

1 This is the accepted version of the following article: Landuyt et al., 2019. Drivers of aboveground understorey
2 biomass and nutrient stocks in temperate forests. *Journal of Ecology* x(x), p. x-x, which has been published in
3 final form at <https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/1365-2745.13318>. This article may
4 be used for non-commercial purposes in accordance with the [Wiley Self-Archiving Policy](#)

5 **Drivers of aboveground understorey biomass and nutrient** 6 **stocks in temperate deciduous forests**

7 ¹Dries Landuyt, ¹Sybryn L. Maes, ¹Leen Depauw, ¹Evy Ampoorter, ¹Haben Blondeel, ^{1,2}Michael P. Perring,
8 ³Guntis Brūmelis, ⁴Jörg Brunet, ⁵Guillaume Decocq, ⁶Jan den Ouden, ⁷Werner Härdtle, ^{8,9}Radim Hédli,
9 ¹⁰Thilo Heinken, ¹¹Steffi Heinrichs, ¹²Bogdan Jaroszewicz, ¹³Keith J Kirby, ^{14,15}Martin Kopecký, ^{16,17}František
10 **Máliš**, ¹⁸Monika Wulf, ¹Kris Verheyen

11 ¹Forest & Nature Lab, Department of Environment, Ghent University, Geraardsbergsesteenweg 267, 9090 Melle-Gontrode, Belgium

12 ²Ecosystem Restoration and Intervention Ecology Research Group, School of Biological Sciences, The University of Western Australia,
13 35 Stirling Highway, Crawley WA 6009, Australia

14 ³Faculty of Biology, University of Latvia, Jelgavas iela 1, Riga LV1004, Latvia

15 ⁴Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Box 49, 23053 Alnarp, Sweden

16 ⁵Ecologie et Dynamique des Systèmes Anthropisés" (EDYSAN, UMR CNRS 7058), Université de Picardie Jules Verne, 1 rue des Louvels,
17 F-80037 Amiens Cedex 1, France

18 ⁶Forest Ecology and Forest Management, Wageningen University, PO Box 47, 6700AA Wageningen, The Netherlands

19 ⁷Leuphana University of Lüneburg, Universitätsallee 1, 21335 Lüneburg, Germany

20 ⁸Institute of Botany of the Czech Academy of Sciences, Lidická 25/27, CZ-60200 Brno, Czech Republic

21 ⁹Department of Botany, Faculty of Science, Palacký University in Olomouc, Šlechtitelů 27, CZ-78371 Olomouc, Czech Republic

22 ¹⁰General Botany, Institute of Biochemistry and Biology, University of Potsdam, 14471 Potsdam, Germany

23 ¹¹Department Silviculture and Forest Ecology of the Temperate Zones, University of Goettingen, Büsngenweg 1, 37077 Göttingen,
24 Germany

25 ¹²Białowieża Geobotanical Station, Faculty of Biology, University of Warsaw, Sportowa 19, 17-230 Białowieża, Poland

26 ¹³Department of Plant Sciences, South Parks Road, Oxford OX2 6TL, United Kingdom

27 ¹⁴Institute of Botany of the Czech Academy of Sciences, Zámek 1, CZ-252 43 Průhonice, Czech Republic

28 ¹⁵Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, CZ-165 00 Prague 6 – Suchbátka,
29 Czech Republic

30 ¹⁶Technical University in Zvolen, Faculty of Forestry, T. G. Masaryka 24, 960 53 Zvolen, Slovakia

31 ¹⁷National Forest Centre, T. G. Masaryka 22, 960 92 Zvolen, Slovakia

32 ¹⁸Leibniz Centre for Agricultural Landscape Research (ZALF) Eberswalder Straße 84, 15374 Müncheberg, Germany

33 *Corresponding author (dries.landuyt@ugent.be)

34 **Summary**

35 **1.** The understorey in temperate forests can play an important functional role, depending on its biomass and
36 functional characteristics. While it is known that local soil and stand characteristics largely determine the
37 biomass of the understorey, less is known about the role of global change. Global change can directly affect

38 understory biomass, but also indirectly by modifying the overstorey, local resource availability and growing
39 conditions at the forest floor.

40 **2.** In this observational study across Europe, we aim at disentangling the impact of global-change drivers on
41 understory biomass and nutrient stocks, from the impact of overstorey characteristics and local site
42 conditions. Using piecewise structural equation modelling, we determine the main drivers of understory
43 biomass and nutrient stocks in these forests and examine potential direct and indirect effects of global-
44 change drivers.

45 **3.** Tree cover, tree litter quality and differences in former land use were the main drivers of understory
46 biomass and nutrient stocks, via their influence on understory light and nitrogen availability and soil acidity.
47 Other global-change drivers, including climate and nitrogen deposition, had similar indirect effects, but these
48 were either weak or only affecting nutrient concentrations, not stocks.

49 **4. Synthesis.** We found that direct effects of global-change drivers on understory biomass and nutrient
50 stocks were absent. The indirect effects of global change, through influencing resource availability and
51 growing conditions at the forest floor, were found to be less important than the effects of overstorey cover
52 and composition. These results suggest that understory biomass and nutrient stocks might respond less to
53 global change in the presence of a dense overstorey, highlighting the buffering role of the overstorey in
54 temperate forests.

55 **Key-words:** ecosystem functioning, ground layer, herb layer, PhytoCalc, piecewise SEM, productivity

56 **1. Introduction**

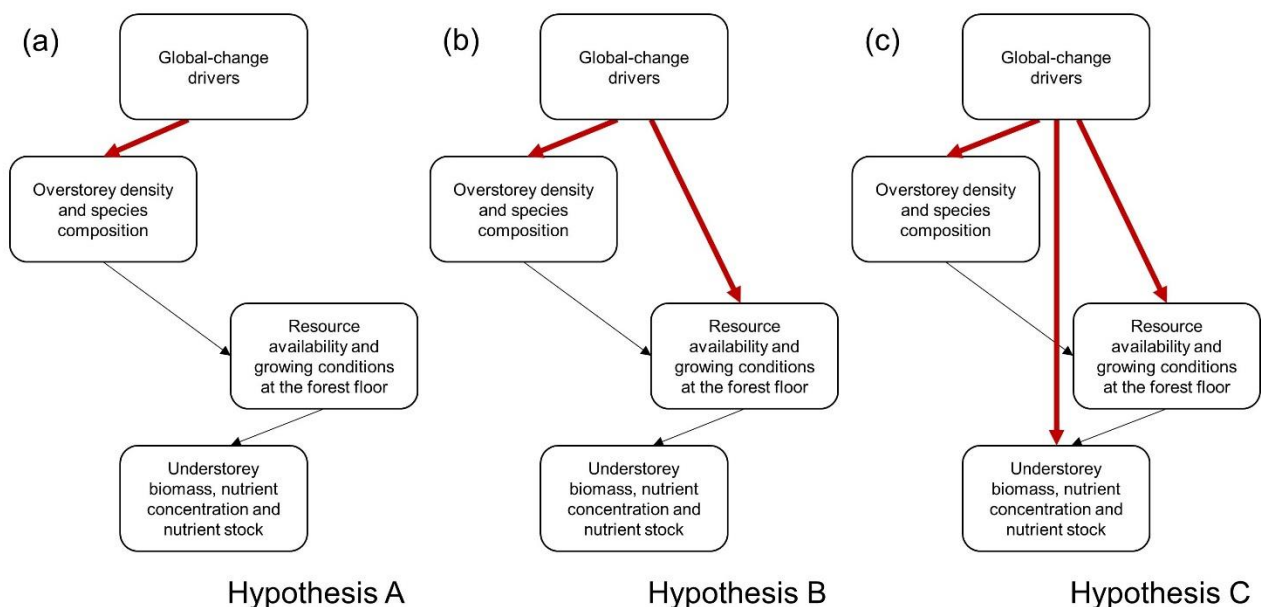
57 Temperate forests cover around 16 % of the world's forest area (Hansen, Stehman, & Potapov, 2010). Being
58 located in the highly-populated temperate climate zone, their biodiversity and functioning is impacted by a
59 complex set of pressures, including climate change, elevated levels of acidifying and eutrophying deposition,
60 invasive species and changes in forest use (Gilliam, 2016; Reich & Frelich, 2002). Investigating how temperate
61 forests respond to these pressures is crucial to be able to conserve these ecosystems and the services they
62 provide.

63 Global-change research in temperate forests has traditionally focussed predominantly on the overstorey
64 (Aber et al., 2001; Dyderski, Paż, Frelich, & Jagodziński, 2018; Pastor & Post, 1988), while global-change
65 responses in the understory have been less studied, although the number of studies has rapidly expanded
66 during the last decade (e.g. Kim, Oren, & Qian, 2016; Perring, Bernhardt-Römermann, et al., 2018; Verheyen
67 et al., 2012). Also the focus of both lines of research has differed considerably. While overstorey research
68 has predominantly focussed on functional responses (e.g. global change affecting overstorey productivity),
69 understory research has predominantly focussed on biodiversity responses, motivated by the knowledge
70 that the understory largely determines the vascular plant diversity in temperate forests (Gilliam, 2007).

71 Although the marginal contribution of the understorey to the total standing biomass in a forest (see for
72 example Zhang, Chen, & Taylor, 2016) might justify the greater interest in the overstorey when it comes to
73 ecosystem functioning, more and more evidence is becoming available that the understorey can play an
74 important functional role as well (Landuyt et al., 2019). The understorey can for example alter tree
75 regeneration and growth rates resulting from competition with trees for water, nutrients and light (Bloor et
76 al., 2008; Giuggiola et al., 2018; Watt, Whitehead, Richardson, Mason, & Leckie, 2003). The understorey can
77 also determine above and belowground food webs (Handa et al., 2014; Scherber et al., 2010), e.g. by acting
78 as a food source for different species groups (Boch et al., 2013; Gill & Beardall, 2001). It further influences
79 nutrient cycling processes (e.g. Jackson, Nilsson, and Wardle 2013; Muller 2003) and can retain a large
80 proportion of throughfall water (e.g. Price et al. 1997). The importance of all these effects jointly depends on
81 understorey biomass and its species composition, the latter driving the understorey's functional signature
82 (Gilliam, 2007; Landuyt et al., 2019). Understorey biomass, however, is generally considered as the most
83 important indicator for understorey functioning, especially when considering the understorey's role in water
84 and nutrient cycling, food provision for ungulates and its effect on tree regeneration (e.g. Mabry, Gerken, &
85 Thompson, 2008; Royo & Carson, 2006; Smolko & Veselovská, 2018; Thrippleton et al., 2018). When looking
86 specifically at the contribution of the understorey to nutrient cycling processes and forage provision,
87 understorey nutrient concentrations will play an important role as well (González-Hernández & Silva-Pando,
88 1999; Pan et al., 2018; Tessier & Raynal, 2003).

89 Research on global-change effects in the understorey of temperate forests has shown that understorey
90 communities, characterised in terms of species richness or functional signature, are sensitive to a multitude
91 of global-change drivers (Ampoorter et al., 2016; De Frenne et al., 2009; Perring, Bernhardt-Römermann, et
92 al., 2018; Verheyen et al., 2012). Most of these responses are, however, context dependent. Whether or not
93 the understorey reacts to global change often depends on local site conditions, defined by the overstorey
94 and the soil (Chen, Biswas, Sobey, Brassard, & Bartels, 2018; Gilliam, 2019; Kim et al., 2016; Perring,
95 Diekmann, et al., 2018; Verheyen et al., 2012). Nitrogen deposition has, for example, the potential to
96 decrease species richness in the understorey by stimulating competitive exclusion (Gilliam, 2006), but this
97 response is often not generalisable (Perring, Diekmann, et al., 2018). Similarly, agricultural land use prior to
98 afforestation has been shown to increase the responsiveness of the understorey to global change (mainly by
99 alleviating nutrient limitations long after agricultural abandonment), but again responses are hard to
100 generalise (Perring et al., 2016). Similar conclusions have been formulated concerning the understorey's
101 response to climate change (e.g. De Frenne et al., 2015). In addition to these context-dependencies, little is
102 known about understorey responses in terms of biomass and nutrient stocks (but see Axmanová, Zelený, Li,
103 & Chytrý, 2011; Welch, Belmont, & Randolph, 2007). Overall, the mechanisms behind these global-change
104 effects (including interactions and context-dependencies) are still poorly understood, making it hard to
105 predict future responses of the understorey to global change or to develop measures to mitigate global-
106 change effects in the understorey (Landuyt et al., 2018).

