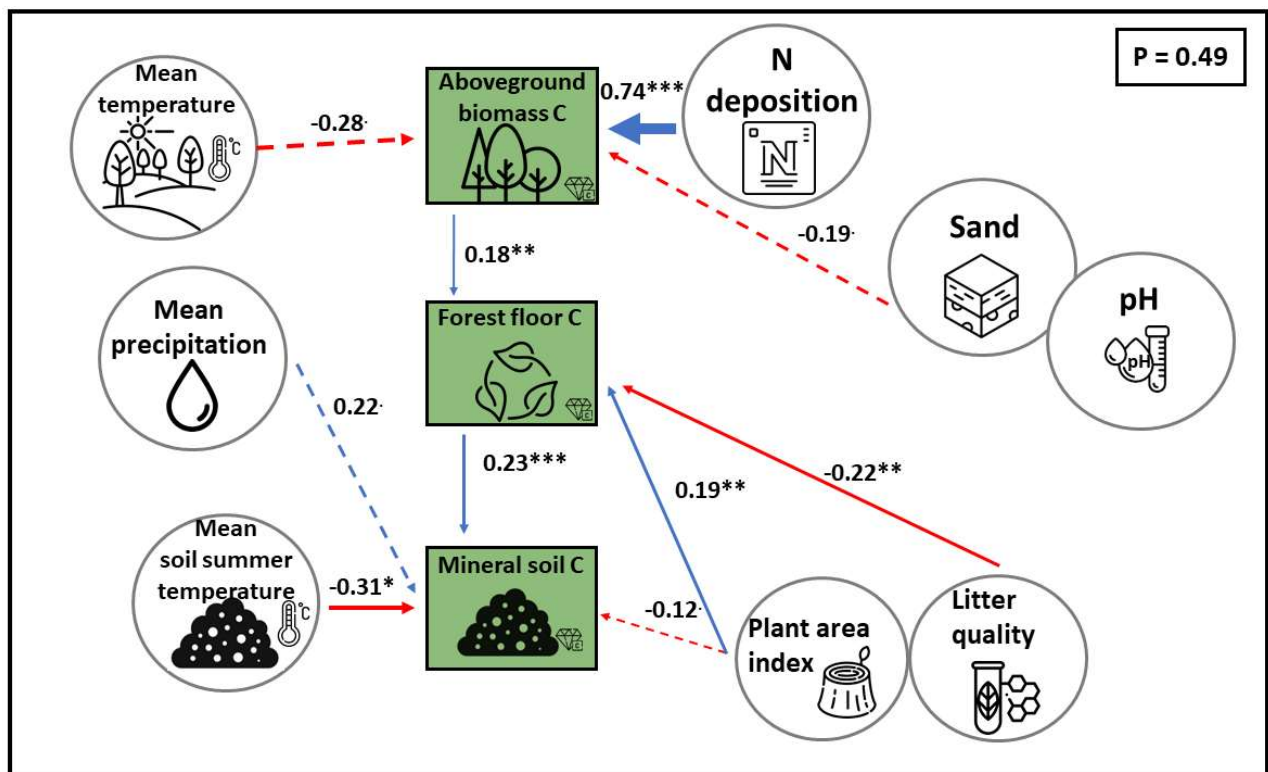
435 3.2 Piecewise structural equation models: drivers of carbon storage

436 Our piecewise SEM, without relationships amongst predictors, reproduced the data well ($p = 0.49$,
 437 $\text{AIC} = 77$) (**Fig. 4**). We found a significant impact of regional drivers and local (soil) characteristics
 438 on the C-stocks. The AGBC-Stock increased with elevated N deposition ($p < 0.001$) whereas a
 439 sandy soil texture ($p = 0.08$) and high MAT ($p = 0.06$) had a close to significant negative impact.
 440 We could not find an impact of N deposition on the C-stocks in the forest floor and mineral soil.
 441 Carbon stocks in the forest floor were affected by the AGBC, litter quality and the plant area index.

442 Hence, the forest floor stock was lowest in forests with a high litter quality ($p = 0.005$) and a low
 443 plant area index ($p = 0.009$). We also found a positive effect of AGBC on the forest floor C-stock (p
 444 $= 0.009$). Further, the stock in the forest floor itself had a significant positive impact on the C-stock
 445 in the mineral topsoil ($p < 0.001$). The MAP and the soil temperature were two additional
 446 determinants of the mineral C-stock. The stock was higher in colder soils ($p = 0.01$) and a higher
 447 precipitation had a marginally positive impact on the mineral C-stock as well ($p = 0.08$).

448 As expected, similar results were detected in the piecewise SEM in which more relationships
 449 between the predictors (e.g. between MAT and soil temperature: see the dashed-dotted lines in **Fig.**
 450 **2**) were included ($p = 0.14$ and AIC = 125) (**Fig. B1**). Marginal and conditional R^2 of all the
 451 component models for both SEMs are shown in **Table B3**.

