

1 **Plant functional trait response to environmental drivers**
2 **across European temperate forest understorey communities**

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61

62

63 **Abstract**

64 (1) Plant functional traits respond to environmental drivers, hence evaluating trait-
65 environment relationships across spatial environmental gradients can help to understand how multiple
66 drivers influence plant communities. Global-change drivers such as changes in atmospheric nitrogen
67 deposition occur worldwide, but they affect community trait distributions at the local scale, where
68 resources (e.g. light availability) and conditions (e.g. soil pH) also influence plant communities.

69 (2) We investigate how multiple environmental drivers affect community trait responses
70 related to resource acquisition (plant height, specific leaf area (SLA), woodiness, and mycorrhizal
71 status) and regeneration (seed mass, lateral spread) of European temperate deciduous forest
72 understoreys. We sampled forest understorey communities and derived trait responses across spatial
73 gradients of global-change drivers (temperature, precipitation, nitrogen deposition, and past land use),
74 while integrating in-situ plot measurements on resources and conditions (soil type, Olsen phosphorus
75 (P), Ellenberg soil moisture, light, litter mass, and litter quality).

76 (3) Among the global-change drivers, mean annual temperature strongly influenced traits
77 related to resource acquisition strategies in the plot understorey communities. Warmer temperatures
78 were associated with on average taller understoreys producing leaves with lower SLA, and a higher
79 proportional cover of woody and obligate mycorrhizal (OM) species. Communities in plots with
80 higher Ellenberg soil moisture content had smaller seeds and lower proportional cover of woody and
81 OM species. Finally, plots with thicker litter layers hosted taller understoreys with larger seeds and a
82 higher proportional cover of OM species.

83 (4) Our findings suggest potential community shifts in temperate forest understoreys with
84 (future) global warming, and highlight the importance of local resources and conditions as well as
85 global-change drivers for community trait variation. We recommend that future studies investigating
86 environmental (change) effects on understorey communities should consider the local environmental
87 context when investigating global-change effects as well as evaluate interactive effects among the
88 different environmental drivers.

89

90 **Introduction**

91 Global environmental changes are causing shifts in the composition and functioning of plant
92 communities (Bernhardt-Römermann et al., 2015; Bjorkman et al., 2018; De Frenne et al., 2011;
93 Hansen et al., 2001; Sala et al., 2000; Walther, 2010). Important global-change drivers affecting
94 temperate plant communities include increased temperatures, changes in precipitation and in
95 atmospheric nitrogen and sulfur deposition, as well as land-use changes (Dentener et al., 2006; Fowler
96 et al., 2013; Millennium Ecosystems Assessment, 2005; Pereira, Navarro, & Martins, 2012; Skov &
97 Svenning, 2004). If we are to accurately predict the effects of future environmental changes on these
98 communities, we need a thorough understanding of whether and how these drivers shape plant
99 communities (Bjorkman et al., 2018; Bruelheide et al., 2018; Landuyt et al., 2018; Vanneste et al.,
100 2018).

101 Functional traits, i.e. measurable characteristics of organisms that ultimately influence their fitness
102 through effects on growth, reproduction and establishment, show great potential to investigate trait-
103 environment relationships (Šímová et al., 2018; Suding et al., 2008). Community-weighted traits
104 depend on the species composition of communities and relate to ecosystem functions, while they may
105 be related to environmental drivers as well, thus connecting ecosystem patterns to ecosystem
106 processes (Laughlin, 2014; Suding et al., 2008; Weiher et al., 1999). Unravelling community trait
107 responses across environmental gradients can therefore advance our understanding of which drivers
108 shape plant communities (Bjorkman et al., 2018; Bruelheide et al., 2018; Dubuis et al., 2013;
109 Vanneste et al., 2018).

110 Community composition and hence trait properties are influenced by environmental drivers acting
111 over different spatial extents (Bruelheide et al., 2018; Perez-Ramos et al., 2017; Vilà-Cabrera,
112 Martínez-Vilalta, & Retana, 2015). Global-change drivers such as changes in atmospheric deposition
113 are being altered on a global scale, but they affect community trait distributions locally, at which scale
114 other resources (e.g. light availability) and conditions (e.g. soil pH) also strongly influence plant
115 communities (Bruelheide et al., 2018; Naaf & Kolk, 2016; Smith, Knapp, & Collins, 2009).
116 Furthermore, global-change drivers can drive changes in plant communities *through* altering local
117 resource availabilities, e.g. soil nitrogen or phosphorus; and local resources and conditions can vice
118 versa determine whether and how global-change drivers affect plant communities (Perring,
119 Diekmann, et al., 2018; Smith et al., 2009). Studies evaluating the functional response of communities
120 to global-change drivers should therefore aim to incorporate effects of local resources and conditions
121 (Bruelheide et al., 2018).

122 In this study, we investigate how concurrent global-change drivers, along with local resources and
123 conditions, are linked with *understorey community* traits in European temperate deciduous forests.
124 Temperate forest understoreys (i) constitute the majority of plant diversity in temperate forests, thus
125 playing a key role in their functioning (Gilliam, 2006; Landuyt et al., 2019), and (ii) are very
126 vulnerable to environmental changes because they are adapted to stable environmental forest
127 conditions (De Frenne et al., 2012; Van Der Veken, Bossuyt, & Hermy, 2004; Verheyen, Honnay,
128 Motzkin, Hermy, & Foster, 2003). Because of the low colonization capacity, specific habitat
129 requirements, and long generation times of many perennial understorey plants (in contrast with e.g.
130 annual grassland plant species), these communities may be hampered in their abilities to track moving
131 climate boundaries or colonize new forest sites. For example, forests on post-agricultural sites may
132 have a different understorey community composition as compared to apparently similar forest sites
133 (e.g. in overstorey composition) but without an agricultural legacy (Baeten, Hermy, Van Daele, &
134 Verheyen, 2010). A better understanding of the relative importance of environmental factors for
135 community trait distributions may improve projections of future changes in understorey community
136 responses. To achieve this, we sampled understorey communities and derived trait responses across
137 spatial environmental gradients of global-change drivers, while integrating *in-situ* measurements on
138 the resources and conditions that may affect these communities as well.

139 Specifically, we evaluate the relationship between community-weighted mean (CWM) trait values
140 and environmental drivers including (i) four *global-change drivers* [mean annual temperature and
141 precipitation, nitrogen deposition, and past land cover], and (ii) six *local resources and conditions*
142 [soil type, bio-available phosphorus, Ellenberg soil moisture, light availability, litter mass, and litter
143 quality]. We examine traits related to two fundamental strategies for plant growth and performance,
144 (i) *resource acquisition* (plant height, specific leaf area (SLA), woodiness and mycorrhizal status),
145 and (ii) *regeneration* (seed mass, lateral spread) (Cornelissen et al., 2003; Diaz et al., 2004; Garnier,
146 Navas, & Grigulis, 2016; Thomson, Moles, Auld, & Kingsford, 2011).

147 We hypothesize that understorey community traits may be affected by both the global-change drivers
148 as well as the local resources and conditions in the plots (Bruehlheide et al., 2018; Perring, Bernhardt-
149 Römermann, et al., 2018; Verheyen et al., 2003). Community plant height as well as SLA were
150 expected to be higher in plots with higher nitrogen deposition, Ellenberg soil moisture, and
151 temperature. Community plant height was expected to be higher in plots with more light, while SLA
152 was expected to be lower in plots with more light, respectively (Dubuis et al., 2013; Garnier et al.,
153 2016; Perring, Bernhardt-Römermann, et al., 2018). The proportion of woody and of obligate
154 mycorrhizal plants in understorey communities might also be related to environmental drivers (e.g.

155 nitrogen deposition) given the demonstrated differences in resource acquisition between woody vs.
156 non-woody as well as non-mycorrhizal vs. mycorrhizal plants (Bardgett, Mommer, & De Vries, 2014;
157 Graves, Peet, & White, 2006; Hempel et al., 2013; Kleyer et al., 2008; Ryser, 1996; Valverde-
158 barrantes, Freschet, Roumet, & Blackwood, 2017). Finally, higher community seed mass was
159 expected to be associated with lower moisture or nutrient levels (DeMalach, Ron, & Kadmon, 2018;
160 Westoby, Leishman, & Lord, 1996), while the mean lateral spread of an understory community
161 could be higher in plots with a differing land-use history, i.e. recent (RF) vs. ancient forests (AFs),
162 because of potentially higher colonization capacities of plant species in RFs (Baeten et al., 2010;
163 Flinn & Vellend, 2005; Verheyen et al., 2003).

