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1 **Impact of patch age and size on forest soil characteristics in European agricultural**
2 **landscapes**

3

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32

33 **Abstract**

34 Many landscapes worldwide are characterized by the presence of a mosaic of forest
35 patches with contrasting age and size embedded in a matrix of agricultural land. However,
36 our understanding of the effects of these key forest patch features on the soil nutrient
37 status (in terms of nitrogen, carbon, and phosphorus) and soil pH is still limited due to a
38 lack of large-scale data. To address this research gap, we analyzed 830 soil samples from
39 nearly 200 forest patches varying in age (recent versus ancient forests) and size (small
40 versus larger patches) along a 2,500-km latitudinal gradient across Europe. We also
41 considered environmental covariates at multiple scales to increase the generality of our
42 research, including variation in macroclimate, nitrogen deposition rates, forest cover in a
43 buffer zone, basal area and soil type. Multiple linear mixed-effects models were performed
44 to test the combined effects of patch features and environmental covariates on soil
45 nutrients and pH. Recent patches had higher total soil phosphorus concentrations and
46 stocks in the mineral soil layer, along with a lower nitrogen to phosphorus ratio within that
47 layer. Small patches generally had a higher mineral soil pH. Mineral soil nitrogen stocks
48 were lower in forest patches with older age and larger size, as a result of a significant
49 interactive effect. Additionally, environmental covariates had significant effects on soil
50 nutrients, including carbon, nitrogen, phosphorus, and their stoichiometry, depending on
51 the specific covariates. In some cases, the effect of patch age on mineral soil P stocks was
52 greater than that of environmental covariates. Our findings underpin the important roles of
53 forest patch age and size for the forest soil nutrient status. Long-term studies assessing
54 edge effects and soil development in post-agricultural forests are needed, especially in a
55 context of changing land use and climate.

56 **Keywords**

57 Fragmentation, forest land-use history, land-use change, macroclimate, soil nutrient
58 balance

59 **1. Introduction**

60 Forest soils play a key role in maintaining forest biogeochemical cycles of carbon (C)
61 and nutrients, like nitrogen (N) and phosphorous (P) (Lal, 2005; Maaroufi and de Long,
62 2020). However, forest soil nutrient concentrations and stocks are sensitive to land-use
63 change and even slight changes in, for instance, their stoichiometry (e.g., C:N ratio, N:P
64 ratios) can induce significant changes in forest community composition and dynamics
65 (Wieder et al., 2015; Jakovac et al., 2016). Therefore, quantifying to what extent forest
66 soil nutrients are affected by land-use change is critical for anticipating potential changes
67 in biogeochemical cycles (Stevenson and Cole, 1999; Sattari et al., 2012; Bradford et al.,
68 2016; Bouwman et al., 2017).

69 Forests throughout the world are strongly affected by habitat fragmentation, a process
70 by which focal habitat gets divided into smaller and isolated patches due to various,
71 typically anthropogenic activities such as land-use change, timber harvesting or
72 construction of infrastructure. Unlike habitat loss per se, in which habitat is directly
73 converted to another habitat type, such as from forest to agricultural land or urban cover,
74 fragmentation refers to a change of the spatial configuration of habitat with increasingly
75 smaller sizes for a given total amount of habitat (Fahrig et al., 2019). More than 70% of
76 the world's forest areas are within 1 km of a forest edge, with most forest patches
77 embedded in artificial landscapes such as arable land (Haddad et al., 2015; Oduro-Appiah
78 and Agyemang-Duah, 2021). In Europe, the situation is even worse, with 40% of the
79 forest area situated within 100 meters from the edge (Estreguil et al., 2012). Conversely,

80 because of changing socio-economic conditions and policies, reforestation of post-
81 agricultural sites is taking place at a large scale. In many countries in Europe, the
82 reforestation of post-agricultural soils stands out as a significant land-use transformation.
83 (Wall and Hytönen, 2005; Olszewska and Smal, 2008; Wellock et al., 2011). At the
84 landscape scale, this often leads to a mosaic comprised of forest patches of various age
85 (ancient vs. recent) and size since reforestation (Honnay et al., 2005; Ziter et al., 2013).

86 Both forest patch age and size are key features of forests that can affect soil
87 characteristics. In terms of age, ancient forests are defined as forests that have not been
88 cleared for agriculture for at least about 200 years, while more recently afforested lands
89 occur on soils that may have been managed and cultivated in the past through agriculture
90 treatment (e.g. fertilization, liming, pesticide addition). Many previous studies have
91 assessed the difference in soil pH and nutrients between ancient and recent forests
92 established on former agricultural land, arable land, pastures or abandoned settlements
93 (Wilson et al., 1997; Graae et al., 2003; Vojta, 2007; Bergès et al., 2017; Abadie et al.,
94 2018). Those studies often detected higher P concentrations, lower C:N ratios and reduced
95 soil acidification in recent forest soils compared to ancient forest soils (Bergès et al., 2017;
96 Brasseur et al., 2018), which can still be detected >100 to 150 years after afforestation
97 (Verheyen et al., 1999; Perring et al., 2008; De Schrijver et al., 2012; Blondeel et al.,
98 2019). Regarding patch size, smaller forest patches are more susceptible to edge effects
99 due to their higher edge-to-core ratio. As a result, they experience higher drift of lime and
100 nutrient inputs (such as nitrogen and phosphate fertilizers) from neighboring, potentially
101 intensively used land, increased nitrogen deposition, higher irradiance and wind speeds,
102 and warmer and drier microclimate conditions compared to larger forest patches (De
103 Schrijver et al., 2007; Wuyts et al., 2008; Remy et al., 2016; Meeussen et al., 2021).

104 Therefore, small forest patches with comparatively strong edge influences might, for
105 instance, show elevated soil pH, N or P concentrations. Forest edges also tend to have
106 higher structural and taxonomic plant diversity which can exert a facilitative effect on
107 litter decomposition (e.g., due to litter mixing and accumulation) (Jastrow, 2007; Bueno
108 and Llambí, 2015; Ramírez et al., 2015), thus higher nutrient cycling rates might be
109 detected in small forest patches than in larger ones. However, due to a lack of data
110 (Brzeziecki et al., 1993; Coudun and Gégout, 2006), few studies have focused on the
111 concurrent impact of patch age and size on soil nutrients and acidity across large spatial
112 extents, using consistent sampling and analytical methods. This is important since soil pH
113 or nutrients are important drivers of forest community composition and forest ecosystem
114 functioning (Salisbury, 1920; Brady and Weil, 1999; Pärtel, 2002). Patches of the same
115 age but small vs large sizes may have different vegetation composition, litter quality, and
116 soil microbial communities (Valdés et al., 2020), thereby influencing soil nutrient cycling
117 processes. For example, smaller patches may have higher proportions of shade-intolerant
118 species, generalist species, or herbaceous species with higher leaf nutrient concentrations
119 (Guirado et al., 2006). Contrasting patch sizes and the associated edge effects can also lead
120 to distinct soil microbial communities, for instance resulting in a higher abundance of
121 arbuscular mycorrhizal fungi closer to edges (Yang et al., 2022) which can then feed back
122 to nutrient cycling. Examining the interactive effects of patch age and size thus bear both
123 theoretical and practical significance.