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



456

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 $= ***$, $p < 0.01 = **$, $p < 0.05 = *$, $p < 0.1 = \cdot$) 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

473 4. Discussion

474 4.1 Gradients in carbon storage

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

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

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

503 For the forest floor, we also found an impact of distance to the edge, though latitude influenced this
504 trend. With decreasing latitude, C-stocks in the forest floor were higher near the edge. A higher
505 stock near the edge in southern regions might be due to a lower decomposition driven by a limiting
506 moisture availability (Riutta et al., 2012). A higher forest floor accumulation near forest edges
507 might also be related to higher disturbances caused by wind, increasing the input but also
508 redistributing the litter (Feeley, 2004; Vasconcelos and Luizão, 2004). Contrary to Remy et al.
509 (2016), no edge-to-interior trends were detected for the mineral C-stock; this might be due to the
510 high spatial variability of this stock potentially masking small-scale variability (e.g. Fahey et al.,
511 2010).

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

629 matter input is of importance, but also the quality (Schulp et al., 2008; Vesterdal et al., 2013).
630 Previous research showed that tree species, and more specifically the chemical composition of their
631 litter, strongly affect the rate of decomposition (*synthesised by* Vesterdal et al., 2013). This is
632 demonstrated by the negative relationship between litter quality and the C-stock in the forest floor
633 in our model. Selecting species with a low litter quality (*e.g. Fagus sylvatica*) can thus benefit forest
634 floor accretion, albeit a low quality can affect soil acidity as shown by the positive impact of litter
635 quality on pH in our additional analyses. Soil acidification causes alterations in nutrient cycling and
636 can subsequently influence understorey growth and diversity, negatively affect soil organisms or
637 eventually lead to a decline in tree species (Sverdrup et al., 1994; Joner et al., 2005; Houle et al.,
638 2007; Bowman et al., 2008; Selvi et al., 2016).

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

649 5. Conclusion

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

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

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683 References

- 684 Ashcroft, M.B., Gollan, J.R., 2013. Moisture, thermal inertia, and the spatial distributions of near-surface soil
685 and air temperatures: Understanding factors that promote microrefugia. *Agric. For. Meteorol.* 176, 77–
686 89. <https://doi.org/10.1016/J.AGRFORMET.2013.03.008>
- 687 Bowman, W.D., Cleveland, C.C., Halada, L., Hreško, J., Baron, J.S., 2008. Negative impact of nitrogen
688 deposition on soil buffering capacity. *Nat. Geosci.* 1, 767–770. <https://doi.org/10.1038/ngeo339>
- 689 Brinck, K., Fischer, R., Groeneveld, J., Lehmann, S., Dantas De Paula, M., Pütz, S., Sexton, J.O., Song, D.,
690 Huth, A., 2017. High resolution analysis of tropical forest fragmentation and its impact on the global
691 carbon cycle. *Nat. Commun.* 8, 1–6. <https://doi.org/10.1038/ncomms14855>
- 692 Cahoon, S.M.P., Sullivan, P.F., Shaver, G.R., Welker, J.M., Post, E., 2012. Interactions among shrub cover