164

165 **Material & Methods**

166 **Study regions**

167 We selected 19 regions along spatial environmental gradients of atmospheric nitrogen deposition and
168 climatic conditions (temperature, precipitation) within the Central-Western European temperate
169 deciduous forest biome (**Fig. 1, Table A1a**). The plots used were selected as part of a vegetation
170 resurvey project investigating land-use history and global-change effects on understorey communities
171 across European forests (ERC-project PASTFORWARD, <http://www.pastforward.ugent.be/>).

172 Mean annual temperature and precipitation (MAT, MAP), and nitrogen deposition (Ndep) at the study
173 regions ranged from 6.1 to 11.9 °C, from 526 to 1586 mm yr⁻¹, and from 7 to 30 kg ha⁻¹ yr⁻¹
174 respectively (**Fig. 1a** – long-term average values from 1980-2015 for MAT and MAP, values for the
175 year 2000 for Ndep). We aimed at maximizing differences in land-use history between plots (within
176 regions, **Fig. 1b**) by sampling in ancient vs. recent forest. We classified ancient forest (AF) plots here
177 as plots that have been continuously forested since at least 1850, whereas recent forest (RF) plots
178 have been afforested after 1850 (Hermy, Honnay, Firbank, Grashof-Bokdam, & Lawesson, 1999).

179 In each region, we selected ten 400m² forest plots (except for 8 plots in Moricsala, 9 plots in Binnen-
180 Vlaanderen, and 15 plots in Białowieża) resulting in a total sample size of 192 plots. Each 400m² plot
181 contained a nested 100m² sub-plot. We tried to minimize differences in parent material and
182 topography between plots and regions. However, plot selection was also constrained by the existence
183 of a prior understorey vegetation survey (not relevant within this spatial study) and information on
184 land-use history.

185 All plots comprised closed-canopy forests with a variable tree and shrub layer composition, but we
186 focused on plots predominantly composed of broadleaved species, although a higher occurrence of
187 coniferous species in the easternmost regions with a hemiboreal climate (Białowieża (BI), Moricsala
188 (MO)) was unavoidable. The canopies consisted mainly of *Fagus sylvatica* (present in 65 of the 192
189 plots), *Fraxinus excelsior* (64/192 plots), *Quercus robur* (60/192 plots), *Carpinus betulus* (52/192
190 plots), *Quercus petraea* (41/192 plots), and *Acer pseudoplatanus* (35/192 plots).

191

192 **Data collection**

193 In May-June 2015 and 2016, we characterized resources and conditions by sampling the mineral
194 topsoil (0-20 cm) and organic forest floor layer, and by taking light measurements, at eye level, with
195 a spherical densiometer in the 100 m² sub-plots. In the 400 m² plots, we took basal area measurements
196 to characterize the overstorey structure and composition based on all trees and shrubs with DBH >
197 7.5 cm. Global-change drivers were estimated from online databases (temperature, precipitation and
198 atmospheric deposition) and plot-level information searches (land-use history). We derived
199 understorey community response variables by conducting standardized vegetation surveys in the 100
200 m² plots, and used trait databases to derive community-level descriptors of trait properties based on
201 species' percentage cover. We also derived the Ellenberg index of moisture availability from these
202 vegetation surveys, using species scores from Ellenberg and Leuschner (2010) (Bartelheimer &
203 Poschlod, 2016; Diekmann, 2003; Scherrer & Guisan, 2019).

204 **Functional trait response**

205 *Understorey community composition*

206 We recorded the species composition and cover through 10 x 10 m plot-level vegetation surveys to
207 calculate descriptors of community trait distributions. Trait values were sourced from several
208 literature databases including e.g. ECOFLORA (Fitter & Peat, 1994) and LEDA (Kleyer et al., 2008)
209 (full list see **Table A2**). We included herbaceous species and low-growing woody species that are
210 structurally and functionally part of the understorey layer (e.g. *Vaccinium myrtillus*), but excluded
211 tree and shrub seedlings and some climber species present in the understorey for two reasons. Many
212 recorded trait values (plant height, SLA, lateral spread) are representative for adult trees, shrubs and
213 climbers rather than the juvenile state found in the understorey. Secondly, we wanted to focus on the
214 species that remain structurally part of the understorey throughout their life cycle, as opposed to those
215 that are only “passing through” (cf. Perring et al., 2018). See **Table A3** for a detailed species list.

216 *Trait data*

217 Previous studies have identified traits that strongly influence plant growth and survival (Bardgett et
218 al., 2014; Cornelissen et al., 2003; Diaz et al., 2004; Laliberté, 2017; Laughlin, 2014; Westoby, 1998;
219 Westoby, Falster, Moles, Vesk, & Wright, 2002). Based on these studies, we focused on six key traits
220 here that capture fundamental trade-offs for plants related to regenerative and resource acquisition
221 strategies: i) *SLA* (mm² mg⁻¹), ii) *plant height* (m), iii) *seed mass* (mg), iv) *woodiness*, v) *mycorrhizal*

222 *status*, and vi) *lateral spread* (m). We first selected three key traits capturing fundamental trade-offs
223 for plants that are incorporated within the “leaf-height-seed” scheme, i.e. SLA or light-capturing area
224 per allocated leaf dry mass, plant height or vegetative height of the plant’s canopy at maturity, and
225 seed mass (Westoby, 1998). Note that in the trait databases from where most of the seed mass records
226 used in our analyses originate, usually the mass of the diaspore is given, but we use the term “seed
227 mass” instead of “diaspore mass” for the sake of simplicity (cf. Sonkoly, Tóthmérész, Deák, & Török,
228 2017).

229 We then added three additional traits of which we expected to find relationships with several of the
230 environmental drivers. Woodiness and mycorrhizal status were included based on the demonstrated
231 differences in resource acquisition between woody/non-woody or herbaceous, as well as between
232 non-mycorrhizal/mycorrhizal plants (Bardgett et al., 2014; Graves et al., 2006; Hempel et al., 2013;
233 Kleyer et al., 2008; Ryser, 1996; Valverde-barrantes et al., 2017). Lateral spread, or the increment of
234 vegetative growth organs in horizontal direction, was included because of the importance of
235 vegetative growth for many understorey species and the potential response to land-use legacies
236 (Baeten et al., 2010; Klimešová, Danihelka, Chrtěk, de Bello, & Herben, 2009).

237 For each of the four continuous plant traits, that is adult plant height, SLA, seed mass, and lateral
238 spread, we calculated the CWM, which was weighted by relative percentage cover (**Fig. 2**). To gain
239 additional information on the community trait distributions and their response to environmental
240 drivers, the coefficient of variation (CV) was calculated for each of the four continuous traits as
241 SD/CWM . We show these results in the appendix (**Table A4, Fig. A6**) and focus on the CWM results
242 in the main text. The categorical traits woodiness and mycorrhizal status were included as the
243 proportional cover of woody species (excluding tree, shrub, and climber species), and species with
244 obligate mycorrhizal (OM) associations in the plots respectively (Bjorkman et al., 2018; Moora,
245 2014) (**Fig. 2**).

246 We used “mean” species values for traits here (following Albert, Grassein, Schurr, Vieilledent, &
247 Violle, 2011; Kazakou et al., 2014), and did not take into account intraspecific trait variation, which
248 also responds to environmental factors (Violle et al., 2012). We followed a two-step procedure to
249 ensure that we had adequate trait data representative of the plot understorey communities. We first
250 checked that trait attributes were present for the most abundant species (present in >5% of the plots
251 and with mean cover >1%), and then ensured that 80% of the plot cover was represented by trait
252 values (**Table A2**) (Pakeman, 2014). An overview of the regional trait variation and distributions is
253 shown in **Table A1b-c** and **Fig. A1**. We also checked pairwise correlations among the traits (**Fig.**
254 **A2**).