124 The objective of this study was to fill the knowledge gap on the impact of forest
125 patch age and size on soil nutrient status and pH in forest patches across agricultural
126 landscapes of western Europe. We used a large-scale study design that covers forest
127 patches varying in age (ancient vs recent) and size (large vs small) along a latitudinal

128 gradient with variable macroclimate from central Sweden and Estonia to southern France.
129 We focused on the concentrations and stocks of soil C, N and P and their stoichiometry in
130 both forest floor (litter layer, fragmentation layer and humus layer) and mineral topsoil
131 layer (0-10 cm), as these are biologically most relevant (e.g., for understory vegetation and
132 forest-floor organisms) and have larger nutrient concentrations compared to deeper soil
133 horizons. As different climates and vegetation types lead to soil types with distinct
134 characteristics, we incorporated five additional ecological variables to increase the
135 generality of our research. These variables capture variation in the data from the
136 continental over the landscape to the patch level (macroclimate, N deposition, forest cover
137 in a buffer zone, total tree basal area and soil type), to account for their potential
138 confounding effects with forest patch age and size.

139 We hypothesized that: (1) recent forest patches have a higher pH, a lower soil C:N
140 ratio and higher soil P concentrations and stocks compared to ancient forest patches; (2)
141 small forest patches have a higher soil pH and higher concentrations and stocks of soil C,
142 N and P than large patches, due to stronger edge deposition effects and a higher drift of
143 lime and nutrient inputs from adjacent agricultural land. We used a sampling design from
144 individual plots to patches, landscapes, and regions, allowing us to assess the relative
145 importance of environmental factors for soil acidity and nutrient status across different
146 spatial scales.

147 **2. Material and methods**

148 2.1 Study sites

149 This study was carried out in eight regions along a 2,500 km-long macroclimatic
150 gradient in Europe, from central Sweden and Estonia to south France (Fig. 1). The broad
151 geographical extent of the study area covers a gradient in macroclimate, and variations in

152 N deposition and forest community composition (Table 1). In each of the eight regions,
153 two 5 km by 5 km landscape windows with predominant agricultural use were selected.
154 Within each window, eleven to sixteen forest patches were chosen to be representative of
155 the variation of patch age (ancient vs recent) and size (large vs small). A total of 199
156 patches were sampled, about half of the patches were large and half were small, and within
157 each of these two size categories, half of the patches were ancient and half were recent.
158 The mean size for ancient and recent patches was 8.4 ± 8.7 ha and 1.1 ± 0.9 ha, respectively;
159 the mean age for ancient and recent patches was 140.3 ± 72.8 year and 31.1 ± 25.1 year,
160 respectively (see detailed summary statistics with mean and range of patch age and size
161 for each region in Table SM. 1 in Supplementary Material). The patches are dominated by
162 broadleaved tree species ($95.76 \pm 13.38\%$ cover across regions, see Table SM. 2 for the
163 proportion in each region). The six most dominant tree genera were *Quercus*, *Alnus*,
164 *Populus*, *Fraxinus*, *Fagus*, and *Betula*, and the detailed information on their relative
165 proportions per region can be found in Table SM. 3 in the Supplementary Material.

166 2.2 Data collection

167 2.2.1 Soil sampling and laboratory analysis

168 Soil samples for chemical analyses were taken during the period from August to
169 October 2012 before leaves were shed. For each patch, we sampled soil evenly along
170 parallel transect lines located 100-m apart from each other. In the smallest patches (less
171 than 1000 m^2), a total of 3-5 soil samples were taken and subsequently pooled. In larger
172 patches, the number of soil samples was related to patch size, ranging from 5 to 31 soil
173 samples per patch. A square wooden frame of $25 \text{ cm} \times 25 \text{ cm}$ was used to collect the
174 forest floor samples following the method by Vesterdal and Raulund-Rasmussen (1998).

175 Living plant parts were cut at the base and removed, and leave litter, fragmented litter and
176 humus were collected by hand for forest floor samples. Great care was taken to ensure that
177 the forest floor and mineral soil samples were not mixed. After removing forest floor, one
178 upper mineral soil sample (0-10 cm) was taken inside the wooden frame using a metal
179 core sampler ($\text{\O}4.2$ cm). A total of 830 samples (forest floor and mineral soil) were
180 collected from 415 sampling locations, placed in marked paper bags and stored dark
181 pending analyses at Forest & Nature laboratory at Ghent University in Belgium.

182 All soil samples were dried at 40°C for analyzing soil C, N and P, and weighed for
183 calculating bulk density. To separate the fine earth and coarse soil fraction, the mineral
184 soil samples were sieved through a 2 mm sieve. The fraction greater than 2 mm which
185 contained roots, small stones, and gravel was removed (Homann et al., 1995). We
186 analyzed soil pH, C and N for both forest floor and homogenized mineral soil samples,
187 and soil P for mineral soil samples. To determine soil pH (CaCl_2), a soil/ CaCl_2 (0.01M)
188 mixture with a ratio of 1:5 was shaken for 5 minutes at 300 rpm. The pH was then
189 measured using a pH meter (Orion 920A) with pH electrode model Ross sure-flow 8172
190 BNWP (Thermo Scientific Orion, Massachusetts, USA). The C and N concentrations were
191 determined using an elemental analyzer (Vario MACRO cube CNS, Elementar,
192 Langensfeld, Germany) through high temperature combustion at 1150°C . Total P
193 concentration was measured after complete destruction with HClO_4 (65%), HNO_3 (70%)
194 and H_2SO_4 (98%) in Teflon bombs for 4 hours at 150°C . Phosphorus and Olsen P
195 concentrations were measured according to the malachite green procedure at 700 nm
196 (Varian, Cary 50 UV-Vis Spectrophotometer, Agilent, Victoria, Australia) (Lajtha et al.,
197 1999; Frossard et al., 2000). Given that soil pH values are lower than 7 in our study
198 (except for one pH data point that falls between 7 and 8), the total carbon measured in our

199 study predominantly represents organic carbon (Ulrich, 1991; Wetzel and Likens, 1991).
200 To check this hypothesis, we plotted the relationship between mineral soil total carbon and
201 total nitrogen by pH group (two groups: low/high pH groups with $\text{pH} < 5$ and $\text{pH} \geq 5$,
202 respectively) (Fig. SM. 1 in Supplementary Material). We found that for the same total N
203 concentration, soil samples with high pH had lower total carbon concentration than those
204 with low pH. This indicates that soil total carbon is more related to organic carbon than to
205 increasing soil inorganic carbon.