693 and the soil microclimate may determine future Arctic carbon budgets. *Ecol. Lett.* 15, 1415–1422.
694 <https://doi.org/10.1111/j.1461-0248.2012.01865.x>
- 695 Chaplin-Kramer, R., Ramler, I., Sharp, R., Haddad, N.M., Gerber, J.S., West, P.C., Mandle, L., Engstrom,
696 P., Baccini, A., Sim, S., Mueller, C., King, H., 2015. Degradation in carbon stocks near tropical forest
697 edges. *Nat. Commun.* 6, 10158. <https://doi.org/10.1038/ncomms10158>
- 698 Chen, J., Saunders, S.C., Crow, T.R., Naiman, R.J., Brosofske, K.D., Mroz, G.D., Brookshire, B.L.,
699 Franklin, J.F., 1999. Microclimate in forest ecosystem and landscape ecology. *Bioscience* 49, 288–297.
700 <https://doi.org/10.2307/1313612>
- 701 Crowther, T.W., Todd-Brown, K.E.O., Rowe, C.W., Wieder, W.R., Carey, J.C., MacHmuller, M.B., Snoek,
702 B.L., Fang, S., Zhou, G., Allison, S.D., Blair, J.M., Bridgham, S.D., Burton, A.J., Carrillo, Y., Reich,
703 P.B., Clark, J.S., Classen, A.T., Dijkstra, F.A., Elberling, B., Emmett, B.A., Estiarte, M., Frey, S.D.,
704 Guo, J., Harte, J., Jiang, L., Johnson, B.R., Kroël-Dulay, G., Larsen, K.S., Laudon, H., Lavallee, J.M.,
705 Luo, Y., Lupascu, M., Ma, L.N., Marhan, S., Michelsen, A., Mohan, J., Niu, S., Pendall, E., Peñuelas,
706 J., Pfeifer-Meister, L., Poll, C., Reinsch, S., Reynolds, L.L., Schmidt, I.K., Sistla, S., Sokol, N.W.,
707 Templer, P.H., Treseder, K.K., Welker, J.M., Bradford, M.A., 2016. Quantifying global soil carbon
708 losses in response to warming. *Nature* 540, 104–108. <https://doi.org/10.1038/nature20150>
- 709 Dagnelie, P., Palm, R., Rondeux, J., & Thill, A. (1999). *Tables de cubage des arbres et des peuplements*
710 *forestiers. Les presses agronomiques de Gembloux.*
- 711 De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B.R., Hylander, K., Luoto, M., Vellend, M.,
712 Verheyen, K., Lenoir, J., 2019. Global buffering of temperatures under forest canopies. *Nat. Ecol. Evol.*
713 3, 744–749. <https://doi.org/10.1038/s41559-019-0842-1>
- 714 De Schrijver, A., Devlaeminck, R., Mertens, J., Wuyts, K., Hermy, M., Verheyen, K., 2007. On the
715 importance of incorporating forest edge deposition for evaluating exceedance of critical pollutant loads.
716 *Appl. Veg. Sci.* 10, 293–298. <https://doi.org/10.1111/j.1654-109X.2007.tb00529.x>
- 717 De Vos, B., Cools, N., Ilvesniemi, H., Vesterdal, L., Vanguelova, E., Carnicelli, S., 2015. Benchmark values
718 for forest soil carbon stocks in Europe: Results from a large scale forest soil survey. *Geoderma* 251–
719 252, 33–46. <https://doi.org/10.1016/j.geoderma.2015.03.008>
- 720 Devlaeminck, R., De Schrijver, A., Hermy, M., 2005. Variation in throughfall deposition across a deciduous
721 beech (*Fagus sylvatica* L.) forest edge in Flanders. *Sci. Total Environ.* 337, 241–252.
722 <https://doi.org/10.1016/J.SCITOTENV.2004.07.005>
- 723 Dieleman, W.I.J., Venter, M., Ramachandra, A., Krockenberger, A.K., Bird, M.I., 2013. Soil carbon stocks
724 vary predictably with altitude in tropical forests: Implications for soil carbon storage. *Geoderma* 204–
725 205, 59–67. <https://doi.org/10.1016/j.geoderma.2013.04.005>
- 726 Doetterl, S., Stevens, A., Six, J., Merckx, R., Van Oost, K., Casanova Pinto, M., Casanova-Katny, A.,
727 Muñoz, C., Boudin, M., Zagal Venegas, E., Boeckx, P., 2015. Soil carbon storage controlled by
728 interactions between geochemistry and climate. *Nat. Geosci.* 8, 780–783.
729 <https://doi.org/10.1038/ngeo2516>