255

Global-change drivers

256 We included two climatic and two atmospheric deposition variables, estimated at the regional scale,
257 to quantify potential drivers of understory trait variation. These were (i) mean annual temperature
258 (MAT, °C), (ii) mean annual precipitation (MAP, mm yr⁻¹), (iii) atmospheric nitrogen deposition
259 (Ndep, kg ha⁻¹ yr⁻¹), and (iv) acidification rate (AcidRate, keq ha⁻¹ yr⁻¹) (**Fig. 2**). For the climatic
260 variables, we extracted monthly climate data from the gridded CRU TS3.24 dataset (Climate
261 Research Unit, 0.1° resolution (ca. ±40 km): Harris, Jones, Osborn, & Lister, 2014), and calculated
262 annual temperature and precipitation values. We used mean annual temperature and precipitation for
263 the time period 1980-2015. Microclimatic buffering effects on below-canopy temperatures were not
264 considered due to the lack of available data, thus the results could differ when using actual measured
265 temperatures at the forest floor (Bhatta & Vetaas, 2016; De Frenne, Rodríguez-Sánchez, et al., 2013;
266 Vanneste et al., 2018).

267 To evaluate potentially eutrophying vs. acidifying effects of increased deposition, we included Ndep
268 as a measure of eutrophication, and AcidRate as a measure of acidification. We extracted total
269 nitrogen deposition (NH₃ + NO_x) and sulfur deposition (SO_x) for the year 2000 based on interpolated
270 model results from the European Monitoring and Evaluation Programme (version 2013,
271 <http://www.emep.int/>) and calculated the acidification rate based on nitrogen and sulfur deposition as
272 (cf. Verheyen et al., 2012):

273

$$AcidRate = \frac{N_{dep}}{14} + 2 * \frac{S_{dep}}{32.06}$$

274 Cumulative deposition values would have been based on backcasting from deposition patterns for the
275 year 2000 (as in Duprè et al. 2010), and thus highly correlated with the 2000 values, leading to high
276 similarity in model results (Henrys et al., 2011). To minimize the number of assumptions in our
277 analysis, we used 2000 values rather than estimated cumulative deposition. We assumed
278 homogeneous environmental conditions within a region, so we extracted all climate and deposition
279 variables on a plot level, and then calculated the mean of all plots for each region.

280 We reconstructed the land-use history of each plot between 1850 and 2015 in a standardized way
281 based on a combination of expert knowledge of our local contact person in each region, a thorough
282 search of region-specific maps and literature, and oral interviews. We tried to maximize differences
283 in past land cover within regions but it was not always possible to find a perfectly even distribution
284 of past land cover categories within each region with the available datasets.

285 We distinguished between ancient forest (AF) plots (n = 131), i.e. plots that have been continuously
286 forested since at least 1850, vs. recent forest (RF) plots (n = 54), i.e. plots that were afforested after
287 *around* 1850. The majority of the recent plots were afforested after 1850, while several were
288 afforested between 1800 and 1850. The previous land cover categories of these recent forest plots
289 were heathland (3), grassland (21), and arable land (30) and they transitioned into forest between
290 1810 and 1900 for the heathland plots, between 1860 and 1912 for former grassland plots, and
291 between 1820 and 1970 for the former arable plots. The past land cover of the recent forest plots may
292 have influenced current understorey communities differently, so we distinguished between the 30
293 post-arable recent forest plots on the one hand, and the 21 post-grassland + 3 post-heathland plots, on
294 the other hand (**Fig. 1b**). Nutrient-enrichment practices such as fertilization and liming and soil
295 disturbance practices (e.g. soil tilling or ploughing) are more likely to have taken place in the post-
296 arable plots vs. more nutrient-depleting practices in the grassland/heathland plots (e.g. burning or
297 sod-cutting). This may have differently altered soil fertility and microbial communities, and
298 potentially influenced understorey trait responses (Buckley & Schmidt, 2001; Fichtner, von Oheimb,
299 Härdtle, Wilken, & Gutknecht, 2014; Matson, Parton, Power, & Swift, 1997).

300 **Resources and conditions**

301 We clustered our plots into three “Soil type” groups (**Fig. 2**) based on soil texture (*% Clay, % Silt, %*
302 *Sand*), and *carbonate or inorganic carbon concentration (%)* using the *hclust* function in R (stats
303 package, ward.D method, Euclidean distances, R Core Team (2016)). See Maes et al. (2019) for
304 details on the soil sampling. The *ClayCarbonate* soils (21 plots) represent silty-clay-carbonate soils
305 with high inorganic carbon concentration, whereas the *ClayNoCarbonate* soils (82 plots) represent
306 silty-clay soils without the presence of carbonates (low inorganic carbon concentration), and the *Sand*
307 soils (82 plots) represent sandy soils with a low inorganic carbon concentration. These clusters
308 represented differences in other topsoil conditions. From the poorer sandy soils to the intermediate
309 clay-no-carbonate to the richer clay-carbonate soils, we observed an increase in proportion of
310 exchangeable base cations (*EBC*), pH (*pH_{KCl}*), and total phosphorus content (*TotP*), and a decrease
311 in litter mass, bulk density, and C/N-ratio (details see Maes et al. (2019)). Since Olsen P was not
312 correlated with the soil type groups, and because it is an important nutrient for plant growth, we
313 included it as a separate predictor here (**Fig. 2**).

314 We expected soil moisture to influence community trait responses (Riegal, Miller, & Krueger, 1991;
315 Schaffers & Sýkora, 2000). We used a proxy that integrates the moisture conditions typically
316 experienced in the plot, since *in situ* measurements are subject to fluctuation from local weather
317 conditions and fine-scale spatio-temporal variation (Kopecký & Čížková, 2010; Korres et al., 2015;

318 Peng et al., 2016). We calculated a presence/absence-based mean community Ellenberg Indicator
319 Value (EIV) score from all the vegetation, including tree, shrub, and understorey species, in the plot
320 (i.e. an ordinal score between 1= species typically growing on dry soils, and 9= species growing on
321 wet soils) – further referred to as “Ellenberg soil moisture” (**Fig. 2**). EIVs indicate species preferences
322 in their realized niche which may characterize the environment in the absence of directly measured
323 variables (Bartelheimer & Poschlod, 2016; Diekmann, 2003; Schaffers & Sýkora, 2000). Although
324 this might be regarded as circular reasoning because both this predictor and the trait responses were
325 based on compositional data (sensu Zelený & Schaffers, 2012), we think that using the EIV for soil
326 moisture is justified here. First, the EIV for soil moisture ignored species abundance while this *was*
327 considered to calculate the CWM trait responses (weighted by relative abundance). Second, EIV for
328 soil moisture was calculated based on *all* the vegetation cover in the plot (i.e. understorey, shrub, and
329 tree species), while the trait responses were calculated for understorey species only. Nevertheless, we
330 should treat our results for soil moisture with some caution, given the potential bias that could be
331 related with the use of this species-derived Ellenberg variable.

332 The overstorey might also influence understorey trait variation across our plots through modifying
333 the leaf litter (quantity and quality) as well as the light availability that reaches the forest floor. We
334 recorded the dry weight of the organic layer as the “Litter mass” (g) for each plot after drying the
335 forest floor samples for 24 hours at 65 °C and included a plot-scale average “Litter quality” score
336 (LQ, **Fig. 2**). This was calculated as a weighted average (by basal area – m² ha⁻¹) of litter quality
337 indices of individual canopy species (trees and shrubs with DBH > 7.5 cm) present within the plot.
338 These species scores reflect the rate of leaf litter decomposition and were obtained from the literature
339 (details see Maes et al., 2019). Finally, we took the average of five densiometer measurements in each
340 plot to attain a canopy openness estimate (%), reflecting the light that reaches the understorey (taken
341 in four plot corners + centre, at eye level i.e. 1.6-1.8 m height, further referred to as “Light”) (**Fig. 2**)
342 (Baudry, Charmetant, Collet, & Ponette, 2014; Lemmon, 1957). To take into account potential
343 confounding effects of canopy development among the different forest regions at the times of
344 sampling, we sampled the regions from west to east, capturing the understorey communities as much
345 as possible at similar stages of canopy development or phenology (when canopy leaf-out was
346 complete).