107 Multiple mechanistic hypotheses can be put forward to explain understorey responses to global-change
 108 drivers and, more specifically, how soil and overstorey characteristics can mediate these responses (Figure
 109 1). The first, most simple, hypothesis (Figure 1a) entails that only the overstorey responds to global change,
 110 and that these changes in the overstorey, mainly changes in crown cover and species composition, influence
 111 understorey resource availability and growing conditions. This hypothesis builds upon the evidence that
 112 overstorey composition can alter light availability through its crown cover (Monsi & Saeki, 2005) and soil
 113 acidity and nutrient availability predominantly via species-specific differences in leaf litter quality (Augusto,
 114 Dupouey, & Ranger, 2003; De Schrijver et al., 2012; van Oijen, Feijen, Hommel, den Ouden, & de Waal, 2005)
 115 with subsequent effects on the understorey (Ali, Chen, You, & Yan, 2019; Axmanová et al., 2011; Falkengren-
 116 Grerup, 1989; McKenzie, Halpern, & Nelson, 2011; Zhang, Chen, & Taylor, 2017). The second hypothesis
 117 (Figure 1b) acknowledges the above-mentioned pathways, but additionally postulates that soil resources can
 118 also change directly in response to global change. This hypothesis relies on the fact that global change is
 119 often associated with direct nutrient inputs into the soil. This accounts for atmospheric nitrogen depositions
 120 (Boring, Swank, Waide, & Henderson, 1988) as well as for recent forests with an agricultural land use history
 121 (e.g. Blondeel et al., 2018). In addition, climate change might affect soil nutrient availability by altering litter
 122 decomposition (Aerts, 1997)). The third, and most complex, hypothesis (Figure 1c) additionally includes direct
 123 global-change effects on the understorey that can, for example, be driven by uptake of nutrients via
 124 aboveground plant organs (as shown by De Frenne et al., 2018) or temperature-induced growth increases
 125 (Farquhar, von Caemmerer, & Berry, 1980).



126

127 **Figure 1.** Graphical representation of three alternative hypotheses that can explain the response of understorey biomass and
 128 nutrient stocks to global change.

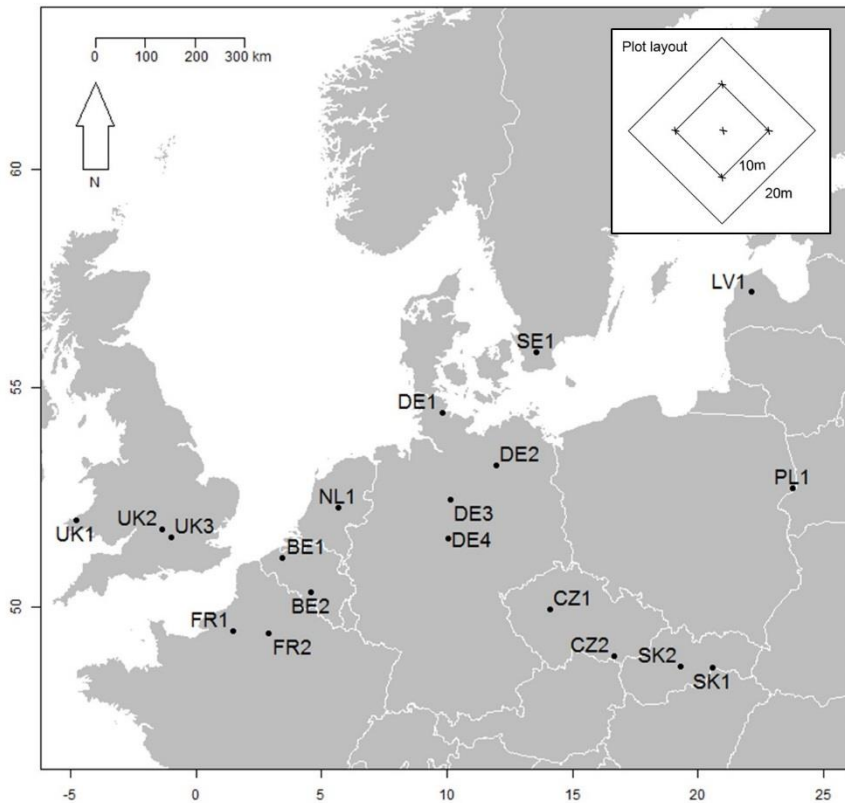
129 In this study, we aim to unravel the mechanisms underlying the response of understorey biomass,
 130 understorey nutrient concentration and understorey nutrient stocks to global change. We evaluate the

131 above-mentioned hypotheses using understorey, overstorey and soil data collected across Europe along a
132 climate and nitrogen deposition gradient in mature temperate forests with contrasting land use histories. By
133 investigating the extent to which understorey characteristics are related to global-change drivers spatially,
134 insights can arguably be gained on the understorey's potential temporal response to global change and the
135 mechanisms behind this response. Using piecewise structural equation modelling, we evaluate the likeliness
136 of each hypothesis, quantify the relative importance of all individual pathways of influence and determine
137 the main drivers of understorey biomass and nutrient stocks.

138 **2. Methods**

139 2.1. Sampling design

140 We sampled 19 regions scattered along a nitrogen deposition and climate gradient in Northwest Europe
141 (Figure 2, S3). In each region, around 10 plots were selected (190 plots in total), mostly including both recent
142 and ancient forests (Table S1). The latter were defined as plots that have been forested continuously since
143 1850 or earlier. Recent forest plots, with similar stand ages as ancient forest plots, were located on former
144 agricultural land, and were divided into plots with an arable land use history and plots that have formerly
145 been used for grazing or other more extensive agricultural practices. Plot selection was based on several
146 criteria: (1) existence of historical understorey surveys (not relevant for this study) (2) an intermediate to
147 high soil nutrient content ($C/N < 20$), (3) an intermediate water holding capacity (Ellenberg Indicator Value
148 for moisture ranging between 3.5 and 6.5, excluding extremely dry and water-logged sites) and (4) a well-
149 documented land use history, resulting in a selection containing both mesophytic deciduous forests and
150 lowland beech forests (according to the European Forest Types classification scheme of Barbati et al. (2014),
151 see also Table S1 for dominant overstorey species and Table S2 for a list of understorey species). We
152 deliberately excluded forests that experience more extreme soil conditions (e.g. very dry or nutrient poor
153 soils). In the latter forests, understorey productivity is generally limited by a single resource (e.g. nutrient or
154 water availability), which should lead to a more predictable understorey response to global change. Although
155 most of the selected plots had a dense canopy layer, the plots still covered a range of light availability
156 conditions, mainly due to differences in tree species composition and management practices. Each plot
157 consisted of two nested square-shaped subplots, one 10 m by 10 m plot, hereafter referred to as the inner
158 plot, and one 20 m by 20 m plot, hereafter referred to as the outer plot (inset Figure 2). Both subplots were
159 used for characterising the shrub layer (shrubs and trees with a height between 1 and 7 m) and the overstorey
160 (trees with a height above 7 m). The inner plot was used for the characterisation of the understorey, light
161 availability, nutrient availability and other soil characteristics. All plots were visited during the late spring of
162 2015 and 2016, when understorey biomass was assumed to be at its maximum.



163

164 **Figure 2.** Geographical spread of the 19 study regions, located in the United Kingdom (UK), France (FR), Belgium (BE), the Netherlands
 165 (NL), Germany (DE), Sweden (SE), Latvia (LV), Poland (PL), the Czech Republic (CZ) and Slovakia (SK). Inset: visualisation of the plot
 166 layout with north-south and east-west oriented diagonals and crosses denoting soil sampling and densitometer measurement
 167 positions.

168 2.2. Global-change drivers at the regional scale

169 We estimated regional-scale explanatory variables from publicly-available databases. Atmospheric nitrogen
 170 deposition data were extracted from EMEP (www.emep.int, v2013) based on plot coordinates recorded in
 171 the field. As cumulative nitrogen deposition has been shown to affect species richness and biomass (De
 172 Schrijver et al., 2011), we chose this indicator to characterise nitrogen inputs rather than current deposition
 173 rates. Both indicators are, however, highly correlated. Cumulative nitrogen deposition was derived from
 174 nitrogen deposition time trends for each plot using the year 2000 value extracted from EMEP as a basis for
 175 extrapolation to the period 1940-2016, based on correction factors published by Duprè et al. (2010).
 176 Cumulative deposition was calculated as the sum of yearly deposition rates between 1940 and 2016. As
 177 within-regional differences in cumulative deposition rates are unlikely, average regional values were used for
 178 the analysis. Climate data, including mean annual precipitation and mean annual temperature were
 179 extracted from CRU TS4.01 (Harris, Jones, Osborn, & Lister, 2014) using the full range of available data from
 180 1900-2015. Again, average regional values were used in the analysis.

181 2.3. Overstorey density and species composition

182 We estimated percentage cover of each tree species based on the horizontal projections of the crowns of
183 trees higher than 7 m. Percentage cover of the shrub layer, being defined as all shrubs and trees with a height
184 between 1 and 7 m, was assessed in a similar way. Both cover percentages were recorded in the inner plot.

185 Overstorey effects on the availability of resources and growing conditions at the forest floor were assumed
186 to be predominantly driven by differences in light transmittance and tree litter quality (Barbier, Gosselin, &
187 Balandier, 2008). To quantify tree litter quality, we calculated an average litter quality score based on species-
188 specific litter quality scores, as described in Maes et al. (2019). For each plot, a weighted average litter quality
189 score was calculated with relative crown cover of each tree species present in the plot as weights. Hence,
190 species composition was not included in the model as such, but instead represented by this litter quality
191 score. Total crown cover of the tree and the shrub layer were assumed to be the main drivers of light
192 availability at the forest floor.

193 *2.4. Resource availability and growing conditions at the forest floor*

194 Soil samples were taken at five locations in the inner plot (inset Figure 2), using a soil auger to sample the
195 upper 20 cm of the mineral soil (0-10 cm samples were used for chemical analyses, 10-20 cm samples for
196 texture analyses). Collected soil samples were pooled across locations but within depths per plot and dried
197 to constant weight at 40°C for 48 h, ground and sieved over a 2 mm mesh. Total phosphorus concentration
198 in the soil was measured colorimetrically according to the malachite green procedure (Lajtha, Driscoll, Jarrell,
199 & Elliott, 1999) after complete destruction of the soil samples with HClO₄ (65%), HNO₃ (70%) and H₂SO₄ (98%)
200 in Teflon bombs for 4 h at 150°C. Total carbon and nitrogen concentrations in the soil were determined by
201 high temperature combustion at 1200°C using an elemental analyser (vario Macro Cube, Elementar,
202 Germany). Inorganic carbon content was obtained running the same analysis after ashing the soil samples
203 for 4 h at 450°C by gradually increasing temperature, leaving inorganic carbon only. Organic carbon
204 concentration was determined by subtracting inorganic carbon concentration from total carbon
205 concentration. Data on organic carbon, total nitrogen and total phosphorus concentration were used for
206 calculating soil organic carbon to total nitrogen (C/N) and organic carbon to total phosphorus (C/P) ratios, as
207 proxies for nitrogen and phosphorus availability, respectively (Leuschner & Ellenberg, 2017). The pH-H₂O of
208 the soil was determined by shaking a 1:5 ratio soil/H₂O mixture for 5 minutes at 300 rpm before measuring
209 with an Orion 920A pH meter equipped with a Ross sure-flow 8172 BNWP pH electrode (Thermo Scientific
210 Orion, USA). Soil texture (% Clay, % Sand and % Silt) was analysed with laser diffraction (Coulter Laser LS 13
211 320 (SIP-050D2) with auto-sampler) after removal of organic material with H₂O₂ (28.5%) and dispersing the
212 sample with Sodium polyphosphate (6%). Data on particle size and inorganic carbon content were used to
213 cluster the soils in three soil type groups with different intrinsic soil characteristics, being sandy soils, clayey
214 soils with high carbonate content and clayey soils with low carbonate content (using hclust in R, for more
215 information see Maes et al. (2019)).