206 For the forest floor, soil bulk density (BD) was calculated as its dry weight divided
207 by the multiplication of depth and area of the sampling square ($25 \text{ cm} \times 25 \text{ cm}$). The C, N
208 and P stocks at this layer were calculated by multiplying the concentrations of C, N and P
209 with BD and soil depth. For the mineral soil layer, BD is the weight of the fine earth
210 fraction ($< 2 \text{ mm}$) divided by the sampling volume after correcting for the presence of
211 stones ($> 2 \text{ mm}$) and roots (Dawud et al., 2016). Stone volume was estimated by dividing
212 the coarse fraction weight by 2.65 g cm^{-3} (density of common minerals). The volume of
213 roots was estimated in a similar way, i.e., by dividing the weight of roots by the root
214 density. A value of 0.56 g cm^{-3} was used for all sites and tree species to represent the root
215 density of broadleaved tree species (Moltesen, 1988). In general, the presence of stones
216 and roots was low. The nutrient stocks for mineral soil were calculated as the
217 concentration of C, N and P multiplied by the fine earth BD and the depth of the soil layer.

218 Finally, because actual soil texture analyses were not feasible on this large amount of
219 soil samples, we extracted the soil texture (clay, sand, and silt contents of 5-15 cm) per
220 patch from the European soil database (<https://soilgrids.org/>) to have comparable data for
221 all windows. The spatial resolution of this database is 1:250.

222 2.2.2 Tree stand inventory

223 During the growing seasons of 2012 and 2013, trees were selected in every sampled
224 plot according to the point-centre quarter method (Cottam and Curtis, 1956). Sampling
225 was restricted to a 20 m radius from the central point, to avoid sampling the same trees
226 twice in nearby locations. For each selected tree, we measured and recorded its diameter at
227 breast height (DBH), azimuth direction and distance towards the centre of the plot.

228 2.2.3 Landscape and patch features

229 At landscape scale, we estimated the proportion of forest in a 500 m buffer ring
230 around each focal patch (Donald and Evans, 2006). We assumed that a larger forest cover
231 can hinder human disturbances and mitigate agricultural fertilizer pollution (Martino, 2001;
232 Andersson and Nordberg, 2017), which might decrease soil nutrient stocks (Cardinale et
233 al., 2012; Vellend et al., 2013). Using a geographic information system (GIS, specifically
234 ArcGIS 9.3 by ESRI), patch size and historical age were determined at the patch scale.
235 This involved analyzing contemporary and historical maps depicting the landscape
236 windows, including recent aerial photographs taken after 2000, as well as maps from the
237 18th, 19th, and 20th centuries. The calculation of patch size entailed the utilization of
238 digitized polygons representing forest patches within each window. To determine the
239 historical age of the patches, we digitized all forest patches from historical maps and
240 estimated their age based on the date of the oldest map in which a focal forest patch was
241 identified. Considering that a patch may consist of a mosaic of patches having different
242 ages, we computed a size-weighted average of the age for all fragments within an isolated
243 patch.

244 2.2.4 Macroclimate and nitrogen deposition

245 We extracted the long-term climatology for mean annual temperature (MAT) and
246 mean annual precipitation (MAP) covering the period 1970-2000 from the WorldClim
247 global geodatabase (1-km resolution, <http://www.worldclim.org/>) and averaged the
248 variables for each forest patch using all 1-km² pixels intersecting it. The N deposition was
249 the sum of nitrate (NO₃⁻-N) and ammonium (NH₄⁺-N), which was derived from the MSC-
250 W model developed within the European Monitoring and Evaluation Program (EMEP)
251 (Simpson et al., 2012) using recalculated emission values. Gridded (50 km × 50 km) data
252 between 1990-2012 was used to cover a period of high deposition (1990) and the lower
253 deposition loads close to the soil sampling event (2012). The model was run by
254 meteorological parameters derived from the European Center of Medium-Range Weather
255 Forecasts (ECMWF). The spatial resolution of both the climate and deposition data often
256 exceeds the distance between the forest patches. Therefore, the calculated values refer to
257 entire landscape windows within regions. Since the macroclimate and N deposition
258 variation within the same landscape of 5 × 5 km² is expected to be quite limited, we used
259 these variables to differentiate between different regions rather than focusing on different
260 patches within the same landscape.

261 2.3 Data analysis

262 Our study included six categories of predictor variables (Table 1). The first and key
263 predictor variables were patch features with patch age and size for testing our two
264 hypotheses. Although we had the classification of ancient vs recent and large vs small to
265 represent patch age and size categories, for data analysis we used the actual estimated
266 numerical value of age and size rather than the categorical variables. To increase the
267 generality of our research, we then included five more categories of variables across patch,
268 landscape, regional and continental scales as covariates, which are often studied and

269 considered as important indicators of forest soil nutrients and soil pH (Martino, 2001; Lal,
270 2005; Pregitzer et al., 2008; Hou et al., 2018): (1) macroclimate with annual mean
271 temperature (MAT) and precipitation (MAP); (2) N deposition rate (N_{deposit}); (3) forest
272 proportion in a 500 m buffer ring around each focal patch (Forest.buffer500); (4) total tree
273 basal area (BA); and (5) soil texture with clay content (Clay). The response variables were
274 soil pH, the concentration and stocks of soil C, N, P and Olsen P, and the stoichiometric
275 ratios of C:N and N:P (Table 1). The response variables were the same for both forest
276 floor and mineral soil layers, except for soil P related variables that were measured only in
277 mineral soil. Each variable had 415 values corresponding to the total number of soil
278 sampling locations, and data was analyzed at the sampling location level. Linear mixed-
279 effects models (LMMs) were applied for each soil response variable, using region and
280 window ID (nested within region) as random intercept terms. Before running the models,
281 we log-transformed some predictor variables (Age, Size, Forest.buffer500 and BA) and
282 response variables (C_{ff} , N_{ms} , P_{ms} , $P_{\text{Olsen}_{\text{ms}}}$, $C:N_{\text{ms}}$, $N:P_{\text{ms}}$, and C_{ff} stocks, N_{ff} stocks and
283 $P_{\text{Olsen}_{\text{ms}}}$ stocks), and scaled all predictor variables. The LMMs had the following
284 structure: Soil variable \sim Age \times Size + MAT + MAP + N_{deposit} + Forest.buffer500 + BA +
285 Clay + (1| (region/window ID)). We used variance inflation factors (VIF) to test for
286 multicollinearity of all LMMs. VIFs for most predictor variables was below 2, except for
287 MAP and N_{deposit} which were between 2 and 3. We therefore kept all predictor variables
288 for each soil variable. Data analysis was performed in R 4.1.1 (R Core Team, 2021). The
289 lme function from the lme4 package (Bates and Maechler, 2016) was applied.