347 For an overview of the regional variation in predictor values and their distribution across all regions,
348 we refer to **Table A1a** and **Fig. A3**, respectively.

349 **Data analysis**

350 We used 185 plots for the analyses from the 192 sampled, excluding 2 plots with very high soil
351 organic matter content, and 5 plots because they had no understorey species. For the analysis of seed
352 mass, *Monilophyta* species (12 fern and 2 *Equisetum* species) were excluded because their very low
353 “diaspore” mass caused a bias in the results (0.000034mg for ferns – Gómez-Noguez, Pérez-García,
354 Mehlreter, Orozco-Segovia, & Rosas-Pérez, 2016)). **Table A5** shows results when including these
355 species. Three additional plots were excluded from the analyses of seed mass, because they only
356 comprised fern species, resulting in a sample size of 182 plots.

357 We evaluated the CWM of the response traits *Plant height*, *SLA*, *Seed mass*, and *Lateral spread*, and
358 the proportional cover of the response traits *Woodiness* and *Obligate mycorrhizal status* in each plot
359 in relation to the global-change drivers and the resources and conditions (**Table A6**). We included
360 Ndep in the global model as a (potential) quadratic effect, because we expected that the effect of
361 deposition on understorey trait responses in our plots might not be linear because of nitrogen
362 saturation effects in several regions where the critical N load for understorey communities was
363 exceeded ($>15\text{-}20 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (**Table A1a**); Bobbink et al., 2017, 2010; Gilliam, 2006).

364 Several predictors and response variables required a transformation prior to the analysis to linearize
365 relationships (**Fig. A1, A3**): *LitterMass* (sqrt), *OlsenP* (log), *Light* (log), and the response *CWM Plant*
366 *height* (log), *CWM Seed Mass* (log). We checked for potential confounding and collinearity issues
367 between the predictor variables by means of boxplots and correlograms (**Fig. A4**). Soil type was
368 slightly correlated with the litter mass as well as litter quality, which should be kept in mind when
369 interpreting results. Otherwise, only nitrogen deposition and acidification rate were highly correlated
370 ($R_p=0.94$) which led to separate models being built using one or the other. All continuous predictors
371 were standardized (scaled and centered) prior to analysis to enable comparison of their effect sizes.

372 We built a model for each trait including all possible combinations of our predictors as main effects.
373 We adopted an AIC-based multi-model inference approach to derive the best-supported models by
374 weighing and ranking all possible models based on a small-sample information criterion (AICc). We
375 derived ‘full’ average parameter estimates and 95% confidence intervals (‘zero-method’ *sensu*
376 Grueber, Nakagawa, Laws, & Jamieson, 2011) based on a reduced set of models with good empirical
377 support ($\Delta\text{AICc} \leq 3$ from lowest AICc model; (Burnham & Anderson, 2002). Models were run using
378 the MuMIn package in R (Barton, 2017).

379 To take into account the hierarchical structure of our data (plots within regions), we included the
380 random intercept *Region* in the models. We used linear mixed effect models (LMM) and generalized
381 linear mixed effect models (GLMM) for the CWM response traits (*Plant height*, *SLA*, *Seed mass*, and
382 *Lateral spread*) and the proportional cover response traits (*Woodiness*, *Obligate mycorrhizal status*),
383 respectively. We modelled *Woodiness* and *Obligate mycorrhizal status* with a Gamma distribution
384 and a log link function because there were several zeroes in the proportional cover data and this
385 provided the best model fit. Because the results of the acidification models largely overlap with the
386 results of the nitrogen deposition models, we report them in the Appendix (**Table A4, A7**), and only
387 highlight new results compared to the deposition models in the main text.

388 We discuss effects where zero was not included in the 95% CI of its parameter estimate (Burnham &
389 Anderson, 2002). We evaluated the global models' performance graphically by looking at plots of
390 the residuals vs. fitted values, and of the fitted vs. observed values (i.e. 'goodness of fit'). For the
391 GLMMs, we additionally checked for heteroscedasticity by evaluating the scaled residual plots, as
392 well as tested for overdispersion by means of the package 'DHARMA'. We also calculated the
393 marginal and conditional R^2 (proportion of variance explained by fixed factors – R^2_m , and by both
394 fixed and random factors – R^2_c) of the global and selected models following Nakagawa & Schielzeth
395 (2013). All statistical analyses and visualizations were performed in R (version 3.3.3: R Core Team
396 (2016) with the packages 'stats', 'MuMIn', 'lme4', 'DHARMA', and 'ggplot2' (Barton, 2017; Hartig,
397 2018; Pinheiro, Bates, DebRoy, & Sarkar, 2016; Wickham, 2009).

398

399 **Results**

400 Some global-change drivers (MAT, Ndep/AcidRate) as well as several resources and conditions
401 (Ellenberg soil moisture, litter mass, and OlsenP) were correlated with variation in trait CWMs in the
402 plots [**Table 1** (models with Ndep), **Table A7** (models with AcidRate)]. We did not observe any
403 effects of past land cover, soil type, litter quality, or light availability on the investigated traits (**Tables**
404 **1, A7**). Overall, lateral spread was much less influenced by the predictors than the other traits (**Table**
405 **1, Fig. 3-4**).

406 Significant trait-environment relationships were found between mean annual temperature (MAT) and
407 CWM of various traits (**Table 1**). CWM plant height, proportional cover of woody and OM species
408 showed a positive, while SLA showed a negative relationship with MAT (**Fig. 4**). Furthermore, we
409 found a quadratic effect of Ndep as well as AcidRate on CWM SLA (**Table 1, A7, Fig. 4**).

410 Ellenberg soil moisture and litter mass also appeared important predictors of understorey trait
411 variation in our plots (**Table 1**). A higher Ellenberg soil moisture was associated with a lower
412 proportional cover of woody and OM species (**Fig. 4**), as well as a lower CWM seed mass (**Fig. 3**).
413 Plots with a higher litter mass showed higher CWM plant height as well as a higher proportional
414 cover of OM species (**Fig. 4**), as well as higher CWM seed mass (**Fig. 3**). Finally, plots with a higher
415 bioavailable phosphorus (Olsen P) also contained lower proportional cover of woody species (**Fig.**
416 **4**).

417 Overall, the R^2 values (R^2_m between 13-41%) suggested that the predictors explained a medium
418 amount of the variation in our response traits. Among the response traits, we observed a positive
419 correlation between woodiness and CWM plant height ($r=0.70$) as well as between woodiness and
420 proportional cover of OM species ($r=0.57$), while CWM plant height and SLA were negatively
421 correlated ($r=-0.60$).

422

423

Table 1: Parameter estimates (i.e. effect sizes) and directions (increase↑ or decrease↓) of the main effects in the average models for the response variables: CWM (first four columns) or proportional cover (last two columns). The last four rows provide information on the selected models that make up the average model: the maximum R² explained with the models by fixed factors only (R^2_m), and by fixed and random factors (R^2_c), the relative weight of the “best-ranked” model based on an AICcutoff of 3 (*max weight*), and the number of models used to derive weighted parameter estimates. The abbreviated response variables *SLA*, *Woody*, and *OM* refer to specific leaf area, proportional cover of woody and obligate mycorrhizal species per plot. The abbreviated predictors (first column) *MAT*, *MAP*, *Ndep*, *AFRF[RF-Grass]*, *AFRF[RF-Arable]*, *SoilType[ClayNoCarb]*, *SoilType[Sand]*, and *OlsenP* refer to mean annual temperature and precipitation, N deposition, recent post-grassland/heathland and post-arable forest plots, clayey soils without carbonate, sandy soils, and Olsen P respectively. Effect sizes are in **bold** if the 95% confidence intervals do not include zero. NA implies that the predictor did not occur in any of the selected models that make up the average model.