216 Plot average light availability was assessed via convex densiometer measurements (Lemmon, 1956) at five
217 locations in the inner plot (one in each corner and one in the centre, indicated by crosses in the inset of Figure
218 2). Mean plot-level light availability was obtained by averaging these five measurements.

219 2.5. Response variables

220 We selected five response variables for analysis, these being aboveground biomass, average nitrogen and
221 phosphorus content per leaf dry mass (hereafter referred to as nitrogen and phosphorus concentration) and
222 total nitrogen and phosphorus stocks in aboveground biomass.

223 The understorey was defined as all woody and non-woody vascular plants not exceeding 1 m in height,
224 including herbs, graminoids, ferns, dwarf shrubs, tree seedlings and small shrubs and trees. First, the
225 percentage cover of all understorey species was quantified via ocular estimation, in the inner plot only. To
226 estimate understorey biomass, the mean shoot length of each species with a cover higher than 5% was
227 additionally recorded. For each of these species, shoot lengths were measured on five randomly selected
228 individuals by elongating the shoots as described in Heinrichs et al. (2010). From the three species with the
229 highest abundances, a subsample of the non-woody aboveground biomass was taken for nutrient analyses.
230 Collected biomass samples were dried to constant weight at 70°C for 48 h, weighed and ground. Nitrogen
231 concentrations in biomass were determined by high temperature combustion at 1150°C using an elemental
232 analyser (Vario MACRO cube CNS, Elementar, Germany). Biomass phosphorus concentration was obtained
233 after digesting 100 mg of the sample with 0.4 ml HClO₄ (65%) and 2 ml HNO₃ (70%) in Teflon bombs for 4 h
234 at 140°C. Phosphorus concentration was measured colorimetrically according to the malachite green
235 procedure (Lajtha et al., 1999).

236 Total understorey biomass was estimated non-destructively via the PhytoCalc model (Bolte, Czajkowski,
237 Bielefeldt, Wolff, & Heinrichs, 2009; Heinrichs et al., 2010), comprising allometric equations to estimate
238 biomass based on cover and shoot length data (Equation 1). The coefficients of these allometric equations
239 (a_g , b_g and c_g) were calibrated and validated for 13 morphological growth forms and eight tree and shrub
240 species commonly found in the understorey of temperate forests (Bolte et al., 2009; Heinrichs et al., 2010).
241 Species data for calibrating the model were sampled in closed beech to more open oak and pine forests with
242 cover values of the tree layer between 15 and 95 % (Bolte, 1999; Schulze, Bolte, Schmidt, & Eichhorn, 2009).

$$243 \text{biomass} \left[\frac{g}{m^2} \right] = \sum_{i=1}^n a_g \cdot C_i^{b_g} S_i^{c_g} \quad (\text{eqn 1})$$

244 Wherein n represents the total number of species within a plot, C_i the cover of species i [%], S_i the elongated
245 shoot length of species i [cm] and a_g , b_g and c_g morphological growth form specific empirical coefficients, as
246 provided by the PhytoCalc model (Table S3). Main morphological growth forms include herbs, grasses, ferns,
247 small shrubs and dwarf shrubs (as well as mosses that have not been considered here). Herbs and grasses
248 were then differentiated by height categories into small, middle and tall. In total 45 species of the ground

249 flora were harvested across Germany to calibrate the morphological growth form specific empirical
250 coefficients. The validity of these coefficients has been tested in independent study areas leading to an
251 extension of the PhytoCalc species list (e.g. Schulze et al., 2009). For woody species, species-specific empirical
252 coefficients exist for the tree species *Fagus sylvatica*, *Quercus robur*, *Quercus petraea*, *Picea abies*, *Pinus*
253 *sylvestris*, *Fraxinus excelsior*, *Acer pseudoplatanus*, *Sorbus aucuparia* and *Betula pendula* and for the shrub
254 species *Cytisus scoparius*, *Rhamnus cathartica* and *Sambucus nigra*. Other woody species are not yet included
255 in the model except for small shrubs mainly representing *Rubus* spec. and *Ribes* spec. and dwarf-shrubs
256 including *Vaccinium* spec. and *Calluna* spec.

257 While cover estimates were recorded for all encountered species, shoot length data were only collected for
258 a subset of these species (those with a cover exceeding 5%). For those species with missing shoot length data
259 (on average 35% of total plot cover, see also Figure S1), default PhytoCalc shoot length values, defined on
260 the level of morphological growth forms, were used (see Table S3). While these group-specific shoot length
261 values agreed well with those observed in the field on average (Figure S2), they do not account for the
262 variability encountered in the field, stressing the need to measure shoot lengths in the field, at least for a
263 subset of the encountered species as done in this study. When recorded species were not included in the
264 PhytoCalc species list, we assigned them to a morphological growth form based on the most occurring
265 morphological growth form for that genus. To avoid errors due to this automated procedure, we manually
266 checked the results to ensure that all species were assigned to the correct morphological growth form. If no
267 match was found at the genus level, species were assumed to have a biomass per cover percentage that
268 equals the mean biomass per cover percentage found in the plot. The percentage cover of species that could
269 not be assigned to one of the morphological growth forms was generally low, ranging between 0 and 10%
270 for the majority of the plots. This percentage was exceeded (up to 40%) only for plots in the Wales region
271 (UK1).

272 While the PhytoCalc model can also be used to estimate nutrient stocks, these estimates have been shown
273 to be prone to error, especially under more open forest conditions (Heinrichs et al., 2010). Moreover, as plant
274 nutrient concentrations are known to be driven by local soil conditions (e.g. Baeten et al., 2011), we used our
275 own field measurements instead. Aboveground nutrient stocks (nitrogen and phosphorus) in the understorey
276 were approximated by multiplying aboveground biomass estimates with the average leaf-level nutrient
277 concentration at the plot-level. Plot-level nutrient concentration was estimated as the average nutrient
278 concentration of the sampled species, weighted by their cover. As unsampled species only represented a
279 minority of the total understorey cover in most plots (see also Figure S1), we do not expect these species to
280 bias our results. However, as nutrient analyses were only conducted on non-woody tissue, which is known
281 to have a higher nutrient concentration than woody tissue, estimated nutrient stock values might
282 overestimate the actual nutrient stocks in the understorey.

283 2.6. Statistical analysis

284 The conceptual graphs, presented in Figure 1, were used to construct three alternative structural equation
285 models (SEMs). For each block in Figure 1, we measured several variables in the field, or extracted data from
286 databases as described above. As global-change drivers, we included mean annual temperature (MAT), mean
287 annual precipitation (MAP), cumulative nitrogen deposition (Ndep) and land use history (to account for
288 historical land use change effects). Overstorey variables included tree cover, shrub cover and tree litter
289 quality. Resource availability and growing conditions at the forest floor were characterised by soil pH, soil
290 C/N, soil C/P and light availability. Table 1 provides an overview of all variables included in the models and
291 their proxies measured in the field. As paths, we included those depicted in Figure 1, but additionally
292 accounted for several known dependencies and independencies to improve the model fit. Light availability
293 was assumed to depend only on tree cover and shrub cover; C/N and C/P were assumed to be correlated and
294 additionally driven by soil pH; and shrub cover was assumed to be driven only by tree cover. Additionally, all
295 soil variables were assumed to be driven by soil type. The full list of paths included in the three alternative
296 models can be found in the online supporting information.

297 The three alternative models were fitted using piecewise SEM (Lefcheck, 2016). In contrast to standard SEM
298 techniques, piecewise SEM allows fitting mixed effect models to all paths of the hypothesised model and can
299 thus account for the blocked design of our data (plots within regions). For each path, we fitted mixed effect
300 models including main effects only and region as random intercept (full model lists for our three alternative
301 hypotheses are provided in the online supporting information). Prior to model fitting, some of the data were
302 log transformed to improve model fit and to ensure residuals were normally distributed (Table 1). The
303 categorical variables past land use and soil type were dummy coded, using “ancient forest” and “clayey soil
304 with high carbonate content” as reference classes, respectively. We repeated the analysis with five different
305 response variables, namely biomass, leaf nitrogen concentration, total aboveground nitrogen stock, leaf
306 phosphorus concentration and total aboveground phosphorus stock.

307 We evaluated the fitted models based on the Fisher’s C statistic (Shiple, 2000), Akaike’s Information
308 Criterion corrected for small sample sizes (AICc), path significance levels and the pseudo R² values (Nakagawa
309 & Schielzeth, 2013) of the fitted linear mixed-effect models. While the Fisher’s C statistic was used to evaluate
310 whether the model accounted for all dependencies in the data, AIC and pseudo R² values were used to
311 evaluate model complexity and model fit. Data preparation and statistical analysis were carried out in R
312 version 3.5.1 (R Core Team, 2018). Structural equation models were fitted using the piecewiseSEM package
313 (Lefcheck, 2016).

314 Finally, we compared the combined indirect effects of nitrogen deposition, climate, past land use and
315 overstorey characteristics on the five understorey response variables considered. We first calculated the
316 magnitude of all indirect effects by multiplication of path coefficients. These indirect effects were defined
317 as significant pathways between a driver (global change or overstorey characteristic) and the understorey
318 response variable, via one or more of the other variables in the model. Next, when there were multiple

319 indirect pathways between a certain driver and understorey response, these were summed, following
 320 Wright's tracing rules (Wright, 1921). The standard deviation and significance of these combined effect was
 321 estimated via a Monte Carlo simulation (10,000 samples), propagating the errors associated to the
 322 estimated standardised path coefficients to obtain a distribution for each combined effect (Preacher &
 323 Selig, 2012). A combined effect was considered significant when its 95% confidence interval (defined by the
 324 2.5% and 97.5% quantiles of the obtained distribution) excluded zero.

325 **Table 1.** Overview of all predictor variables included in the structural equation models, the chosen proxy and the applied data
 326 transformation for statistical analysis. See also Figure S3 for a comparison of these ranges with full ranges encountered in temperate
 327 forests. More information on the soil types can be found in Maes et al. (2019).

Variable	Proxy	Range	Units	Transformation
Global-change drivers				
Climate	Mean annual precipitation	547 - 1585	mm	NA
	Mean annual temperature	6.5 - 12.1	°C	NA
Nitrogen deposition	Cumulative nitrogen deposition	459 - 1925	kg.ha ⁻¹	Log(X)
Past land use	Three types of past land use	1.Recent forest with past arable agricultural use 2.Recent forest with past non-arable agricultural use 3.Ancient forest	NA	NA
Overstorey density and species composition				
Litter quality	Litter quality score (weighted on tree species cover)	0.9 - 4.9	NA	Log(X)
Tree cover	Estimated cover	0 - 98	%	NA
Shrub cover	Estimated cover	0 - 97	%	NA
Soil type				
Soil type	Three types of soil based on clay content and inorganic carbon content	1.Sandy soils 2.Clayey soils with high carbonate content 3.Clayey soils with low carbonate content	NA	NA
Resource availability and growing conditions				
Soil acidity	pH _{H₂O}	3.7 - 8.2	NA	Log(X)
Nitrogen availability	C/N ratio	9 - 26	NA	Log(X)
Phosphorus availability	C/P ratio	22 - 922	NA	Log(X)
Light availability	Canopy openness	2 - 73	%	Log(X)

328

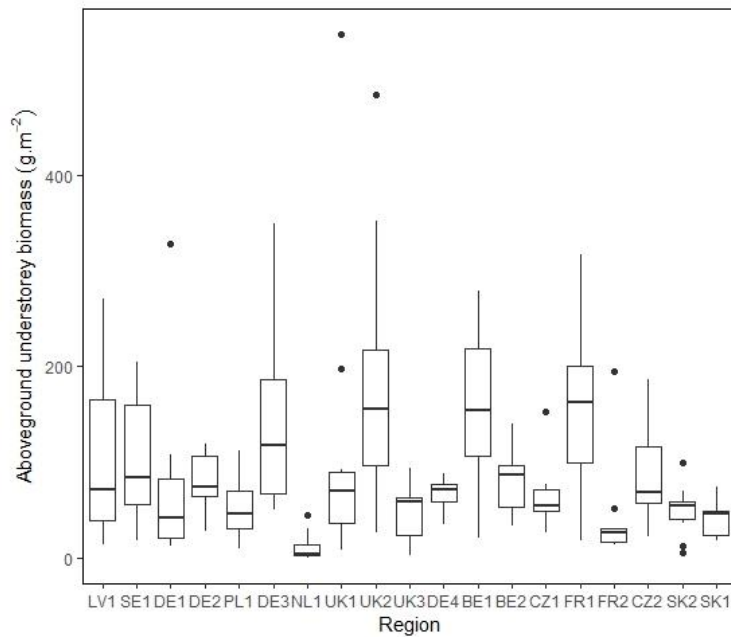
329 3. Results

329

330 3.1. Understorey biomass, nutrient concentrations and stocks

330

331 Understorey biomass in the sampled forests ranged between 0 and >500 g.m⁻², with a high within and among
 332 region variability (Figure 3). While the mean understorey biomass was 87.4 g.m⁻² across all plots, half of the
 333 plots had an understorey biomass that was lower than 63.8 g.m⁻² (inter quartile range: 33.3-106.6 g.m⁻²).



