

Global environmental change effects on plant community composition trajectories depend upon management legacies

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Funding information

European Research Council (ERC), Grant/
Award Numbers: 614839 & 278065;
Research Foundation – Flanders (FWO);
Société Botanique de France; Czech Science
Foundation, Grant/Award Number: GACR
17-09283S

Abstract

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

KEYWORDS

biodiversity change, climate change, disturbance regime, forestREplot, herbaceous layer, management intensity, nitrogen deposition, plant functional traits, time lag, vegetation resurvey

1 | INTRODUCTION

Ecology has shifted from simply explaining the contemporary state of ecosystems towards predicting their temporal dynamics, taking

account of simultaneous environmental changes, including land-use change, climate change and atmospheric pollution. Functional traits i.e. measurable characteristics of organisms that ultimately influence their fitness through effects on reproduction and growth, show great

potential assisting these predictions (Laughlin & Messier, 2015; McGill, Enquist, Weiher, & Westoby, 2006; Violle et al., 2007). Traits respond to and cause effects on their environment, thus connecting both ecosystem patterns (e.g., species diversity and composition) and processes (Bardgett, Mommer, & De Vries, 2014; Eviner & Chapin, 2003; Suding et al., 2008). The understanding of trait variation across spatial environmental gradients is relatively advanced (e.g., Cornwell & Ackerly, 2009; Fonseca, Overton, Collins, & Westoby, 2000; Laliberté et al., 2010; Messier, McGill, & Lechowicz, 2010; Moles et al., 2009). However, knowledge of temporal trait change across environmental gradients remains limited (Amatangelo, Johnson, Rogers, & Waller, 2014; Dwyer, Hobbs, & Mayfield, 2014; Hedwall & Brunet, 2016; Li & Waller, 2017). This lack of knowledge makes it difficult to predict future ecosystem structure and functioning, especially as space-for-time approaches can produce biased results (Johnson & Miyanishi, 2008).

Predictions of how ecosystems might change into the future can be improved by considering past environmental conditions, and time lags in response (Ogle et al., 2015; Ryan et al., 2015). Legacies of past land management on the abiotic and biotic environment influence at least two fundamental plant community processes: ecological selection and dispersal (Perring et al., 2016; Vellend, 2010). Resources and conditions, influenced by legacies, determine organism performance as mediated by their traits, selecting for certain species over others. Land management legacies can also affect dispersal dynamics, which can be an important influence on community structure (Burton, Mladenoff, Clayton, & Forrester, 2011), with these dispersal effects mediated by constituent traits e.g. seed mass and plant height (Baeten, Hermy, Van Daele, & Verheyen, 2010). Together, these processes determine the trajectories of communities and ecosystems following changes to land management practices (e.g., Bürgi, Östlund, & Mladenoff, 2017; Gimmi et al., 2013; Löhmus, Paal, & Liira, 2014). Successional trajectories of ecological change are further influenced by recent global environmental changes, due to chronic alterations in resources and conditions (Smith, Knapp, & Collins, 2009).

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

ecosystem responses to environmental change (e.g., Garnier, Navas, & Grigulis, 2016; Vellend et al., 2017).

Here, we test for interactions between land-use legacies and environmental change using understorey resurvey data from temperate forests across Europe, where we can exploit large spatial variability in both historical management (Durak, 2012; McGrath et al., 2015; Rackham, 2003) and global environmental change factors. Forest plant communities display slow dynamics and trajectories of change (Dornelas et al., 2013; Peterken & Game, 1984) and in the absence of continuous long-term monitoring, we can only reveal these changes through resurveys (Kapfer et al., 2017). More generally, resurveys across broad, potentially orthogonal, environmental gradients offer the opportunity to disentangle the interacting effects of multiple ecological drivers (Verheyen et al., 2017) providing such observational results are carefully interpreted (Smart et al., 2012).

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

Traditional CWS systems involve regular opening of the canopy through cutting multitemmed individuals of species such as oak (*Quercus* sp.), hornbeam (*Carpinus betulus*), and hazel (*Corylus avellana*), on short rotation cycles (typically 7–30 years). Cutting provides wood for charcoal, fencing and other products that can use small diameter poles. In the “true” CWS system, single stemmed timber trees (standards of e.g., oak) are chosen and then grown through multiple coppicing cycles until suitable for harvest (Altman et al., 2013). The regular opening of the canopy in coppice and CWS creates cyclic variation in light and warm temperatures in the forest understorey and also reduces humidity (e.g., Ash & Barkham, 1976). Intensive removal of wood tends to lead to substantial depletion of nutrients (Hölscher, Schade, & Leuschner, 2001; Rackham, 2003; Šrámek, Volařík, Ertas, & Matula, 2015). On the other hand, traditional HF systems focus on producing timber over much longer rotation lengths than CWS systems, but often using the same species e.g. oak. Regeneration is encouraged through clear felling, single tree selection, or group selection of trees in belts and/or in increasing radii from central points, depending on site topography and road networks (Matthews, 1989). The longer period of canopy closure in HF systems leads to shadier, cooler and more moist understorey microclimates compared to CWS (Scolastri et al., 2017). High forest

systems also tend to maintain nutrient stocks, with stem only harvesting in particular (Vangansbeke et al., 2015). Such differences in disturbance regimes between silvicultural systems, and subsequent effects on resources and conditions, lead to understorey plant communities with divergent species compositions and associated trait distributions (Decocq et al., 2004; Keith, Newton, Morecroft, Bealey, & Bullock, 2009; Scolastri et al., 2017; Ujházy et al., 2017).