		CWM/Proportional cover					
		<u>Regeneration</u>		<u>Resource acquisition</u>			
		Seed Mass	Lateral Spread	Plant Height	SLA	Woody	OM
Global-change drivers	Intercept	1.82	0.15	-0.71	28.88	-2.96	-1.40
	MAT	-0.07↓	0.00	0.30↑	-4.22↓	1.01↑	0.35↑
	MAP	-0.23↓	0.00	0.00	0.02↑	0.01↑	0.26↑
	Ndep	-0.08↓	0.00	0.00	1.26↑	-0.01↓	0.07↑
	Ndep ²	0.00*	0.00	0.00	-0.80↓	0.00	0.01↑
	AFRF [RF-Grass]	-0.01↓	NA	NA	-0.08↓	0.03↑	0.03↑
	AFRF [RF-Arable]	-0.09↓	NA	NA	-0.34↓	0.05↑	0.03↑
Resources and conditions	SoilType [ClayNoCarb]	NA	-0.02↓	0.02↑	NA	NA	0.00
	SoilType [Sand]	NA	-0.02↓	0.01↑	NA	NA	-0.01↓
	OlsenP	-0.05↓	0.00	0.03↑	-0.39↓	-0.35↓	-0.11↓
	SoilMoisture (EIV)	-0.29↓	0.00	0.00	0.07↑	-0.51↓	-0.26↓
	LitterMass	0.24↑	0.00	0.14↑	-0.06↓	0.32↓	0.28↑
	LitterQuality	0.02↑	0.00	0.00	0.13↑	-0.30↓	0.01↑
	Light	0.00	0.00	0.06↑	-0.19↓	0.30↑	0.00
	Max R ² _m	0.28	0.13	0.37	0.41	0.22	0.25
	Max R ² _c	0.48	0.42	0.53	0.44	0.44	0.33
	Max weight	0.06	0.05	0.15	0.08	0.29	0.11
	No models	41	51	16	33	8	22

425 **Discussion**

426 **Regeneration traits**

427 Lateral spread showed no relationship with environmental drivers, while seed mass was related
428 to some of the resources and conditions i.e. Ellenberg soil moisture and litter mass.
429 Communities in moister plots having on average lower seed mass is in accordance with other
430 studies on the relationship between seed mass and Ellenberg soil moisture (Baker, 1972; Dubuis
431 et al., 2013; Sonkoly et al., 2017; Westoby, Jurado, & Leishman, 1992). Larger seed mass has
432 been linked with a higher resilience to various seedling disturbances such as drought, likely due
433 to the tendency of larger seeds to retain more metabolic reserves (DeMalach et al., 2018;
434 Westoby, 1998; Westoby et al., 1996).

435 Communities in plots with more litter had on average larger seeds. This may be because more
436 seed reserves enable the initial seedlings to penetrate these thicker litter layers (Baltzinger,
437 Archaux, & Dumas, 2012; Kidson & Westoby, 2000). Reduced light availabilities beneath litter
438 layers may also prevent small seeds from germinating, whereas large-seeded species are less
439 dependent on light for germination success (Milberg, Andersson, & Thompson, 2000; Simpson,
440 Richardson, & Laughlin, 2016; Zhang, Hu, Baskin, Baskin, & Wang, 2017).

441 **Resource acquisition traits**

442 Mean annual temperature (MAT) showed a relationship to all resource acquisition traits in our
443 plots. This result agrees with findings from previous trait studies showing that temperature is a
444 key factor for understorey composition and functioning (Bjorkman et al., 2018; De Frenne,
445 Graae, et al., 2013; Lu et al., 2017; Moles et al., 2014; Murray, Brown, Dickman, & Crowther,
446 2004; Reich & Oleksyn, 2004; Wright et al., 2004). Besides temperature, a strong link between
447 Ellenberg soil moisture and several traits was found in our plots as well (Riegal et al., 1991;
448 Schaffers & Sýkora, 2000).

449 Understoreys were taller and had leaves with lower CWM SLA in warmer regions (De Frenne,
450 Graae, et al., 2013; Moles et al., 2009; Vanneste et al., 2018). SLA represents a trade-off
451 between potential carbon gain (biomass production) and resource conservation (Wright et al.,
452 2004). Species in resource-rich environments (i.e. resources such as water or nutrients) tend to
453 have larger SLA i.e. focus on rapid resource acquisition through thinner leaves with shorter life
454 span than those in resource-stressed environments, which focus on resource conservation

455 through thicker leaves with longer life span (Ordoñez et al., 2009; Westoby et al., 2002; Wright
456 et al., 2004). Producing leaves with lower SLA (*sclerophyllous*) in warmer regions with higher
457 potential evapotranspiration rates might be more an (indirect) water-conserving rather than a
458 nutrient-conserving strategy. This could become increasingly important in regions with
459 increasing temperatures without concurrent increases in precipitation (Soudzilovskaia et al.,
460 2013). If so, we could expect to find an effect between CWM SLA and MAP as well though,
461 which was not the case. On the other hand, the lower CWM SLA in warmer regions might be
462 linked to the higher proportions of woody species cover in those regions, since woody plants
463 have lower SLA and growth rates than herbaceous plants due to large energy requirements for
464 formation of woody structures (de Vries, Brunsting, & Van Laar, 1974; Jarvis & Jarvis, 1964;
465 Poorter & Evans, 1998).

466 CWM SLA showed a quadratic hump-shaped relationship with nitrogen deposition as well as
467 acidification rate, although this was weaker than the negative linear relationship with
468 temperature. Greater N availability from increased atmospheric deposition can increase SLA
469 (and growth rates) through favouring highly resource competitive species over more N-efficient
470 species (Boutin et al., 2017; Poorter, Niinemets, Poorter, Wright, & Villar, 2009; Reich,
471 Walters, & Ellsworth, 1997; Westoby et al., 2002), while beyond a certain threshold or critical
472 load of deposition (here ca. $18 \text{ kg ha}^{-1} \text{ yr}^{-1}$), growth reductions from N saturation and potential
473 acidification may occur, as suggested by these results (Aber, 1992, 1998; Bobbink et al., 2017).
474 Due to potential confounding effects with the topsoil conditions in this result, we should not
475 overinterpret this. That is, the Speulderbos (NL) region receiving the highest Ndep also had
476 poorer topsoil properties (sandy soil type, lower pH) and lower species numbers.

477 Interestingly, both the proportional cover of woody and of OM species was positively related
478 to temperature, and negatively to Ellenberg soil moisture. A higher abundance of woody plant
479 species (not counting tree and shrub seedlings that were excluded from the analysis) in the
480 understorey may result in a stronger mycorrhizal fungal network leading to higher occurrences
481 of species forming mycorrhizal associations (Hempel et al., 2013; Veresoglou, Wulf, & Rillig,
482 2017; Wang, Qiu, & Qiu, 2006). This might also explain the positive correlation between
483 proportional cover of woody and OM species ($R_p=0.57$). Species forming mycorrhizal
484 associations appeared to thrive better (i.e. they had greater relative cover) in plots with lower
485 Ellenberg soil moisture as compared to species that do not as fungal associations aid water
486 uptake (Bennett & Klironomos, 2018; Wang et al., 2006). The decrease in woody species cover
487 with higher Ellenberg soil moisture (and also with bioavailable P) seems in line with the

488 hypothesis that higher available resources promote herbaceous but constrain woody
489 understorey species growth because of the higher resources per unit biomass required for
490 herbaceous species development (Graves et al., 2006).

491 Besides temperature and Ellenberg soil moisture, litter mass also affected CWM of some
492 resource acquisition traits, with communities in plots with more litter being taller, having larger
493 seeds, and harbouring more OM species (cover). These results support previous studies
494 demonstrating the importance of (deciduous) litter in structuring understorey communities,
495 through forming a chemical, physical, as well as biological barrier for seeds, seedlings, and
496 adult plants (Baltzinger et al., 2012; Maes et al., 2019; Xiong & Nilsson, 1999).