334

335 **Figure 3.** Variability of aboveground understory biomass across all regions, ordered from north to south. Region codes refer to the
 336 regions' countries: United Kingdom (UK), France (FR), Belgium (BE), the Netherlands (NL), Germany (DE), Sweden (SE), Latvia (LV),
 337 Poland (PL), the Czech Republic (CZ) and Slovakia (SK).

338 Similarly, nitrogen and phosphorus concentrations in the understory's aboveground biomass varied
 339 considerably (Figure S4). Nitrogen concentrations were between 1.0 and 4.4% with a mean nitrogen
 340 concentration of 2.7%. High nitrogen concentrations were found in some plots located in Belgium, the
 341 Netherlands and the UK. Phosphorus concentrations varied between 0.8 and 6.9‰ with a mean phosphorus
 342 concentration of 2.7‰. Again, high concentrations were found in some plots located in Belgium, the
 343 Netherlands and the UK. Nutrient stock patterns were similar to those found for biomass (Figure S5),
 344 indicating that, as expected, biomass strongly determined nutrient stocks in the understory. Nitrogen stocks
 345 ($2.3 \pm 2.2 \text{ g.m}^{-2}$) were on average 10-times higher than phosphorus stocks ($0.2 \pm 0.3 \text{ g.m}^{-2}$), with values
 346 ranging as high as 17.9 g.m^{-2} and 2.0 g.m^{-2} , for nitrogen and phosphorus respectively.

347 *3.2. Direct or indirect effects of global change on understory biomass, nutrient concentration and stock*

348 All 15 fitted models (3 hypotheses x 5 response variables) yielded a Fisher's C-statistic with a p-value ranging
 349 between 0.17 (hypothesis A, phosphorus concentration as response variable) and 0.51 (hypothesis B,
 350 nitrogen stock as response variable), suggesting that even the most simple hypothesis (hypothesis A)
 351 accounted for all dependencies among the variables included in the model. The AICc of the fitted models
 352 increased with increasing model complexity from hypothesis A to hypothesis C, denoting that, based on AICc,
 353 hypothesis A represented the relationships among the included variables the best (Figure S6). When looking
 354 specifically at model fit, we saw an increase of the average marginal R^2 (proportion of variance explained by
 355 fixed effects alone) from hypothesis A to hypothesis B, and no or a small increase from hypothesis B to
 356 hypothesis C (Figure S6). Compared to fitted hypothesis B, fitted hypothesis C only included a few additional
 357 significant pathways (i.e. direct links between global-change drivers and the understory response variables)

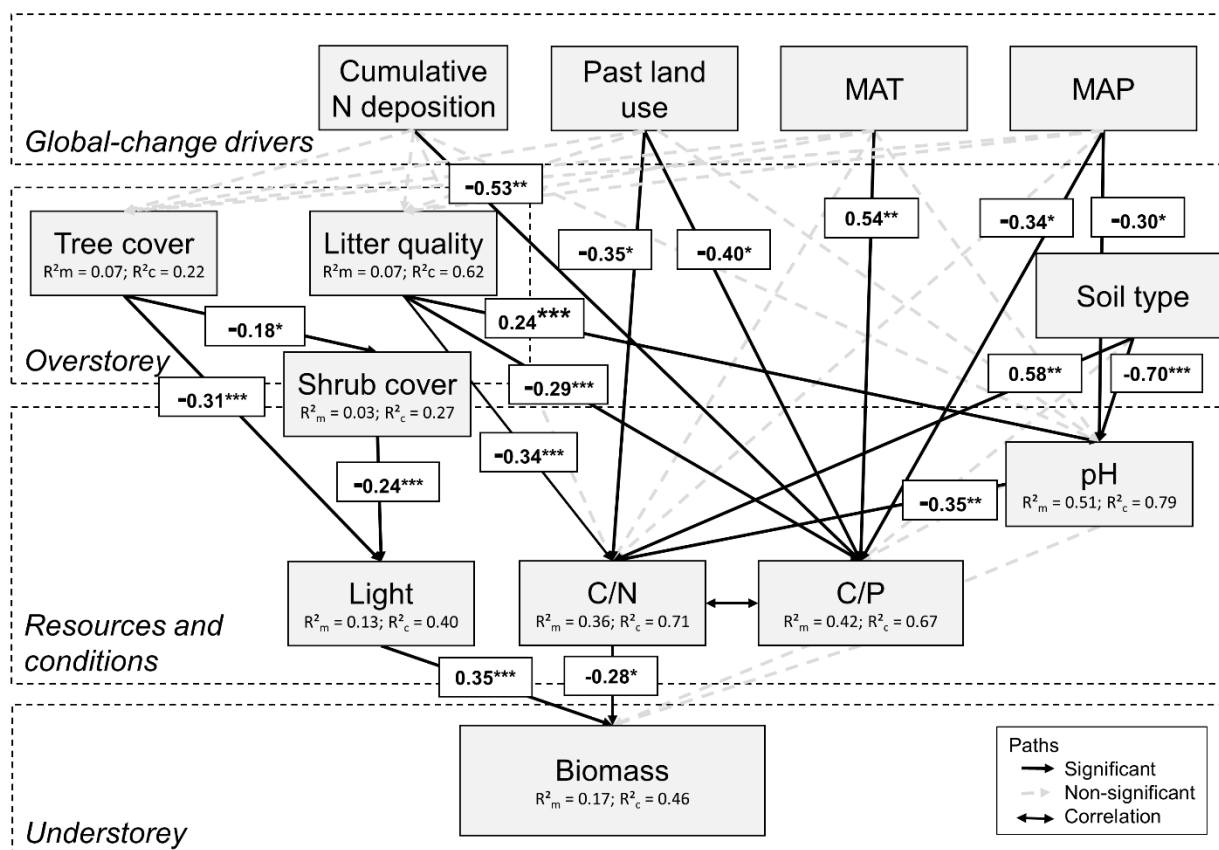
358 with only a very small increase of the model's average marginal R^2 value. Based on these results we retained
359 hypothesis B for all response variables, as the best model balancing model complexity and model fit,
360 suggesting that global-change drivers affect understorey biomass, nutrient concentrations and nutrient
361 stocks mainly indirectly. In the following, we use this hypothesised model as the basis to discuss the main
362 drivers of biomass, nutrient concentration and nutrient stocks in the understorey of temperate forests.

363 *3.3. Drivers of understorey biomass*

364 As suggested by hypothesis B, global-change drivers were found to affect understorey biomass mainly
365 indirectly via two alternative pathways: (1) via affecting the overstorey with cascading effects on resource
366 availability and growing conditions at the forest floor, and eventually understorey biomass, and (2) via an
367 additional direct effect on resource availability and growing conditions, with cascading effects on understorey
368 biomass (Figure 1b). However, when looking specifically at the significant paths in the model (Figure 4), we
369 did not find empirical evidence for global-change effects on tree composition (quantified in terms of litter
370 quality) or density.

371 In contrast, we did find support for global-change effects on resource availability and growing conditions at
372 the forest floor. Past arable land use, nitrogen deposition and MAP negatively affected the C/P ratio of the
373 soil, while MAT had a positive effect on this soil variable. Past arable land use had a negative effect on the
374 C/N ratio of the soil, while MAP was found to have an indirect positive influence, via soil pH. Next to these
375 global-change drivers, also tree litter quality was found to negatively affect the soil's C/N and C/P ratios, the
376 effect on soil C/N reinforced by an indirect effect via soil pH. Tree cover had a direct negative effect on light
377 availability and a positive indirect effect via its influence on shrub cover. Also intrinsic soil characteristics
378 that were captured by the soil type variable were found to influence soil pH and soil C/N. Biomass was
379 positively affected by light availability and, although only marginally significant, negatively by the C/N ratio
380 of the soil.

381 For all fitted mixed-effect models, marginal R^2 values differed considerably from conditional R^2 values,
382 indicating that the region, included as a random effect, explained a large proportion of the variation in the
383 data. In summary, global-change drivers were found to directly affect resource availability and growing
384 conditions at the forest floor, but the cascading effects on understorey biomass were found to be marginally
385 significant only (via soil C/N). Instead, understorey biomass was largely driven by light availability, fully
386 determined by the overstorey, whose canopy density (and litter quality) was not influenced by the considered
387 global-change drivers.



388

389 **Figure 4.** Fitted structural equation model (hypothesis B) visualizing all pathways and drivers that determine understory biomass.
 390 Marginal (R^2_m) and conditional (R^2_c) R^2 values of the fitted linear mixed-effect models are shown below each variable. The boxes on
 391 all significant paths display standardised coefficients and significance levels. *, **, *** denote significance levels with p-values lower
 392 than 0.05, 0.01 and 0.001, respectively. For past land use and soil type, we only displayed standardised coefficients for one level
 393 compared to its baseline. Displayed standardised path coefficients for soil type are those that quantify the effect of clayey soils with
 394 low carbonate content compared to clayey soils with a high carbonate content. The effect of a sandy soil compared to a clayey soil
 395 with a high carbonate content was only significant for pH (-1.39***), but was not shown in the graph. Displayed standardised path
 396 coefficients for past land use are those that quantify the effect of past arable land use compared to ancient forest. The effects of
 397 non-arable past land use compared to ancient forest were all not significant.

398 **3.4. Drivers of understory nutrient concentrations and stocks**

399 The fitted SEM models for understory nutrient concentrations and stocks were all similar to the one
 400 presented in Figure 4, except for the arrows representing the effects of light, soil C/N, C/P and pH on the
 401 model's main response variable (understorey biomass, nutrient concentrations or stocks). Standardised
 402 coefficients that quantify these effects for all response variables are provided in Table 2. While nutrient stock
 403 responses were similar to biomass responses, nutrient concentrations responded differently. Phosphorus
 404 concentration in the understory was found to be negatively affected by soil C/P and pH, while none of the
 405 predictors were found to have a significant effect on understory nitrogen concentration. Again, marginal R^2
 406 values differed considerably from the conditional ones, denoting that the random effect explained most of
 407 the variance in the data.

408 **Table 2.** Standardised coefficients and marginal and conditional R² values for the mixed-effect models, predicting biomass, nutrient
 409 concentrations and stocks. *, **, *** denote significance levels with p-values lower than 0.05, 0.01 and 0.001, respectively. N.S.
 410 represents non-significant path coefficients.

