Long-term community change: bryophytes are more responsive than vascular plants to nitrogen deposition and warming

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Abstract

Aims: Many studies of vegetation change over multiple decades have focused on vascular plants, but very few on bryophytes, despite the importance of bryophytes for overall plant biodiversity and ecosystem functioning. Using a repeated survey of vascular plants and bryophytes in a forest ecosystem, we tested predictions of the hypotheses that: (1) vegetation change has been driven by N deposition and climate warming, and (2) bryophytes are more responsive to environmental change than vascular plants.

Location: Lowland temperate forest, northwest France.

Methods: In forest plots initially surveyed in 1976, we re-surveyed both vascular plants and bryophytes in 2009 and 2012, respectively. We analysed changes in α-diversity, β-diversity, and species composition, and we used community-weighted mean values of species affinities for temperature, light, pH, soil moisture and N to assess the temporal responses potentially caused by warming, N deposition, or possibly a changing light regime.

Results: We observed significantly increased species richness of bryophytes and decreased richness of vascular plants. Community affinities to N, pH and temperature increased significantly for bryophytes, but not for vascular plants, although the change over time in N affinities for vascular plants was qualitatively in the predicted direction. Bryophytes showed a higher magnitude of temporal community change than vascular plants, both in terms of overall species composition and environmental affinities, indicating a higher responsiveness of bryophytes to environmental change.

Conclusion: Overall, the result of more marked temporal community change for bryophytes suggests that the many studies of changes in vascular plant communities over time might underestimate the sensitivity of the broader plant community (including cryptogams) to environmental change.

Introduction

Spatial variation in plant community composition is strongly influenced by abiotic factors (e.g. soil chemistry and climatic conditions), site history and biotic interactions. Changes in such factors are therefore expected to cause temporal changes in the structure and composition of plant communities (Smith et al. 2009; De Keersmaeker et al. 2014; Kempel et al. 2015; McGill et al. 2015; Vellend et al. 2017). However, for long-lived perennial plants, which dominate most of the world's vegetation, temporal responses may take many decades to manifest, thus requiring long-term monitoring or the use of historical data to document (Vellend et al. 2013a,b, 2017; Chytrý et al. 2014).

In recent decades, anthropogenic global changes have caused major modifications of the physical and chemical characteristics of the Earth's surface, with important consequences for the structure of ecological communities (Poiani et al. 2000; Rooney et al. 2004; Wiegmann & Waller 2006; Bernhardt-Römermann et al. 2015). In communities that have not undergone major land-use transitions, dominant global change factors include climate change (especially warming) and atmospheric N deposition (Field

et al. 1992). As predicted by climate warming, several studies have documented 'thermophilization' – decreased abundance of cold-adapted species and/or increases in warm-adapted species (Bertrand et al. 2011; De Frenne et al. 2013) – or shifts in species distributions toward higher altitudes (Le Roux & McGeoch 2008; Savage & Vellend 2015) and latitudes (Chen et al. 2011). In the context of N deposition, other studies have documented 'eutrophication' of vegetation, involving a shift in composition toward more N-demanding species (Thimonier et al. 1994; Gilliam 2007; Delgado & Ederra 2013) and a decrease in species richness and evenness (Bobbink et al. 2010; Armitage et al. 2014; Field et al. 2014).

A powerful and increasingly prevalent method for assessing the pattern and causes of long-term vegetation change involves 'legacy data', such as phytosociological plots that were initially surveyed decades ago (Vellend et al. 2013a,b, 2017; Chytrý et al. 2014). Using data on species' ecological affinities (Diekmann 2003) such as Ellenberg indices (Ellenberg 1988), we can formulate *a priori* predictions about how communities should have changed over time under different hypotheses (e.g. a strong influence of warming or nutrient deposition) (Diekmann 2003; Delgado & Ederra 2013), and then test these predictions (Hédl et al. 2017).