290 **3. Results**

291 Higher concentration and stocks of mineral soil P (P_{ms} and P_{ms} stocks) were found in
292 more recent than in more ancient forest patches (Table 2 and Fig. 2). A standardized unit

293 change in age caused 0.13 standardized unit decrease of P_{ms} , 0.31 standardized unit
294 decrease of P_{ms} stocks, and 0.20 standardized unit increase of $N:P_{ms}$. Patch age did not
295 have any effects on soil pH, C:N or the concentration or stocks of soil C and N in both
296 forest floor and mineral soil layers.

297 Smaller patches showed higher pH_{ms} than larger forest patches (Table 2 and Fig. 3). A
298 standardized unit change in patch size caused 0.10 standardized unit decrease of pH_{ms} .
299 Patch size did not have significant effects on pH_{ff} , the concentration or stocks of soil C, N,
300 and P, or their ratios ($C:N_{ff}$, $C:N_{ms}$ and $N:P_{ms}$) in both the forest floor and mineral soil
301 layers. For the interactive effect of patch age and size, lower mineral soil N stocks in
302 patches with older age and larger size was detected (Table 2).

303 For annual mean temperature (MAT) and precipitation (MAP), N deposition ($N_{deposit}$),
304 forest proportion in 500 m buffer zone (Forest.buffer500), total tree basal area (BA) and
305 soil texture (Clay), we found inconsistent responses of soil C and N between forest floor
306 and mineral soil to MAT. More specifically, C_{ms} and N_{ms} decreased, while C_{ff} stocks and
307 N_{ff} stocks increased with increasing MAT (Table 2 and Fig. SM.2 in supplementary
308 material). MAP did not show significant effects on soil variables (Table 2 and Fig. SM.3
309 in supplementary material). The $P_{Olsen_{ms}}$ and $P_{Olsen_{ms}}$ stocks increased with increasing
310 $N_{deposit}$ (Fig. SM.4 in supplementary material). Forest.buffer500 showed a positive effect
311 on $C:N_{ms}$ and the BA had a negative effect on $C:N_{ms}$ and $N:P_{ms}$ (Fig. SM.5 & SM.6 in
312 supplementary material). Furthermore, decreased N_{ff} , N_{ms} and $N:P_{ms}$ with increasing clay
313 content were found (Fig. SM.7 in supplementary material).

314 Finally, the effect of patch age on P_{ms} stocks was sometimes much stronger than
315 macroclimate or BA (Table 2). A standardized unit change in patch age had an almost

316 three times and five times higher impact than MAT and N_{deposit} , or a four times higher
317 impact than BA on P_{ms} stocks.

318 **4. Discussion**

319 4.1 Effects of patch age and size on soil nutrients and pH

320 Since soils of more recent forest patches had higher mineral soil P concentration and
321 stocks than soils of more ancient forest patches, we detect an important role of past land-
322 use history and fertilization legacy on soil nutrients in forests across a latitudinal gradient
323 in Europe. More recently afforested lands have been previously managed and cultivated
324 through agricultural management, which could result in a higher soil P concentration or
325 stocks. For instance, the application of P-based fertilizers, along with the use of livestock
326 manure and organic waste as natural fertilizers, introduces P to agricultural fields
327 (Almeida et al., 2019; Bindraban et al., 2020). Over time, these inputs can lead to the
328 accumulation of forest soil P. Previous studies also found a higher P concentration (few
329 studies tested P stocks as we did) in post-agricultural forest soils compared to ancient
330 forest soils (Verheyen et al., 1999; De Schrijver et al., 2012; Blondeel et al., 2019). Those
331 studies showed that the legacies of soil P can persist for decades, indicating that the
332 geochemical mechanisms associated with soil P availability operate over long time-scales
333 (Walker and Syers, 1976; Vitousek and Farrington, 1997; McDowell et al., 2001;
334 Dupouey et al., 2002; De Schrijver et al., 2012). For example, in previous local studies on
335 similar forest soil layers (0 to 30 cm), Verheyen et al. (1999) and Honnay et al. (1999)
336 showed that mixed hardwood forests with a history of agricultural land use experienced a
337 significant increase in soil phosphate, especially in the twentieth century. Likewise, Bergè
338 s et al. (2017) and Blondeel et al. (2019) found that post-agricultural forests, even after

339 afforestation for several decades or centuries, still had higher P concentration compared to
340 ancient forests. Some studies also observed variations in different soil P fractions. For
341 example, De Schrijver et al. (2012) demonstrated that as forests age, labile and slowly
342 cycling inorganic soil phosphorus fractions decrease, while organic fractions exhibit a
343 significant increase. In our study, we did not detect a change in Olsen P with patch age. In
344 addition, some of the studies that reported higher soil P levels also observed higher pH
345 values (e.g., Honnay et al., 1999; Blondeel et al., 2019). However, we did not find changes
346 in soil pH with patch age. Yet, there are also studies showing that soil pH remains
347 relatively unchanged in the upper soil layer, for instance in northern hardwood forests in
348 the U.S. (Goodale and Aber, 2001), reforested forests in Spain (Hevia et al., 2014), and
349 former agricultural land in Belgium forests (Bossuyt et al., 1999).