- 730 Fahey, T.J., Woodbury, P.B., Battles, J.J., Goodale, C.L., Hamburg, S.P., Ollinger, S. V, Woodall, C.W.,
731 2010. Forest carbon storage: ecology, management, and policy. *Front. Ecol. Environ.* 8, 245–252.
732 <https://doi.org/10.1890/080169>
- 733 Feeley, K.J., 2004. The effects of forest fragmentation and increased edge exposure on leaf litter
734 accumulation. *J. Trop. Ecol.* 20, 709–712. <https://doi.org/10.1017/S0266467404001828>
- 735 Frey, S.J.K., Hadley, A.S., Johnson, S.L., Schulze, M., Jones, J.A., Betts, M.G., 2016. Spatial models reveal
736 the microclimatic buffering capacity of old-growth forests. *Sci. Adv.* 2, e1501392.
737 <https://doi.org/10.1126/sciadv.1501392>
- 738 Gao, W., Yang, H., Kou, L., Li, S., 2015. Effects of nitrogen deposition and fertilization on N
739 transformations in forest soils: a review. *J. Soils Sediments* 15, 863–879.
740 <https://doi.org/10.1007/s11368-015-1064-z>
- 741 Gilliam, F.S., 2019. Excess nitrogen in temperate forest ecosystems decreases herbaceous layer diversity and
742 shifts control from soil to canopy structure. *Forests* 10, 66. <https://doi.org/10.3390/f10010066>
- 743 Govaert, S., Meeussen, C., Vanneste, T., Bollmann, K., Brunet, J., Cousins, S.A.O., Diekmann, M., Graae,
744 B.J., Hedwall, P.O., Heinken, T., Iacopetti, G., Lenoir, J., Lindmo, S., Orczewska, A., Perring, M.P.,
745 Ponette, Q., Plue, J., Selvi, F., Spicher, F., Tolosano, M., Vermeir, P., Zellweger, F., Verheyen, K.,
746 Vangansbeke, P., De Frenne, P., 2020. Edge influence on understorey plant communities depends on
747 forest management. *J. Veg. Sci.* 31, 281–292. <https://doi.org/10.1111/jvs.12844>
- 748 Gower, S.T., Kucharik, C.J., Norman, J.M., 1999. Direct and indirect estimation of leaf area index, f(APAR),
749 and net primary production of terrestrial ecosystems. *Remote Sens. Environ.* 70, 29–51.
750 [https://doi.org/10.1016/S0034-4257\(99\)00056-5](https://doi.org/10.1016/S0034-4257(99)00056-5)
- 751 Greiser, C., Meineri, E., Luoto, M., Ehrlén, J., Hylander, K., 2018. Monthly microclimate models in a
752 managed boreal forest landscape. *Agric. For. Meteorol.* 250–251, 147–158.
753 <https://doi.org/10.1016/J.AGRFORMET.2017.12.252>
- 754 Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton,
755 J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins,
756 C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O.,
757 Orrock, J.L., Song, D.-X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on
758 Earth's ecosystems. *Sci. Adv.* 1, e1500052. <https://doi.org/10.1126/sciadv.1500052>
- 759 Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S.,
760 Roberts, D., Jaiteh, M.S., Esseen, P.-A., 2005. Edge influence on forest structure and composition in
761 fragmented landscapes. *Conserv. Biol.* 19, 768–782. <https://doi.org/10.1111/j.1523-1739.2005.00045.x>
- 762 Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. *Biometrical*
763 *J.* <https://doi.org/10.1002/bimj.200810425>
- 764 Houle, D., Tremblay, S., Ouimet, R., 2007. Foliar and wood chemistry of sugar maple along a gradient of
765 soil acidity and stand health. *Plant Soil* 300, 173–183. <https://doi.org/10.1007/s11104-007-9401-7>
- 766 Hyvönen, R., Persson, T., Andersson, S., Olsson, B., Ågren, G.I., Linder, S., 2008. Impact of long-term
767 nitrogen addition on carbon stocks in trees and soils in northern Europe. *Biogeochemistry* 89, 121–137.
768 <https://doi.org/10.1007/s10533-007-9121-3>
- 769 International Civil Aviation Organization., 1993. Manual of the ICAO standard atmosphere: extended to 80
770 kilometres (262 500 feet), 3rd ed. International Civil Aviation Organization, Montreal, Quebec.
- 771 IPCC, 2006. IPCC Guidelines for National Greenhouse Gas Inventories, Agriculture, forestry and other land
772 use. Chapter 4.
- 773 Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D.W., Minkkinen, K.,
774 Byrne, K.A., 2007. How strongly can forest management influence soil carbon sequestration?
775 *Geoderma* 137, 253–268. <https://doi.org/10.1016/j.geoderma.2006.09.003>
- 776 Janssens, I.A., Dieleman, W., Luysaert, S., Subke, J.A., Reichstein, M., Ceulemans, R., Ciais, P., Dolman,