These management “types”, as well as encompassing variation within them (Duguid & Ashton, 2013), have not been static entities in any given area throughout preceding centuries. Changing socio-economic conditions have led to the abandonment of active timber management in some regions (i.e., zero management), commencing at different times across Europe, and affecting both CWS and HF stands (Hédli, Kopecký, & Komárek, 2010; McGrath et al., 2015; Munteanu, Nita, Abrudan, & Radeloff, 2016; Szabó, 2010; Van Calster et al., 2008). Elsewhere, within and among regions, timber management has been maintained but typically with HF systems at the expense of CWS (Baeten et al., 2009). This decline in CWS management has been tempered by recent reintroductions of this strategy in a few forests, typically as a conservation measure (Vild, Roleček, Hédli, Kopecký, & Utinek, 2013) but also with increasing demand to harvest biomass for fuelwood or to mitigate climate change (Borchard et al., 2017; Lasserre et al., 2011). Overall, European forests are characterized by dynamic silvicultural management systems and legacies driven by abiotic environmental conditions and socio-economic pressures. We are thus presented with an exceptional opportunity to test whether the response of plant communities to recent environmental change depends on these historical management transitions, and/or on coarse categories of historical or more recent management types that reflect distinct silvicultural regimes. Furthermore, we can also investigate whether any responses to these dynamic legacies may be related to the silvicultural regimes’ hypothesized effects on resources and conditions, properties that provide a bridge to observed ecological responses.

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

In addition to fundamental trait-based community properties, we also considered whether responses in species richness (a commonly reported diversity metric), and community-level Ellenberg Indicator Values (EIVs) (Ellenberg, Weber, Düll, Wirth, & Werner, 2001) showed evidence for interactions between management legacies and recent environmental changes. Indicator values, widely calculated and used in vegetation investigations across Europe (as well as

elsewhere e.g., Klinka, Krajina, Ceska, & Scagel, 1989) indicate species preferences for underlying environmental conditions and help understand community responses, and can also be related to the considered traits (Shipley et al., 2017). The indicators are considered robust in the absence of directly measured resource and condition variables (Diekmann, 2003), which is the situation faced here. Although there is variability among species within groups, and individuals within species, these latter analyses complement the core trait-based investigation and enable preliminary investigation of the potential for community responses being related to resources and conditions engendered by the management legacies.

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

Overall though, we expect that these responses will be modulated by the trajectories of change engendered by previous silvicultural management. In particular, we predict that likely depleted nutrient resources in former CWS systems would dampen community responses to increased N deposition (e.g., lessen increases in SLA and EIV_N) due to limitation by other resources (e.g., P) compared to systems that have been under long-term HF management. We also predict that the change to less intensive management in former CWS forests would lead to a general loss of species, as warm- and light-adapted species would be unable to persist in cooler, shadier microclimates. These losses could be lessened in stands undergoing warming as previously adapted species continued to persist. In contrast, former HF systems would remain on relatively stable species richness trajectories subsequently influenced by environmental changes e.g. many systems show declines associated with increasing N deposition (Bobink et al., 2010; Gilliam et al., 2016; Simkin et al., 2016). We also expect that prolonged absence of high light conditions e.g. through the implementation of zero management, would lead to loss of species across the forests (Plue et al., 2013). In sum, changes in species abundance in all these systems, together with species losses and gains, would lead to changes in trait attribute and indicator values. Therefore, we would expect variation in these properties to relate to historical management as well as recent global environmental changes.

2 | MATERIALS AND METHODS

2.1 | Vegetation surveys

We used resurvey data across deciduous temperate forests in Europe from the forestREplot network (www.forestreplot.ugent.be), a

database of vegetation plot records for woodland understoreys. Each dataset in this database is composed of multiple nonoverlapping (in space) plot records from two time points (Table 1). The time interval between surveys in the 40 datasets and 1814 plots analysed here is considered sufficient to detect directional change in the herbaceous layer (a mean interval of 38.6 ± 14.7 [1 SD] years) (De Frenne et al., 2013). Each dataset comes from a relatively homogeneous area in terms of climate and atmospheric deposition such that we considered all plots within a given dataset to have experienced the same macro climatic and atmospheric deposition conditions.

A priori, our analysis focused on European temperate broad-leaved deciduous forests and we therefore excluded plots from North America in the database, and any conifer-dominated plots which were often also associated with broad-scale disturbance between surveys e.g. clearfelling and replanting. We also omitted forested plots known to be located on former agricultural land, and any remaining deciduous plots that also had large-scale management interventions between surveys (see also Appendix S1). These choices removed confounding influences on community change e.g. successional responses to clearfelling (Ujházy et al., 2017).

2.2 | Response variables

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

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

these species were generally rare, virtually all cover and all species in all plots tended to be characterized for plant height at both the time of the initial and resurvey.

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

$$R = \frac{\ln\left(\frac{i_{t+\Delta t}}{i_t}\right)}{\Delta t} \quad (1)$$

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 most recent survey and Δt the number of years between surveys.

2.3 | Explanatory variables

2.3.1 | Rates of global environmental change

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

2.3.2 | Management transitions

Individual dataset contributors assigned plots within their dataset as belonging to one of seven management transitions for the period between 1800 and the resurvey date: CWS to HF, CWS to zero, CWS to HF to zero, HF throughout, HF to zero, zero throughout, and Unknown management. Contributors based their decisions on their local knowledge, and previous research, having been informed of the basis for categorization (see Appendix S4 for further details). We used 1800 as a baseline because we had evidence of forest management classes from this date, and we were focussing on whether long-term legacies interacted with recent environmental change. We excluded from analyses plots classified as *Unknown management*. We also excluded plots classified as *CWS to zero management* and *zero throughout management* because these plots covered very limited ranges of environmental conditions preventing strong tests of management-environmental change interactions

TABLE 1 Datasets from forestREplot (www.forestreplot.ugent.be) in ancient forests with management information. Map ID refers to Figure 1. Datasets 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 and shade casting information. Latitudes and longitudes are indicative of plot locations; precise co-ordinates for plots are available in the data files 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	Rychebské 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
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	1,964–1973	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

(Continues)

TABLE 1 (Continued)

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?
29	EU_36	Hodonínská dubrava	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

(Appendix S4). The four retained management transitions were distributed across Europe (Figure 1). Thirteen of the 40 datasets were characterized by having more than one management transition among their constituent plots (Table 1 and Figure 1).