350 However, consistent with our hypothesis, smaller forest patches had a higher pH in
351 the mineral soil than larger forest patches. This indicated potentially higher drift of K^+ ,
352 Ca^{2+} and Mg^{2+} into forest edges from nearby agricultural soil particles (Valdés et al.,
353 2015), which reduces soil acidity. Previous studies have reported elevated pH values and
354 higher concentrations of K^+ , Ca^{2+} and Mg^{2+} in the organic layer or mineral soil at the
355 edges of deciduous and coniferous forests (Honnay et al., 2002; Malmivaara-Lämsä et al.,
356 2008; Govaert et al., 2019; Meeussen et al., 2021). These studies have attributed the
357 observed differences to factors such as increased base cation input through throughfall and
358 litterfall, or increased leaching of ions, dry deposition, due to the edge effects, which could
359 also counteract or outweigh the soil acidification effect caused by higher levels of
360 acidifying deposition at the edge (Lovett and Reiners, 1986; Beier and Gundersen, 1989;
361 Devlaeminck et al., 2005). Therefore, patches with small size are probably more affected

362 by surrounding agricultural practices due to edge effects, while patch age effects on soil P,
363 are the result of the agricultural legacy in afforested, post-agricultural forests.

364 Our study also suggested that patch features may not be the determinants of soil C
365 and N in the upper soil layer, since we did not observe any significant effects of forest
366 patch age or size on the concentrations and stocks of soil C and N in the forest floor and
367 mineral soil layers. Similar to our results, Von Oheimb et al. (2008) showed no significant
368 differences in mineral soil C and N concentrations with the land-use conversion from
369 agricultural land to forest over 150 years. Mund and Schulze (2006) found no forest age
370 effect on the mineral soil C stocks of beech forests. Nitsch et al. (2018) concluded that, the
371 studies that did not detect changes in soil C or N were because only the uppermost soil
372 layers down to a depth of 10-15 cm were considered. Significant difference in pH or soil
373 nutrients were previously only detected deeper, up to about 30 cm, rather than at the forest
374 floor or top of the mineral soil layer (Wulf, 2022). Leuschner et al. (2014) and Nitsch et al.
375 (2018) showed that decades or centuries of former land use have reduced the C and
376 nutrient storage of the subsoil. This might be because the organic and mineral soil layers
377 accumulate C more rapidly than the subsoil, allowing for the rebuilding of C stocks
378 characteristic of the organic layer or mineral soil layer in continuously forested sites. New
379 equilibrium at these two layers is typically reached after several decades or 50-130 years
380 of forest development (Jandl et al., 2007; Leuschner et al., 2014). On the contrary, the
381 recovery of C stocks in the mineral soil is a much slower process, driven by inputs of fine
382 litter, dead roots, root fragments, as well as the accumulation of dead microbial and soil
383 animal biomass in the soil profile (Gregorich et al., 1998; Pregitzer and Euskirchen, 2004).
384 The absence of effect of patch size on soil C or N was contrary to a study by Remy et al.
385 (2016) in temperate forests, who found strong interior-to-edge trends for the mineral C and

386 N stocks. This may also suggest that higher soil C and N levels can only be detected at the
387 soil point strictly located at the forest edge compared to the forest interior. Yet, our study
388 is consistent with Meeussen et al. (2021) at the European scale who found no interior-to-
389 edge variation of soil C stocks for the mineral topsoil. Schedlbauer et al. (2022) showed
390 that edge effects altered soil C cycling by increasing soil respiration rates but with non-
391 significant difference in soil C pools between forest edge and the interior. Finally, it was
392 only when estimating the interactive effects of patch age and size that the variation in soil
393 N could be detected. Specifically, we observed lower mineral N stocks in patches with
394 older age and larger size.

395 4.2 Effects of other predictor variables on soil nutrients and pH

396 Contrasting to previous local studies that solely focused on patch features, our study
397 also assessed the impact of other environmental factors across different scales on soil
398 nutrients. The response direction and magnitude of patch-scale soil nutrients to the other
399 predictor variables (MAT, MAP, N_{deposit} , Forest.buffer500, BA and Clay) were generally
400 consistent with previous findings at regional/continental or at local levels. High
401 temperatures facilitate rapid immobilization and mineralization (Wallenstein et al., 2011;
402 Hou et al., 2018), which could speed up the natural processes of forest soil nutrient loss at
403 a continental or global extent (Singh et al., 2022). High-latitude temperate regions are
404 expected to experience a temperature rise that surpasses the average global increase (IPCC,
405 2022). We found decreased soil C and N concentrations in mineral soil layers with
406 increasing MAT along the latitudinal gradient. Similarly, in a comprehensive analysis by
407 Crowthe et al. (2015), significantly lower soil C stocks were observed in high-latitude
408 areas across North America, Europe, and Asia. Although high precipitation was found to
409 generally increase nutrient levels, in our case, precipitation did not affect soil pH or

410 nutrient stocks. On the other hand, high temperature and high N deposition may increase
411 plant productivity (if no other resources are limiting) and the accumulation of surface litter
412 and soil organic matter (Lützow et al., 2006; Paul, 2016), which might contribute to the
413 increased soil C and N stocks in the forest floor or increased mineral soil Olsen P as we
414 found (Berg and Matzner, 1997; Hinsinger 2001; Pregitzer et al., 2008). Both the studies
415 by Zhang et al. (2014) and by Tian et al. (2015) also showed that N addition significantly
416 increased the Olsen P concentration in grassland soils. The decrease in soil pH caused by
417 N addition led to a reduction in exchangeable cations, thereby resulting in decreased soil P
418 resorption to cations. Our findings also suggested a potential link between increasing
419 nitrogen deposition and a decrease in soil pH, although the decrease was not statistically
420 significant. This might explain our results because we also found a decrease in soil pH
421 (though not statistically significant) with increasing N deposition.

422 Moreover, at landscape scale, the role of Forest.buffer500 generally had a weak effect
423 on soil nutrients, with only a positive effect on C:N_{ms}. For the effect of BA, stands with
424 high BA might represent highly productive stands and thus induce high organic matter (e.g.
425 high plant leaf and root residues) input into the soil (Li et al., 2010; Lal, 2005; Paul, 2016;
426 Rasse et al., 2005; Mooshammer et al., 2016), i.e., low C:N, or N:P ratios of mineral soil
427 in our study. The result that increasing clay content decreased soil N in both forest floor
428 and mineral soil or N:P in mineral soil suggested that soils with higher clay content have
429 higher cation exchange capacity, which decreased N concentrations by increasing
430 biological activity, and N mainly forms in the organic rather than in the clay (Pepper and
431 Brusseau, 2019). The relatively stronger effect of patch age on soil P stocks than
432 macroclimate (MAT or N_{deposit}) also highlighted the importance of forest fragmentation
433 effect when predicting forest soil nutrient status.

