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8 **Title: Global environmental change effects on plant community composition trajectories**  
9 **depend upon management legacies.**

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11 **Running Head:** Legacies determine community trajectories.

12

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93 layer, Nitrogen deposition, Management intensity, Plant functional traits, Time lag, Vegetation  
94 resurvey.

95

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97 **ABSTRACT**

98 The contemporary state of functional traits and species richness in plant communities depends on  
99 legacy effects of past disturbances. Whether temporal responses of community properties to current  
100 environmental changes are altered by such legacies is, however, unknown. We expect global  
101 environmental changes to interact with land-use legacies given different community trajectories  
102 initiated by prior management, and subsequent responses to altered resources and conditions. We  
103 tested this expectation for species richness and functional traits using 1814 survey-resurvey plot  
104 pairs of understorey communities from 40 European temperate forest datasets, syntheses of  
105 management transitions since the year 1800, and a trait database. We also examined how plant  
106 community indicators of resources and conditions changed in response to management legacies and  
107 environmental change. Community trajectories were clearly influenced by interactions between  
108 management legacies from over 200 years ago and environmental change. Importantly, higher rates  
109 of nitrogen deposition led to increased species richness and plant height in forests managed less  
110 intensively in 1800 (i.e. high forests), and to decreases in forests with a more intensive historical  
111 management in 1800 (i.e. coppiced forests). There was evidence that these declines in community  
112 variables in formerly coppiced forests were ameliorated by increased rates of temperature change  
113 between surveys. Responses were generally apparent regardless of sites' contemporary management  
114 classifications, although sometimes the management transition itself, rather than historic or  
115 contemporary management types, better explained understorey responses. Main effects of  
116 environmental change were rare, although higher rates of precipitation change increased plant  
117 height, accompanied by increases in fertility indicator values. Analysis of indicator values  
118 suggested the importance of directly characterising resources and conditions to better understand  
119 legacy and environmental change effects. Accounting for legacies of past disturbance can reconcile  
120 contradictory literature results and appears crucial to anticipating future responses to global  
121 environmental change.

## 122 **Introduction**

123 Ecology has shifted from simply explaining the contemporary state of ecosystems towards  
124 predicting their temporal dynamics, taking account of simultaneous environmental changes,  
125 including land-use change, climate change, and atmospheric pollution. Functional traits i.e.  
126 measurable characteristics of organisms that ultimately influence their fitness through effects on  
127 reproduction and growth, show great potential assisting these predictions (Laughlin & Messier,  
128 2015; McGill, Enquist, Weiher, & Westoby, 2006; Violle et al., 2007). Traits respond to and cause  
129 effects on their environment, thus connecting both ecosystem patterns (e.g. species diversity and  
130 composition) and processes (Bardgett, Mommer, & De Vries, 2014; Eviner & Chapin III, 2003;  
131 Suding et al., 2008). The understanding of trait variation across spatial environmental gradients is  
132 relatively advanced (e.g. Cornwell & Ackerly, 2009; Fonseca, Overton, Collins, & Westoby, 2000;  
133 Laliberté et al., 2010; Messier, McGill, & Lechowicz, 2010; A.T. Moles et al., 2009). However,  
134 knowledge of temporal trait change across environmental gradients remains limited (Amatangelo,  
135 Johnson, Rogers, & Waller, 2014; Dwyer, Hobbs, & Mayfield, 2014; Hedwall & Brunet, 2016; Li  
136 & Waller, 2017). This lack of knowledge makes it difficult to predict future ecosystem structure and  
137 functioning, especially as space-for-time approaches can produce biased results (Johnson &  
138 Miyanishi, 2008).

139

140 Predictions of how ecosystems might change into the future can be improved by considering past  
141 environmental conditions, and time lags in response (Ogle et al., 2015; Ryan et al., 2015). Legacies  
142 of past land management on the abiotic and biotic environment influence at least two fundamental  
143 plant community processes: ecological selection and dispersal (Perring et al., 2016; Vellend, 2010).  
144 Resources and conditions, influenced by legacies, determine organism performance as mediated by  
145 their traits, selecting for certain species over others. Land management legacies can also affect  
146 dispersal dynamics, which can be an important influence on community structure (Burton,  
147 Mladenoff, Clayton, & Forrester, 2011), with these dispersal effects mediated by constituent traits

148 e.g. seed mass and plant height (Baeten, Hermy, Van Daele, & Verheyen, 2010). Together, these  
149 processes determine the trajectories of communities and ecosystems following changes to land  
150 management practices (e.g. Bürgi, Östlund, & Mladenoff, 2017; Gimmi et al., 2013; Lohmus, Paal,  
151 & Liira, 2014). Successional trajectories of ecological change are further influenced by recent  
152 global environmental changes, due to chronic alterations in resources and conditions (M. D. Smith,  
153 Knapp, & Collins, 2009).

154  
155 Studies often focus on one of the two focal explanatory variables (i.e. legacies or global  
156 environmental change) yet interactions between them are likely (Perring et al., 2016). For instance,  
157 the impact of nitrogen (N) deposition on plant diversity can depend on soil pH (Simkin et al., 2016),  
158 a property that can be altered by previous management. Legacies of high phosphorus (P) from  
159 former intensive agricultural land use can increase community responsiveness to increased N  
160 availability (Marrs, 1993). In the absence of increased P, similar ecosystems lacking an intensive  
161 agricultural history may not respond as strongly to N addition (Kopecký, Hédli, & Szabó, 2013;  
162 Ollinger, Aber, Reich, & Freuder, 2002; Perring et al., 2016). This expectation that community  
163 responses to N addition, and other environmental changes, depend on previous management has  
164 rarely been tested (Gill, 2014; Li & Waller, 2017) and never, to our knowledge, across broad  
165 environmental gradients. The potential for such interactions with N and other recent environmental  
166 changes has fundamentally important implications for our ability to predict future ecosystem  
167 responses to environmental change, and may help reconcile contradictory literature patterns in  
168 ecosystem responses to environmental change (e.g. Garnier, Navas, & Grigulis, 2016; Vellend et  
169 al., 2017).

170  
171 Here, we test for interactions between land-use legacies and environmental change using  
172 understorey resurvey data from temperate forests across Europe, where we can exploit large spatial  
173 variability in both historical management (Durak, 2012; McGrath et al., 2015; Rackham, 2003) and

174 global environmental change factors. Forest plant communities display slow dynamics and  
175 trajectories of change (Dornelas et al., 2013; Peterken & Game, 1984) and in the absence of  
176 continuous long-term monitoring, we can only reveal these changes through resurveys (Kapfer et  
177 al., 2017). More generally, resurveys across broad, potentially orthogonal, environmental gradients  
178 offer the opportunity to disentangle the interacting effects of multiple ecological drivers (Verheyen  
179 et al., 2017) providing such observational results are carefully interpreted (Smart et al., 2012).

180

181 Our analyses focus on two widespread historical forest management systems in Europe, coppice  
182 (hereafter CWS, “coppice with standards” reflecting the presence of standard trees in some  
183 implementations) and high forest (HF), treated in classical texts as different silvicultural systems  
184 (e.g. Matthews, 1989; D. M. Smith, Larson, Kelty, & Ashton, 1997). These systems have been used  
185 as a basis to make comparisons in recent research (e.g. Bottalico et al., 2014; Scolastri, Cancellieri,  
186 Iocchi, & Cutini, 2017) while numerous papers refer to one or the other system. The basis for the  
187 clear difference in these silvicultural systems is the method of regeneration of tree species: CWS  
188 involves vegetative reproduction from coppice stools, while HF systems tend to regenerate from  
189 seed. There is likely variability within these systems due to abiotic environmental conditions,  
190 variation in management intensity depending on socio-economic pressures, and socio-cultural  
191 differences in forestry methods, but the different regeneration methods create distinct forest  
192 environments.

193

194 Traditional CWS systems involve regular opening of the canopy through cutting multi-stemmed  
195 individuals of species such as oak (*Quercus* sp.), hornbeam (*Carpinus betulus*), and hazel (*Corylus*  
196 *avellana*), on short rotation cycles (typically 7 – 30 years). Cutting provides wood for charcoal,  
197 fencing and other products that can use small diameter poles. In the ‘true’ CWS system, single  
198 stemmed timber trees (standards of e.g. oak) are chosen and then grown through multiple coppicing  
199 cycles until suitable for harvest (Altman et al., 2013). The regular opening of the canopy in coppice



200 and CWS creates cyclic variation in light and warm temperatures in the forest understorey and also  
201 reduces humidity (e.g. Ash & Barkham, 1976). Intensive removal of wood tends to lead to  
202 substantial depletion of nutrients (Hölscher, Schade, & Leuschner, 2001; Rackham, 2003; Šrámek,  
203 Volařík, Ertas, & Matula, 2015). On the other hand, traditional HF systems focus on producing  
204 timber over much longer rotation lengths than CWS systems, but often using the same species e.g.  
205 oak. Regeneration is encouraged through clear felling, single tree selection, or group selection of  
206 trees in belts and / or in increasing radii from central points, depending on site topography and road  
207 networks (Matthews, 1989). The longer period of canopy closure in HF systems leads to shadier,  
208 cooler and more moist understorey microclimates compared to CWS (Scolastri et al., 2017). High  
209 forest systems also tend to maintain nutrient stocks, with stem only harvesting in particular  
210 (Vangansbeke et al., 2015). Such differences in disturbance regimes between silvicultural systems,  
211 and subsequent effects on resources and conditions, lead to understorey plant communities with  
212 divergent species compositions and associated trait distributions (Decocq et al., 2004; Keith,  
213 Newton, Morecroft, Bealey, & Bullock, 2009; Scolastri et al., 2017; Ujházy et al., 2017).