497 **Lack of effects of light availability and past land cover**

498 The lack of effects of light availability on the investigated traits is surprising, as light is
499 considered a key driver of the functional composition and dynamics of understorey
500 communities (Bartels & Chen, 2009; Bartemucci, Messier, & Canham, 2006; Bernhardt-
501 Römermann et al., 2015; De Frenne et al., 2015; Lieffers, Messier, Stadt, Gendron, & Comeau,
502 1999; Sercu et al., 2017). We sampled in quite closed mature forests with a mean canopy
503 openness of 18.3% (min. 1.4%, max. 69.8%), so perhaps there was too little variation in light
504 availability to result in functional trait variation. Other explanations could be that light
505 heterogeneity rather than availability is more important for understorey functioning (Bartels &
506 Chen, 2009; Burton, Perakis, McKenzie, Lawrence, & Puettmann, 2017; F. Valladares &
507 Niinemets, 2008), or that we missed community trait responses to light here by using single
508 trait values per species. Intraspecific trait variation or plasticity to light may be particularly
509 strong because of the asymmetric nature of competition for light (Roscher, Schumacher,
510 Schmid, & Schulze, 2015; Fernando Valladares, Laanisto, Niinemets, & Zavala, 2016). Finally,
511 although several studies have demonstrated the reliability of densiometer measurements as an
512 alternative for estimating light availability below the canopy (e.g. compared to hemispherical
513 photography) (Bellow & Nair, 2003; Parker, 2014), using this “indirect” method to estimate
514 light availability could still be partly responsible for the lack of effects here (Engelbrecht &
515 Hertz, 2001; Jennings, 1999).

516 We also expected to find land-use legacies in the functional signature (e.g. lateral spread) of the
517 present-day understorey communities (Flinn & Vellend, 2005; Holmes & Matlack, 2018;
518 Verheyen et al., 2003), but past land cover did not affect any of the traits. This could suggest

519 that land-use legacies do not necessarily affect the functional signature of understorey
520 communities, even if compositional shifts from land-use legacies might occur.

521 **Implications for future understorey communities**

522 Community-level resource acquisition traits in temperate forest understoreys seemed driven by
523 both global-change drivers and local resources and conditions. Considering the local context is
524 not always straightforward, as *in situ* measurements of local resources and conditions can be
525 laborious, costly and logistically challenging, especially across larger-scale environmental
526 gradients. Global-change drivers may affect forests *through* (indirectly) altering other local
527 conditions, as well as these local conditions may influence how forests respond to global
528 changes (Landuyt et al., 2018; Naaf & Kolk, 2016; Simpson et al., 2016; Smith et al., 2009).
529 Because of this, it will be crucial to also evaluate interactive effects among environmental
530 drivers, not only among global-change drivers or among local resources and conditions, but
531 also between the two, e.g. by performing structural equation modelling and evaluating
532 interactive effects.

533 Among the studied global-change drivers, MAT appeared more important than N deposition,
534 MAP, or past land cover. Based on our findings, future warming could lead to understorey
535 community changes benefiting taller species with more resource conservative leaves (lower
536 SLA) across the investigated environmental gradients. Future warming may also benefit woody
537 species and species forming mycorrhizal associations residing in understorey communities.
538 Future studies should consider microclimatic buffering effects on below-canopy temperatures
539 by including measured temperatures at the forest floor, since this buffering effect (i.e. likely
540 reduced temperature ranges) may confound the temperature-trait relationships found here
541 (Zellweger et al., 2019). That is, our plots comprised closed canopy forests that have not had
542 much disturbance in the recent past, and where canopy cover has increased over time. Thus, we
543 might expect even stronger temperature effects on the understorey trait responses if this
544 buffering was not to occur or was to be altered, e.g. through opening up of the canopy. Note
545 that we excluded tree and shrub seedlings in this study since these do not remain part of the
546 understorey, so these results do not consider effects on tree regeneration. Furthermore, future
547 responses may also depend on other local resources and conditions such as e.g. the size of the
548 litter layer or phosphorus availability. Due to the heterogeneous nature of these resources and
549 conditions below the forest canopy, they can differ considerably among sites, and potentially
550 confound the expected understorey responses to global change.

551 Spatial environmental gradients only allowed us to hint at potential future changes in
552 understorey community trait composition and functioning (Blois, Williams, Fitzpatrick,
553 Jackson, & Ferrier, 2013; De Lombaerde et al., 2018; Elmendorf et al., 2015; Kratz, Deegan,
554 Harmon, & Lauenroth, 2003). Future studies using plot resurveys should investigate temporal
555 changes as well, to test the validity of our results (Hedwall & Brunet, 2016; Perring, Bernhardt-
556 Römermann, et al., 2018; Perring et al., 2016; Verheyen et al., 2016). More work is needed to
557 take into account biotic influences on understorey communities (e.g. herbivory pressure)
558 (Bernhardt-Römermann et al., 2015; de la Peña et al., 2016; Morecroft, Taylor, & Ellwood,
559 2001; Rooney, 2009), as well as more in-depth analysis of individual species responses. We
560 also did not take into account potential effects of forest size/fragmentation here because most
561 of our regions comprised medium- to large-sized forests. Future studies should consider this,
562 since potential time lags in composition turnover from fragmentation effects, and even potential
563 extinction debts, could have an influence on the composition of the understorey, indirectly
564 affecting trait responses (Vanneste et al., 2018). Given the broad environmental gradients
565 covered here, we expected trait variation to be dominated by inter-specific differences rather
566 than intraspecific variation (Auger & Shipley, 2013). However, for certain traits such as SLA,
567 intraspecific trait variation (ITV) might play a more important role in driving trait variation,
568 hence considering ITV is also a necessary priority for future research. Furthermore, intra-
569 specific trait variation has been suggested as a useful early-warning signal where changes in
570 traits at the individual level may forecast future shifts at community level, reiterating the
571 importance of evaluating ITV as well (Smith et al., 2009).

572 **Conclusion**

573 To conclude, warmer temperatures were associated with on average taller understoreys
574 producing leaves with lower SLA, and a higher relative cover of woody and obligate
575 mycorrhizal species. These findings may hint at community shifts in temperate forest
576 understoreys with (future) global warming. Furthermore, local resources and conditions
577 including Ellenberg soil moisture, litter mass, and to a lesser extent P availability, were
578 associated with community trait variation across the spatial environmental gradients as well.
579 Based on these findings, we recommend that studies investigating global environmental
580 (change) effects on understorey communities should consider the local environmental context.
581 Further investigations should evaluate interactive effects among the different environmental

582 drivers, incorporate intraspecific trait variation, as well as perform temporal studies to validate
583 how understoreys are already changing in response to changing environments.

584

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600 **Data accessibility**

601 We intend to archive all data used in this paper on our public website:
602 www.pastforward.ugent.be.

603 **Conflict of interest**

604 The authors have no conflicts of interest to declare.

605 **Author contributions**

606 SLM, MPP and KV conceived and designed the study with significant contributions from SG,
607 DL, LD, and HB. GB, JB, GD, JDO, WH, RH, TH, SH, BJ, KK, MK, FM, MW, and KV
608 assessed historical land-use information for the study regions, and participated in the field
609 campaign (as well as MPP, SG, DL, LD, and HB). SLM, MBR, and SG compiled the trait
610 information from various literature sources. SLM, with input from MPP, DL, LH, TV, and KV
611 performed data quality checks, and subsequent statistical analyses on the data. SLM wrote the
612 first draft of the paper. All co-authors provided revisions and comments.