434 **5. Conclusions**

435 Despite the global concerns on the impact of forest fragmentation on forest
436 ecosystems, there is still a research gap in our overall understanding of the relationship
437 between forest patch features and the soil nutrient status. Our study addressed this gap by
438 using a large-scale sampling design to assess how the age and size of forest patches affect
439 soil nutrients at the continental extent of Europe. We highlighted that recent and small
440 forest patches, respectively, have higher P concentration and stocks in soils and a less
441 acidic soil. Moreover, considering multi-scale environmental factors allowed for these key
442 findings general and applicable for ecologists and forest managers. Our intensive sampling
443 design could not detect the effects of age or size on other soil nutrients in addition to soil P,
444 as found in some case studies. With increasing climate and land-use changes, long-term
445 studies on assessing edge effects on soil nutrients and soil system recovery (including
446 subsoil layer) of forest patches are needed for better predicting forest soil health in a
447 habitat fragmentation background.

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Table 1 Mean, SD and range of predictor and response variables used in the LMM models.

	Abbreviation	Explanation	Unit	Mean	SD	Range
Predictor variables	Region	Estonia, central Sweden, south Sweden, west Germany, east Germany, Belgium, north France, South France, used as random effect	-	-	-	-
	Window	Landscape window	-	-	-	-
	MAT	Mean annual temperature	°C	8.5	3.1	3.6-14.7
	MAP	Mean annual precipitation	mm	677.7	85.3	550.5-820.0
	N _{deposit}	Annual 2012 N deposition	kg N ha ⁻¹ yr ⁻¹	12.8	5.1	4.8-24.9
	Forest.buffer500	Proportion of forest in a 500 m buffer around the patch	%	12.8	15.8	0.0-99.9
	Age	Patch age (weighted by size)	yr	110.4	81.9	12.0-326.3
	Size	Patch size	ha	9.3	10.3	0.1-44.1
	Clay	Percentage of clay (from SoilGrids)	%	19.3	9.1	5.4-35.8
	BA	Total tree basal area	m ² ha ⁻¹	30.0	23.0	5.0-200.6
Response variables	pH _{ff}	pH in the forest floor	-	5.1	0.7	3.2-7.9
	C _{ff}	Carbon concentration in the forest floor	g kg ⁻¹	449.0	54.6	150.9-536.8
	N _{ff}	Nitrogen concentration in the forest floor	g kg ⁻¹	15.2	4.0	6.8-29.7
	C:N _{ff}	Carbon to nitrogen ratio in the forest floor	-	31.7	9.8	15.4-73.8
	C _{ff} stocks	Carbon stocks in the forest floor	Mg ha ⁻¹	4.7	6.1	0.0-73.7
	N _{ff} stocks	Nitrogen stocks in the forest floor	Mg ha ⁻¹	0.2	0.3	0.0-3.8
	pH _{ms}	pH in the mineral soil	-	4.4	1.0	2.8-6.9
	C _{ms}	Carbon concentration in the mineral soil	g kg ⁻¹	60.0	36.6	12.0-195.9
	N _{ms}	Nitrogen concentration in the mineral soil	g kg ⁻¹	4.8	2.4	1.3-16.4
	P _{ms}	Phosphorus concentration in the mineral soil	mg kg ⁻¹	514.8	302.9	77.2-2848.7
	P_Olsen _{ms}	Olsen phosphorus concentration in the mineral soil	mg kg ⁻¹	24.6	19.1	0.2-188.8
	C:N _{ms}	Carbon to nitrogen ratio in the mineral soil	-	12.1	2.8	7.8-32.6
	N:P _{ms}	Nitrogen to phosphorus ratio in the mineral soil	-	10.7	5.3	1.9-45.8
	C _{ms} stocks	Carbon stocks in the mineral soil	Mg ha ⁻¹	40.3	16.5	1.2-146.2
	N _{ms} stocks	Nitrogen stocks in the mineral soil	Mg ha ⁻¹	3.3	1.1	0.1-8.6
	P _{ms} stocks	Phosphorus stocks in the mineral soil	kg ha ⁻¹	373.9	195.2	11.1-1365.8
	P_Olsen _{ms} stocks	Olsen phosphorus stocks in the mineral soil	kg ha ⁻¹	17.1	19.1	0.2-132.0

Table 2 Relationships between forest patch age and size, environmental covariates and the forest floor and mineral soil properties (soil pH and nutrients concentrations and stocks in the forest floor and mineral soil layers). Values are standardized parameter estimates from general LMM with region and landscape type as random effect.

Soil layer	Predictor variable	Patch features variables			Environmental covariates					
		Age	Size	Age × Size	MAT	MAP	N _{deposit}	Forest.buffer500	BA	Clay
Forest floor	pH _{ff}	-0.08	-0.05	0.05	0.14	0.12	-0.30	-0.11	0.06	0.12
	C _{ff}	-0.09	0.02	-0.05	-0.28	0.29	-0.33	-0.01	0.02	-0.27
	N _{ff}	-0.07	-0.03	-0.03	0.03	0.18	0.03	0.00	-0.02	-0.42***
	C:N _{ff}	-0.04	0.07	-0.03	-0.23	0.00	-0.24	0.05	0.01	0.05
	C _{ff} stocks	0.11	-0.08	-0.02	0.40***	-0.25	0.14	0.07	-0.02	-0.06
	N _{ff} stocks	0.10	-0.08	-0.02	0.41***	-0.20	0.16	0.05	-0.02	-0.13
Mineral soil	pH _{ms}	-0.07	-0.10*	0.01	0.20	0.11	-0.34	-0.02	0.05	0.09
	C _{ms}	0.04	0.02	0.00	-0.33*	0.00	0.20	-0.01	-0.05	-0.19
	N _{ms}	0.05	-0.04	-0.04	-0.36*	0.14	0.00	-0.05	-0.03	-0.28*
	P _{ms}	-0.13*	-0.03	-0.05	-0.31	-0.05	-0.06	-0.07	0.06	0.01
	P_Olsen _{ms}	-0.03	0.02	0.03	-0.39	-0.40	0.59*	0.01	-0.07	0.00
	C:N _{ms}	0.12	0.07	0.08	-0.25	-0.22	0.39	0.13*	-0.12***	0.02
	N:P _{ms}	0.20***	-0.01	0.02	-0.08	0.29	0.02	0.02	-0.10*	-0.39*
	C _{ms} stocks	0.01	-0.05	-0.06	-0.12	-0.16	0.11	0.00	-0.08	-0.17
	N _{ms} stocks	-0.05	-0.08	-0.14*	-0.09	0.02	-0.14	-0.09	-0.02	-0.13
	P _{ms} stocks	-0.31***	0.00	-0.09	0.00	-0.22	-0.06	-0.07	0.08	0.23
P_Olsen _{ms} stocks	-0.05	0.01	0.01	-0.27	-0.47	0.59*	0.03	-0.07	0.15	