2.3.3 | Covariates

We included covariates given their potential influence on community change (Austrheim, Evju, & Mysterud, 2005; Simkin et al., 2016; Smart et al., 2014). Covariates included altitude (alt), plot size (plot-size), initial survey year, mean annual temperature/precipitation (MAT/MAP), and cumulative N deposition (baseN), estimated at the time of the initial survey. Given the inclusion of time between surveys in the denominator of community response variables (Equation 1) and therefore its implicit impact on the rate of change, we did not include this descriptor as a covariate in the analysis. We also characterized the environment through cover-weighted EIV for reaction (EIV_R), fertility (EIV_N), moisture (EIV_F), and light (EIV_L) at the time of the initial survey (Ellenberg et al., 2001). We did not use EIV for temperature (EIV_T) as a covariate given the inclusion of climate variables at the dataset scale; however, as noted above, we included EIV_T in community response analyses. EIVs indicate species preferences in their realized niche and are argued to be a robust method to characterize the environment in the absence of directly measured variables (Diekmann, 2003). We used the absolute change in EIV_L between surveys (ΔEIV_L) as a proxy for potential management actions between surveys, in the absence of other information. Initial survey herbaceous richness (herb_{rich}) and cover (herb_{cover}) were included in models examining trait responses between surveys. Appendix S5 further outlines the rationale for covariate inclusion in statistical models, and correlations among them. Covariates could also be correlated with management transitions and/or recent environmental changes, confounding interpretation. We first tested the evidence for potential confounding (Appendix S5; arrows “a” on Figure 2), prior to estimating the effects of covariates on response variables (*Testing the Hypothesis: Analytical Approach*; and arrow “b” on Figure 2). The potential for confounding was generally absent, and almost entirely so when relating covariates to historical management type (Appendix S5).

2.4 | Testing the hypothesis: Analytical approach

We adopted a multilevel, mixed-effect modelling approach to test our hypothesis, analysing data using R Version 3.3.2 (R Core Team, 2017) and the associated package “nlme” (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2016). Dataset was treated as a random effect with varied intercepts only. We also incorporated dataset as a weights term, i.e. we controlled for heterogeneity in residual spread. We considered focal explanatory variables (i.e., the four forest management transitions, and the three environmental changes) and covariates to be fixed effects. All continuous/ordinal fixed effects were standardized (plot size was natural log transformed prior to this procedure), and we used an identity link function and assumed a

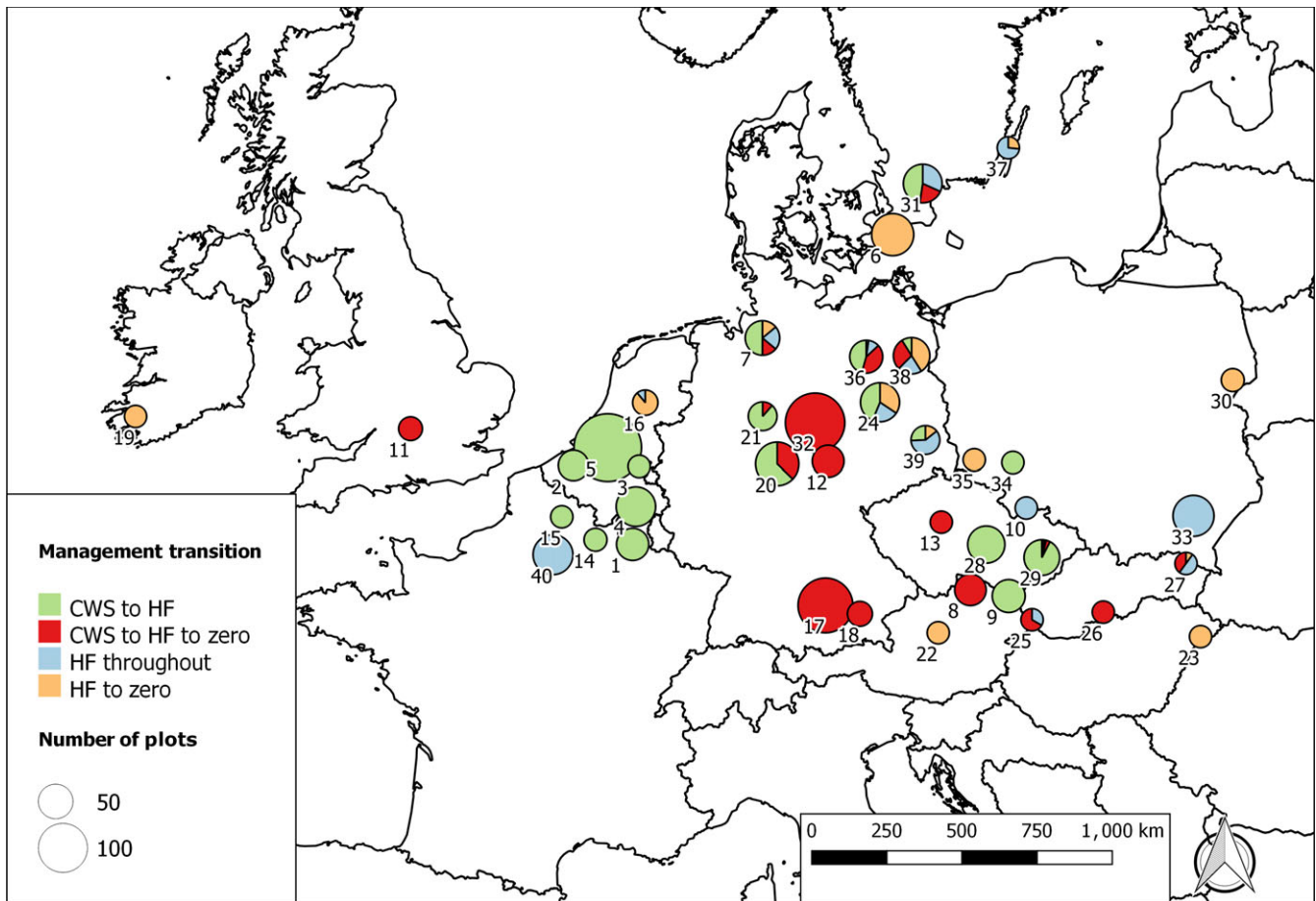


FIGURE 1 Management transitions across European temperate forest understories sourced from forestREplot (www.forestreplot.ugent.be) and expert testimony. Each circle indicates an included dataset and its approximate geographical location (some have been moved for better visibility), with circle size proportional to the number of included resurvey plots. Circle number refers to Map ID in Table 1. Single colours denote that a single management transition, as indicated by the legend, characterizes all analysed plots within a dataset. Multiple colours per circle, and the size of slices indicate multiple management transitions within a given dataset and the proportion of plots with a given transition, respectively

Gaussian error distribution. We graphically checked model assumptions (e.g., Zuur, Ieno, Walker, Saveliev, & Smith, 2009); transformations and alternative error structures were not deemed necessary following these procedures.