Many legacy studies have been conducted to date, but almost all of them have focused only on vascular plants, despite the fact that bryophytes are major contributors to both plant diversity and ecosystem functioning (Turetsky 2003; Lindo & Gonzalez 2010). Bryophyte communities fix both C and N, often enhance soil organic matter content and water retention, capture nutrients from the air and provide habitat for a diverse community of microorganisms and invertebrates (During & Van Tooren 1990; Turetsky 2003; Vanderpoorten & Goffinet 2009; Lindo & Gonzalez 2010).

Different taxa do not necessarily respond in a similar fashion or with the same intensity to environmental change (Grytnes et al. 2006; Bagella 2014), and it has been hypothesized that bryophytes and vascular plants might respond differently (Möls et al. 2013). However, these taxa have very rarely been studied jointly in long-term temporal analyses (Økland et al. 2004; Lalanne et al. 2008, 2010), likely due to the paucity of historical data available for bryophytes (Gignac 2001; Molau & Alatalo 1998; but see Delgado & Ederra 2013). We thus have extremely limited knowledge of how these different components of the plant community compare in terms of the nature and magnitude of long-term responses to environmental change. Nevertheless, our knowledge of the basic biology of vascular plants and bryophytes provides a basis for hypotheses related to their relative sensitivity to environmental change. For instance, widespread dispersal of bryophyte spores (Vanderpoorten & Goffinet 2009) can permit more rapid colonization of suitable habitats, thus accelerating community responses to environmental change (Cottenie & De Meester 2004). In addition, because bryophytes absorb water through above-ground tissues, they should be more responsive than vascular plants to the chemical composition of rainfall (Turetsky 2003; Bobbink et al. 2010).

Here we report an analysis of community changes over ~35 yr for both understorey vascular plants (i.e. herbaceous plants, ferns and shrubs) and bryophytes (i.e. mosses and liverworts) in a lowland forested region of northwest France, initially surveyed in 1976 (Bardat 1978), and then re-surveyed in 2009 and 2012 using the same protocols and location. Here we used community-weighted mean (CWM) values of species affinities for temperature, light, pH, soil moisture and N to assess the temporal responses potentially caused by warming, N deposition or possibly a changing light regime.

We first conducted exploratory analyses of temporal changes in multivariate species composition and diversity, and then tested the following specific hypotheses and predictions: (1) N deposition and climate warming have had a major influence on changes in plant community composition. *Predictions*: for both vascular plants and bryophytes, CWM for ecological affinities to N, pH and temperature should have increased over the ~35-yr period. (2) Bryophyte communities are more responsive to environmental change than understorey vascular plant communities. *Prediction*: the magnitude of community responses has been larger for bryophytes than for vascular plants. Specifically, we expect larger increases for bryophytes than for vascular plants in the analyses described under hypothesis (1).

Methods

Study area

Fieldwork was conducted in a 7450-ha site located in the Brotonne forest (Normandy, France; 49.4–49.52° N, 0.65–0.80° E), an Atlantic *Fagus–Quercus* even-aged forest dominated by *Fagus sylvatica* L., *Quercus robur* L. and *Quercus petraea* L. Elevation ranges from 0 to 200 m a.s.l., with distinct geology and soil types: plateaus are characterized by quaternary loess (silt) with variable amounts of clay; slopes are calcareous; and valleys are covered mostly by old alluvial soils. The climate is oceanic, with an average annual rainfall of 800–900 mm evenly distributed throughout the year, and a mean annual temperature of 10 °C. Our study region, Upper Normandy, was a major industrial region in France, with a high level of atmospheric nutrient deposition, especially NO_x (NO, NO_2) and SO_x (SO_2, SO_3), which reached their peaks in the 1970s and 1980s in France, with subsequent declines (CITEPA

2003; PRQA 2009). Thus, while soils continue to accumulate N from the atmosphere, soil acidity may have declined in recent decades. The region has also experienced considerable climate warming over the past half century (Fig. 1). Beech forests in this region are managed for harvesting as even-age stands, with a cutting cycle of ~140 yr. Although we selected plots without any recent anthropogenic or natural disturbances (e.g. clearing, planting or windstorms), successional shifts in the light regime might contribute to temporal community change.