The variable abbreviations and explanations are mentioned in Table 1. ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

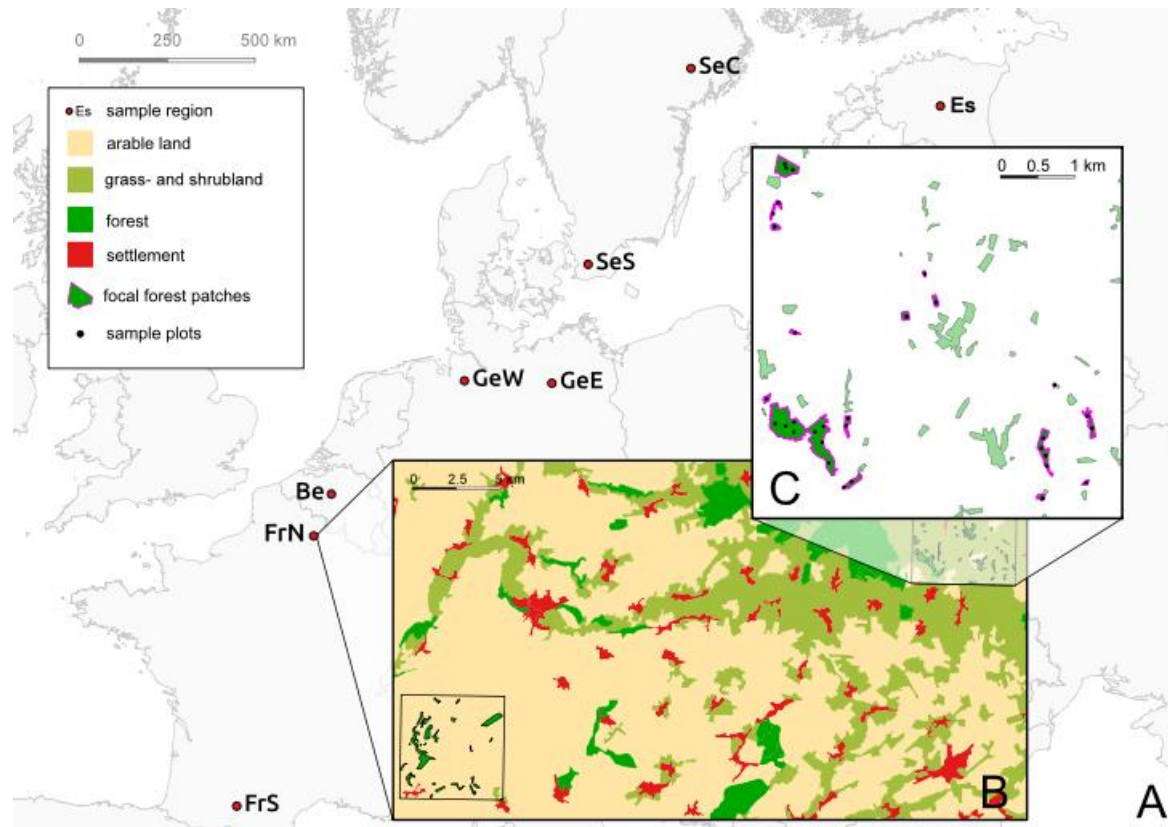


Fig. 1 Sampling design. (A) Location of the eight study regions along a macroclimatic gradient in Europe (Es, Estonia; SeC, central Sweden; SeS, south Sweden; FrN, north France; FrS, south France; Be, Belgium; GeW, west Germany; GeE, east Germany). (B) Detail of the forest patches and the surrounding land uses in northern France. (C) Soil sampling plots in selected forest patches.