214

215 These management ‘types’, as well as encompassing variation within them (Duguid & Ashton,  
216 2013), have not been static entities in any given area throughout preceding centuries. Changing  
217 socio-economic conditions have led to the abandonment of active timber management in some  
218 regions (i.e. zero management), commencing at different times across Europe, and affecting both  
219 CWS and HF stands (Hédl, Kopecký, & Komárek, 2010; McGrath et al., 2015; Munteanu, Nita,  
220 Abrudan, & Radeloff, 2016; Szabó, 2010; Van Calster et al., 2008). Elsewhere, within and among  
221 regions, timber management has been maintained but typically with HF systems at the expense of  
222 CWS (Baeten et al., 2009). This decline in CWS management has been tempered by recent  
223 reintroductions of this strategy in a few forests, typically as a conservation measure (Vild, Roleček,  
224 Hédl, Kopecký, & Utinek, 2013) but also with increasing demand to harvest biomass for fuelwood  
225 or to mitigate climate change (Borchard et al., 2017; Lasserre et al., 2011). Overall, European

226 forests are characterized by dynamic silvicultural management systems and legacies driven by  
227 abiotic environmental conditions and socio-economic pressures. We are thus presented with an  
228 exceptional opportunity to test whether the response of plant communities to recent environmental  
229 change depends on these historical management transitions, and / or on coarse categories of  
230 historical or more recent management types that reflect distinct silvicultural regimes. Further, we  
231 can also investigate whether any responses to these dynamic legacies may be related to the  
232 silvicultural regimes' hypothesized effects on resources and conditions, properties that provide a  
233 bridge to observed ecological responses.

234

235 We focus our analyses on community-level values of three traits (specific leaf area (SLA), plant  
236 height, and seed mass) that arguably capture fundamental trade-offs for plants (Díaz et al., 2016;  
237 Laughlin, 2014; Weiher et al., 1999; Westoby, 1998), and given the need to understand temporal  
238 trait responses to aid predictive responses to environmental change. Community weighted mean  
239 trait values are often associated with responses to environmental gradients and community assembly  
240 (Funk et al., 2017), while the range of trait values is an indicator of the breadth of diversity in a plot.  
241 Other indicators of diversity for single traits are available (Mouillot, Mason, Dumay, & Wilson,  
242 2005) but we chose to examine range, because of its simplicity and ease of interpretation.

243

244 In addition to fundamental trait-based community properties, we also considered whether responses  
245 in species richness (a commonly reported diversity metric), and community-level Ellenberg  
246 Indicator Values (EIVs) (Ellenberg, Weber, Düll, Wirth, & Werner, 2001) showed evidence for  
247 interactions between management legacies and recent environmental changes. Indicator values,  
248 widely calculated and used in vegetation investigations across Europe (as well as elsewhere e.g.  
249 Klinka, Krajina, Ceska, & Scagel, 1989) indicate species preferences for underlying environmental  
250 conditions and help understand community responses, and can also be related to the considered  
251 traits (Shipley et al., 2017). The indicators are considered robust in the absence of directly measured

252 resource and condition variables (Diekmann, 2003), which is the situation faced here. Although  
253 there is variability among species within groups, and individuals within species, these latter  
254 analyses complement the core trait-based investigation and enable preliminary investigation of the  
255 potential for community responses being related to resources and conditions engendered by the  
256 management legacies.

257

258 We expect that recent alterations in resources and conditions due to environmental change (e.g. N  
259 deposition, climate change) will lead to community trait and indicator value responses and altered  
260 species richness. Accounting for recent environmental change only, and based on prior research  
261 from spatial gradients, we might expect mean SLA and plant height to increase in response to  
262 greater availability of soil resources (e.g. moisture and N) (Garnier et al., 2016). Increasing soil  
263 resource availability will also favour species with higher EIV for fertility ( $EIV_N$ ) (Naaf & Kolk,  
264 2016). We might also expect no relationship between seed mass and changing resource conditions  
265 (Fortunel et al., 2009), and a unimodal response for species richness (Fraser et al., 2015).

266

267 Overall though, we expect that these responses will be modulated by the trajectories of change  
268 engendered by previous silvicultural management. In particular, we predict that likely depleted  
269 nutrient resources in former CWS systems would dampen community responses to increased N  
270 deposition (e.g. lessen increases in SLA and  $EIV_N$ ) due to limitation by other resources (e.g. P)  
271 compared to systems that have been under long-term HF management. We also predict that the  
272 change to less intensive management in former CWS forests would lead to a general loss of species,  
273 as warm- and light-adapted species would be unable to persist in cooler, shadier microclimates.  
274 These losses could be lessened in stands undergoing warming as previously adapted species  
275 continued to persist. In contrast, former HF systems would remain on relatively stable species  
276 richness trajectories subsequently influenced by environmental changes e.g. many systems show  
277 declines associated with increasing N deposition (Bobbink et al., 2010; Gilliam et al., 2016; Simkin

278 et al., 2016). We also expect that prolonged absence of high light conditions e.g. through the  
279 implementation of zero management, would lead to loss of species across the forests (Plue et al.,  
280 2013). In sum, changes in species abundance in all these systems, together with species losses and  
281 gains, would lead to changes in trait attribute and indicator values. Therefore, we would expect  
282 variation in these properties to relate to historical management as well as recent global  
283 environmental changes.

284

## 285 **Materials and Methods**

### 286 *Vegetation Surveys*

287 We used resurvey data across deciduous temperate forests in Europe from the forestREplot network  
288 ([www.forestreplot.ugent.be](http://www.forestreplot.ugent.be)), a database of vegetation plot records for woodland understoreys. Each  
289 dataset in this database is composed of multiple non-overlapping (in space) plot records from two  
290 time points (Table 1). The time interval between surveys in the 40 datasets and 1814 plots analysed  
291 here is considered sufficient to detect directional change in the herbaceous layer (a mean interval of  
292  $38.6 \pm 14.7$  [1 sd] years) (De Frenne et al., 2013). Each dataset comes from a relatively  
293 homogeneous area in terms of climate and atmospheric deposition such that we considered all plots  
294 within a given dataset to have experienced the same climatic and atmospheric deposition conditions.  
295 *A priori*, our analysis focused on European temperate broadleaved deciduous forests and we  
296 therefore excluded plots from North America in the database, and any conifer-dominated plots  
297 which were often also associated with broad-scale disturbance between surveys e.g. clearfelling and  
298 replanting. We also omitted forested plots known to be located on former agricultural land, and any  
299 remaining deciduous plots that also had large-scale management interventions between surveys (see  
300 also Appendix S1 in Supplementary Information). These choices removed confounding influences  
301 on community change e.g. successional responses to clearfelling (Ujházy et al., 2017).

302

303 *Response Variables*

304 We calculated between-survey responses for species richness and for community weighted mean  
305 (hereafter mean) and range of SLA, plant height and seed mass. We also examined EIVs for soil  
306 reaction ( $EIV_R$ , associated with soil acidity and soil pH), soil fertility ( $EIV_N$ ), temperature ( $EIV_T$ ),  
307 and soil moisture ( $EIV_F$ ), with attribute values for particular species derived from Ellenberg et al.  
308 (2001). The latter analysis can relate community responses to suggested effects of management  
309 regimes and environmental changes on resources and conditions, given indicators reflect species'  
310 habitat affinities. There is also some recent evidence that the key functional traits measured here can  
311 be used to predict species' affinities, providing a further link between these community  
312 compositional properties (Shipley et al., 2017).

313

314 Species richness was a simple count of herbaceous species. For trait and EIV analyses, we only  
315 considered herbaceous species and some low-growing woody species that are functionally part of  
316 the ground layer, such as *Calluna* and *Vaccinium*. Species-specific trait values were derived from a  
317 number of sources (Appendix S2) including the LEDA trait database (Kleyer et al., 2008). We  
318 calculated mean trait values and EIVs for each plot, weighting by species' cover. We calculated  
319 trait ranges as the difference between the lowest and highest attribute values across species within a  
320 plot. Using a single attribute value per species (EIV or functional trait) is appropriate given our  
321 inability to estimate time-specific values and the stability of ranking across a regional set of species  
322 (Albert, Grassein, Schurr, Vieilledent, & Violle, 2011; Kazakou et al., 2014). We show in Appendix  
323 S3 that there were few missing trait values to compromise interpretation of our results. In particular,  
324 only 40 out of the 963 species across all datasets were missing values for plant height. Since these  
325 species were generally rare, virtually all cover and all species in all plots tended to be characterised  
326 for plant height at both the time of the initial and resurvey.

327 For each response variable  $i$ , we calculated its change over time (R) in each plot as:

$$328 \quad R = \frac{\ln\left(\frac{i_{t+\Delta t}}{i_t}\right)}{\Delta t}$$

329 **Equation [1]**

330 where  $i_t$  is the value for  $i$  at the time of the initial survey,  $i_{t+\Delta t}$  refers to its value at the time of the  
331 most recent survey, and  $\Delta t$  the number of years between surveys.