For each response variable (R), we first explained variation as a function of all possible, not highly correlated (Spearman's $\rho < 0.65$), methodological and environmental covariates (Equation 2 where “~” represents “is some function of”). We dropped EIV_N and *initial survey year* at this stage, given high correlations with EIV_R and *baseN*, respectively. As noted above, we only included herbaceous richness ($herb_{rich}$) and cover ($herb_{cover}$) from Equation (2) when assessing trait responses. We then performed stepwise backwards selection, allowing us to choose the most parsimonious explanation for the data in the absence of information on management history and environmental change. Dropped variables (i.e., EIV_N and *initial survey year*) were tested for inclusion if we removed their correlated variable during model selection. We found a covariates model with the fewest parameters without significantly compromising its likelihood based on the Akaike Information Criterion (AIC) ($p > .05$ in a

model comparison, and no more than 2 units greater than the lowest AIC model).

$$R \sim \text{plotsize} + \text{alt} + EIV_R + EIV_F + \text{MAT} + \text{MAP} + \text{baseN} + EIV_L + \Delta EIV_L + herb_{rich} + herb_{cover} \quad (2)$$

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

$$R \sim \text{covars} + \text{man}_j * (\text{temp}\Delta + \text{precip}\Delta + \text{Ndep}\Delta) \quad (3)$$

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

For the management variable, we separately tested models using three different a priori syntheses: (i) historical management type in 1800 alone (two levels: CWS or HF), (ii) contemporary

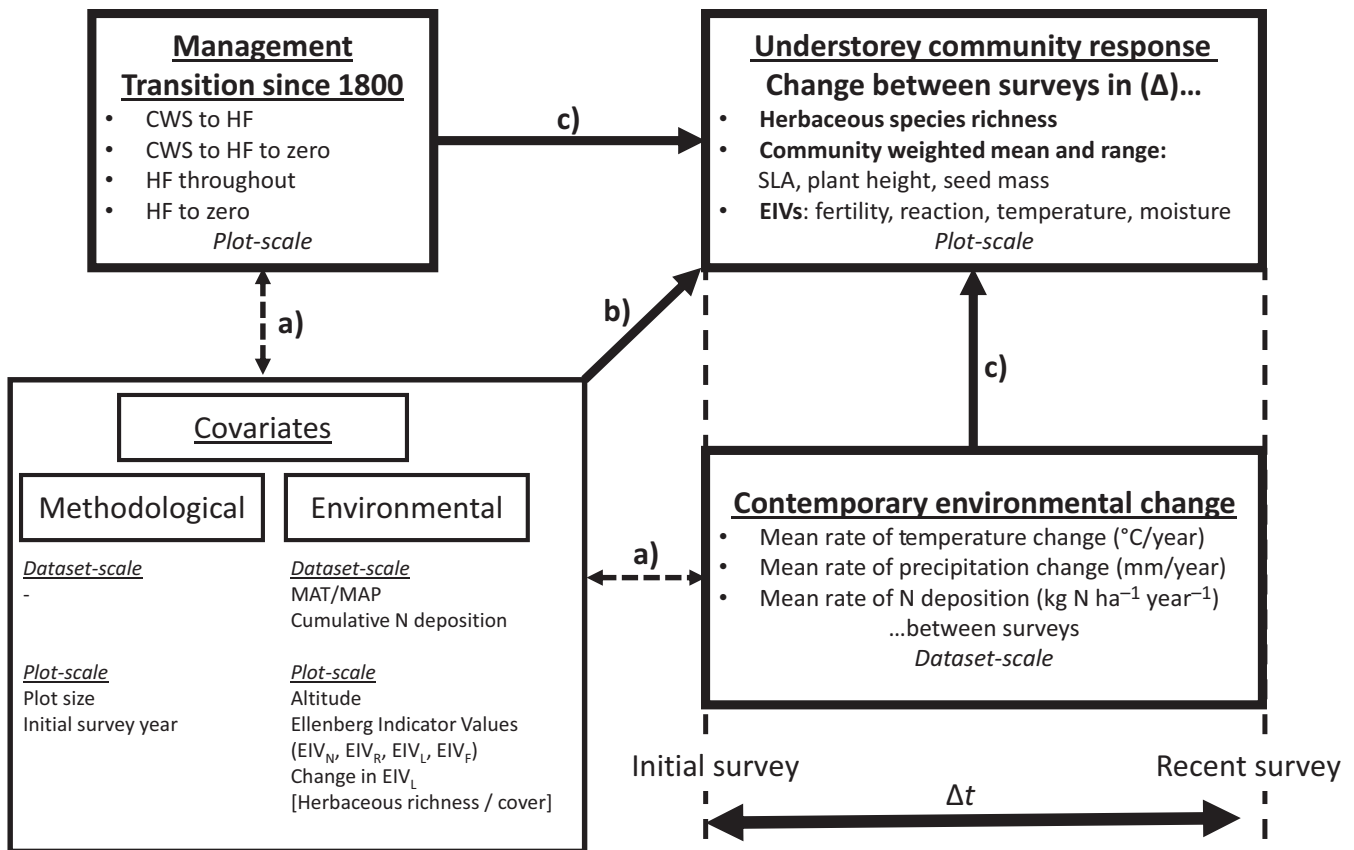


FIGURE 2 Summary of analytical approach: (a) assessment of potential confounding between named methodological/environmental covariates and management transitions/environmental changes at different scales; (b) modelling of understorey community responses, estimated according to Equation (1), as a function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