Plot selection and field data collection

Between 1975 and 1977, 500 plots within the study area were surveyed during spring and summer (Bardat 1978). Plots in the original survey were mapped at a fine scale (1/5000), and we were able to relocate the old plots with high precision using QGIS 2.8.2. For the recent surveys, we selected plots according to three criteria: (1) plots must occur in one of two oak and beech forest Natura 2000 habitats: *Endymionon scriptae-Fagetum sylvaticae* (Durin et al. 1967) and *Iliciaquifolii-Fagetum sylvaticae* (Durin et al. 1967; Royer et al. 2006); (2) plots must not have experienced major disturbances (e.g. clear-cutting) in recent decades; (3) plots have maintained forest cover since the 1970s. Applying these criteria resulted in 74 plots for vascular

plant sampling, 46 of which were also used for bryophyte sampling (bryophyte plots require a comparatively larger investment of resources, given time-consuming identifications).

Using identical methods for the two time periods, the abundance of all species of vascular plant (herbaceous species, ferns, shrubs and trees) and bryophytes (*Bryophyta* and *Marchantiophyta*) were recorded following a phytosociological approach (Bardat 1978). In each plot (400 m^2) or subplot (see below), the abundance of all vascular plant and bryophyte species present in the plot was recorded using Braun-Blanquet's phytosociological coefficients (abundance–dominance index; Braun-Blanquet et al. (1952); *see* Appendices S1 and S2 for frequency of occurrence of all species). For vascular plants, the recent surveys were conducted in 2009 during two time windows – in April for spring flowering species and in June/July for summer flowering species – and abundances were recorded for two vegetation layers, shrubs and ground-layer plants. Our analysis thus focused only on understorey plants (i.e. not canopy trees). For bryophytes, recent surveys were conducted in April 2012, and in each plot we sampled up to four microhabitats ('subplots'), corresponding to different substrates: soil, rock, tree stumps and fallen branches. Not all substrates were present in a given plot, so the total number of subplots (93: 44 soil + 2 rock + 32
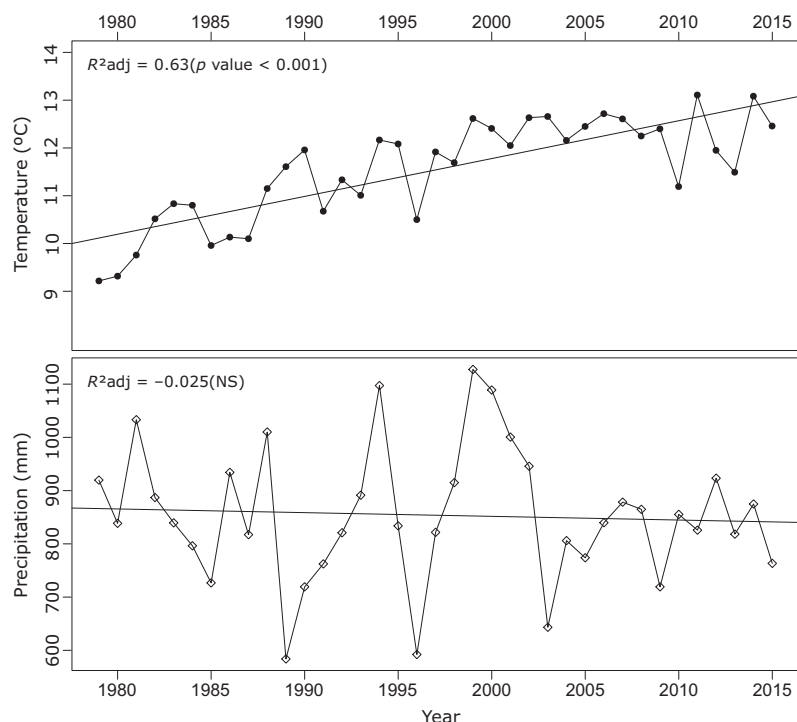

Fig. 1. Temporal trends in mean annual temperature and total annual precipitation, calculated from monthly mean values between Jan 1979 and Dec 2015. Data are from the *Météo-France* meteorological station in Jumièges (n. 76378001), [49.434, 0.821], located 7 km from the study site.

stump + 15 branch) is <46 × 4, but identical for the two time periods (balanced design). Because there are only two subplots on rock per year, we removed these from analyses, leaving 91 subplots per year. Because Braun-Blanquet coefficients do not scale linearly with abundance, we first converted each coefficient to the midpoint of the range of proportional cover values for a given coefficient. We merged '+' (some individuals) and '1' (<5% cover) into the same category. We then calculated relative abundances by dividing each species' raw abundance by the sum of abundances across species within a plot.