- 777 A.J., Grace, J., Matteucci, G., Papale, D., Piao, S.L., Schulze, E.D., Tang, J., Law, B.E., 2010.
778 Reduction of forest soil respiration in response to nitrogen deposition. *Nat. Geosci.*
779 <https://doi.org/10.1038/ngeo844>
- 780 Jenkins, J.C., Chojnacky, D.C., Heath, L.S., Birdsey, R.A., 2003. National-Scale Biomass Estimators for
781 United States Tree Species. *For. Sci.* 49, 12–35. <https://doi.org/10.1093/forestscience/49.1.12>
- 782 Jobbágy, E.G., Jackson, R.B., 2000. The vertical distribution of soil organic carbon and its relation to climate
783 and vegetation. *Ecol. Appl.* 10, 423–436. [https://doi.org/10.1890/1051-0761\(2000\)010\[0423:TVDOSO\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0423:TVDOSO]2.0.CO;2)
- 785 Johnson, D.W., Curtis, P.S., 2001. Effects of forest management on soil C and N storage: Meta analysis. *For.*
786 *Ecol. Manage.* 140, 227–238. [https://doi.org/10.1016/S0378-1127\(00\)00282-6](https://doi.org/10.1016/S0378-1127(00)00282-6)
- 787 Joner, E.J., Eldhuset, T.D., Lange, H., Frostegård, Å., 2005. Changes in the microbial community in a forest
788 soil amended with aluminium in situ, in: *Plant and Soil*. Springer, pp. 295–304.
789 <https://doi.org/10.1007/s11104-005-2287-3>
- 790 Jucker, T., Bouriaud, O., Coomes, D.A., 2015. Crown plasticity enables trees to optimize canopy packing in
791 mixed-species forests. *Funct. Ecol.* 29, 1078–1086. <https://doi.org/10.1111/1365-2435.12428>
- 792 Jucker, T., Hardwick, S.R., Both, S., Elias, D.M.O., Ewers, R.M., Milodowski, D.T., Swinfield, T., Coomes,
793 D.A., 2018. Canopy structure and topography jointly constrain the microclimate of human-modified
794 tropical landscapes. *Glob. Chang. Biol.* 24, 5243–5258. <https://doi.org/10.1111/gcb.14415>
- 795 Juodvalkis, A., Kairiukstis, L., Vasiliauskas, R., 2005. Effects of thinning on growth of six tree species in
796 north-temperate forests of Lithuania. *Eur. J. For. Res.* 124, 187–192. <https://doi.org/10.1007/s10342-005-0070-x>
- 798 Kalácska, M., Calvo-Alvarado, J.C., Sánchez-Azofeifa, G.A., 2005. Calibration and assessment of seasonal
799 changes in leaf area index of a tropical dry forest in different stages of succession. *Tree Physiol.* 25,
800 733–744. <https://doi.org/10.1093/TREEPHYS/25.6.733>
- 801 Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder,
802 H.P., Kessler, M., 2017. Climatologies at high resolution for the earth’s land surface areas. *Sci. Data* 4,
803 170122. <https://doi.org/10.1038/sdata.2017.122>
- 804 Kovács, B., Tinya, F., Ódor, P., 2017. Stand structural drivers of microclimate in mature temperate mixed
805 forests. *Agric. For. Meteorol.* 234–235, 11–21. <https://doi.org/10.1016/j.agrformet.2016.11.268>
- 806 Laurance, W.F., Laurance, S.G., Ferreira, L. V., Rankin-de Merona, J.M., Gascon, C., Lovejoy, T.E., 1997.
807 Biomass collapse in Amazonian forest fragments. *Science* (80-.). 278, 1117–1118.
808 <https://doi.org/10.1126/science.278.5340.1117>
- 809 Lefcheck, J.S., 2016. piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution,
810 and systematics. *Methods Ecol. Evol.* 7, 573–579. <https://doi.org/10.1111/2041-210X.12512>
- 811 Lovett, G.M., Arthur, M.A., Weathers, K.C., Fitzhugh, R.D., Templer, P.H., 2013. Nitrogen addition
812 increases carbon storage in soils, but not in trees, in an Eastern U.S. deciduous forest. *Ecosystems* 16,
813 980–1001. <https://doi.org/10.1007/s10021-013-9662-3>
- 814 Luyssaert, S., Inglima, I., Jung, M., Richardson, A.D., Reichstein, M., Papale, D., Piao, S.L., Schulze, E.-D.,
815 Wingate, L., Matteucci, G., Aragao, L., Aubinet, M., Beer, C., Bernhofer, C., Black, K.G., Bonal, D.,
816 Bonnefond, J.-M., Chambers, J., Ciais, P., Cook, B., Davis, K.J., Dolman, A.J., Gielen, B., Goulden,
817 M., Grace, J., Granier, A., Grelle, A., Griffis, T., Grünwald, T., Guidolotti, G., Hanson, P.J., Harding,
818 R., Hollinger, D.Y., Hutrya, L.R., Kolari, P., Kruijt, B., Kutsch, W., Lagergren, F., Laurila, T., Law,
819 B.E., Le Maire, G., Lindroth, A., Loustau, D., Malhi, Y., Mateus, J., Migliavacca, M., Misson, L.,
820 Montagnani, L., Moncrieff, J., Moors, E., Munger, J.W., Nikinmaa, E., Ollinger, S. V., Pita, G.,
821 Rebmann, C., Roupsard, O., Saigusa, N., Sanz, M.J., Seufert, G., Sierra, C., Smith, M.-L., Tang, J.,
822 Valentini, R., Vesala, T., Janssens, I.A., 2007. CO₂ balance of boreal, temperate, and tropical forests
823 derived from a global database. *Glob. Chang. Biol.* 13, 2509–2537. <https://doi.org/10.1111/j.1365-2486.2007.01439.x>