332

### 333 *Explanatory Variables*

#### 334 i) *Rates of Global Environmental Change*

335 We calculated mean annual temperature and precipitation by averaging annual values for the 10  
336 years preceding the initial and the recent survey (as per Bernhardt-Römermann et al., 2015),  
337 sourcing data from Harris et al. (2014). Such an approach accounts for slow responses of long-lived  
338 forest plants to environmental change (i.e. the weather during the year of the survey has little  
339 influence on community composition) and accounts for time lags in dynamics (Bertrand et al.,  
340 2016; De Frenne et al., 2013; Li & Waller, 2017). We compiled data on N deposition from the  
341 EMEP database, applied correction factors for different decades from Duprè et al. (2010), and then  
342 calculated cumulative amounts of N deposited at the time of the initial and recent survey, starting  
343 from 1800 (as per Bernhardt-Römermann et al., 2015). For each environmental variable in each  
344 plot, we then calculated the difference between the recent and the initial survey, and divided this by  
345 the number of years between surveys, effectively to calculate a slope assuming linear change. For a  
346 given dataset, we then calculated the mean slope across all its plots, to give us the dataset level  
347 predictors used in our analyses.

#### 348 ii) *Management Transitions*

349 Individual dataset contributors assigned plots within their dataset as belonging to one of seven  
350 management transitions for the period between 1800 and the resurvey date: *CWS to HF*, *CWS to*  
351 *zero*, *CWS to HF to zero*, *HF throughout*, *HF to zero*, *zero throughout*, and *Unknown management*.  
352 Contributors based their decisions on their local knowledge, and previous research, having been

353 informed of the basis for categorisation (see Appendix S4 for further details). We used 1800 as a  
354 baseline because we had evidence of forest management classes from this date, and we were  
355 focussing on whether long-term legacies interacted with recent environmental change. We excluded  
356 from analyses plots classified as *Unknown management*. We also excluded plots classified as *CWS*  
357 *to zero* management and *zero throughout* management because these plots covered very limited  
358 ranges of environmental conditions preventing strong tests of management-environmental change  
359 interactions (Appendix S4). The four retained management transitions were distributed across  
360 Europe (Fig. 1). Thirteen of the 40 datasets were characterised by having more than one  
361 management transition among their constituent plots (Table 1 and Fig. 1).

### 362 iii) *Covariates*

363 We included covariates given their potential influence on community change (Austrheim, Evju, &  
364 Mysterud, 2005; Simkin et al., 2016; Smart et al., 2014). Covariates included altitude (*alt*), plot size  
365 (*plotsize*), initial survey year, mean annual temperature / precipitation (*MAT / MAP*), and  
366 cumulative N deposition (*baseN*), estimated at the time of the initial survey. Given the inclusion of  
367 time between surveys in the denominator of community response variables (Equation [1]) and  
368 therefore its implicit impact on the rate of change, we did not include this descriptor as a covariate  
369 in the analysis. We also characterised the environment through cover-weighted EIV for reaction  
370 (*EIV<sub>R</sub>*), fertility (*EIV<sub>N</sub>*), moisture (*EIV<sub>F</sub>*), and light (*EIV<sub>L</sub>*) at the time of the initial survey (Ellenberg  
371 et al., 2001). We did not use EIV for temperature (*EIV<sub>T</sub>*) as a covariate given the inclusion of  
372 climate variables at the dataset scale; however, as noted above, we included *EIV<sub>T</sub>* in community  
373 response analyses. EIVs indicate species preferences in their realised niche and are argued to be a  
374 robust method to characterise the environment in the absence of directly measured variables  
375 (Diekmann, 2003). We used the absolute change in *EIV<sub>L</sub>* between surveys ( $\Delta EIV_L$ ) as a proxy for  
376 potential management actions between surveys, in the absence of other information. Initial survey  
377 herbaceous richness (*herb<sub>rich</sub>*) and cover (*herb<sub>cover</sub>*) were included in models examining trait  
378 responses between surveys. Appendix S5 further outlines the rationale for covariate inclusion in

379 statistical models, and correlations among them. Covariates could also be correlated with  
380 management transitions and / or recent environmental changes, confounding interpretation. We first  
381 tested the evidence for potential confounding (Appendix S5; arrows ‘a’ on Fig. 2), prior to  
382 estimating the effects of covariates on response variables (*Testing the Hypothesis: Analytical*  
383 *Approach*; and arrow ‘b’ on Fig. 2). The potential for confounding was generally absent, and almost  
384 entirely so when relating covariates to historical management type (Appendix S5).

385

### 386 *Testing the Hypothesis: Analytical Approach*

387 We adopted a multi-level, mixed-effect modelling approach to test our hypothesis, analysing data  
388 using R Version 3.3.2 (R Core Team, 2017) and the associated package ‘nlme’ (Pinheiro, Bates,  
389 DebRoy, Sarkar, & Team, 2016). Dataset was treated as a random effect with varied intercepts only.  
390 We also incorporated dataset as a weights term, i.e. we controlled for heterogeneity in residual  
391 spread. We considered focal explanatory variables (i.e. the four forest management transitions, and  
392 the three environmental changes) and covariates to be fixed effects. All continuous / ordinal fixed  
393 effects were standardized (plot size was natural log transformed prior to this procedure), and we  
394 used an identity link function and assumed a Gaussian error distribution. We graphically checked  
395 model assumptions (e.g. Zuur, Ieno, Walker, Saveliev, & Smith, 2009); transformations and  
396 alternative error structures were not deemed necessary following these procedures.

397

398 For each response variable (R), we first explained variation as a function of all possible, not highly  
399 correlated (Spearman’s  $\rho < 0.65$ ), methodological and environmental covariates (Equation [2]  
400 where ‘~’ represents “is some function of”). We dropped  $EIV_N$  and *initial survey year* at this stage,  
401 given high correlations with  $EIV_R$  and *baseN* respectively. As noted above, we only included  
402 herbaceous richness (*herb<sub>rich</sub>*) and cover (*herb<sub>cover</sub>*) from Equation [2] when assessing trait  
403 responses. We then performed stepwise backwards selection, allowing us to choose the most  
404 parsimonious explanation for the data in the absence of information on management history and



405 environmental change. Dropped variables (i.e.  $EIV_N$  and *initial survey year*) were tested for  
406 inclusion if we removed their correlated variable during model selection. We found a covariates  
407 model with the fewest parameters without significantly compromising its likelihood based on the  
408 Akaike Information Criterion (AIC) ( $p > 0.05$  in a model comparison, and no more than 2 units  
409 greater than the lowest AIC model).

410

$$411 \quad R \sim \text{plotsize} + \text{alt} + EIV_R + EIV_F + MAT + MAP + \text{baseN} + EIV_L + \Delta EIV_L + \text{herb}_{rich} + \text{herb}_{cover}$$

412

**Equation [2]**

413 For each R and its associated covariate model (*covars*; Appendix S6), we then tested our main  
414 hypothesis by asking whether there was any evidence for interactions among management legacy  
415 and environmental changes, also taking account of main effects of focal explanatory variables  
416 (Equation [3]):

417

$$418 \quad R \sim \text{covars} + \text{man}_j * (\text{temp } \Delta + \text{precip } \Delta + N \text{ dep } \Delta)$$

419

**Equation [3]**

420 where  $\text{man}_j$  refers to the management legacy  $j$  and  $\text{temp } \Delta$ ,  $\text{precip } \Delta$  and  $N \text{ dep } \Delta$  refer to dataset-  
421 level scaled and centred rates of change in temperature, precipitation and N deposition between  
422 surveys.

423

424 For the management variable, we separately tested models using three different *a priori* syntheses:  
425 (i) historical management type in 1800 alone (two levels: CWS or HF), (ii) contemporary  
426 management type alone (two levels: HF or zero), and (iii) the management transition (four levels:  
427 CWS to HF to zero, CWS to HF, HF to zero and HF throughout). The first and third approaches test  
428 for evidence that historic management (either as a type in 1800, or as transitions since that time)  
429 interacts with recent environmental change to influence community property trajectories. The  
430 second analysis tests whether contemporary management, regardless of historic management and

431 when the contemporary management began, influences trajectories. We emphasize that our  
432 synthesis of the management legacy information into types does not imply that such types  
433 characterise management actions throughout the time series, nor does the management type in 1800  
434 necessarily denote predominant management before that time. However, we contend that despite  
435 likely variations within management types, such categorisation provides a means to rigorously test  
436 our overarching expectation that there are interactions among management legacies and  
437 environmental change.

438

439 We simplified the full model of Equation [3] using a stepwise backward selection procedure as for  
440 the covariates model alone, but retaining all initially chosen covariates. All models were fit with  
441 maximum likelihood (ML) to enable comparison testing; the most parsimonious model was then  
442 refit with restricted maximum likelihood (REML) to derive parameter estimates (shown in full in  
443 Appendix S7). For a given response variable and to aid comparison among models, we present AIC  
444 values of the most parsimonious ML model among the different management transitions, as well as  
445 the goodness-of-fit indicated by marginal and conditional  $R^2$  (Nakagawa & Schielzeth, 2013). We  
446 tested the robustness of community property results (i.e. species richness, trait values, indicator  
447 values) to different decisions concerning the characterisation of the overstorey at the time of the  
448 initial survey and its dynamic between surveys, the inclusion of woody seedlings, and diaspore size  
449 for ferns (see Appendices S8 – S12). When presenting regression lines, all variables not shown  
450 were assumed to be at their mean value. Note also that when interpreting community weighted  
451 mean responses, we discuss changes in relative cover. For instance, an increased mean EIV for a  
452 particular factor could reflect species with low demand for that factor decreasing while species with  
453 high demand remaining unchanged between surveys, or low demand species not changing in  
454 absolute cover but species with high demand increasing, and finally low demand species decreasing  
455 in cover and high demand species increasing. All three scenarios would lead to an increased mean  
456 EIV due to the increase in relative cover of high demand species.