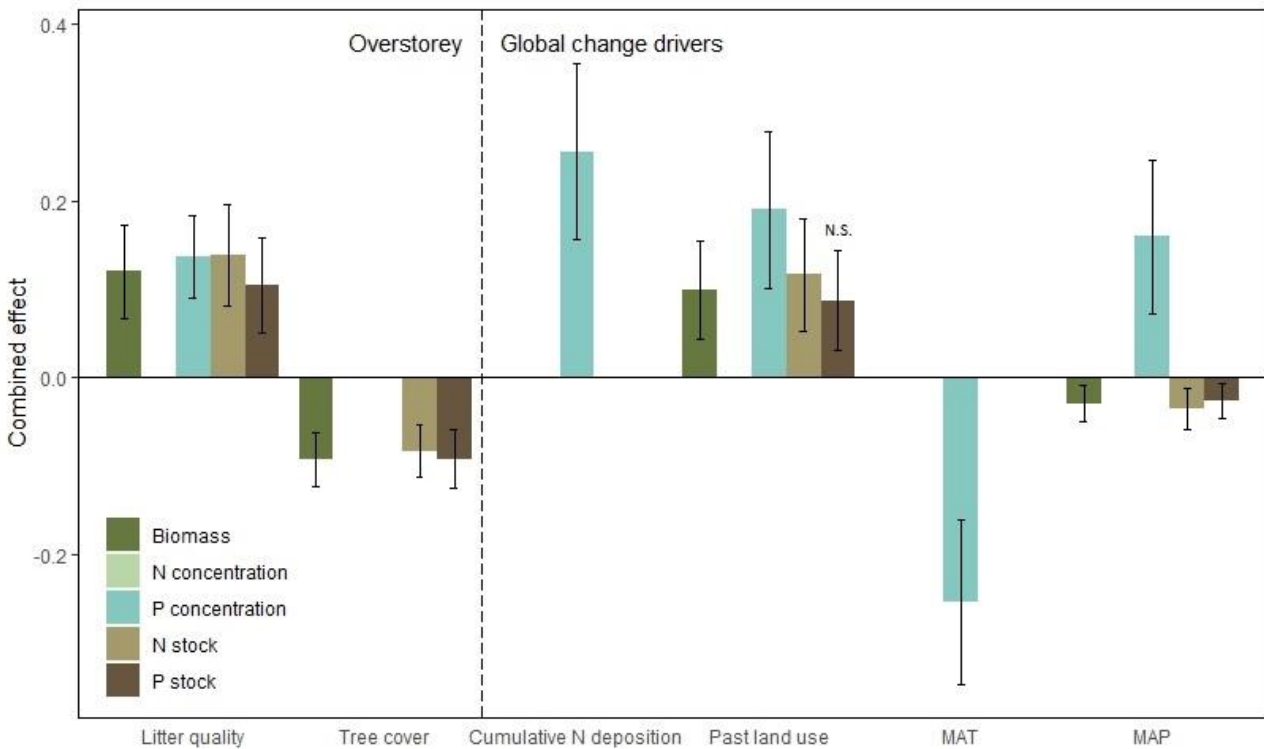
Response variable	Standardised coefficients				Marginal R ²	Conditional R ²
	Light	C/N	C/P	pH		
Biomass	0.35***	-0.28*	N.S.	N.S.	0.17	0.46
Nitrogen concentration	N.S.	N.S.	N.S.	N.S.	0.05	0.54
Nitrogen stock	0.31***	-0.33**	N.S.	N.S.	0.17	0.38
Phosphorus concentration	N.S.	N.S.	-0.47***	-0.26*	0.16	0.43
Phosphorus stock	0.34***	-0.25*	N.S.	N.S.	0.16	0.39

411

412 3.5. Combined effects of global-change drivers and overstorey characteristics

413 The combined effect of each global-change driver and overstorey variable differed depending on the
 414 response variable considered (Figure 5). For biomass and nutrient stocks, overstorey characteristics and past
 415 land use generally came out as most important predictors when looking at their direct and indirect effects
 416 combined. Tree cover affected understory biomass and nutrient stocks negatively, while litter quality had a
 417 positive effect. This positive litter quality effect, however, was driven by the effect of soil C/N on understory
 418 biomass, which was only marginally significant (Figure 4, Table 2). For understory phosphorus concentration,
 419 tree cover was less important, while other predictors, including nitrogen deposition, MAT and MAP became
 420 more important.

421



422

423 **Figure 5.** Combined direct and indirect effects of all driving variables in determining understory biomass, leaf nutrient concentration
 424 and aboveground nutrient stocks. Combined effect values were obtained through multiplication and summation of all significant

425 standardised path coefficients along each driving variable's pathways of influence, following Wright's tracing rules. The effect of past
426 land use represents the effect of past arable land versus ancient forest. Error bars (standard deviation) and the significance of the
427 combined effects were estimated via a Monte Carlo simulation (see section 2.6 for more details). N.S. indicates non-significant effects.

428 **4. Discussion**

429 We did not find direct effects of the global-change drivers considered (climate, nitrogen deposition and past
430 land use) on understorey biomass, nutrient concentration and stocks. These drivers do affect understorey
431 biomass, nutrient concentrations and stocks, but only via influencing soil characteristics that, in turn, affect
432 the understorey. We additionally found that it is mainly the overstorey, and more specifically its density and
433 litter quality, that determines understorey biomass, nutrient concentrations and stocks. These findings
434 suggest that understorey responses to global change might be limited in the relatively dense forests stands
435 under investigation. In these forests, overstorey characteristics mainly determined understorey resource
436 availability and growing conditions rather than the global-change drivers considered.

437 4.1. Understorey biomass, nutrient concentration and stocks and their main predictors

438 Understorey biomass, nutrient concentration and stock estimates were generally within similar ranges as
439 those reported in previous studies (e.g. Axmanová et al., 2011; Ernst, 1979; Ewald, Braun, Zeppenfeld, Jehl,
440 & Heurich, 2014; Siccama, Bormann, & Likens, 1970; Smolko & Veselovská, 2018; Thrippleton, Bugmann,
441 Kramer-priewasser, & Snell, 2016; Welch et al., 2007; Whittaker, Bormann, Likens, & Siccama, 1974). The
442 high variability of biomass estimates in this study (both among and within regions), however, suggests that
443 comparing understorey biomass values among studies is challenging and not necessarily insightful. The
444 agreement nevertheless suggests that the applied biomass estimation procedure, based on cover and shoot
445 length data, yields realistic results, as has been shown by other studies that have applied and evaluated
446 PhytoCalc (Mölder, Bernhardt-Römermann, & Schmidt, 2008; Mölder, Streit, & Schmidt, 2014). Our data also
447 illustrate the potential importance of the understorey for nutrient cycling in temperate forests. As found in
448 our study, the biomass of the understorey can reach values that are comparable to the biomass of leaves
449 produced in the overstorey, generally ranging between 100 and 900 g.m⁻² (Sayer, 2006). As both biomass
450 pools largely determine the yearly litter input to the soil, the understorey's contribution to this flux can be
451 considered significant.

452 Understorey biomass was found to be predominantly driven by light and nitrogen availability. The effect of
453 nitrogen availability on understorey biomass, however, was less significant than the effect of light, confirming
454 the idea that understorey productivity is predominantly light-, rather than nutrient-, limited (De Frenne et
455 al., 2015; Verheyen et al., 2012), especially in mature stands (Gilliam & Turrill, 1993). Although understorey
456 biomass responses to phosphorus availability have been reported in the past (Axmanová et al., 2011; Welch
457 et al., 2007), we did not detect such a response. Nitrogen and phosphorus stocks were driven by similar
458 variables as those driving biomass. Soil phosphorus availability and soil pH jointly affected the understorey's
459 phosphorus concentration, while none of the drivers considered affected the understorey's nitrogen

460 concentration. These findings agree with observations in post-agricultural forests, where understory plants
461 have been shown to increase their phosphorus concentration in aboveground biomass as a response to
462 elevated soil phosphorus availability (Baeten et al., 2011). The absence of a nitrogen concentration response
463 to elevated nitrogen availability in the soil might be surprising but agrees with findings in systems where
464 nitrogen is not limiting plant growth (Tessier & Raynal, 2003).

465 4.2. The effects of global-change drivers on understory biomass, nutrient concentration and stocks

466 Our study showed that the global-change drivers considered affect the understory mainly via affecting
467 nitrogen and phosphorus availability in tandem with the overstorey. As expected, soil nutrient availability
468 responded positively (decreasing soil C/N and C/P ratios indicate increasing nutrient availability) to tree litter
469 quality (see also Maes et al. (2019)). Past land use, however, was found to be an equally important driver of
470 soil nutrient availability. Past arable land use was found to increase nitrogen and phosphorus availability,
471 confirming other observations in forest stands planted on former agricultural fields (Baeten et al., 2011;
472 Blondeel et al., 2018; Falkengren-Grerup, ten Brink, & Brunet, 2006; Flinn & Marks, 2007).

473 Climate was found to affect the understory via its influence on soil nutrient availability. While soil nutrient
474 availability is generally expected to increase with increasing MAT, due to higher decomposition rates (as
475 found in many short-term warming experiments (Kirschbaum, 1995)), we found no trend for soil nitrogen
476 availability and an opposite trend for soil phosphorus availability. MAP was found to increase phosphorus
477 availability and decrease nitrogen availability, the latter via decreasing the soil's pH. While an increase of
478 leaching can explain the decrease of nitrogen availability, the link between climate and phosphorus
479 availability might be more complex than our hypotheses suggest. Long-term soil development processes,
480 differences in phosphorus deposition or intraspecific tree litter quality responses to climate, i.e. links that we
481 did (and could) not include in any of the hypothesized models, may have driven the observed phosphorus
482 availability responses to climate (Sohrt, Lang, & Weiler, 2017).

483 For nitrogen deposition we expected two counteracting effects: a positive effect on understory biomass (as
484 found for example by Gilliam (2019) for cover) as a result of increasing soil nitrogen availability (Falkengren-
485 Grerup, Brunet, & Diekmann, 1998) and a negative effect as a result of increasing overstorey biomass
486 reducing light availability (Hyvönen et al., 2007; Reyer, 2015). Neither of those was detected in our analysis.
487 The absence of a response of soil nitrogen availability was especially surprising, but might be related to the
488 low spatial resolution of the EMEP data or potential mismatches between atmospheric nitrogen deposition
489 (used as predictor here) and throughfall nitrogen (i.e. nitrogen deposited at the forest floor) determined by
490 canopy structure and composition (De Schrijver et al., 2007). Surprisingly, at first glance, we found a positive
491 effect of nitrogen deposition on phosphorus availability in the soil. Various mechanisms though can explain
492 increased phosphorus availability following nitrogen addition, including release of extracellular phosphatase
493 enzymes (Treseder & Vitousek, 2001), increased rock weathering rates and/or increased uptake of

494 phosphorus from deeper soil layers by the overstorey, with subsequent litterfall returning phosphorus to the
495 soil surface. However, evidence for temperate forests contradicts the latter hypothesis (Van Diepen et al.
496 2015), and active weathering profiles are probably at depth in these forests. Explaining this finding of
497 increased phosphorus availability with greater nitrogen deposition therefore requires further investigation.

498 The retained hypothesis B also indicates that the considered global-change drivers do not directly affect
499 understorey biomass, nutrient concentrations and stocks. This could be because of the buffering capacity of
500 the overstorey. The overstorey, including both shrubs and trees, can act as a thermal insulator (De Frenne et
501 al., 2019), can intercept precipitation (Crockford & Richardson, 2000) and nitrogen (Adriaenssens et al.,
502 2012), decoupling to some extent the growing conditions experienced by the understorey from those
503 experienced above the canopy. In more open stands, this buffering effect of the overstorey will decrease, so
504 direct effects of the considered global-change drivers might then become more likely. However, testing for
505 such interactions between tree cover and global change would require a dataset that covers a wider gradient
506 of canopy openness than the one considered in our study.

507 Large conditional R^2 values for the models predicting tree litter quality, soil nutrient availability, soil pH and
508 understorey characteristics (Figure 4, Table 2) suggest that there might be other important drivers acting at
509 the regional scale that influence soil resources, overstorey composition and the understorey. These might
510 include differences in herbivory dynamics, overstorey and understorey species pools and soil characteristics
511 not accounted for in our analysis. Additionally accounting for these potential drivers could shed more light
512 on the individual importance of drivers acting at the regional scale. As we do not expect these drivers to be
513 strongly correlated with the ones we considered in our analysis, we do not expect them to change our
514 findings related to climate, nitrogen deposition and overstorey effects.

515 4.3. From spatial environmental gradients to temporal responses to global change

516 Our study has identified contemporary drivers of understorey biomass, nutrient concentration and stocks
517 across Europe. These responses across spatial environmental gradients might also be used to deduce
518 potential temporal changes in the understorey following future global change. Multiple studies have shown
519 that spatial environmental gradients can be used to study temporal responses (Blois, Williams, Fitzpatrick,
520 Jackson, & Ferrier, 2013; Elmendorf et al., 2015; Newbold et al., 2015), although the rates of change might
521 not always coincide (see, for example, Adler & Levine, 2007). While differences among plant communities
522 across spatial environmental gradients are often a result of long-term responses to a specific regional driver,
523 temporal responses might lag behind due to rather slow immigration or local extinction rates of plant species
524 as a response to global change (Vellend et al., 2006; Verheyen, Honnay, Motzkin, Hermy, & Foster, 2003).
525 We, therefore, believe that (long-term) temporal global-change responses of understorey biomass and
526 nutrient stocks will go in the same direction as the responses we have observed across spatial environmental
527 gradients. However, the magnitude of the response will likely differ for the reasons given above.