management type alone (two levels: HF or zero), and (iii) the management transition (four levels: CWS to HF to zero, CWS to HF, HF to zero and HF throughout). The first and third approaches test for evidence that historic management (either as a type in 1800, or as transitions since that time) interacts with recent environmental change to influence community property trajectories. The second analysis tests whether contemporary management, regardless of historic management and when the contemporary management began, influences trajectories. We emphasize that our synthesis of the management legacy information into types does not imply that such types characterize management actions throughout the time series, nor does the management type in 1800 necessarily denote predominant management before that time. However, we contend that despite likely variations within management types, such categorization provides a means to rigorously test our overarching expectation that there are interactions among management legacies and environmental change.

We simplified the full model of Equation (3) using a stepwise backward selection procedure as for the covariates model alone, but retaining all initially chosen covariates. All models were fit with maximum likelihood (ML) to enable comparison testing; the most parsimonious model was then refit with restricted maximum likelihood

(REML) to derive parameter estimates (shown in full in Appendix S7). For a given response variable and to aid comparison among models, we present AIC values of the most parsimonious ML model among the different management transitions, as well as the goodness-of-fit indicated by marginal and conditional R^2 (Nakagawa & Schielzeth, 2013). We tested the robustness of community property results (i.e., species richness, trait values, indicator values) to different decisions concerning the characterization of the overstorey at the time of the initial survey and its dynamic between surveys, the inclusion of woody seedlings, and diaspore size for ferns (see Appendices S8, S9, S10, S11 and S12). When presenting regression lines, all variables not shown were assumed to be at their mean value. Note also that when interpreting community weighted mean responses, we discuss changes in relative cover. For instance, an increased mean EIV for a particular factor could reflect species with low demand for that factor decreasing while species with high demand remaining unchanged between surveys, or low demand species not changing in absolute cover but species with high demand increasing, and finally low demand species decreasing in cover and high demand species increasing. All three scenarios would lead to an increased mean EIV due to the increase in relative cover of high demand species.

3 | RESULTS

Forest management type over 200 years ago (i.e., CWS or HF) and the transition since that time, interacted significantly with environmental changes to determine many plant community attribute temporal trajectories (first and last column in Table 2a, Appendix S7 for parameter estimates). For herbaceous species richness, and mean

and range of plant height, interactions were apparent regardless of contemporary management type and mainly involved rates of temperature change and nitrogen deposition. There was also evidence for management transitions since 1800 interacting with environmental changes, and this was the most likely model (from those compared) for change in mean SLA, and for moisture-indicating values (EIV_F) (Table 2b). Only EIV_T showed evidence for contemporary

TABLE 2 Understorey plant community responses to management transition legacies and potential interactions with environmental changes (T = rate of temperature change, P = rate of precipitation change, N = annual rate of N deposition) in the most parsimonious model

Δ in understorey response variable	Management type in 1800 CWS vs. HF		Contemporary management type (time of most recent survey) HF vs. Zero		Management transition from 1800							
	Main effect	Interaction with environmental change	Main effect	Interaction with environmental change	Main effect	Interaction with environmental change						
(a)												
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 _R (reaction)	n.s. (N)	n.s.	– (N)	(P) *	– (N)	(P) *						
EIV _N (fertility)	n.s. (P)	n.s.	n.s. (P)	n.s.	n.s. (P)	n.s.						
EIV _F (moisture)	n.s.	n.s.	n.s.	n.s.	(P) *	(T,N) *						
EIV _T (temperature)	n.s. (T,P,N)	n.s.	– (P,N)	(T) *	n.s. (T,P,N)	n.s.						
Δ in understorey response variable	Covariates model			Management type in 1800			Contemporary management type			Management transition from 1800		
	AIC	R _m ²	R _c ²	AIC	R _m ²	R _c ²	AIC	R _m ²	R _c ²	AIC	R _m ²	R _c ²
(b)												
Herbaceous species richness	–10,924.7	14.3	56.1	–10,926.6	17.6	56.6	See covariates model			See covariates model		
Mean SLA	–14,804.3	26.1	35.9	See covariates model			–14,813.5	29.5	36.8	–14,820.7	30.8	35.8
Mean plant height	–11,961.4	19.6	48.8	–11,992.5	41.2	52.6	–11,979.0	37.6	52.4	–11,991.7	44.3	52.8
Mean seed mass	–8,520.7	2.9	12.4	See covariates model			See covariates model			See covariates model		
Range SLA	–11,351.3	8.2	26.4	See covariates model			See covariates model			See covariates model		
Range plant height	–13,655.4	27.0	34.0	–13,668.4	36.4	39.8	–13,661.2	31.3	36.3	–13,663.4	36.7	40.8
Range seed mass	–7,852.5	6.8	31.9	See covariates model			See covariates model			See covariates model		
EIV _R (reaction)	–17,104.4	38.0	48.2	–17,109.2	39.7	49.8	–17,109.1	39.9	50.0	–17,105.0	39.2	49.1
EIV _N (fertility)	–15,733.6	31.5	60.9	–15,740.2	40.7	62.3	See management type in 1800 model			See management type in 1800 model		
EIV _F (moisture)	–17,881.0	42.7	64.4	See covariates model			See covariates model			–17,887.0	46.4	62.2
EIV _T (temperature)	–18,171.9	9.9	16.5	–18,178.3	12.9	17.1	–18,178.8	13.7	17.3	–18,178.3	12.9	17.1