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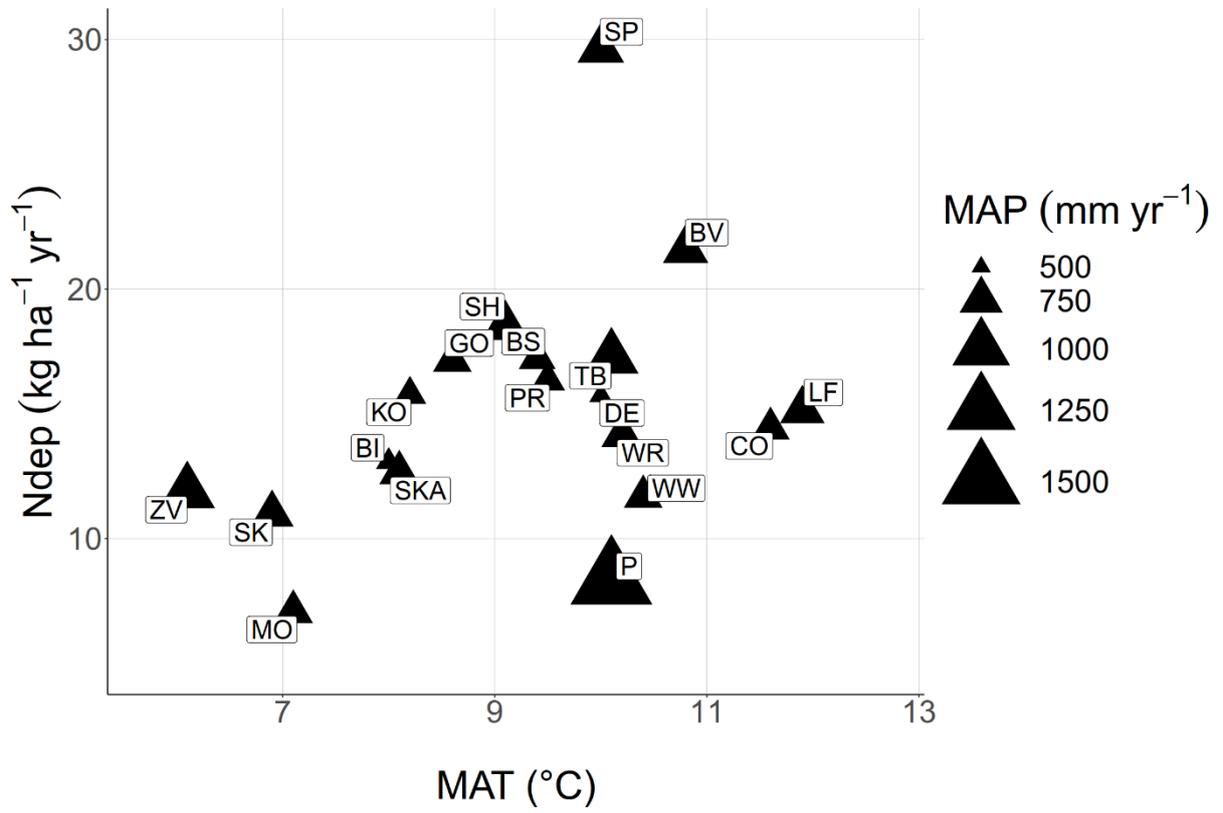
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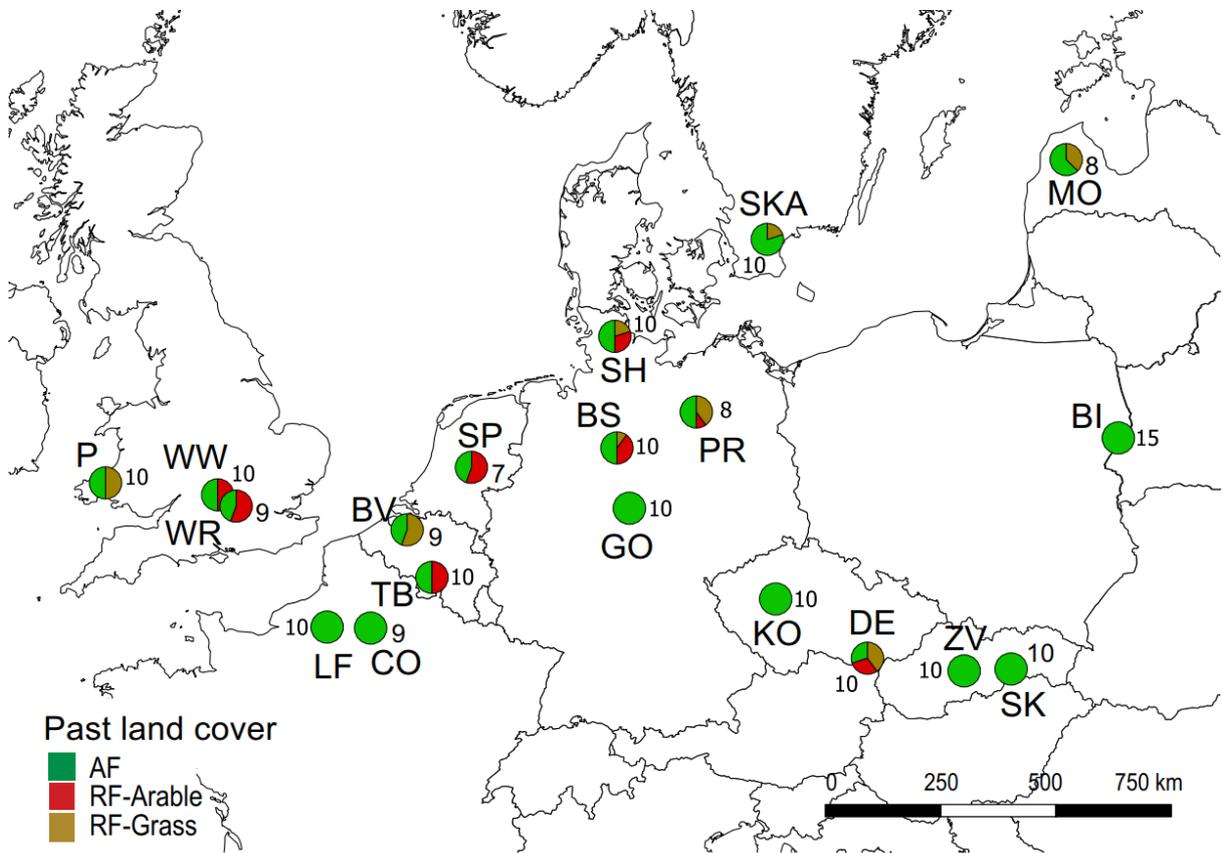
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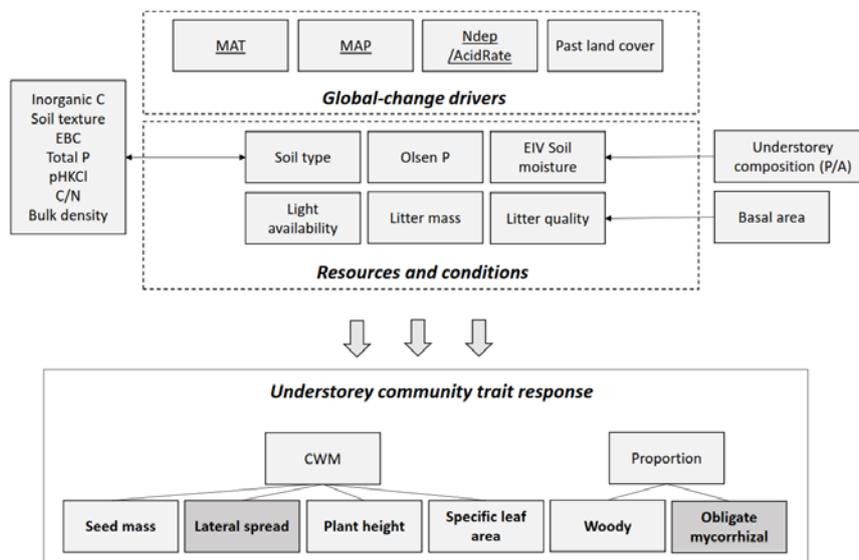
960 **Figure 1:**

961 **a)** Environmental gradients covered by the 19 forest regions where plots were sampled: nitrogen
962 deposition ($Ndep - kg\ ha^{-1}\ yr^{-1}$) vs. mean annual temperature ($MAT - ^\circ C$) is plotted, with the
963 symbol size reflecting the total annual precipitation ($MAP - mm\ yr^{-1}$) in that region. Values
964 from the year 2000 were used for $Ndep$, and average values for 1980-2015 were used for MAT
965 and MAP .

966

967 **b)** Geographical distribution of the 19 forest regions where plots were sampled. Per region, the
968 pie chart visualizes the proportion of ancient forest (AF : green) vs. recent forest plots with past
969 arable land use (RF -*Arable*: red) vs. recent plots with past heathland/grassland as past land use
970 (RF -*Grass*: brown). The Region code and total number of plots used per region is indicated
971 next to the pie charts. *Note*: the 185 plots that were used in the analyses (out of 192 initially
972 sampled) are shown in this figure.

973



974

975 **Figure 2:** Graphical representation of the predictors including global-change drivers and
 976 resources and conditions, and investigated understory community trait responses (*left:*
 977 community-weighted means (CWM), *right:* proportional cover of species). Underlined
 978 predictor variables were calculated at the regional scale, while all others were calculated at the
 979 plot scale. Aboveground traits are shaded in light grey, while belowground traits are in dark
 980 grey. Variables outside the boxes have been used to calculate other variables inside the box (i.e.
 981 basal area-weighted litter quality score and presence-absence based mean Ellenberg Indicator
 982 value for soil moisture), or reflect variation in other topsoil physicochemical variables (soil
 983 type).