457 **Results**

458 Forest management type over 200 years ago (i.e. CWS or HF) and the transition since that time,  
459 interacted significantly with environmental changes to determine many plant community attribute  
460 temporal trajectories (first and last column in Table 2a, Appendix S7 for parameter estimates). For  
461 herbaceous species richness, and mean and range of plant height, interactions were apparent  
462 regardless of contemporary management type and mainly involved rates of temperature change and  
463 nitrogen deposition. There was also evidence for management transitions since 1800 interacting  
464 with environmental changes, and this was the most likely model (from those compared) for change  
465 in mean SLA, and for moisture-indicating values ( $EIV_F$ ) (Table 2b). Only  $EIV_T$  showed evidence for  
466 contemporary management type interacting with environmental change as being a more likely  
467 explanation for responses than other management syntheses (Table 2b). Unmanaged forests at the  
468 time of the most recent survey show a greater decline in relative cover of high temperature  
469 indicating species as compared to managed forests with increasing rates of temperature change (see  
470 parameter estimates in Appendix S12). Trajectories of change in mean and range of seed mass, and  
471 range of SLA, were most likely (and parsimoniously) explained by covariates models alone. Main  
472 effects of environmental change were sometimes important, with greater rates of increase in  
473 precipitation predicting increased mean and range of plant height, decreased influence of higher  
474  $EIV_T$  species, and increased influence of higher  $EIV_N$  species. The relative cover of species with  
475 higher values of  $EIV_R$  and  $EIV_T$  increased between surveys with greater rates of N deposition  
476 (Appendices S7 and S12).

477

478 The importance of incorporating management and / or environmental change in models explaining  
479 community trajectories varied among those response variables where such factors aided model fit  
480 (Table 2b). For mean plant height, the contribution of fixed factors went from 19.6 % in the  
481 covariates model alone to 41.2 % in a model incorporating interactions among environmental  
482 changes and 1800 management type. In contrast, for herbaceous richness only 3 % more variation

483 was explained by fixed effects that incorporate such interactions. Approximately 4 % more  
484 variation was explained for those responses best modelled by management transition and  
485 environmental change interactions (mean SLA and  $EIV_F$ ). The additional explanation provided by  
486 environmental change and management legacy (interactively or not) aids understanding of what  
487 appears to be limited mean directional change across response variables (Figure S7.1, Appendix  
488 S7). The conditional  $R^2$  show the importance of considering the random effect of dataset, and  
489 confirm the overall good model fits for models incorporating management type in 1800 (ranging  
490 from 50 - 55 %), with varied fits when considering management transitions (36 % (mean SLA) -  
491 62.2 % ( $EIV_F$ ); Table 2b).

492  
493 These patterns are generally robust to alternative analysis decisions (Appendices S8, S9, S11, and  
494 S12). Interactions between land management legacies and environmental changes, as well as the  
495 importance of land management legacies alone, are also clearly observed in functional-structural  
496 group (sensu Box, 1996) understory cover responses (Appendix S13). These results confirm the  
497 importance of taking management legacies into account when predicting community responses to  
498 environmental change. Mean seed mass was also predicted by an interaction between management  
499 type in 1800 and N deposition or temperature change when the covariate model included direct  
500 overstorey characterisation, including when spore mass was incorporated (Appendix S8, Appendix  
501 S11). In the data subset including tree and shrub seedlings in understory richness, there was no  
502 longer evidence for interactions among environmental changes and historical management type.  
503 This is likely due to the increasing tree species' cover that was also observed in the understoreys of  
504 former CWS systems (Appendix S13), made up of different species to compensate for the loss of  
505 herbaceous species in such systems, and thus removing evidence for an interaction. However,  
506 interactions remained when considering herbaceous species richness only in this data subset  
507 (Appendix S9). In a reduced data analysis with only those plots with direct overstorey  
508 characterisation of the stand, AIC values marginally indicated  $EIV_R$  response ratios were better

509 predicted by an interaction between contemporary management and precipitation change. However,  
510 slope estimates were close to 0, while the significant main effect of N deposition remained across  
511 management legacies. For  $EIV_T$ , the weight of evidence shifted towards a main effect of  
512 precipitation being important, regardless of management legacy.  $EIV_N$  was better predicted by  
513 considering an interaction between management transition since 1800 and precipitation change in  
514 the reduced dataset. This reflected CWS to HF to Zero management transitions increasing more in  
515 fertile indicator species relative cover than the increases observed in other transitions with greater  
516 rates of precipitation change.

517

518 Overall, and across analyses, change in mean and range in plant height and herbaceous species  
519 richness between surveys showed the clearest evidence for interactions among environmental  
520 changes and management type in 1800 (Figure 3). Forests with a CWS management type in 1800  
521 showed a decline in mean plant height as N deposition increases. In contrast, forests managed as HF  
522 in 1800 showed an increase in plant height between surveys, in response to N deposition (Fig. 3a).  
523 Similar responses were found for trait range across N deposition, although the difference in slopes  
524 between management types were not significant (Appendix S7). In contrast, the overall decline in  
525 the range in plant height in forests managed as CWS in 1800 was ameliorated at higher rates of  
526 temperature change, while those managed as HF in 1800 are relatively unaffected across the  
527 temperature change gradient (Fig. 3b). These changes in traits were accompanied by changes in  
528 herbaceous species richness (despite a lack of correlation between mean trait response and species  
529 richness (Table S7.1)). We record greater richness declines in former CWS forests between surveys  
530 at higher rates of N deposition, while species richness change in HF remains unaffected (Fig. 3c).  
531 Declines in species richness in former CWS forests were predicted to be marginally lower at higher  
532 rates of temperature change, while HF response ratios decline with greater temperature change (Fig.  
533 3d).

534

535 Management transitions since 1800, rather than management types in 1800 or at the time of the  
536 most recent survey, were important for explaining changes in  $EIV_F$  along environmental change  
537 gradients. All transitions except CWS to HF had greater relative cover of more moist indicating  
538 species between surveys (i.e. a positive response ratio for  $EIV_F$ ), a response unaltered by  
539 environmental changes. However, the lack of overall response in CWS to HF systems masked two  
540 clear interactions in response to this management legacy: greater rates of N deposition led to an  
541 increase in relative cover of moisture indicating species between surveys (Fig. 4a) while greater  
542 rates of temperature change led to a decline in moisture-indicating species' relative cover (Fig. 4b).

543

## 544 **Discussion**

545 Using data from 1814 plots in 40 datasets across temperate European forests, overall we found  
546 support for our hypothesis that land management legacies significantly interact with recent  
547 environmental changes to determine changes in plant communities. Variation in six out of eleven  
548 understorey community response variables was best explained by incorporating information on  
549 management legacies and their interaction with environmental changes, while variation in an  
550 additional two attributes was better explained by considering management legacies or  
551 environmental changes as compared with models that considered covariates alone. For three  
552 attributes (change between surveys in: herbaceous species richness, mean and range of plant  
553 height), the management type approximately 200 years ago in conjunction with environmental  
554 change best explained variation in response ratios, regardless of management at the time of the most  
555 recent survey.

556

557 To our knowledge, this is the first demonstration of interactive effects of environmental change and  
558 management legacies on the change in plant community properties between two time points. This is  
559 despite the widespread appreciation of historical effects on current ecosystem states (Foster et al.,  
560 2003), knowledge about the different timescales at which resource alterations act (M. D. Smith et

561 al., 2009), huge variation in management histories in European forests (McGrath et al., 2015), and a  
562 growing interest in time lags in ecosystems (Bertrand et al., 2016; Bürgi et al., 2017; Ogle et al.,  
563 2015). Local-scale temporal changes in plant diversity show tremendous variability from site to site  
564 (Vellend et al., 2017), and our results can help to explain some of this variation.

565

566 Having demonstrated the importance of management legacies for dictating community responses to  
567 environmental change, the question then becomes “Why are such legacies ecologically important?”  
568 We suggest that the patterns we have revealed can be understood through the dynamics of both  
569 resources and conditions in response to different forest silvicultural regimes, and the “ecological  
570 memory” (Ogle et al., 2015) such management regimes engender. We are unable to unequivocally  
571 substantiate this suggestion with the data herein, partly because they are observational and also  
572 because we do not have direct characterisation of management-induced changes in resources and  
573 conditions. We can though assess how functional trait and species richness results align with  
574 expectations from expected resource and condition dynamics, supported by analyses of indicator  
575 value responses.

576

577 We expected that former CWS forests would exhibit different dynamics to forests managed as HF  
578 in 1800, likely due to the different legacies in resources and conditions these alternative  
579 management intensities and their associated disturbance regimes create. For species richness, we  
580 expected that former CWS would lose species, particularly warm- and light-adapted ones, as  
581 communities adjusted to HF or zero management, based on unimodal responses to resource  
582 gradients (Fraser et al., 2015) and the reduction in management intensity. We also expected that a  
583 lack of soil resources in CWS systems would constrain community property responses to N  
584 deposition in contrast to HF systems e.g. in plant height and SLA as well as species richness. In HF,  
585 we expected communities would remain on relatively stable trajectories, sensitive to subsequent

586 environmental changes e.g. richness declines associated with increasing N deposition (Bobbink et  
587 al., 2010; Gilliam et al., 2016).