528 We did find regional differences in species pools in the understorey and that single species can have a large
529 influence on understorey biomass (in accordance to the mass ratio hypothesis of Grime (1998) and as found
530 by Wasof et al. (2018) and Liu et al.(2019)). Plots dominated by *Deschampsia cespitosa*, *Rubus idaeus*, *Ribes*
531 *rubrum*, *Pteridium aquilinum* or *Urtica dioica* were all plots with a high biomass (between 100 and 200 g.m⁻²
532 ²), while plots dominated by *Mercurialis perennis*, *Allium ursinum*, *Anemone nemorosa* or tree seedlings were
533 all plots with a low biomass (<100 g.m⁻²). The biomass responses discussed in this study can hence
534 predominantly be considered a result of compositional differences, and not only a result of increased plant
535 growth in forests that experience higher resource levels and better growing conditions. This suggest that our
536 findings are indeed likely to overestimate temporal changes as a response to global change, as species
537 turnover might lag behind (Smith, Knapp, & Collins, 2009).

538 Knowing that our findings likely overestimate temporal changes, it is especially surprising that we found that
539 the overstorey, in terms of litter quality and density, might not be responsive to global change. Note,
540 however, that this no change in litter quality does not necessarily correspond to a no change in tree species
541 composition. Tree species composition might have changed, but not in a directional way towards tree species
542 with a lower or higher litter quality. We believe, however, that this lack of response might be related to the
543 relatively narrow regional gradients in our dataset or to our selection of sampling sites (Table 1). The
544 considered environmental gradients might have been too narrow to invoke changes in tree cover or tree
545 litter quality. Current evidence on tree species responses to global change indeed suggest that compositional
546 changes in the tree layer are expected under more extreme climatic conditions characterised by hotter
547 drought periods (Allen et al., 2010; Buras & Menzel, 2019; Fekete et al., 2017). Hence, including more
548 southern regions of Europe could have provided more insights on this. Another reason for this lack of
549 response might be related to the selection of forest stands, often dominated by *Quercus robur* and *Fagus*
550 *sylvatica* (Table S1), species that are found to be less responsive to climate change compared to evergreen
551 coniferous species, such as *Pinus sylvestris* and *Picea abies* (Buras & Menzel, 2019). Also for tree cover, we
552 did not see a response to climate and/or nitrogen deposition, contradicting previous studies that predict an
553 increase of overstorey density as a response to higher temperatures and nitrogen deposition rates, especially
554 when water availability is not limiting growth (Hyvönen et al., 2007; Reyer, 2015). An explanation for this
555 lack of response might be forest management. Since most of the investigated forests were actively managed,
556 thinning activities in the near past could have obfuscated potential effects of environmental drivers on tree
557 cover.

558 Our findings do suggest that when changes in the overstorey as a response to global change occur, they could
559 significantly affects understorey biomass and nutrient stocks, mainly via altering light availability at the forest
560 floor. Our findings, however, also show that tree cover changes can result in opposite changes in shrub cover
561 that will codetermine forest floor light availability (see also Sercu et al., 2017). Hence, accounting for shrub

562 layer responses to a changing overstorey cover will additionally be important to predict future understorey
563 responses to global change.

564 **5. Conclusions**

565 This study shows that understorey aboveground biomass, nutrient concentrations and stocks in mature
566 temperate forests across Northwest Europe are predominantly determined by the characteristics of the
567 overstorey, but also by past land use. These drivers influence resource availability and growing conditions at
568 the forest floor which in turn determine understorey biomass, nutrient concentrations and stocks. We also
569 found that direct effects of global-change drivers on understorey biomass and nutrient stocks were absent
570 and that their indirect effects (influencing resource availability and growing conditions at the forest floor)
571 were less important than the indirect effects of the overstorey (except for past land use effects). Our findings
572 suggest that understorey biomass and nutrient stock responses to global change might be limited in the
573 presence of a dense overstorey, highlighting the buffering role of the overstorey in temperate forests.

574 **Authors' contribution statement**

575 DL, SM, LD, HB, EA, MPP and KV designed the study; SM and LD collected the data supported by DL, HB, MPP,
576 GB, JB, GD, WH, RH, TH, SH, BJ, KJK, MK, FM, MW and KV; DL analysed the data and led the writing of the
577 manuscript. All authors contributed to the drafts and gave final approval for publication.

578 **Data accessibility**

579 Data are available via the PASTFORWARD project website: pastforward.ugent.be

580 **Conflict of interest**

581 The authors have no conflicts of interest to declare

582 **Acknowledgements**

583 DL is supported by a postdoctoral fellowship of the Research Foundation-Flanders (FWO). The European
584 Research Council (ERC), through a Consolidator Grant awarded to KV, supports MPP, HB, SLM, LD, and KV
585 (614839, the PASTFORWARD project). FM was supported by grants APVV-15-0270 and APVV-18-0086. MK
586 and RH were supported by project RVO67985939 from The Czech Academy of Sciences. RH was additionally
587 supported by project 17-09283S from the Grant Agency of the Czech Republic. We thank the Nature
588 Conservation Agency of Latvia who granted permission to work in the Moricsala Strict Nature Reserve. We
589 also thank Kris Ceunen, Filip Ceunen, Robbe De Beelde, Emiel De Lombaerde, Jorgen Op de Beeck, Pieter De
590 Frenne, Bram Bauwens, Sanne Govaert, Wolfgang Schmidt, Abbe Hamilton, Déborah Closset-Kopp and many
591 others for their support during the fieldwork. Luc Willems and Greet De Bruyn for chemical analyses and
592 Stephanie Schelfhout for describing chemical analyses. We also thank three anonymous reviewers for their
593 insightful comments that improved this manuscript considerably.

594

595 **6. References**

- 596 Aber, J., Neilson, R. P., McNulty, S., Lenihan, J. M., Bachelet, D., & Drapek, R. J. (2001). Forest Processes and
597 Global Environmental Change: Predicting the Effects of Individual and Multiple Stressors. *Bioscience*,
598 51(9), 735–751.
- 599 Adler, P. B., & Levine, J. M. (2007). Contrasting relationships between precipitation and species richness in
600 space and time. *Oikos*, 116(2), 221–232. doi:10.1111/j.0030-1299.2007.15327.x
- 601 Adriaenssens, S., Hansen, K., Staelens, J., Wuyts, K., De Schrijver, A., Baeten, L., ... Verheyen, K. (2012).
602 Throughfall deposition and canopy exchange processes along a vertical gradient within the canopy of
603 beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst). *Science of the Total Environment*,
604 420(2012), 168–182. doi:10.1016/j.scitotenv.2011.12.029
- 605 Aerts, R. (1997). Climate , Leaf Litter Chemistry and Leaf Litter Decomposition in Terrestrial Ecosystems : A
606 Triangular Relationship. *Oikos*, 79(3), 439–449.
- 607 Ali, A., Chen, H. Y. H., You, W. H., & Yan, E. R. (2019). Multiple abiotic and biotic drivers of aboveground
608 biomass shift with forest stratum. *Forest Ecology and Management*, 436, 1–10.
609 doi:10.1016/j.foreco.2019.01.007
- 610 Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., ... Cobb, N. (2010).
611 A global overview of drought and heat-induced tree mortality reveals emerging climate change risks
612 for forests. *Forest Ecology and Management*, 259(4), 660–684. doi:10.1016/j.foreco.2009.09.001
- 613 Ampoorter, E., Selvi, F., Auge, H., Baeten, L., Berger, S., Carrari, E., ... Verheyen, K. (2016). Driving
614 mechanisms of overstorey-understorey diversity relationships in European forests. *Perspectives in*
615 *Plant Ecology, Evolution and Systematics*, 19, 21–29. doi:10.1016/j.ppees.2016.02.001
- 616 Augusto, L., Dupouey, J.-L., & Ranger, J. (2003). Effects of tree species on understory vegetation and
617 environmental conditions in temperate forests. *Annals of Forest Science*, 60, 823–831.
618 doi:10.1051/forest
- 619 Axmanová, I., Zelený, D., Li, C., & Chytrý, M. (2011). Environmental factors influencing herb layer
620 productivity in Central European oak forests : insights from soil and biomass analyses and a
621 phytometer experiment. *Plant Soil*, 342, 183–194. doi:10.1007/s11104-010-0683-9
- 622 Baeten, L., Verstraeten, G., de Frenne, P., Vanhellefont, M., Wuyts, K., Hermy, M., & Verheyen, K. (2011).
623 Former land use affects the nitrogen and phosphorus concentrations and biomass of forest herbs.
624 *Plant Ecology*, 212(5), 901–909. doi:10.1007/s11258-010-9876-9
- 625 Barbati, A., Marchetti, M., Chirici, G., & Corona, P. (2014). European Forest Types and Forest Europe SFM

- 626 indicators: Tools for monitoring progress on forest biodiversity conservation. *Forest Ecology and*
627 *Management*, 321, 145–157. doi:10.1016/j.foreco.2013.07.004
- 628 Barbier, S., Gosselin, F., & Balandier, P. (2008). Influence of tree species on understory vegetation diversity
629 and mechanisms involved-A critical review for temperate and boreal forests. *Forest Ecology and*
630 *Management*, 254(1), 1–15. doi:10.1016/j.foreco.2007.09.038
- 631 Blois, J. L., Williams, J. W., Fitzpatrick, M. C., Jackson, S. T., & Ferrier, S. (2013). Space can substitute for time
632 in predicting climate-change effects on biodiversity. *Proceedings of the National Academy of Sciences*,
633 110(23), 9374–9379. doi:10.5061/dryad.d5f1r.1
- 634 Blondeel, H., Perring, M. P., Bergès, L., Brunet, J., Decocq, G., Depauw, L., ... Verheyen, K. (2018). Context-
635 dependency of agricultural legacies in temperate forest soils. *Ecosystems*, 1–15. doi:10.1007/s10021-
636 018-0302-9
- 637 Bloor, J. M. G., Leadley, P. W., Barthes, L., Ecology, S. P., Feb, N., Bloor, J. M. G., & Leadley, P. W. (2008).
638 Responses of *Fraxinus excelsior* seedlings to grass- above- and below-ground competition. *Plant*
639 *Ecology*, 194, 293–304. doi:10.1007/s11258-007-9292-y
- 640 Boch, S., Berlinger, M., Fischer, M., Knop, E., Nentwig, W., Türke, M., & Prati, D. (2013). Fern and bryophyte
641 endozoochory by slugs. *Oecologia*, 172(3), 817–822. doi:10.1007/s00442-012-2536-0
- 642 Bolte, A. (1999). *Abschätzung von Trockensubstanz-, Kohlenstoff- und Nährelementvorräten der*
643 *Waldbodenflora: Verfahren, Anwendung und Schätztafeln.* (A. Roloff, Ed.) (Forstwissen). Tharandt:
644 Eugen Ulmer Verlag.
- 645 Bolte, A., Czajkowski, T., Bielefeldt, J., Wolff, B., & Heinrichs, S. (2009). Schätzung der oberirdischen
646 Biomassevorräte des Baum-und Strauchunterwuchses in Wäldern auf der Basis von
647 Vegetationsaufnahmen. *Forstarchiv*, 80, 222–228. doi:10.237603004112-80-222
- 648 Boring, L. R., Swank, W. T., Waide, J. B., & Henderson, G. S. (1988). Sources , fates , and impacts of nitrogen
649 inputs to terrestrial ecosystems : review and synthesis. *Biogeochemistry*, 6(2), 119–159.
- 650 Buras, A., & Menzel, A. (2019). Projecting tree species composition changes of european forests for 2061–
651 2090 under RCP 4.5 and RCP 8.5 scenarios. *Frontiers in Plant Science*, 9(January), 1–13.
652 doi:10.3389/fpls.2018.01986
- 653 Chen, H. Y. H., Biswas, S. R., Sobey, T. M., Brassard, B. W., & Bartels, S. F. (2018). Reclamation strategies for
654 mined forest soils and overstorey drive understory vegetation. *Journal of Applied Ecology*, 55, 926–
655 936. doi:10.1111/1365-2664.13018
- 656 Crockford, R. H., & Richardson, D. P. (2000). Partitioning of rainfall into throughfall, stemslow and
657 interception effect of forest type, ground cover and climate. *Hydrological Processes*, 14(16–17), 2903–