- 825 Maes, S.L., Blondeel, H., Perring, M.P., Depauw, L., Brümelis, G., Brunet, J., Decocq, G., den Ouden, J.,
826 Härdtle, W., Hédli, R., Heinken, T., Heinrichs, S., Jaroszewicz, B., Kirby, K., Kopecký, M., Máliš, F.,
827 Wulf, M., Verheyen, K., 2019. Litter quality, land-use history, and nitrogen deposition effects on
828 topsoil conditions across European temperate deciduous forests. *For. Ecol. Manage.* 433, 405–418.
829 <https://doi.org/10.1016/J.FORECO.2018.10.056>
- 830 Magnani, F., Mencuccini, M., Borghetti, M., Berbigier, P., Berninger, F., Delzon, S., Grelle, A., Hari, P.,
831 Jarvis, P.G., Kolari, P., Kowalski, A.S., Lankreijer, H., Law, B.E., Lindroth, A., Loustau, D., Manca,
832 G., Moncrieff, J.B., Rayment, M., Tedeschi, V., Valentini, R., Grace, J., 2007. The human footprint in
833 the carbon cycle of temperate and boreal forests. *Nature* 447, 848–850.
834 <https://doi.org/10.1038/nature05847>
- 835 Manning, P., Saunders, M., Bardgett, R.D., Bonkowski, M., Bradford, M.A., Ellis, R.J., Kandeler, E.,
836 Marhan, S., Tscherko, D., 2008. Direct and indirect effects of nitrogen deposition on litter
837 decomposition. *Soil Biol. Biochem.* 40, 688–698. <https://doi.org/10.1016/J.SOILBIO.2007.08.023>
- 838 Matlack, G.R., 1993. Microenvironment variation within and among forest edge sites in the eastern United
839 States. *Biol. Conserv.* 66, 185–194. [https://doi.org/10.1016/0006-3207\(93\)90004-K](https://doi.org/10.1016/0006-3207(93)90004-K)
- 840 Mayer, M., Prescott, C.E., Abaker, W.E.A., Augusto, L., Cécillon, L., Ferreira, G.W.D., James, J., Jandl, R.,
841 Katzensteiner, K., Laclau, J.P., Laganière, J., Nouvellon, Y., Paré, D., Stanturf, J.A., Vanguelova, E.I.,
842 Vesterdal, L., 2020. Influence of forest management activities on soil organic carbon stocks: A
843 knowledge synthesis. *For. Ecol. Manage.* 466, 118127. <https://doi.org/10.1016/j.foreco.2020.118127>
- 844 MCPFE. (2011). State of Europe's Forests 2011 - Status and Trends in Sustainable Forest
845 Management in Europe. FOREST EUROPE, UNECE and FAO, Oslo.
- 846 Meeussen, C., Govaert, S., Vanneste, T., Calders, K., Bollmann, K., Brunet, J., Cousins, S.A.O., Diekmann,
847 M., Graae, B.J., Hedwall, P.O., Krishna Moorthy, S.M., Iacopetti, G., Lenoir, J., Lindmo, S.,
848 Orczewska, A., Ponette, Q., Plue, J., Selvi, F., Spicher, F., Tolosano, M., Verbeeck, H., Verheyen, K.,
849 Vangansbeke, P., De Frenne, P., 2020. Structural variation of forest edges across Europe. *For. Ecol.*
850 *Manage.* 462, 117929. <https://doi.org/10.1016/j.foreco.2020.117929>
- 851 Meier, I.C., Leuschner, C., 2010. Variation of soil and biomass carbon pools in beech forests across a
852 precipitation gradient. *Glob. Chang. Biol.* 16, 1035–1045. <https://doi.org/10.1111/j.1365-2486.2009.02074.x>
- 854 Mourelle, C., Kellman, M., Kwon, L., 2001. Light occlusion at forest edges: an analysis of tree architectural
855 characteristics. *For. Ecol. Manage.* 154, 179–192. [https://doi.org/10.1016/S0378-1127\(00\)00624-1](https://doi.org/10.1016/S0378-1127(00)00624-1)
- 856 Nadelhoffer, K.J., Giblin, A.E., Shaver, G.R., Laundre, J.A., 1991. Effects of temperature and substrate
857 quality on element mineralization in six Arctic soils. *Ecology* 72, 242–253.
858 <https://doi.org/10.2307/1938918>
- 859 Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R² from generalized linear
860 mixed-effects models. *Methods Ecol. Evol.* 4, 133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
- 862 Naudts, K., Chen, Y., McGrath, M.J., Ryder, J., Valade, A., Otto, J., Luysaert, S., 2016. Forest
863 management: Europe's forest management did not mitigate climate warming. *Science (80-.)*. 351, 597–
864 599. <https://doi.org/10.1126/science.aad7270>
- 865 Niinemets, Ü., 2010. A review of light interception in plant stands from leaf to canopy in different plant
866 functional types and in species with varying shade tolerance. *Ecol. Res.* 25, 693–714.
867 <https://doi.org/10.1007/s11284-010-0712-4>
- 868 Ordway, E.M., Asner, G.P., 2020. Carbon declines along tropical forest edges correspond to heterogeneous
869 effects on canopy structure and function. *Proc. Natl. Acad. Sci.* 117, 201914420.
870 <https://doi.org/10.1073/pnas.1914420117>
- 871 Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A.,
872 Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen,