588

589 In line with expectations, former CWS stands lost species between surveys but greater rates of  
590 temperature change reduced the magnitude of decline. This reduction in magnitude was not  
591 accompanied by clear changes in  $EIV_T$  suggesting that species indicator values for temperature had  
592 been maintained in a given former CWS plot between surveys. Indeed, across the entire dataset,  
593 there was a tendency for a decrease in the relative contribution of warm-adapted species cover with  
594 increasing temperature change (significantly different in the case of HF vs Zero management at the  
595 time of the contemporary survey) which may reflect microclimatic effects (De Frenne et al., 2013)  
596 and species responses to increased overstorey cover (measured directly, and also reflected in  $EIV_L$   
597 responses (Appendix S10)). The relatively subtle temperature effect in former CWS (see also Figure  
598 S14.1) might be explained by previous adaptation of the flora to cyclic variation in relatively warm  
599 temperatures in the understorey due to canopy opening. This potentially prevents the further decline  
600 in mean  $EIV_T$  observed in other silvicultural systems.

601

602 Contrary to our expectation that N deposition would have less of an effect in former CWS stands,  
603 models predicted even greater decline in species richness as N deposition increased, although  
604 greater rates of N deposition are associated with greater relative cover of flora indicative of warm  
605 temperatures i.e. mean  $EIV_T$  increases. The greater richness decline in CWS forests is in line with  
606 overall expectations for loss of species at higher soil resource availability (Fraser et al., 2015).  
607 Indeed, N deposition may speed up the loss of species through more rapid competitive exclusion by  
608 species adapted to shaded conditions, already present in the flora or capable of invading, if other  
609 resources do not become limiting to their growth (Härdtle, von Oheimb, & Westphal, 2003; Hautier,  
610 Niklaus, & Hector, 2009; Peppeler-Lisbach, Beyer, Menke, & Mentges, 2015). There may also be a  
611 role for mycorrhizal fungi in determining such interactions; herbaceous species that are lost may



612 have arbuscular or ectomycorrhizal fungal partners that have been adversely affected by historic  
613 levels of N deposition (Phillips, Brzostek, & Midgley, 2013; van Strien, Boomsluitter, Noordeloos,  
614 Verweij, & Kuyper, 2017). These ideas would require further analysis of individual species  
615 responses, which would also be useful from a biodiversity conservation standpoint, but are beyond  
616 the scope of the present investigation, focussing as it does on synthetic community descriptors.  
617

618 In HF, and in contrast to theoretical predictions, additional N deposition did not affect herbaceous  
619 species richness responses, and there was even evidence for an increase when N deposition is above  
620 critical threshold rates (Figure S14.2). Invasion by species that benefit from increased soil N  
621 together with continued persistence of oligotrophic species has led previously to observations of  
622 increasing species richness under high N deposition (Dirnböck et al., 2014). Our species richness  
623 results complement experimental investigations, which have shown the importance of interacting  
624 effects of temperature, light and N on community dynamics (De Frenne et al., 2015). Importantly,  
625 our results also support the prediction that N deposition may have variable effects depending on  
626 context (Simkin et al., 2016). Interestingly, the interactions observed for herbaceous richness  
627 between environmental changes and management type in 1800 disappear when total understorey  
628 richness is considered (Appendix S9). This reflects an increase in woody species cover (Appendix  
629 S13) made up of different species. Greater richness increases in former CWS than HF to remove  
630 evidence for any interactions with environmental change is in line with expectations that lower  
631 available soil resources in CWS constrain herbaceous and promote woody understorey community  
632 development (Graves, Peet, & White, 2006). However, former HF, assumed to have greater levels  
633 of soil resources, increased in woody species number, suggesting the importance of other factors  
634 determining woody expansion. Elucidating species richness dynamics, together with consideration  
635 of indicator values, in relation to land management legacies significantly adds to our understanding,  
636 compared to analyses that showed limited overall change (Bernhardt-Römermann et al., 2015;

637 Verheyen et al., 2012) but also reinforces the need to characterise the environment experienced by  
638 the plants.

639

640 Interactive effects of management legacies and recent environmental change also influenced  
641 indicator values and key functional traits, especially plant height. Trait responses, particularly for  
642 community weighted means, were uncorrelated with species richness responses (Table S7.1). This  
643 disconnect between taxonomic and functional responses has been highlighted for a North American  
644 forest, as has an interaction between management legacies (fire exclusion) and environmental  
645 change in understorey functional response (Li & Waller, 2017). This emphasizes the value of  
646 community investigations into functional properties across management legacies and environmental  
647 change. In our investigation, herbaceous vegetation was predicted to become dominated by taller  
648 species as N deposition increased in HF systems, in line with expectations (summarized by Garnier  
649 et al., 2016). However, rather than this response being constrained in former CWS systems, as we  
650 expected, plant height was predicted to decline in such systems as N deposition increased. This  
651 might be because the trait syndromes (Laughlin, 2014) that allow persistence in these particular  
652 management transitions are different to those found in former HF systems. It could also be due to  
653 the aforementioned mycorrhizal effects, or because historical changes in resources and conditions in  
654 particular systems do not match literature findings, such that responses do not match expectations.  
655 That soil resource conditions are likely important in determining community dynamics was  
656 indicated by the increase in plant height and  $EIV_N$  in response to greater rates of precipitation, and  
657 increases in  $EIV_R$  in response to N deposition. The increase in height confirms a response observed  
658 at a global scale (A. T. Moles et al., 2014), while interactions between fertility indicators and  
659 moisture and N addition have been observed previously (Thomas, Halpern, Falk, Liguori, & Austin,  
660 1999).

661

662 We also expected SLA to increase in response to N deposition, with this response being constrained  
663 in former CWS systems due to the aforementioned resource constraints. Indeed, in shaded  
664 conditions, we would expect species with high SLA to dominate because of a selective advantage  
665 (Poorter, Niinemets, Poorter, Wright, & Villar, 2009). We do not know why SLA did not respond as  
666 expected in former CWS stands as compared to HF stands. Unmeasured driving factors (such as  
667 grazing pressure Díaz et al., 2007) or more immediate changes in resources and conditions e.g. the  
668 light environment, could be predominant factors in determining SLA response between surveys.  
669 This may explain why contemporary management interacted with environmental changes to effect  
670 SLA response between surveys (Table 2), and the importance of covariates such as overstorey  
671 cover,  $EIV_L$  and change in  $EIV_L$  in determining responses (Table S10.1).

672

673 While our analysis succeeded in explaining some site-to-site variation in plant community trends,  
674 much variation remains unexplained. Accounting for other variables, such as grazing pressures,  
675 current and previous landscape context, or land ownership, may improve the amount of variation  
676 explained in response trajectories (Bergès, Avon, Verheyen, & Dupouey, 2013; Kimberley,  
677 Blackburn, Whyatt, & Smart, 2014, 2016). However, the implications of our results, i.e. that we  
678 need to account for historic management in future projections of response to environmental change,  
679 would only be altered if unmeasured variables were confounded with management transitions and /  
680 or environmental changes. We have no *a priori* reasons for such expectations for landscape context  
681 and ownership. However, former HF stands may be more attractive to game animals than CWS, but  
682 we are unable to test this possibility at present. Some HF designated-stands also had nutrient-  
683 depleting and more intensive management practices in former times (e.g. litter raking and use as  
684 wood pasture (Gimmi et al., 2013)) such that we may have underestimated the importance of past  
685 management conditions.

686

687 A better mechanistic understanding of links between historical management, environmental changes  
688 and present-day plant community trajectories would be further improved by direct characterisation  
689 of long-term temporal dynamics of resource and conditions (Ogle et al., 2015). The fact that  
690 indicator values did not respond to direct changes in their equivalent regional-scale environmental  
691 drivers, but did respond to other drivers (e.g.  $EIV_T$  significantly responding to precipitation and  
692 nitrogen but not temperature change (even with a tendency to decline with increasing temperature);  
693  $EIV_R$  increasing with N deposition while  $EIV_N$  remained unaffected) also suggests more direct  
694 characterisation of resources and conditions would be helpful. These non-obvious indicator value  
695 responses likely also reflect the fact that original indicator values were based on spatial  
696 relationships with many (co)-varying environmental factors, rather than on temporal responses to  
697 altered resources and conditions. The endeavour to provide better mechanistic understanding will be  
698 further aided by:

- 699 a) more detailed studies of how plants perceive environmental gradients across time and space  
700 (Garnier et al., 2016);
- 701 b) continuous characterisation of historical and contemporary management intensities based on  
702 alternative data sources than those used here (Szabó & Hédli, 2011); and,
- 703 c) experiments that manipulate resources and conditions (De Frenne et al., 2015; Hahn & Orrock,  
704 2016; Rollinson, Kaye, & Leites, 2012).

705

706 We have shown that across European temperate forest understoreys, community property dynamics  
707 depend upon interactions among historic land management legacies and environmental changes.  
708 Given that functional traits (SLA and plant height) and species richness responses were affected by  
709 past and contemporary management, our results imply that only considering the main effects of  
710 recent environmental changes on ecosystem dynamics could obscure the importance of  
711 management history for determining trajectories of community change. In other words, future  
712 projections of ecosystem dynamics that only consider contemporary environmental change may be

713 flawed, without consideration of the trajectories of change systems are already on. Our results could  
714 explain some of the highly variable patterns of local diversity change in the literature (Vellend et  
715 al., 2017). Further progress on mechanistic understanding likely requires the direct characterisation  
716 of historical trajectories in resources and conditions engendered by management legacies, both for  
717 temperate forests and other ecosystems. Our results are a first demonstration, at broad  
718 environmental scales, that account needs to be taken of previous land management if we are to  
719 understand how plant communities, and their important functional properties, will change in the  
720 Anthropocene.