Species ecological affinities

The affinity of each species for different environmental conditions was characterized using Ellenberg and related indicator values for vascular plants from *Plantatt* (Hill et al. 2004 based on Ellenberg et al. 1991) and equivalent indices for bryophytes from *Bryoatt* (Hill et al. 2007; based on Ellenberg et al. 1991). Ellenberg's indices were used for light (L), moisture (F), pH (R) and nitrogen (N) (Appendix S3). We did not have directional hypotheses concerning light and moisture affinities, although light was used to test the possibility that increasing canopy cover over time (i.e. decreased light due to forest succession) drove some community changes. For temperature affinities, we calculated a proxy of average annual temperature as the average of July mean temperature (i.e. the warmest month) and January mean temperature (i.e. the coolest month) throughout the range of each species in the United Kingdom (see 'Geographic attributes: climatic means' in Hill et al. 2004 for vascular plants and Hill et al. 2007 for bryophytes). For each species, we can consider this 'species temperature index' (STI) represents species' associations with temperature (Thuiller et al. 2005; Devictor et al. 2008).

In each time period, for each plot k, we calculated the average for each indicator value j, weighted by the relative abundance of each species i as follows (Garnier et al. 2004; Shipley et al. 2011):

$$CWM_{jk} = \sum_i p_{ik}\, t_{ij}$$

where p_{ik} is the relative abundance of species i in plot k, and t_{ij} the affinity index j of species i.

Statistical analysis

All statistical analysis was done using R v. 3.2.3 (R Foundation for Statistical Computing, Vienna, AT).

To test for temporal change in species richness (number of species per plot or subplot) for vascular plants and bryophytes separately, we used linear mixed effect models

(LMM). Given the difference in data structure between vascular plants (no subplots) and bryophytes (subplots), the models were different for the two taxa. In univariate response models, for bryophytes, we used subplot nested within plot as a random effect (1|plot/subplot), whereas for vascular plants, we used only plot as a random effect (1|plot). In all models, year was a fixed effect factor with two levels. Using plot as a random factor accounts for the fact that the same plot was measured at the two time points. These analyses were conducted with the *lmer* function in the *lme4* package
(v. 1.1-10; Bates et al. 2015).

The calculation of *P*-values for these kinds of models is not straightforward. Here we report the 95% credible intervals (CrI) for the fixed effect of time using the *sim* function with 2000 simulations by the package arm (v. 1.9-3). The effect of a variable is considered 'significant' if the 95% credible interval excludes zero and 'highly significant' with 99.9%.

For β-diversity, we tested differences across time with PERMutational analysis of multivariate DISPersion (PERMDISP) using the Bray-Curtis index of compositional dissimilarity in the *betadisper* function in the *vegan* package (v.2.3-1). To test for significant temporal shifts in species composition, we used PERMANOVA (Anderson 2001) with 999 permutations across all plots in the *adonis* function in *vegan*, also using the Bray-Curtis dissimilarity index. Permutations involved swapping the data for a given plot (vascular plants) or subplot (bryophytes) across years.

As described above, each plot or subplot was characterized by CWM values for each of five indicators of environmental affinity. These data were analysed using both multivariate and univariate analyses, separately for vascular plants and bryophytes in all cases. First, in order to visualize relationships between ecological affinities across plots and across time, we performed a PCA using normalized (scaled and centred) CWM per plot and year. Second, LMM were used to test for a difference in CWM between years; these univariate models were implemented in the exact same way as the models for species richness described above. See Appendix S4 for more information on CWM models.