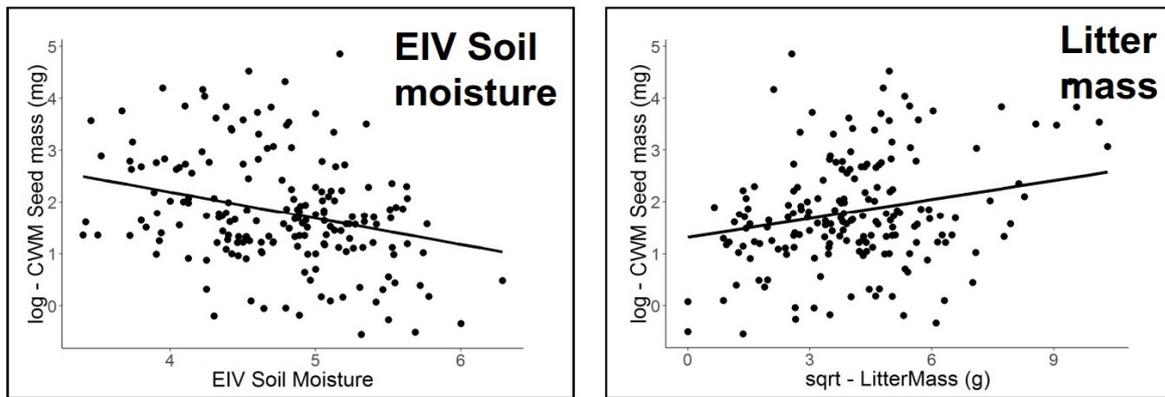
984 Abbreviations used in the figure represent mean annual temperature and precipitation ($MAT -$
 985 $^{\circ}C$, $MAP - mm\ yr^{-1}$), nitrogen deposition ($Ndep - kg\ ha^{-1}\ yr^{-1}$), acidification rate ($AcidRate -$
 986 $keq\ ha^{-1}\ yr^{-1}$), Olsen phosphorus ($Olsen\ P - mg\ kg^{-1}$), Presence/Absence (P/A), Inorganic carbon
 987 content ($Inorganic\ C - \%$), proportion of exchangeable base cations (EBC), total phosphorus
 988 ($Total\ P - mg\ kg^{-1}$), and organic carbon/total nitrogen ratio (C/N).

989 Note that (i) Olsen P is included as a separate predictor here as it is an important nutrient for
 990 plant growth and was not correlated with soil type, and (ii) lateral spread is “mainly” a

991 belowground trait (e.g. rhizomes), but understorey species also have aboveground
992 characteristics for lateral spread (e.g. stolons).

993

Resources and conditions

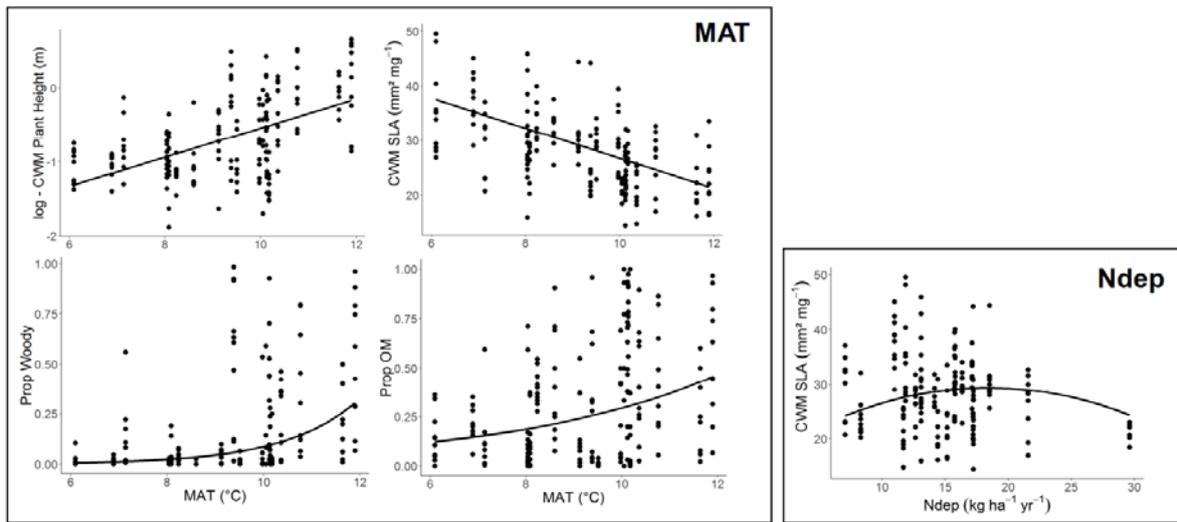


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995 **Figure 3:** Trait-environment relationships for the regeneration trait *seed mass*. Effects of EIV
996 soil moisture (*left*) and litter mass (*right*) on the community-weighted mean seed mass (*CWM*
997 *seed mass*). Actual data points (*dots*) and average model estimates of the effects (*full lines*), in
998 which the values of the other continuous variables were set at their observed mean, are shown.

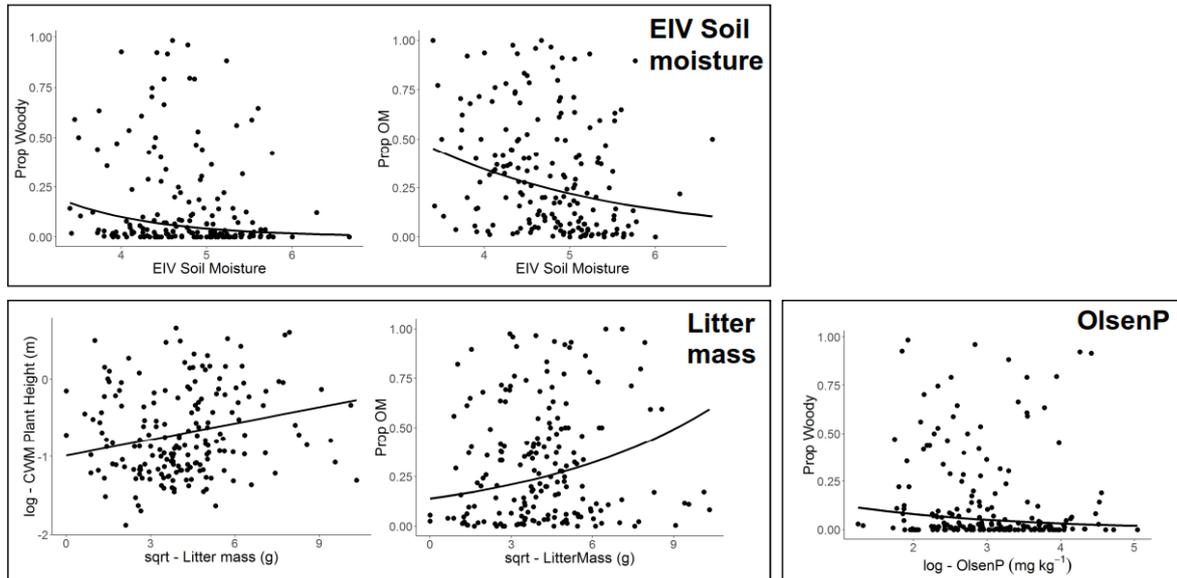
999

a) Global-change drivers



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b) Resources and conditions



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Figure 4: Trait-environment relationships for resource acquisition traits.

1003

a) Effects of global-change drivers: of MAT (°C) on community-weighted mean plant height (CWM plant height (m)), CWM specific leaf area (CWM SLA ($\text{mm}^2 \text{mg}^{-1}$)), proportional cover of woody species (Prop Woody), and proportional cover of obligate mycorrhizal species (Prop OM) (left); and of Ndep ($\text{kg ha}^{-1} \text{yr}^{-1}$) on CWM SLA (right).

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1006

1007

b) Effects of local resources and conditions: of EIV soil moisture on Prop Woody and Prop OM (top left); of litter mass (g) on CWM plant height and Prop OM (bottom left); and of OlsenP on Prop Woody (bottom right).

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