721

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1063

1064 **Table 1:** Datasets from forestREplot ([www.forestreplot.ugent.be](http://www.forestreplot.ugent.be)) in ancient forests with management information. Map ID refers to Fig 1. Datasets  
 1065 that did not record tree and shrub seedlings in the herbaceous layer indicated by **N**, as are datasets that did not have information on overstorey cover  
 1066 and shade casting information. Latitudes and longitudes are indicative of plot locations; precise co-ordinates for plots are available in the data files  
 1067 sourced from the forestREplot website.

Map ID	forestREplot ID	Name	Country	Latitude (°N)	Longitude (°E)	# Plots	Management Transitions (per dataset)	Initial Survey Year	Most Recent Survey Year	Overstorey cover and shade casting information?	Tree and shrub seedlings in understorey layer?
1	EU_01	Gaume	Belgium	49.6	5.6	43	1	1953-1963	2008	Y	Y
2	EU_02	Binnen Vlaanderen	Belgium	51.1	3.5	39	1	1980	2009	Y	Y
3	EU_06	Meerdaalwoud	Belgium	50.8	4.7	21	1	1954	2000	Y	Y
4	EU_07	Florenne	Belgium	50.2	4.6	65	1	1957	2005	N	N
5	EU_08	Tournibus	Belgium	50.3	4.6	190	1	1967	2005	Y	N
6	EU_09	Dalby	Sweden	55.7	13.3	74	1	1935	2010	Y	Y
7	EU_11	Elbe-Weser	Germany	53.4	9.2	50	4	1986-1987	2008	Y	Y
8	EU_12	Děvín Wood	Czech Republic	48.9	16.6	41	1	1953-1964	2002-2003	Y	Y
9	EU_13	Milovice Wood	Czech Republic	48.8	16.7	46	1	1953	2006	Y	N
10	EU_14	Rychlebské hory Mountains	Czech Republic	50.3	17.1	21	1	1941-1944	1998-1999	Y	Y
11	EU_15	Wytham Woods	UK	51.8	-1.3	24	1	1974	1999	N	N
12	EU_16	Göttingen SFB	Germany	51.5	10.1	42	1	1980	2001	Y	Y
13	EU_17	Milíčovský les	Czech Republic	50.0	14.5	16	1	1986	2008	Y	Y
14	EU_19	Hirson	France	50.0	4.1	22	1	1956-1965	1996-1999	Y	Y
15	EU_20	Andigny	France	50.0	3.6	19	1	1957-1965	1993-1996	Y	Y
16	EU_21	Speulderbos	Netherlands	52.3	5.7	27	2	1957-1959	1987-1988	Y	Y
17	EU_23	Echinger-Lohe	Germany	48.3	11.6	125	1	1986	2003	Y	Y
18	EU_23b	Echinger-Lohe	Germany	48.3	11.6	26	1	1961-1986	2003	Y	Y
19	EU_24	County Kerry	Eire	52.0	-9.6	16	1	1991	2011	Y	Y
20	EU_25	Göttingen-Carici-Fagetum	Germany	51.6	10.0	78	2	1955-1959	2011-2012	Y	Y
21	EU_26	Göttingen-Hordelymo-Fagetum	Germany	51.6	10.0	35	2	1955-1966	2009	Y	Y
22	EU_27	Zöbelboden	Austria	47.8	14.4	18	1	1993	2005-2010	Y	Y
23	EU_28	Nyírség	Hungary	47.8	22.3	10	1	1933	1990	Y	Y

Map ID	forestREplot ID	Name	Country	Latitude (°N)	Longitude (°E)	# Plots	Management Transitions (per dataset)	Initial Survey Year	Most Recent Survey Year	Overstorey cover and shade casting information?	Tree and shrub seedlings in understorey layer?
24	EU_30	Brandenburg	Germany	51.8	14.0	64	3	1962-1964	2012	Y	Y
25	EU_31	South West Slovakia	Slovakia	48.4	17.3	18	2	1966-1972	2007	Y	Y
26	EU_32	Central Slovakia	Slovakia	48.3	19.4	21	1	1964-1973	2005-2007	Y	Y
27	EU_33	North East Slovakia	Slovakia	49.2	21.8	10	3	1974	2006	Y	Y
28	EU_35	Krumlov Wood	Czech Republic	49.1	16.4	58	1	1964-1968	2012	Y	N
29	EU_36	Hodonínská dúbrava	Czech Republic	48.9	17.1	53	4	1965	2012	Y	N
30	EU_38	Białowieża	Poland	52.8	23.9	22	1	1966	2012	Y	Y
31	EU_41	Skåne	Sweden	55.9	13.7	63	3	1983	2014	N	N
32	EU_44	Göttingen-Hunstollen	Germany	51.6	10.0	147	1	1992	2012	Y	Y
33	EU_46	Sanocko-Turczańskie Mountains	Poland	49.5	22.4	71	1	1972-1973	2005-2007	Y	Y
34	EU_47	Bazaltowa Mountains	Poland	51.0	16.1	4	1	1993-1994	2010-2014	Y	Y
35	EU_48	Buki Sudeckie	Poland	50.9	16.0	16	1	1990	2014	Y	Y
36	EU_50	Prignitz	Germany	53.1	12.3	46	4	1954-1960	2014	Y	N
37	EU_51	Öland	Sweden	56.7	16.5	15	2	1988	2014	Y	Y
38	EU_52	North Brandenburg	Germany	53.1	13.7	56	4	1963-1964	2014	Y	Y
39	EU_53	South Brandenburg	Germany	51.8	13.8	35	3	1960-1965	2014	Y	Y
40	EU_58	Compiègne	France	49.4	2.9	67	1	1970	2015	Y	Y

1068

1069 **Table 2:** Understorey plant community responses to management transition legacies and potential interactions with environmental changes (T = rate of  
1070 temperature change, P = rate of precipitation change, N = annual rate of N deposition) in the most parsimonious model. In **a)** ‘\*’ indicates that for a  
1071 given management legacy, or its interaction with a given environmental change, there is a significant effect on understorey response ( $p \leq 0.05$ ); ‘-’  
1072 indicates management legacy inclusion in the most parsimonious model with parameter estimates of differences between legacies not significantly  
1073 different from 0; and, ‘n.s.’ indicates that there is no evidence for variable inclusion. A letter in parentheses in the Main Effect column in bold indicates  
1074 there is a significant ( $p \leq 0.05$ ) main effect of the given environmental change (T, P or N), regardless of management; if normal text, the variable is  
1075 included but it is not different from 0 ( $p > 0.05$ ). Full parameter estimates shown in Appendices S7 and S12. In **b)**, we show model comparison  
1076 statistics between the most parsimonious covariates model and the most parsimonious models that include main effects and / or interactions among  
1077 environmental change, and management legacies. AIC: Akaike Information Criterion;  $R^2_m$  indicates a goodness-of-fit associated with a given model’s  
1078 fixed variables, while  $R^2_c$  indicates goodness-of-fit for the fixed and random components of the model (Nakagawa & Schielzeth, 2013); both are  
1079 indicated in %. We fitted models using maximum likelihood estimation; we indicate the model with the lowest AIC among comparisons in bold.

1080 **a)**

<b>Δ in Understorey Response Variable</b>	<b>Management Type in 1800 CWS vs HF</b>		<b>Contemporary Management Type (time of most recent survey) HF vs Zero</b>		<b>Management Transition from 1800</b>	
	<b>Main Effect</b>	<b>Interaction with environmental change</b>	<b>Main Effect</b>	<b>Interaction with environmental change</b>	<b>Main Effect</b>	<b>Interaction with environmental change</b>
Herbaceous species richness	-	* (T, N)	n.s.	n.s.	n.s.	n.s.
Mean SLA	n.s.	n.s.	-	* (T,N)	* (N)	* (T, P)
Mean plant height	* (P)	* (N)	n.s. (P)	n.s.	* (P)	* (N)
Mean seed mass	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Range SLA	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Range plant height	* (P)	* (T)	n.s. (P)	n.s.	* (P)	* (T)
Range seed mass	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
EIV <sub>R</sub> (reaction)	n.s. (N)	n.s.	- (N)	* (P)	- (N)	* (P)
EIV <sub>N</sub> (fertility)	n.s. (P)	n.s.	n.s. (P)	n.s.	n.s. (P)	n.s.
EIV <sub>F</sub> (moisture)	n.s.	n.s.	n.s.	n.s.	* (P)	* (T,N)
EIV <sub>T</sub> (temperature)	n.s. (T,P,N)	n.s.	- (P,N)	* (T)	n.s. (T,P,N)	n.s.