In (a) “*” indicates that for a given management legacy, or its interaction with a given environmental change, there is a significant effect on understorey response ($p \leq .05$); “–” indicates management legacy inclusion in the most parsimonious model with parameter estimates of differences between legacies not significantly 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 there is a significant ($p \leq .05$) main effect of the given environmental change (T, P or N), regardless of management; if normal text, the variable is included but it is not different from 0 ($p > .05$). Full parameter estimates shown in Appendix S7 and S12. In (b), we show model comparison statistics between the most parsimonious covariates model and the most parsimonious models that include main effects and/or interactions among environmental change, and management legacies. AIC: Akaike Information Criterion; R_m² indicates a goodness-of-fit associated with a given model's fixed variables, while R_c² indicates goodness-of-fit for the fixed and random components of the model (Nakagawa & Schielzeth, 2013); both are indicated in %. We fitted models using maximum likelihood estimation; we indicate the model with the lowest AIC among comparisons in bold.

management type interacting with environmental change as being a more likely explanation for responses than other management syntheses (Table 2b). Unmanaged forests at the time of the most recent survey show a greater decline in relative cover of high temperature indicating species as compared to managed forests with increasing rates of temperature change (see parameter estimates in Appendix S12). Trajectories of change in mean and range of seed mass, and range of SLA, were most likely (and parsimoniously) explained by covariates models alone. Main effects of environmental change were sometimes important, with greater rates of increase in precipitation predicting increased mean and range of plant height, decreased influence of higher EIV_T species, and increased influence of higher EIV_N species. The relative cover of species with higher values of EIV_R and EIV_T increased between surveys with greater rates of N deposition (Appendices S7 and S12).

The importance of incorporating management and/or environmental change in models explaining community trajectories varied among those response variables where such factors aided model fit (Table 2b). For mean plant height, the contribution of fixed factors went from 19.6% in the covariates model alone to 41.2% in a model incorporating interactions among environmental changes and 1800 management type. In contrast, for herbaceous richness only 3% more variation was explained by fixed effects that incorporate such interactions. Approximately 4% more variation was explained for those responses best modelled by management transition and environmental change interactions (mean SLA and EIV_F). The additional explanation provided by environmental change and management legacy (interactively or not) aids understanding of what appears to be limited mean directional change across response variables (Figure S7.1, Appendix S7). The conditional R^2 values show the importance of considering the random effect of dataset, and confirm the overall good model fits for models incorporating management type in 1800 (ranging from 50% to 55%), with varied fits when considering management transitions (36% [mean SLA] – 62% [EIV_F]; Table 2b).

These patterns are generally robust to alternative analysis decisions (Appendices S8, S9, S11, and S12). Interactions between land management legacies and environmental changes, as well as the importance of land management legacies alone, are also clearly observed in functional-structural group (*sensu* Box, 1996) understorey cover responses (Appendix S13). These results confirm the importance of taking management legacies into account when predicting community responses to environmental change. Mean seed mass was also predicted by an interaction between management type in 1800 and N deposition or temperature change when the covariate model included direct overstorey characterization, including when spore mass was incorporated (Appendix S8 and S11). In the data subset including tree and shrub seedlings in understorey richness, there was no longer evidence for interactions among environmental changes and historical management type. This is likely due to the increasing tree/shrub seedling species' cover that was also observed in the understoreys of former CWS systems (Appendix S13), made up of different species to compensate for the

loss of herbaceous species in such systems, and thus removing evidence for an interaction. However, interactions remained when considering herbaceous species richness only in this data subset (Appendix S9). In a reduced data analysis with only those plots with direct overstorey characterization of the stand (Appendix S12), AIC values marginally indicated EIV_R response ratios were better predicted by an interaction between contemporary management and precipitation change. However, slope estimates were close to 0, while the significant main effect of N deposition remained across management legacies. For EIV_T, the weight of evidence shifted towards a main effect of precipitation being important, regardless of management legacy. EIV_N was better predicted by considering an interaction between management transition since 1800 and precipitation change in the reduced dataset. This reflected CWS to HF to Zero management transitions increasing more in fertile indicator species relative cover than the increases observed in other transitions with greater rates of precipitation change.