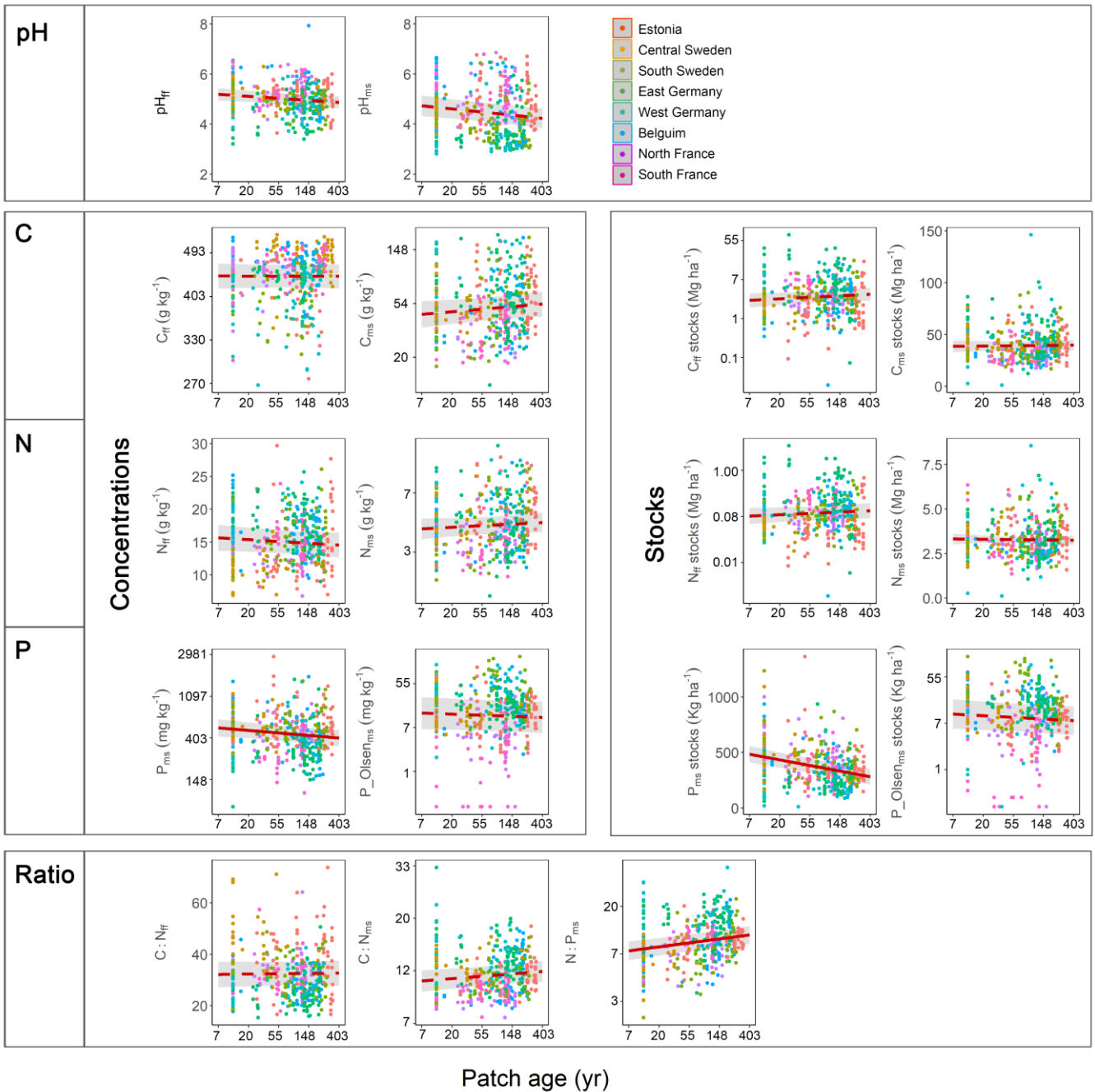


Fig. 2 The relationships between forest patch age (in years, the X axis was log transformed) and soil variables including soil pH and the concentrations and stocks of soil C, N and P and their ratios for both forest floor and mineral soil layers. The abbreviations and explanations for the variables are in Table 1. The soil variables of C_{ff} , N_{ms} , P_{ms} , P_Olsen_{ms} , $C:N_{ms}$, $N:P_{ms}$, C_{ff} stocks, N_{ff} stocks and P_Olsen_{ms} stocks are log transformed. The solid red lines represent the significant trends ($P < 0.05$) and dashed red lines represent non-significant trends ($P > 0.05$). The shaded area represents 95% confidence intervals.

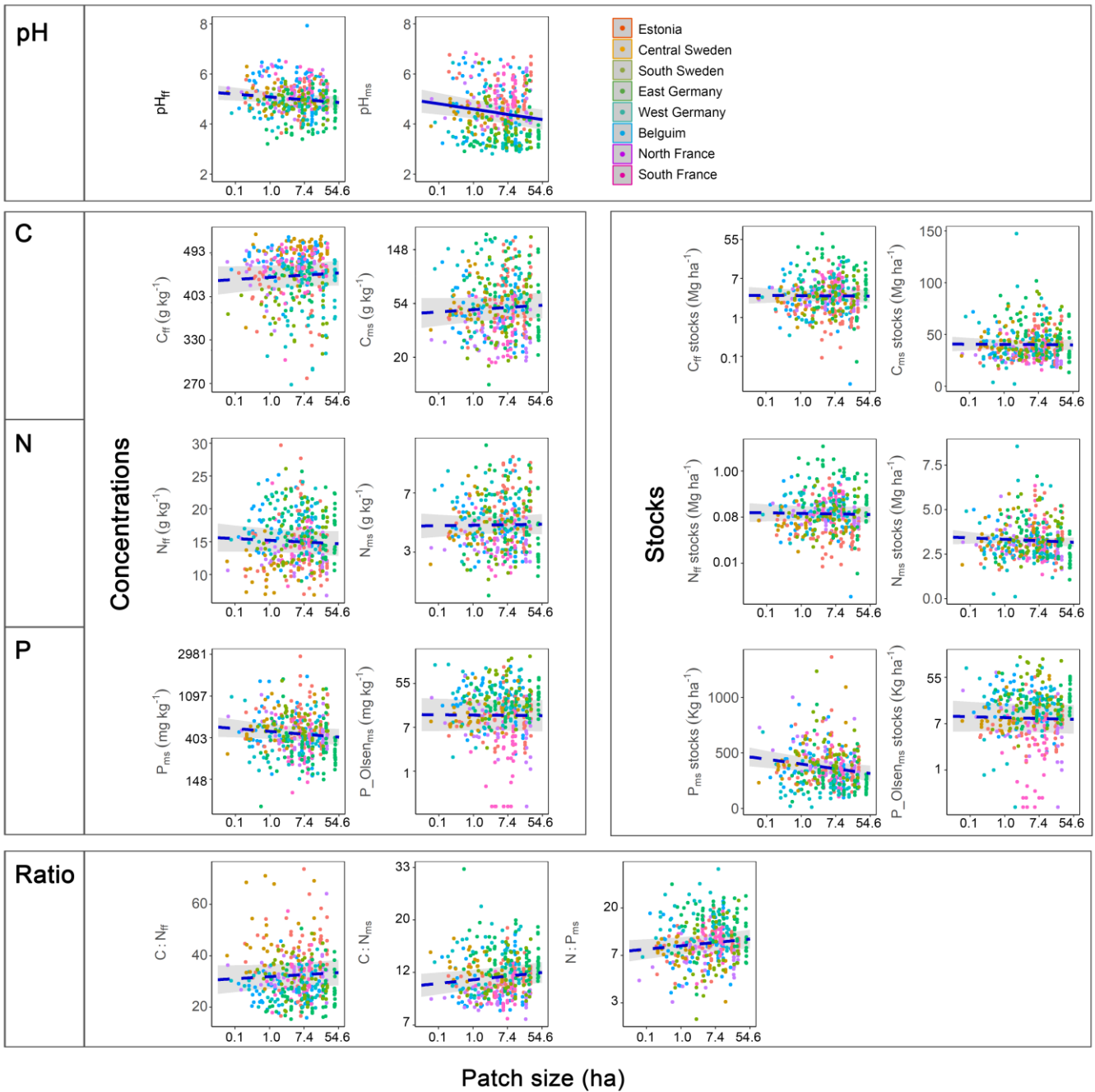


Fig. 3 The relationships between forest patch size (in hectares, the X axis was log transformed) and soil variables including soil pH and the concentrations and stocks of soil C, N and P and their ratios for both forest floor and mineral soil layers. The abbreviations and explanations for the variables are in Table 1. The soil variables of C_{ff} , N_{ms} , P_{ms} , $P_{Olsen_{ms}}$, $C:N_{ms}$, $N:P_{ms}$, C_{ff} stocks, N_{ff} stocks and $P_{Olsen_{ms}}$ stocks are log transformed. The solid blue lines represent the significant trends ($P < 0.05$) and dashed blue lines represent non-significant trends ($P > 0.05$). The shaded area represents 95% confidence intervals.