Results

Diversity and composition

For bryophytes, the total number of species across all sample plots increased from 18 in 1976 to 52 in 2012 (Table 1). Of the 37 new species, 30 were present in fewer than 10% of plots in 2012. Three species found in the initial survey in 1976 were not found in the resurvey (*Pleurozium schreberi*, *Brachythecium velutinum* and *Hylocomium splendens*).

Bryophyte species richness per plot increased significantly over time, by more than twofold, with the same qualitative trend for Shannon diversity (Table 1). Richness increased in all four subplot types (Appendix S5). The PERMANOVA analysis showed a significant temporal shift in bryophyte community composition, but there was no significant temporal change in β-diversity (PERMDISP, see Table 1).

For vascular plants, the total number of species declined from 87 in 1976 to 62 in 2009, while mean plot-scale species richness also showed a significant decrease over time (Table 1). As was the case for bryophytes, there was no significant temporal change in β-diversity (PERMDISP, Table 1), but there was a significant shift in community composition over time (PERMANOVA, Table 1).

Ecological affinities

For bryophytes, there was a clear multivariate temporal shift in environmental affinities associated with a shift toward higher N, pH and temperature affinities (Fig. 2a). Univariate analyses for bryophytes showed significant temporal increases for average annual temperature, N and pH affinities (consistent with Fig. 2a) and a decrease for light affinity (Table 2). There was no significant temporal change for moisture affinity.

In contrast, vascular plants did not show any clear directional multivariate changes, but a small decrease of the CWM multivariate dispersion between 1976 and 2009 (Fig. 2b). None of the temporal changes were significant in univariate analyses, although the mean change for N was qualitatively in the predicted positive direction (95% CrI over time = [−0.1, 0.3], mean = 0.1; see Table 2, Appendix S4).

Discussion

Support for our first hypothesis – that temperature and N indices would increase over time – was mixed. Community

affinities to N, pH and temperature increased significantly for bryophytes, but not for vascular plants, although the change over time in N affinities for vascular plants was suggestive of a weak effect in the predicted direction (Table 2). Our second hypothesis – that bryophytes are more responsive to environmental change – was clearly supported by the data. CWM changes for vascular plants were not significant while those for bryophytes were significant and of substantially larger raw magnitude (Table 2).

Bryophytes showed a higher magnitude of temporal community change than vascular plants both in terms of overall species composition (Table 1) and environmental affinities (Table 2, Fig. 2a). The greater sensitivity of bryophytes than vascular plants to environmental change likely results from aspects of their basic morphology and life history. Bryophytes possess no vascular system or true roots, and have limited ability to resist desiccation, with water and nutrients absorbed largely through leaves, thus making them highly sensitive to atmospheric N inputs and the acidity of rain (Turetsky 2003; Tuba et al. 2011). Compared to vascular plants, bryophytes also have relatively strong dispersal and high spore (or propagule) production, thus increasing the local availability of species from the regional pool (Gignac 2001; Raabe et al. 2010), which can potentially enhance community-level responses to environmental change (Cottenie & De Meester 2004). Few studies have made similar comparisons between bryophytes and vascular plants. In one study, Carleton (1990) found results consistent with ours: higher responsiveness of bryophyte species composition than vascular plant composition to a lowland-to-upland environmental gradient in the Canadian boreal forest.

Our first hypothesis predicted important roles for climate warming and N deposition in causing temporal community change. Our results for N affinities were at least roughly consistent for both bryophytes and vascular plants, but the results were mixed for warming, as discussed in the following paragraphs.

Table 1. Biodiversity indices for bryophyte and vascular plant communities in 1976 and 2012 or 2009. Species richness differences were tested with LMM; 95% credible intervals were calculated using posterior distributions. PERMDISP and PERMANOVA analyses were performed on Bray-Curtis compositional dissimilarities among pairs of plots. Distance to median is the average distance of a plot to the centroid of the plots in that year in multivariate space. Significance levels were calculated based on the position of zero relative to the posterior distributions: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. Background shading indicates significant differences ($P < 0.05$).