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

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

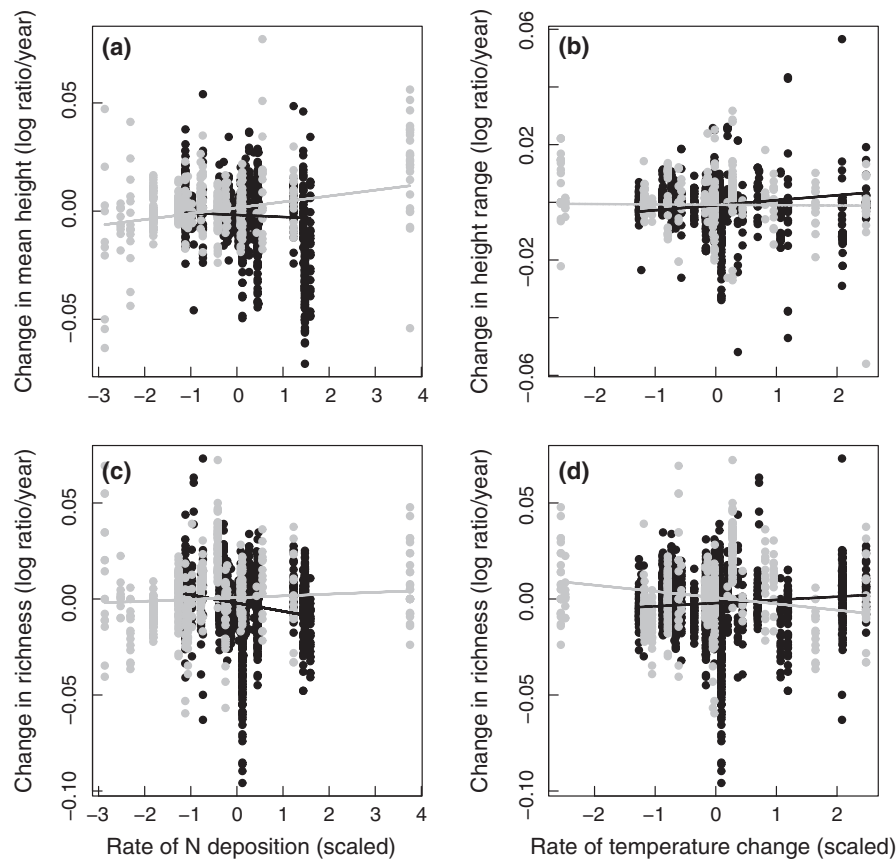


FIGURE 3 Community temporal trajectories interactively depend on historic management type and environmental change. All subpanels show understorey community attribute responses of plots within stands either managed as CWS (black dots and lines) or HF (grey dots and lines) in 1800, regardless of management at the time of the most recent survey and transitions since that time, against a given environmental change. Change in (a) mean plant height vs. N deposition; (b) range in plant height vs. temperature change; (c) species richness vs. N deposition; (d) species richness vs. temperature change. Responses above 0 on the y-axis indicate an increase in a given attribute between surveys while those below 0 indicate a decline; mean (± 1 SD) N deposition (i.e. 0 value on x-axis in [a] and [c]) is 16.94 (4.02) kg N/ha/year and mean (± 1 SD) temperature change (i.e. 0 value on x-axis in [b] and [d]) is 0.029 (0.0146) °C/year

4 | DISCUSSION

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

To our knowledge, this is the first demonstration of interactive effects of environmental change and management legacies on the change in plant community properties between two time points. This

is despite the widespread appreciation of historical effects on current ecosystem states (Foster et al., 2003), knowledge about the different timescales at which resource alterations act (Smith et al., 2009), huge variation in management histories in European forests (McGrath et al., 2015), and a growing interest in time lags in ecosystems (Bertrand et al., 2016; Bürgi et al., 2017; Ogle et al., 2015). Local-scale temporal changes in plant diversity show tremendous variability from site to site (Vellend et al., 2017), and our results can help to explain some of this variation.

Having demonstrated the importance of management legacies for dictating community responses to environmental change, the question then becomes “Why are such legacies ecologically important?” We suggest that the patterns we have revealed can be understood through the dynamics of both resources and conditions in response to different forest silvicultural regimes, and the “ecological memory” (Ogle et al., 2015) such management regimes engender. We are unable to unequivocally substantiate this suggestion with the data herein, partly because they are observational and also because we do not have direct characterization of management-induced changes in resources and conditions. We can though assess

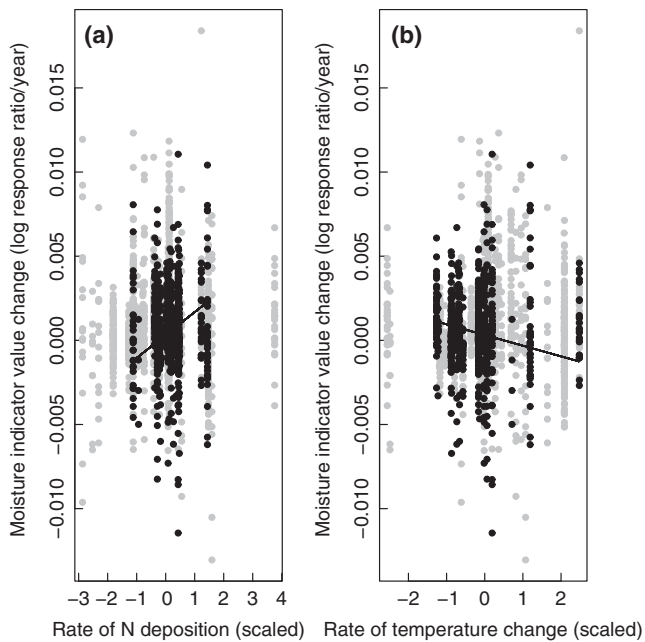


FIGURE 4 EIV_F trajectories interactively depend on management transition since 1800 and environmental change. All subpanels show moisture indicator value responses of plots within stands managed as one of four different transitions since 1800 against a given environmental change. Grey points refer to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

how functional trait and species richness results align with expectations from expected resource and condition dynamics, supported by analyses of indicator value responses.

We expected that former CWS forests would exhibit different dynamics to forests managed as HF in 1800, likely due to the different legacies in resources and conditions these alternative management intensities and their associated disturbance regimes create. For species richness, we expected that former CWS would lose species, particularly warm- and light-adapted ones, as communities adjusted to HF or zero management, based on unimodal responses to resource gradients (Fraser et al., 2015) and the reduction in management intensity. We also expected that a lack of soil resources in CWS systems would constrain community property responses to N deposition in contrast with HF systems e.g. in plant height and SLA as well as species richness. In HF, we expected communities would remain on relatively stable trajectories, sensitive to subsequent environmental changes e.g. richness declines associated with increasing N deposition (Bobbink et al., 2010; Gilliam et al., 2016).

In line with expectations, former CWS stands lost species between surveys but greater rates of temperature change reduced the magnitude of decline. This reduction in magnitude was not accompanied by clear changes in EIV_T suggesting that species indicator values for temperature had been maintained in a given former

CWS plot between surveys. Indeed, across the entire dataset, there was a tendency for a decrease in the relative contribution of warm-adapted species cover with increasing temperature change (significantly different in the case of HF vs. Zero management at the time of the contemporary survey) which may reflect microclimatic effects (De Frenne et al., 2013) and species responses to increased overstorey cover (measured directly, and also reflected in EIV_L responses [Appendix S10]). The relatively subtle temperature effect in former CWS (see also Figure S14.1) might be explained by previous adaptation of the flora to cyclic variation in relatively warm temperatures in the understorey due to canopy opening. This potentially prevents the further decline in mean EIV_T observed in other silvicultural systems.