- 873 A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. *Science* 333,
874 988–93. <https://doi.org/10.1126/science.1201609>
- 875 Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and The R Core Development Team. 2020. nlme: linear and
876 nonlinear mixed effects models. R package version 3.1– 147
- 877 R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical
878 Computing, Vienna, Austria. URL <https://www.R-project.org/>
- 879 Reinmann, A.B., Hutyra, L.R., 2017. Edge effects enhance carbon uptake and its vulnerability to climate
880 change in temperate broadleaf forests. *Proc. Natl. Acad. Sci. U. S. A.* 114, 107–112.
881 <https://doi.org/10.1073/pnas.1612369114>
- 882 Remy, E., Wuyts, K., Boeckx, P., Ginzburg, S., Gundersen, P., Demey, A., Van Den Bulcke, J., Van Acker,
883 J., Verheyen, K., 2016. Strong gradients in nitrogen and carbon stocks at temperate forest edges. *For.*
884 *Ecol. Manage.* 376, 45–58. <https://doi.org/10.1016/j.foreco.2016.05.040>
- 885 Remy, E., Wuyts, K., Van Nevel, L., De Smedt, P., Boeckx, P., Verheyen, K., 2018. Driving factors behind
886 litter decomposition and nutrient release at temperate forest edges. *Ecosystems* 21, 755–771.
887 <https://doi.org/10.1007/s10021-017-0182-4>
- 888 Riutta, T., Slade, E.M., Bebbler, D.P., Taylor, M.E., Malhi, Y., Riordan, P., Macdonald, D.W., Morecroft,
889 M.D., 2012. Experimental evidence for the interacting effects of forest edge, moisture and soil
890 macrofauna on leaf litter decomposition. *Soil Biol. Biochem.* 49, 124–131.
891 <https://doi.org/10.1016/j.soilbio.2012.02.028>
- 892 Schmidt, M., Jochheim, H., Kersebaum, K.-C., Lischeid, G., Nendel, C., 2017. Gradients of microclimate,
893 carbon and nitrogen in transition zones of fragmented landscapes – a review. *Agric. For. Meteorol.* 232,
894 659–671. <https://doi.org/10.1016/J.AGRFORMET.2016.10.022>
- 895 Schulp, C.J.E., Nabuurs, G.-J., Verburg, P.H., de Waal, R.W., 2008. Effect of tree species on carbon stocks
896 in forest floor and mineral soil and implications for soil carbon inventories. *For. Ecol. Manage.* 256,
897 482–490. <https://doi.org/10.1016/J.FORECO.2008.05.007>
- 898 Seidl, R., Schelhaas, M.J., Rammer, W., Verkerk, P.J., 2014. Increasing forest disturbances in Europe and
899 their impact on carbon storage. *Nat. Clim. Chang.* 4, 806–810. <https://doi.org/10.1038/nclimate2318>
- 900 Selvi, F., Carrari, E., Coppi, A., 2016. Impact of pine invasion on the taxonomic and phylogenetic diversity
901 of a relict Mediterranean forest ecosystem. *For. Ecol. Manage.* 367, 1–11.
902 <https://doi.org/10.1016/J.FORECO.2016.02.013>
- 903 Serreze, M.C., Barry, R.G., 2011. Processes and impacts of Arctic amplification: A research synthesis. *Glob.*
904 *Planet. Change* 77, 85–96. <https://doi.org/10.1016/j.gloplacha.2011.03.004>
- 905 Shipley, B., 2009. Confirmatory path analysis in a generalized multilevel context. *Ecology* 90, 363–368.
906 <https://doi.org/10.1890/08-1034.1>
- 907 Smith, I.A., Hutyra, L.R., Reinmann, A.B., Marrs, J.K., Thompson, J.R., 2018. Piecing together the
908 fragments: elucidating edge effects on forest carbon dynamics. *Front. Ecol. Environ.* 16, 213–221.
909 <https://doi.org/10.1002/fee.1793>
- 910 Smith, I.A., Hutyra, L.R., Reinmann, A.B., Thompson, J.R., Allen, D.W., 2019. Evidence for edge
911 enhancements of soil respiration in temperate forests. *Geophys. Res. Lett.* 46, 4278–4287.
912 <https://doi.org/10.1029/2019GL082459>
- 913 Staude, I.R., Waller, D.M., Bernhardt-Römermann, M., Bjorkman, A.D., Brunet, J., De Frenne, P., Hédli, R.,
914 Jandt, U., Lenoir, J., Máliš, F., Verheyen, K., Wulf, M., Pereira, H.M., Vangansbeke, P., Ortman-
915 Ajkai, A., Pielech, R., Berki, I., Chudomelová, M., Decocq, G., Dirnböck, T., Durak, T., Heinken, T.,
916 Jaroszewicz, B., Kopecký, M., Macek, M., Malicki, M., Naaf, T., Nagel, T.A., Petřík, P., Reczyńska,
917 K., Schei, F.H., Schmidt, W., Standovár, T., Świerkosz, K., Teleki, B., Van Calster, H., Vild, O.,
918 Baeten, L., 2020. Replacements of small- by large-ranged species scale up to diversity loss in Europe's
919 temperate forest biome. *Nat. Ecol. Evol.* 4, 802–808. <https://doi.org/10.1038/s41559-020-1176-8>