1081

1082 b)

$\Delta$ in Understorey Response Variable	Covariates Model			Management Type in 1800			Contemporary Management Type			Management Transition from 1800		
	AIC	R <sup>2</sup> <sub>m</sub>	R <sup>2</sup> <sub>c</sub>	AIC	R <sup>2</sup> <sub>m</sub>	R <sup>2</sup> <sub>c</sub>	AIC	R <sup>2</sup> <sub>m</sub>	R <sup>2</sup> <sub>c</sub>	AIC	R <sup>2</sup> <sub>m</sub>	R <sup>2</sup> <sub>c</sub>
Herbaceous species richness	-10924.7	14.3	56.1	<b>-10926.6</b>	17.6	56.6	See covariates model			See covariates model		
Mean SLA	-14804.3	26.1	35.9	See covariates model			-14813.5	29.5	36.8	<b>-14820.7</b>	30.8	35.8
Mean plant height	-11961.4	19.6	48.8	<b>-11992.5</b>	41.2	52.6	-11979.0	37.6	52.4	-11991.7	44.3	52.8
Mean seed mass	<b>-8520.7</b>	2.9	12.4	See covariates model			See covariates model			See covariates model		
Range SLA	<b>-11351.3</b>	8.2	26.4	See covariates model			See covariates model			See covariates model		
Range plant height	-13655.4	27.0	34.0	<b>-13668.4</b>	36.4	39.8	-13661.2	31.3	36.3	-13663.4	36.7	40.8
Range seed mass	<b>-7852.5</b>	6.8	31.9	See covariates model			See covariates model			See covariates model		
EIV <sub>R</sub> (reaction)	-17104.4	38.0	48.2	<b>-17109.2</b>	39.7	49.8	-17109.1	39.9	50.0	-17105.0	39.2	49.1
EIV <sub>N</sub> (fertility)	-15733.6	31.5	60.9	<b>-15740.2</b>	40.7	62.3	See management type in 1800 model			See management type in 1800 model		
EIV <sub>F</sub> (moisture)	-17881.0	42.7	64.4	See covariates model			See covariates model			<b>-17887.0</b>	46.4	62.2
EIV <sub>T</sub> (temperature)	-18171.9	9.9	16.5	-18178.3	12.9	17.1	<b>-18178.8</b>	13.7	17.3	-18178.3	12.9	17.1

1083

1084 **Figure Captions**

1085 **Figure 1: Management transitions across European temperate forest understoreys** sourced  
1086 from forestREplot ([www.forestreplot.ugent.be](http://www.forestreplot.ugent.be)) and expert testimony. Each circle indicates an  
1087 included dataset and its approximate geographical location (some have been moved for better  
1088 visibility), with circle size proportional to the number of included resurvey plots. Circle number  
1089 refers to Map ID in Table 1. Single colours denote that a single management transition, as indicated  
1090 by the legend, characterises all analysed plots within a dataset. Multiple colours per circle, and the  
1091 size of slices indicate multiple management transitions within a given dataset and the proportion of  
1092 plots with a given transition respectively.

1093

1094 **Figure 2: Summary of analytical approach:** **a)** assessment of potential confounding between  
1095 named methodological / environmental covariates and management transitions / environmental  
1096 changes at different scales; **b)** modelling of understorey community responses, estimated according  
1097 to Equation [1], as a function of covariates to find the most parsimonious covariates model; **c)**  
1098 modelling of understorey community responses as a function of potential interactions among  
1099 management transitions and environmental changes taking account of the most parsimonious  
1100 covariates model. See main text for further details.

1101

1102 **Figure 3: Community temporal trajectories interactively depend on historic management type**  
1103 **and environmental change.** All subpanels show understorey community attribute responses of  
1104 plots within stands either managed as CWS (black dots and lines) or HF (grey dots and lines) in  
1105 1800, regardless of management at the time of the most recent survey and transitions since that  
1106 time, against a given environmental change. Change in **a)** mean plant height vs N deposition; **b)**  
1107 range in plant height vs temperature change; **c)** species richness vs N deposition; **d)** species richness  
1108 vs temperature change. Responses above 0 on the y-axis indicate an increase in a given attribute  
1109 between surveys while those below 0 indicate a decline; mean ( $\pm 1$  s.d.) N deposition (i.e. 0 value

1110 on x-axis in a) and c)) is 16.94 (4.02) kg N / ha / yr and mean ( $\pm$  1 s.d.) temperature change (i.e. 0  
1111 value on x-axis in b) and d)) is 0.029 (0.0146) °C / yr.

1112

1113 **Figure 4:  $EIV_F$  trajectories interactively depend on management transition since 1800 and**  
1114 **environmental change.** All subpanels show moisture indicator value responses of plots within  
1115 stands managed as one of four different transitions since 1800 against a given environmental  
1116 change. Grey points refer to management transitions that do not exhibit an interaction with  
1117 environmental change (i.e. CWS to HF to Zero, HF to Zero and HF throughout) while black dots  
1118 refer to a CWS to HF transition, with the line fitting the most parsimonious model parameters.  
1119 Interpretation of axes is as per Figure 3. Change between surveys in **a)**  $EIV_F$  against N deposition;  
1120 and **b)**  $EIV_F$  against temperature change.

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1125 **Supporting Information Captions**

- 1126 **Appendix S1:** Quality assurance of forestREplot data
- 1127 **Appendix S2:** Trait attribute sources
- 1128 **Appendix S3:** Comprehensiveness of trait data
- 1129 **Appendix S4:** Management characterisation, and location in contemporary environmental  
1130 space
- 1131 **Appendix S5:** Rationale for covariate inclusion; covariate summaries.  
1132 Investigations into confounding of management transitions / environmental  
1133 changes with covariates.
- 1134 **Appendix S6:** Most parsimonious covariate models: Parameter estimates
- 1135 **Appendix S7:** Considering interactions among management legacies and environmental  
1136 changes: Parameter estimates
- 1137 **Appendix S8:** Direct overstorey characterisation: Parameter estimates
- 1138 **Appendix S9:** Total understorey species richness response: Parameter estimates
- 1139 **Appendix S10:** Synthesis of covariate models across datasets
- 1140 **Appendix S11:** CWM and range of seed mass when including spore-producing plants:  
1141 Parameter estimates
- 1142 **Appendix S12:** Community Ellenberg Indicator Value response analysis
- 1143 **Appendix S13:** Community structural form analysis
- 1144 **Appendix S14:** Threshold interpretation graphs
- 1145 **Appendix S15:** Supplementary information references

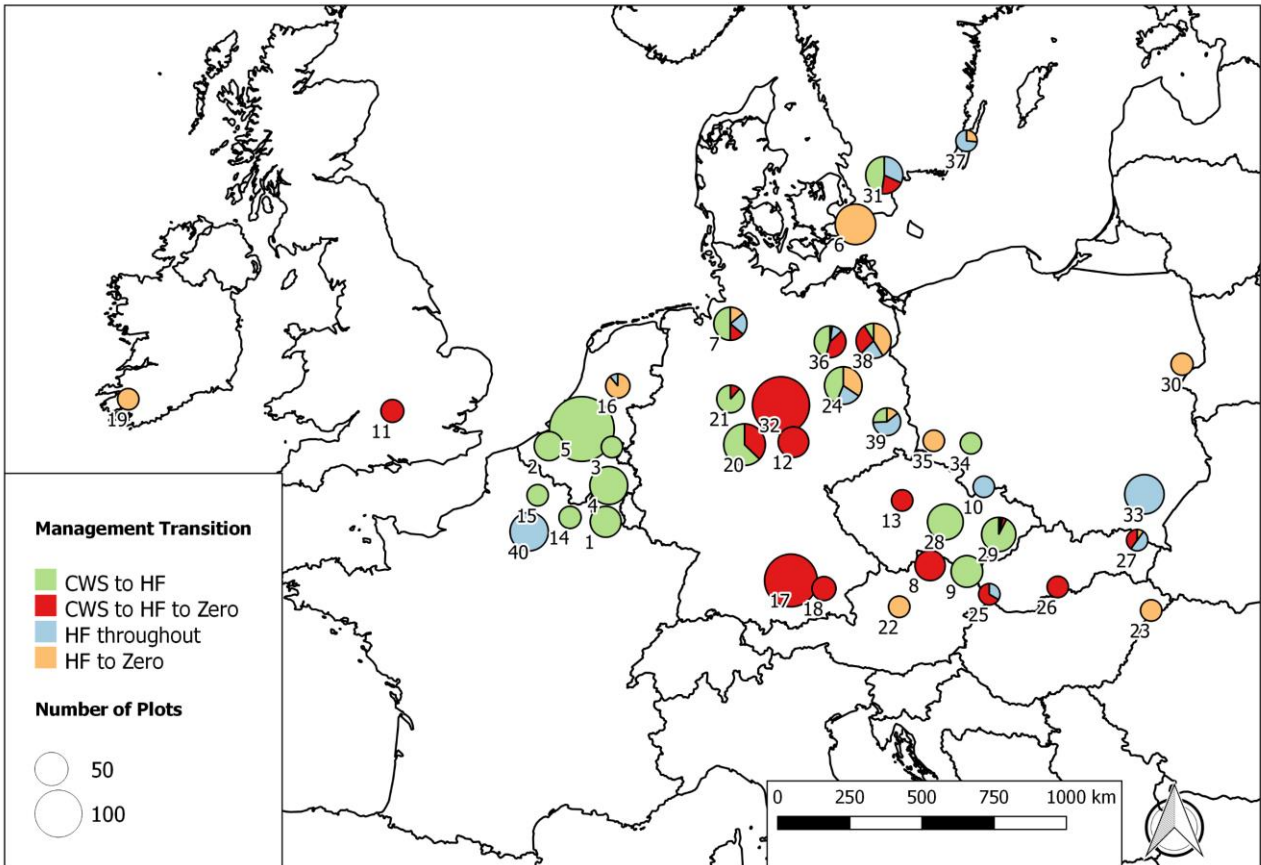
1146 **Data Accessibility**

1147 Data supporting results are archived at a Ghent University institutional repository, and available  
1148 through the forestREplot website ([www.forestreplot.ugent.be](http://www.forestreplot.ugent.be)). Original forest community resurvey  
1149 data, also deposited at forestREplot, can be accessed by contacting the Management Committee  
1150 (details on the website) who obtained individual permissions for data use from dataset contributors.  
1151 Conflicting policies from funding sources at the time of initial and resurveys prevents unsupervised  
1152 public accessibility of raw vegetation resurvey data.