Contrary with our expectation that N deposition would have less of an effect in former CWS stands, models predicted even greater decline in species richness as N deposition increased, although greater rates of N deposition are associated with greater relative cover of flora indicative of warm temperatures i.e. mean EIV_T increases. The greater richness decline in CWS forests is in line with overall expectations for loss of species at higher soil resource availability (Fraser et al., 2015). Indeed, N deposition may speed up the loss of species through more rapid competitive exclusion by species adapted to shaded conditions, already present in the flora or capable of invading, if other resources do not become limiting to their growth (Härdtle, von Oheimb, & Westphal, 2003; Hautier, Niklaus, & Hector, 2009; Pepler-Lisbach, Beyer, Menke, & Mentges, 2015). There may also be a role for mycorrhizal fungi in determining such interactions; herbaceous species that are lost may have arbuscular or ectomycorrhizal fungal partners that have been adversely affected by historic levels of N deposition (Phillips, Brzostek, & Midgley, 2013; van Strien, Boomsliuter, Noordeloos, Verweij, & Kuyper, 2017). These ideas would require further analysis of individual species responses, which would also be useful from a biodiversity conservation standpoint, but are beyond the scope of the present investigation, focussing as it does on synthetic community descriptors.

In HF, and in contrast to theoretical predictions, additional N deposition did not affect herbaceous species richness responses, and there was even evidence for an increase when N deposition is above critical threshold rates (Figure S14.2). Invasion by species that benefit from increased soil N together with continued persistence of oligotrophic species has led previously to observations of increasing species richness under high N deposition (Dirnböck et al., 2014). Our species richness results complement experimental investigations, which have shown the importance of interacting effects of temperature, light and N on community dynamics (De Frenne et al., 2015). Importantly, our results also support the prediction that N deposition may have variable effects depending on context (Simkin et al., 2016). Interestingly, the interactions observed for herbaceous richness between environmental changes and management type in 1800 disappear when total understorey richness is considered (Appendix S9). This reflects an increase in woody seedling species cover (Appendix S13) made up of different species. Greater richness

increases in former CWS than HF to remove evidence for any interactions with environmental change is in line with expectations that lower available soil resources in CWS constrain herbaceous and promote woody understorey community development (Graves, Peet, & White, 2006). However, former HF, assumed to have greater levels of soil resources, increased in woody species number, suggesting the importance of other factors determining woody expansion. Elucidating species richness dynamics, together with consideration of indicator values, in relation to land management legacies significantly adds to our understanding, compared to analyses that showed limited overall change (Bernhardt-Römermann et al., 2015; Verheyen et al., 2012) but also reinforces the need to characterize the environment experienced by the plants.

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

We also expected SLA to increase in response to N deposition, with this response being constrained in former CWS systems due to the aforementioned resource constraints. Indeed, in shaded conditions, we would expect species with high SLA to dominate because of a selective advantage (Poorter, Niinemets, Poorter, Wright, & Villar, 2009). We do not know why SLA did not respond as expected in former CWS stands as compared to HF stands. Unmeasured driving factors (such as grazing pressure Díaz et al., 2007) or more immediate changes in resources and conditions e.g. the light environment, could be predominant factors in determining SLA response between

surveys. This may explain why contemporary management interacted with environmental changes to effect SLA response between surveys (Table 2), and the importance of covariates such as overstorey cover, EIV_L and change in EIV_L in determining responses (Table S10.1).

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

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

1. more detailed studies of how plants perceive environmental gradients across time and space (Garnier et al., 2016);
2. continuous characterization of historical and contemporary management intensities based on alternative data sources than those used here (Szabó & Hédl, 2011); and,
3. experiments that manipulate resources and conditions (De Frenne et al., 2015; Hahn & Orrock, 2016; Rollinson, Kaye, & Leites, 2012).

We have shown that across European temperate forest understoreys, community property dynamics depend upon interactions among historic land management legacies and environmental changes. Given that functional traits (SLA and plant height) and

species richness responses were affected by past and contemporary management, our results imply that only considering the main effects of recent environmental changes on ecosystem dynamics could obscure the importance of management history for determining trajectories of community change. In other words, future projections of ecosystem dynamics that only consider contemporary environmental change may be flawed, without consideration of the trajectories of change systems are already on. Our results could explain some of the highly variable patterns of local diversity change in the literature (Vellend et al., 2017). Further progress on mechanistic understanding likely requires the direct characterization of historical trajectories in resources and conditions engendered by management legacies, both for temperate forests and other ecosystems. Our results are a first demonstration, at broad environmental scales, that account needs to be taken of previous land management if we are to understand how plant communities, and their important functional properties, will change in the Anthropocene.

ACKNOWLEDGEMENTS

We thank three anonymous reviewers and the Subject Editor for comments that significantly improved and clarified the arguments within the manuscript. We also thank all those vegetation surveyors, historians, and trait measurers, past and present, whose endeavours allowed us to test our hypothesis. The European Research Council (ERC), through a Consolidator Grant awarded to KV, supports MPP, HB, SLM, LD, EDL, DL and KV (614839; the PASTFORWARD project). DL is also supported by the Research Foundation – Flanders (FWO). Data from Zöbelboden, Austria (Thomas Dirnböck) were recorded in the framework of UNECE CLRTAP ICP Integrated Monitoring Program; data collection for Compiègne (GD and Déborah Closset-Kopp) was aided by Société Botanique de France. Data collection for FM (Slovakia) was supported by APVV-15-0270 and APVV-15-0176. MC, RH, and OV received funding from the Czech Science Foundation, project GACR 17-09283S, and MC, RH, MK, and OV through the ERC LONGWOOD project, ERC Grant agreement no. 278065 and from project RVO 67985939. PP was supported by Centre of Excellence PLADIAS, no. 14-15414S (Czech Science Foundation). We thank Safaa Wasof (Ghent University) for assistance with R.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA ACCESSIBILITY

Data supporting results are archived at a Ghent University institutional repository, and available through the forestREplot website (www.forestreplot.ugent.be). Original forest community resurvey data, also deposited at forestREplot, can be accessed by contacting the Management Committee (details on the website) who obtained individual permissions for data use from dataset contributors. Conflicting policies from funding sources at the time of initial and

resurveys prevents unsupervised public accessibility of raw vegetation resurvey data.

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How to cite this article: Perring MP, Bernhardt-Römermann M, Baeten L, et al. Global environmental change effects on plant community composition trajectories depend upon management legacies. *Glob Change Biol*. 2018;00:1–19. <https://doi.org/10.1111/gcb.14030>