- 920 Sverdrup, H., Warfvinge, P., Nihlgård, B., 1994. Assessment of soil acidification effects on forest growth in
921 Sweden. *Water, Air, Soil Pollut.* 78, 1–36. <https://doi.org/10.1007/BF00475665>
- 922 Tashi, S., Singh, B., Keitel, C., Adams, M., 2016. Soil carbon and nitrogen stocks in forests along an
923 altitudinal gradient in the eastern Himalayas and a meta-analysis of global data. *Glob. Chang. Biol.* 22,
924 2255–2268. <https://doi.org/10.1111/gcb.13234>
- 925 Thomas, R.Q., Canham, C.D., Weathers, K.C., Goodale, C.L., 2010. Increased tree carbon storage in
926 response to nitrogen deposition in the US. *Nat. Geosci.* 3, 13–17. <https://doi.org/10.1038/ngeo721>
- 927 Valdés, A., Lenoir, J., De Frenne, P., Andrieu, E., Brunet, J., Chabrierie, O., Cousins, S.A.O., Deconchat, M.,
928 De Smedt, P., Diekmann, M., Ehrmann, S., Gallet- Moron, E., Gärtner, S., Giffard, B., Hansen, K.,
929 Hermy, M., Kolb, A., Le Roux, V., Liira, J., Lindgren, J., Martin, L., Naaf, T., Paal, T., Proesmans, W.,
930 Scherer- Lorenzen, M., Wulf, M., Verheyen, K., Decocq, G., 2020. High ecosystem service delivery
931 potential of small woodlands in agricultural landscapes. *J. Appl. Ecol.* 57, 4–16.
932 <https://doi.org/10.1111/1365-2664.13537>
- 933 Vande Walle, I., Van Camp, N., Perrin, D., Lemeur, R., Verheyen, K., Van Wesemael, B., Laitat, E., 2005.
934 Growing stock-based assessment of the carbon stock in the Belgian forest biomass. *Ann. For. Sci.* 62,
935 853–864. <https://doi.org/10.1051/forest:2005076>
- 936 Vanneste, T., Govaert, S., De Kesel, W., Van Den Berge, S., Vangansbeke, P., Meeussen, C., Brunet, J.,
937 Cousins, S.A.O., Decocq, G., Diekmann, M., Graae, B.J., Hedwall, P.-O., Heinken, T., Helsen, K.,
938 Kapás, R.E., Lenoir, J., Liira, J., Lindmo, S., Litza, K., Naaf, T., Orczewska, A., Plue, J., Wulf, M.,
939 Verheyen, K., De Frenne, P., 2020. Plant diversity in hedgerows and road verges across Europe. *J.*
940 *Appl. Ecol.* <https://doi.org/10.1111/1365-2664.13620>
- 941 Vasconcelos, H.L., Luizão, F.J., 2004. Litter production and litter nutrient concentrations in a fragmented
942 amazonian landscape. *Ecol. Appl.* 14, 884–892. <https://doi.org/10.1890/03-5093>
- 943 Verheyen, K., Baeten, L., De Frenne, P., Bernhardt-Römermann, M., Brunet, J., Cornelis, J., Decocq, G.,
944 Dierschke, H., Eriksson, O., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Kirby, K., Naaf, T.,
945 Peterken, G., Petřík, P., Pfadenhauer, J., Van Calster, H., Walther, G.R., Wulf, M., Verstraeten, G.,
946 2012. Driving factors behind the eutrophication signal in understorey plant communities of deciduous
947 temperate forests. *J. Ecol.* 100, 352–365. <https://doi.org/10.1111/j.1365-2745.2011.01928.x>
- 948 Vesterdal, L., Clarke, N., Sigurdsson, B.D., Gundersen, P., 2013. Do tree species influence soil carbon stocks
949 in temperate and boreal forests? *For. Ecol. Manage.* 309, 4–18.
950 <https://doi.org/10.1016/J.FORECO.2013.01.017>
- 951 von Arx, G., Graf Pannatier, E., Thimonier, A., Rebetez, M., 2013. Microclimate in forests with varying leaf
952 area index and soil moisture: potential implications for seedling establishment in a changing climate. *J.*
953 *Ecol.* 101, 1201–1213. <https://doi.org/10.1111/1365-2745.12121>
- 954 Wamelink, G.W.W., Wieggers, H.J.J., Reinds, G.J., Kros, J., Mol-Dijkstra, J.P., van Oijen, M., de Vries, W.,
955 2009. Modelling impacts of changes in carbon dioxide concentration, climate and nitrogen deposition
956 on carbon sequestration by European forests and forest soils. *For. Ecol. Manage.* 258, 1794–1805.
957 <https://doi.org/10.1016/j.foreco.2009.05.018>
- 958 Wang, S., Huang, Y., 2020. Determinants of soil organic carbon sequestration and its contribution to
959 ecosystem carbon sinks of planted forests. *Glob. Chang. Biol.* 26, 3163–3173.
960 <https://doi.org/10.1111/gcb.15036>
- 961 Weathers, K.C., Cadenasso, M.L., Pickett, S.T.A., 2001. Forest edges as nutrient and pollutant concentrators:
962 Potential synergisms between fragmentation, forest canopies, and the atmosphere. *Conserv. Biol.* 15,
963 1506–1514. <https://doi.org/10.1046/j.1523-1739.2001.01090.x>
- 964 Wiesmeier, M., Urbanski, L., Hobbey, E., Lang, B., von Lützw, M., Marin-Spiotta, E., van Wesemael, B.,
965 Rabot, E., Ließ, M., Garcia-Franco, N., Wollschläger, U., Vogel, H.J., Kögel-Knabner, I., 2019. Soil
966 organic carbon storage as a key function of soils - A review of drivers and indicators at various scales.
967 *Geoderma* 333, 149–162. <https://doi.org/10.1016/j.geoderma.2018.07.026>

- 968 Wuyts, K., De Schrijver, A., Staelens, J., Gielis, L., Vandenbruwane, J., Verheyen, K., 2008. Comparison of
969 forest edge effects on throughfall deposition in different forest types. *Environ. Pollut.* 156, 854–861.
970 <https://doi.org/10.1016/j.envpol.2008.05.018>
- 971 Zianis, D., 2008. Predicting mean aboveground forest biomass and its associated variance. *For. Ecol.*
972 *Manage.* 256, 1400–1407. <https://doi.org/10.1016/j.foreco.2008.07.002>
- 973 Zianis, D., Muukkonen, P., Mäkipää, R., Mencuccini, M., 2005. Biomass and stem volume equations for tree
974 species in Europe. *Silva Fenn. Monogr.*
- 975 Ziter, C., Bennett, E.M., Gonzalez, A., 2014. Temperate forest fragments maintain aboveground carbon
976 stocks out to the forest edge despite changes in community composition. *Oecologia* 176, 893–902.
977 <https://doi.org/10.1007/s00442-014-3061-0>
- 978