1153

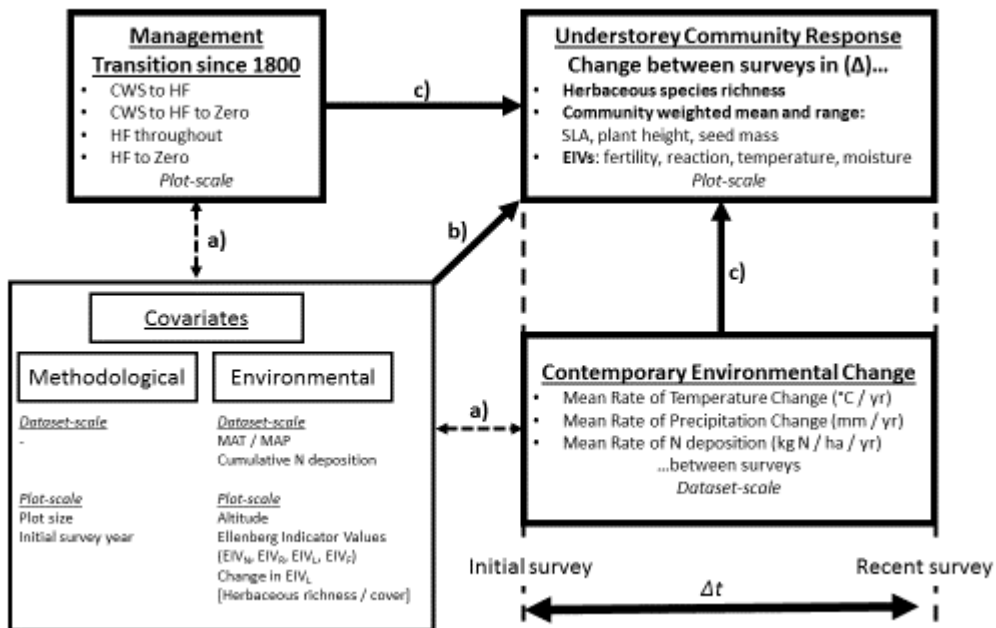
1154 **Supporting Information** is included for the manuscript as detailed above, and available at

1155 [[weblink](#)].



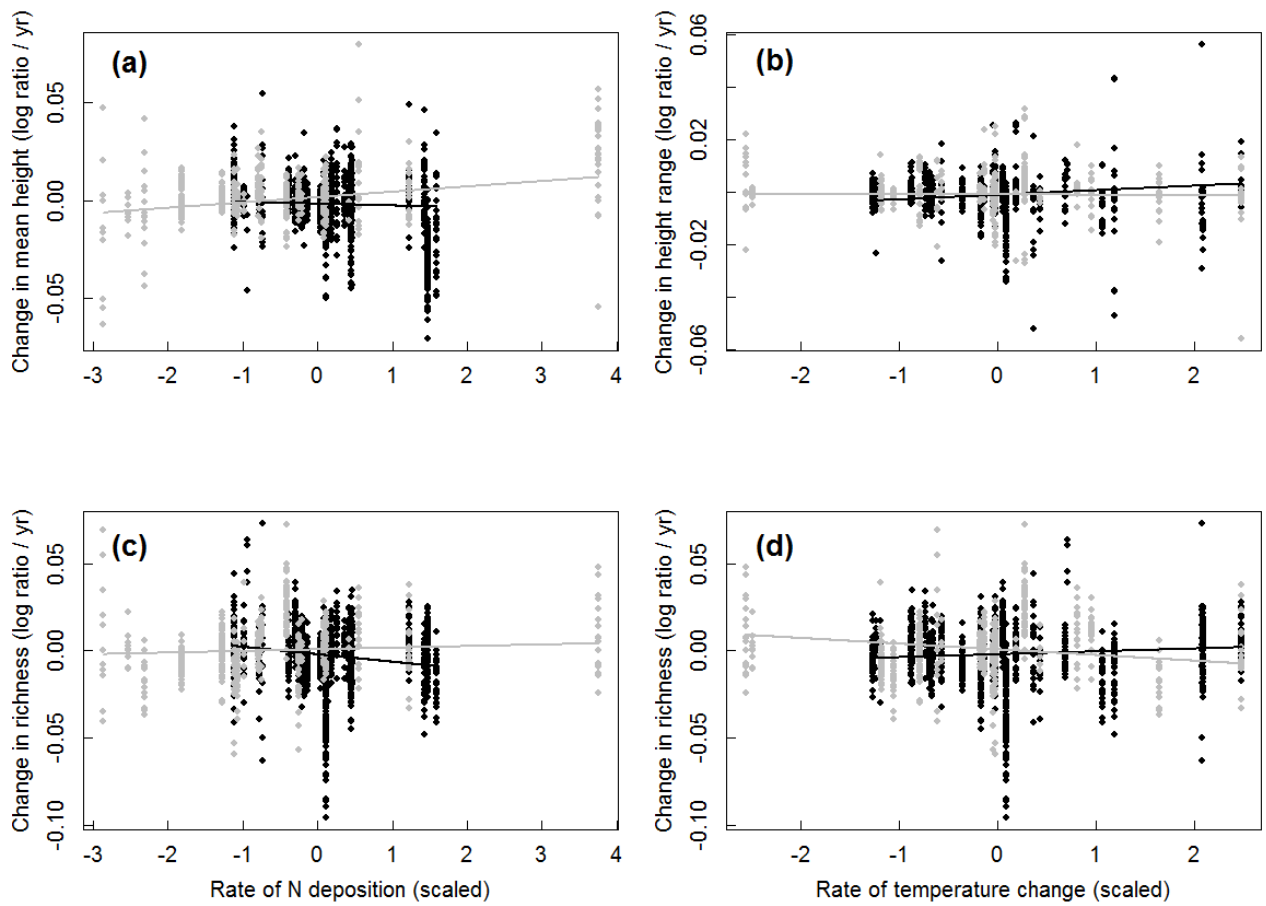
1157

1158 **Figure 1**



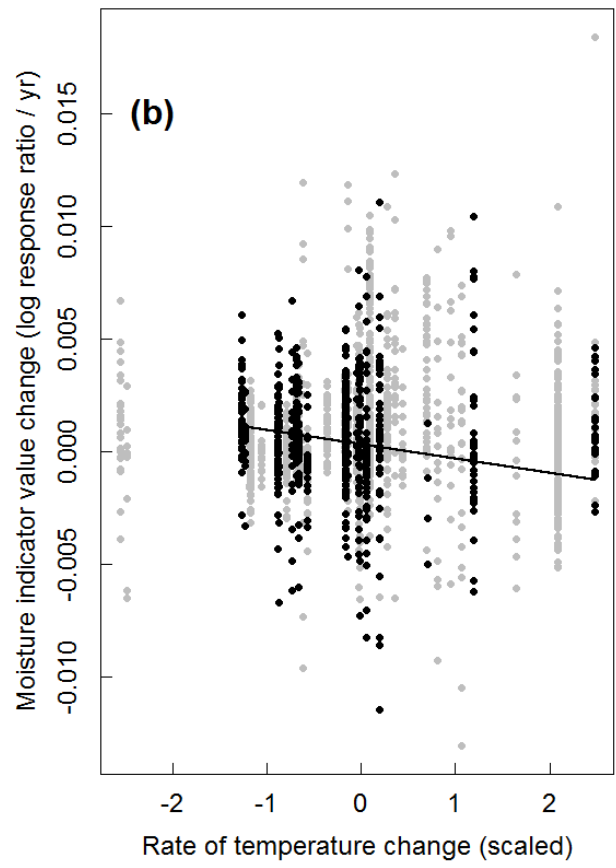
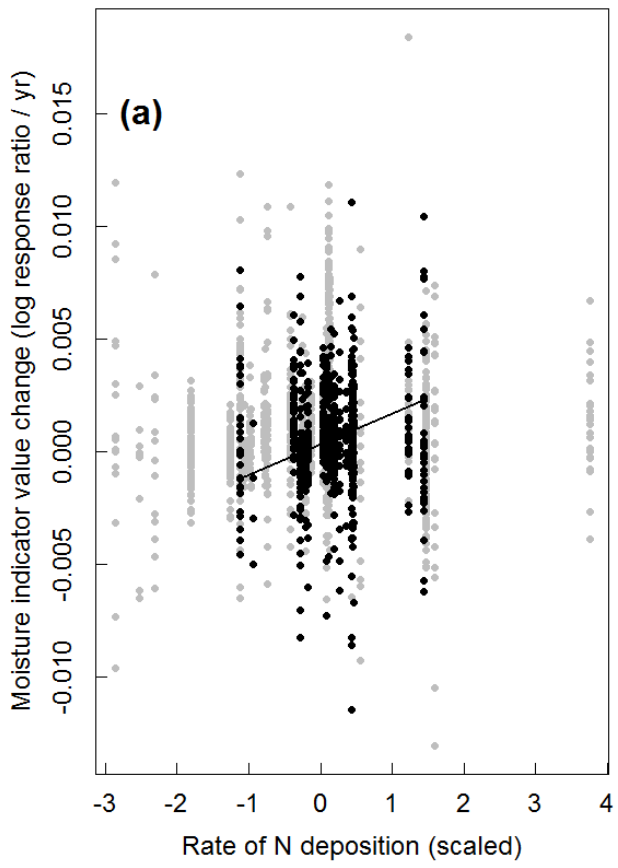
1159

1160 **Figure 2**



1161

1162 **Figure 3**



1163

1164 **Figure 4**

1165

1166