- 658 2920. doi:10.1002/1099-1085(200011/12)14:16/17<2903::AID-HYP126>3.0.CO;2-6
- 659 De Frenne, P., Blondeel, H., Brunet, J., Carón, M. M., Chabrierie, O., Cougnon, M., ... Verheyen, K. (2018).
660 Atmospheric nitrogen deposition on petals enhances seed quality of the forest herb *Anemone*
661 *nemorosa*. *Plant Biology*, *20*(3), 619–626. doi:10.1111/plb.12688
- 662 De Frenne, P., Kolb, A., Verheyen, K., Brunet, J., Chabrierie, O., Decocq, G., ... Graae, B. J. (2009). Unravelling
663 the effects of temperature, latitude and local environment on the reproduction of forest herbs. *Global*
664 *Ecology and Biogeography*, *18*(6), 641–651. doi:10.1111/j.1466-8238.2009.00487.x
- 665 De Frenne, P., Rodríguez-Sánchez, F., De Schrijver, A., Coomes, D. A., Hermy, M., Vangansbeke, P., &
666 Verheyen, K. (2015). Light accelerates plant responses to warming. *Nature Plants*, *1*(9), 15110.
667 doi:10.1038/nplants.2015.110
- 668 De Frenne, P., Zellweger, F., Rodríguez-sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., ... Lenoir, J.
669 (2019). Global buffering of temperatures under forest canopies. *Nature Ecology and Evolution*.
670 doi:10.1038/s41559-019-0842-1
- 671 De Schrijver, A., De Frenne, P., Ampoorter, E., Van Nevel, L., Demey, A., Wuyts, K., & Verheyen, K. (2011).
672 Cumulative nitrogen input drives species loss in terrestrial ecosystems. *Global Ecology and*
673 *Biogeography*, *20*(6), 803–816. doi:10.1111/j.1466-8238.2011.00652.x
- 674 De Schrijver, A., De Frenne, P., Staelens, J., Verstraeten, G., Muys, B., Vesterdal, L., ... Verheyen, K. (2012).
675 Tree species traits cause divergence in soil acidification during four decades of postagricultural forest
676 development. *Global Change Biology*, *18*(3), 1127–1140. doi:10.1111/j.1365-2486.2011.02572.x
- 677 De Schrijver, A., Geudens, G., Augusto, L., Staelens, J., Mertens, J., Wuyts, K., ... Verheyen, K. (2007). The
678 effect of forest type on throughfall deposition and seepage flux a review. *Oecologia*, *153*(3), 663–674.
679 doi:10.1007/s00442-007-0776-1
- 680 Duprè, C., Stevens, C. J., Ranke, T., Bleeker, A., Peppler-Lisbach, C., Gowing, D. J. G., ... Diekmann, M. (2010).
681 Changes in species richness and composition in European acidic grasslands over the past 70 years: The
682 contribution of cumulative atmospheric nitrogen deposition. *Global Change Biology*, *16*(1), 344–357.
683 doi:10.1111/j.1365-2486.2009.01982.x
- 684 Dyderski, M. K., Paź, S., Frelich, L. E., & Jagodziński, A. M. (2018). How much does climate change threaten
685 European forest tree species distributions? *Global Change Biology*, *24*(3), 1150–1163.
686 doi:10.1111/gcb.13925
- 687 Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Fosaa, A. M., Gould, W. A., Hermanutz, L., ... Walker, M.
688 (2015). Experiment, monitoring, and gradient methods used to infer climate change effects on plant
689 communities yield consistent patterns. *Proceedings of the National Academy of Sciences of the United*

690 *States of America*, 112(2), 448–452. doi:10.1073/pnas.1410088112

691 Ernst, W. H. O. (1979). Population Biology of *Allium Ursinum* in Northern Germany. *Journal of Ecology*,
692 67(1), 347–362. doi:10.2307/2259355

693 Ewald, J., Braun, L., Zeppenfeld, T., Jehl, H., & Heurich, M. (2014). Estimating the distribution of forage mass
694 for ungulates from vegetation plots in Bavarian forest national park. *Tuexenia*, 34(1), 53–70.
695 doi:10.14471/2014.34.006

696 Falkengren-Grerup, U. (1989). Soil acidification and its impact on ground vegetation. *Ambio*, 18(3), 179–
697 183. Retrieved from <http://www.jstor.org/stable/4313559>

698 Falkengren-Grerup, U., Brunet, J., & Diekmann, M. (1998). Nitrogen mineralisation in deciduous forest soils
699 in south Sweden in gradients of soil acidity and deposition. *Environmental Pollution*, 102(S1), 415–
700 420. doi:10.1016/S0269-7491(98)80062-6

701 Falkengren-Grerup, U., ten Brink, D.-J., & Brunet, J. (2006). Land use effects on soil N , P , C and pH persist
702 over 40 – 80 years of forest growth on agricultural soils. *Forest Ecology and Management*, 225, 74–81.
703 doi:10.1016/j.foreco.2005.12.027

704 Farquhar, G. D., von Caemmerer, S., & Berry, J. A. (1980). A biochemical model of photosynthetic CO₂
705 assimilation in leaves of C₃ species. *Planta*, 149(1), 78–90. doi:10.1007/BF00386231

706 Fekete, I., Lajtha, K., Kotrocó, Z., Várbíró, G., Varga, C., Tóth, J. A., ... Berki, I. (2017). Long-term effects of
707 climate change on carbon storage and tree species composition in a dry deciduous forest. *Global*
708 *Change Biology*, 23(8), 3154–3168. doi:10.1111/gcb.13669

709 Flinn, K. M., & Marks, P. L. (2007). Agricultural legacies in forest environments : tree communities , soil
710 properties , and light availability. *Ecological Applications*, 17(2), 452–463. doi:10.1890/05-1963

711 Gill, R. M. A., & Beardall, V. (2001). The impact of deer on woodlands: The effects of browsing and seed
712 dispersal on vegetation structure and composition. *Forestry*, 74(3), 209–218.
713 doi:10.1093/forestry/74.3.209

714 Gilliam, F. S. (2006). Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition.
715 *Journal of Ecology*, 94(6), 1176–1191. doi:10.1111/j.1365-2745.2006.01155.x

716 Gilliam, F. S. (2007). The ecological significance of the herbaceous layer in temperate forest ecosystems.
717 *BioScience*, 57(10), 845–858. doi:10.1641/B571007

718 Gilliam, F. S. (2016). Forest ecosystems of temperate climatic regions: from ancient use to climate change.
719 *New Phytologist*, 212, 871–887. doi:10.1111/nph.14255

720 Gilliam, F. S. (2019). Excess nitrogen in temperate forest ecosystems decreases herbaceous layer diversity

721 and shifts control from soil to canopy structure. *Forests*, 10(1), 66. doi:10.3390/f10010066

722 Gilliam, F. S., & Turrill, N. L. (1993). Herbaceous Layer Cover and Biomass in a Young Versus a Mature Stand
723 of a Central Appalachian Hardwood Forest. *Bulletin of the Torrey Botanical Club*, 120(4), 445–450.

724 Giuggiola, A., Zweifel, R., Feichtinger, L. M., Vollenweider, P., Bugmann, H., Haeni, M., & Rigling, A. (2018).
725 Competition for water in a xeric forest ecosystem – Effects of understory removal on soil micro-
726 climate, growth and physiology of dominant Scots pine trees. *Forest Ecology and Management*, 409,
727 241–249. doi:10.1016/j.foreco.2017.11.002

728 González-Hernández, M. P., & Silva-Pando, F. J. (1999). Nutritional attributes of understory plants known as
729 components of deer diets. *Journal of Rangeland Management*, 52(2), 132–138.

730 Grime, J. P. (1998). Benefits of plant diversity to ecosystems: immediate filter and founder effects. *Journal*
731 *of Ecology*, 86, 902–910.

732 Handa, I. T., Aerts, R., Berendse, F., Berg, M. P., Bruder, A., Butenschoen, O., ... Hättenschwiler, S. (2014).
733 Consequences of biodiversity loss for litter decomposition across biomes. *Nature*, 509(7499), 218–
734 221. doi:10.1038/nature13247

735 Hansen, M. C., Stehman, S. V., & Potapov, P. V. (2010). Quantification of global gross forest cover loss.
736 *Proceedings of the National Academy of Sciences of the United States of America*, 107(19), 8650–8655.
737 doi:10.1073/pnas.0912668107

738 Harris, I., Jones, P. D., Osborn, T. J., & Lister, D. H. (2014). Updated high-resolution grids of monthly climatic
739 observations - the CRU TS3.10 Dataset. *International Journal of Climatology*, 34(3), 623–642.
740 doi:10.1002/joc.3711

741 Heinrichs, S., Bernhardt-Römermann, M., & Schmidt, W. (2010). The estimation of aboveground biomass
742 and nutrient pools of understorey plants in closed Norway spruce forests and on clearcuts. *European*
743 *Journal of Forest Research*, 129(4), 613–624. doi:10.1007/s10342-010-0362-7

744 Hyvönen, R., Ågren, G. I., Linder, S., Persson, T., Cotrufo, F., Ekblad, A., ... Sigurdsson, B. D. (2007). The likely
745 impact of elevated [CO₂], nitrogen deposition, increased temperature and management on carbon
746 sequestration in temperate and boreal forest ecosystems : a literature review. *New Phytologist*, 173,
747 463–480. doi:10.1111/j.1469-8137.2007.01967.x

748 Jackson, B. G., Nilsson, M. C., & Wardle, D. A. (2013). The effects of the moss layer on the decomposition of
749 intercepted vascular plant litter across a post-fire boreal forest chronosequence. *Plant and Soil*,
750 367(1–2), 199–214. doi:10.1007/s11104-012-1549-0

751 Kim, D., Oren, R., & Qian, S. S. (2016). Response to CO₂ enrichment of understory vegetation in the shade
752 of forests. *Global Change Biology*, 22, 944–956. doi:10.1111/gcb.13126

- 753 Kirschbaum, M. U. F. (1995). 1995 THE TEMPERATURE DEPENDENCE OF SOIL ORGANIC.pdf, 27(6), 753–760.
754 doi:10.13140/RG.2.2.34459.67369
- 755 Lajtha, K., Driscoll, C. T., Jarrell, W. M., & Elliott, E. T. (1999). Soil phosphorus: characterization and total
756 element analysis. In G. P. Robertson, D. C. Coleman, C. S. Bledsoe, & P. Sollins (Eds.), *Standard Soil*
757 *Methods for Long-term Ecological Research* (pp. 115–142). New York: Oxford University Press.
- 758 Landuyt, D., De Lombaerde, E., Perring, M. P., Hertzog, L. R., Ampoorter, E., Maes, S. L., ... Verheyen, K.
759 (2019). The functional role of temperate forest understorey vegetation in a changing world. *Global*
760 *Change Biology*. doi:10.1111/gcb.14756
- 761 Landuyt, D., Perring, M. P., Seidl, R., Taubert, F., Verbeeck, H., & Verheyen, K. (2018). Modelling
762 understorey dynamics in temperate forests under global change—Challenges and perspectives.
763 *Perspectives in Plant Ecology, Evolution and Systematics*, 31, 44–54. doi:10.1016/j.ppees.2018.01.002
- 764 Lefcheck, J. S. (2016). PIECEWISE SEM : Piecewise structural equation modelling in R for ecology, evolution,
765 and systematics. *Methods in Ecology and Evolution*, 7, 573–579. doi:10.1111/2041-210X.12512
- 766 Lemmon, P. E. (1956). A spherical densiometer for estimating forest overstorey density. *Forest Science*, 2(4),
767 314–320. doi:10.1093/forestscience/2.4.314
- 768 Leuschner, C., & Ellenberg, H. (2017). *Ecology of Central European Forests*. Cham: Springer International
769 Publishing.
- 770 Liu, B., Chen, H. Y. H., & Yang, J. (2019). Linking understory species diversity, community-level traits and
771 productivity in a Chinese boreal forest. *Journal of Vegetation Science*, (October 2017), 247–256.
772 doi:10.1111/jvs.12714
- 773 Mabry, C. M., Gerken, M. E., & Thompson, J. R. (2008). Seasonal storage of nutrients by perennial
774 herbaceous species in undisturbed - and disturbed deciduous hardwood forests. *Applied Vegetation*
775 *Science*, 11, 37–44. doi:10.3170/2007-7-18302
- 776 Maes, S. L., Blondeel, H., Perring, M. P., Depauw, L., Brūmelis, G., Brunet, J., ... Verheyen, K. (2019). Litter
777 quality, land-use history, and nitrogen deposition effects on topsoil conditions across European
778 temperate deciduous forests. *Forest Ecology and Management*, 433, 405–418.
779 doi:10.1016/j.foreco.2018.10.056
- 780 McKenzie, D., Halpern, C. B., & Nelson, C. R. (2011). Overstorey influences on herb and shrub communities in
781 mature forests of western Washington, U.S.A. *Canadian Journal of Forest Research*, 30(10), 1655–
782 1666. doi:10.1139/x00-091
- 783 Mölder, A., Bernhardt-Römermann, M., & Schmidt, W. (2008). Herb-layer diversity in deciduous forests:
784 Raised by tree richness or beaten by beech? *Forest Ecology and Management*, 256(3), 272–281.

785 doi:10.1016/j.foreco.2008.04.012

786 Mölder, A., Streit, M., & Schmidt, W. (2014). When beech strikes back: How strict nature conservation
787 reduces herb-layer diversity and productivity in Central European deciduous forests. *Forest Ecology
788 and Management*, 319, 51–61. doi:10.1016/j.foreco.2014.01.049

789 Monsi, M., & Saeki, T. (2005). On the factor light in plant communities and its importance for matter
790 production. *Annals of Botany*, 95(3), 549–567. doi:10.1093/aob/mci052

791 Muller, R. N. (2014). Nutrient relations of the herbaceous layer in deciduous forest ecosystems. In F. S.
792 Gilliam (Ed.), *The Herbaceous Layer in Forests of Eastern North America* (pp. 13–34). New York: Oxford
793 University Press.

794 Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R² from generalized
795 linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142. doi:10.1111/j.2041-
796 210x.2012.00261.x

797 Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., ... Purvis, A. (2015). Global
798 effects of land use on local terrestrial biodiversity. *Nature*, 520(7545), 45–50.
799 doi:10.1038/nature14324

800 Pan, P., Zhao, F., Ning, J., Zhang, L., Ouyang, X., & Zang, H. (2018). Impact of understory vegetation on soil
801 carbon and nitrogen dynamic in aerially seeded *Pinus massoniana* plantations. *PLoS ONE*, 13(1),
802 e0191952.

803 Pastor, J., & Post, W. M. (1988). Response of northern forests to CO₂-induced climate change. *Nature*,
804 334(6177), 55–58. doi:10.1038/334055a0

805 Perring, M. P., Bernhardt-Römermann, M., Baeten, L., Midolo, G., Blondeel, H., Depauw, L., ... Verheyen, K.
806 (2018). Global environmental change effects on plant community composition trajectories depend
807 upon management legacies. *Global Change Biology*, 24(4), 1722–1740. doi:10.1111/gcb.14030

808 Perring, M. P., De Frenne, P., Baeten, L., Maes, S. L., Depauw, L., Blondeel, H., ... Verheyen, K. (2016). Global
809 environmental change effects on ecosystems: The importance of land-use legacies. *Global Change
810 Biology*, 22(4), 1361–1371. doi:10.1111/gcb.13146

811 Perring, M. P., Diekmann, M., Midolo, G., Schellenberger Costa, D., Bernhardt-Römermann, M., Otto, J. C. J.,
812 ... Verheyen, K. (2018). Understanding context dependency in the response of forest understorey
813 plant communities to nitrogen deposition. *Environmental Pollution*, 242, 1787–1799.
814 doi:10.1016/j.envpol.2018.07.089

815 Preacher, K. J., & Selig, J. P. (2012). Advantages of Monte Carlo Confidence Intervals for Indirect Effects.
816 *Communication Methods and Measures*, 6(2), 77–98. doi:10.1080/19312458.2012.679848

- 817 Price, A. G., Dunham, K., Carleton, T., & Band, L. (1997). Variability of water fluxes through the black spruce
818 (Picea mariana) canopy and feather moss (Pleurozium schreberi) carpet in the boreal forest of
819 Northern Manitoba. *Journal of Hydrology*, 196(1–4), 310–323. doi:10.1016/S0022-1694(96)03233-7
- 820 R Core Team. (2018). R: a language and environment for statistical computing. Vienna, Austria: R
821 Foundation for Statistical Computing.
- 822 Reich, P. B., & Frelich, L. (2002). Temperate Deciduous Forests. In H. A. Mooney & J. G. Canadell (Eds.),
823 *Encyclopedia of Global Environmental Change - Volume 2: The Earth system: biological and ecological*
824 *dimensions of global environmental change* (pp. 565–569). Chichester: John Wiley & Sons.
- 825 Reyer, C. (2015). Forest productivity under environmental change—A review of stand-scale modeling
826 studies. *Current Forestry Reports*, 1(2), 53–68. doi:10.1007/s40725-015-0009-5
- 827 Royo, A. A., & Carson, W. P. (2006). On the formation of dense understory layers in forests worldwide:
828 consequences and implications for forest dynamics, biodiversity, and succession. *Canadian Journal of*
829 *Forest Research*, 36(6), 1345–1362. doi:10.1139/x06-025
- 830 Sayer, E. J. (2006). Using experimental manipulation to assess the roles of leaf litter in the functioning of
831 forest ecosystems. *Biological Reviews of the Cambridge Philosophical Society*, 81(1), 1–31.
832 doi:10.1017/S1464793105006846
- 833 Scherber, C., Eisenhauer, N., Weisser, W. W., Schmid, B., Voigt, W., Fischer, M., ... Tscharrntke, T. (2010).
834 Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*,
835 468(7323), 553–556. doi:10.1038/nature09492
- 836 Schulze, I.-M., Bolte, A., Schmidt, W., & Eichhorn, J. (2009). Phytomass, litter and net primary production of
837 herbaceous layer. In R. Brumme & P. K. Khanna (Eds.), *Functioning and Management of European*
838 *Beech Ecosystems* (p. 501). Berlin: Springer-Verlag Berlin Heidelberg. doi:10.1007/978
- 839 Sercu, B. K., Baeten, L., van Coillie, F., Martel, A., Lens, L., Verheyen, K., & Bonte, D. (2017). How tree
840 species identity and diversity affect light transmittance to the understory in mature temperate
841 forests. *Ecology and Evolution*, 7(24), 10861–10870. doi:10.1002/ece3.3528
- 842 Shipley, B. (2000). A new inferential test for path models based on directed acyclic graphs. *Structural*
843 *Equation Modeling*, 7(2), 206–218. doi:10.1207/S15328007SEM0702
- 844 Siccama, T. G., Bormann, F. H., & Likens, G. E. (1970). The Hubbard Brook Ecosystem Study : productivity ,
845 nutrients , and phytosociology of the herbaceous layer. *Ecological Monographs*, 40(4), 389–402.
846 doi:10.2307/1942337
- 847 Smith, M. D., Knapp, A. K., & Collins, S. L. (2009). A framework for assessing ecosystem dynamics in
848 response to chronic resource alterations induced by global change. *Ecology*, 90(12), 3279–3289.

849 doi:10.1890/08-1815.1

850 Smolko, P., & Veselovská, A. (2018). Seasonal dynamics of forage for red deer in temperate forests :
851 importance of the habitat properties , stand development stage and overstorey dynamics. *Wildlife*
852 *Biology*, 2018(1). doi:10.2981/wlb.00366

853 Sohrt, J., Lang, F., & Weiler, M. (2017). Quantifying components of the phosphorus cycle in temperate
854 forests, 4(December). doi:10.1002/wat2.1243

855 Tessier, J. T., & Raynal, D. J. (2003). Vernal nitrogen and phosphorus retention by forest understory
856 vegetation and soil microbes. *Plant and Soil*, 256, 443–453.

857 Thrippleton, T., Bugmann, H., Folini, M., & Snell, R. S. (2018). Overstorey–understorey interactions intensify
858 after drought-induced forest die-off: long-term effects for forest structure and composition.
859 *Ecosystems*, 21(4), 723–739. doi:10.1007/s10021-017-0181-5

860 Thrippleton, T., Bugmann, H., Kramer-Priewasser, K., & Snell, R. S. (2016). Herbaceous understory : an
861 overlooked player in forest landscape dynamics ? *Ecosystems*, 19(7), 1240–1254. doi:10.1007/s10021-
862 016-9999-5

863 Treseder, K. K., & Vitousek, P. M. (2001). Effects of soil nutrient availability on investment in acquisition of
864 N and P in Hawaiian rain forests. *Ecology*, 82(4), 946–954. doi:10.1890/0012-
865 9658(2001)082[0946:EOSNAO]2.0.CO;2

866 Van Diepen, L. T. A., Frey, S. D., Sthultz, C. M., Morrison, E. W., Minocha, R., Pringle, A., & Peters, D. P. C.
867 (2015). Changes in litter quality caused by simulated nitrogen deposition reinforce the N-induced
868 suppression of litter decay. *Ecosphere*, 6(10), 1–16. doi:10.1890/ES15-00262.1

869 van Oijen, D., Feijen, M., Hommel, P., den Ouden, J., & de Waal, R. (2005). Effects of tree species
870 composition on within-forest distribution of understory species. *Applied Vegetation Science*, 8(2),
871 155–166.

872 Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G., & Hermy, M. (2006).
873 Extinction debt of forest plants persists for more than a century following habitat fragmentation.
874 *Ecology*, 87(3), 542–548.

875 Verheyen, K., Baeten, L., De Frenne, P., Bernhardt-Römermann, M., Brunet, J., Cornelis, J., ... Verstraeten, G.
876 (2012). Driving factors behind the eutrophication signal in understory plant communities of
877 deciduous temperate forests. *Journal of Ecology*, 100(2), 352–365. doi:10.1111/j.1365-
878 2745.2011.01928.x

879 Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., & Foster, D. R. (2003). Response of forest plant species
880 to land-use change: a life-history trait-based approach. *Journal of Ecology*, 91(4), 563–577.

881 doi:10.1046/j.1365-2745.2003.00789.x

882 Wasof, S., Lenoir, J., Hattab, T., Jamoneau, A., Decocq, G., Evy, E. G., ... Verheyen, K. (2018). Dominance of
883 individual plant species is more important than diversity in explaining plant biomass in the forest
884 understorey. *Journal of Vegetation Science*, 29(3), 521–531. doi:10.1111/jvs.12624

885 Watt, M. S., Whitehead, D., Richardson, B., Mason, E. G., & Leckie, A. C. (2003). Modelling the influence of
886 weed competition on the growth of young *Pinus radiata* at a dryland site. *Forest Ecology and*
887 *Management*, 178, 271–286. doi:10.1139/X06-254

888 Welch, N. T., Belmont, J. M., & Randolph, J. C. (2007). Summer ground layer biomass and nutrient
889 contribution to above-ground litter in an Indiana temperate deciduous forest. *The American Midland*
890 *Naturalist*, 157(1), 11–26. doi:10.1674/0003-0031(2007)157[11:SGLBAN]2.0.CO;2

891 Whittaker, R. H., Bormann, F. H., Likens, G. E., & Siccama, T. G. (1974). The Hubbard Brook Ecosystem
892 Study: forest biomass and production. *Ecological Monographs*, 44(2), 233–254. doi:10.2307/1942313

893 Wright, S. (1921). Correlation and Causation. *Journal of Agricultural Research*, 20, 557–585.
894 doi:10.2307/3966855

895 Zhang, Y., Chen, H. Y. H., & Taylor, A. R. (2016). Aboveground biomass of understorey vegetation has a
896 negligible or negative association with overstorey tree species diversity in natural forests. *Global*
897 *Ecology and Biogeography*, 25(2), 141–150. doi:10.1111/geb.12392

898 Zhang, Y., Chen, H. Y. H., & Taylor, A. R. (2017). Positive species diversity and above-ground biomass
899 relationships are ubiquitous across forest strata despite interference from overstorey trees.
900 *Functional Ecology*, 31(2), 419–426. doi:10.1111/1365-2435.12699

901