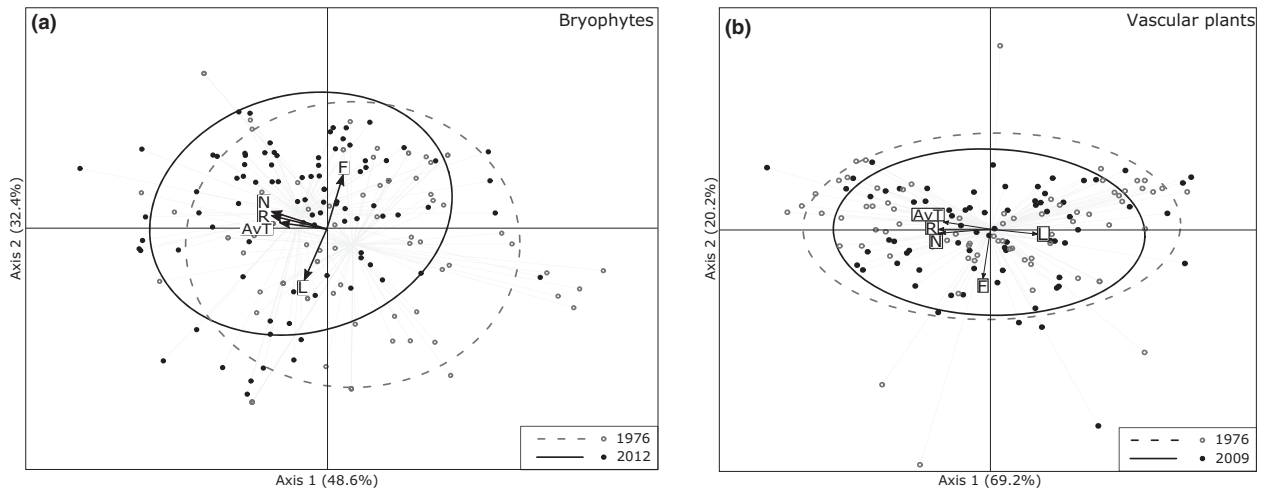|	Number of (sub)Plots	Total Species Number	Species Richness			PERMDISP			PERMANOVA		
			2.5%	Estimate (50%)	97.5%	Dist. to Median	F	P	F	R^2	P
Bryophytes	(plots) subplots			Per subplot							
1976	(46) 91	18	2.8	3.3	3.8	0.56	0.02	0.89	12.84	0.07	0.001
2012	(46) 91	53	6.3	6.8***	7.3	0.56					
Vascular plants	Plots			Per plot							
1976	74	87	14.2	15.8	17.4	0.55	0.98	0.33	6.8	0.04	0.001
2009	74	62	8.3	9.8***	11.5	0.54					

Fig. 2. PCA ordination of CWM for affinities with average annual temperature (AvT), light (L), moisture (F), soil pH (R) and nitrogen (N) for (**a**) bryophytes and (**b**) vascular plants. 80% confidence ellipses are shown for each time period.

Table 2. Temporal changes of CWM of ecological affinities for bryophytes and vascular plants. Coefficient estimates (50%) are the modelled means from LMM; also shown are the 95% credible intervals around the means. Initial values are estimates for the 1976 surveys, and temporal changes are the differences between the initial and contemporary (2009 or 2012) surveys. Significance levels were calculated based on the position of zero relative to the posterior distributions: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. Background shading indicates significant differences ($P < 0.05$).

		Bryophytes CWM			Vascular Plants CWM		
		2.5%	Estimate (50%)	97.5%	2.5%	Estimate (50%)	97.5%
AvT - Affinity to average annual temperature	Initial	8.9	8.9	9	9	9	9.1
	Temporal change	0.04	0.1***	0.1	−0.03	−0.001	0.03
R - affinity to pH	Initial	3.7	3.8	4	4.2	4.5	4.7
	Temporal change	0.1	0.3***	0.4	−0.2	0.03	0.3
N - affinity to nitrogen	Initial	3.4	3.5	3.6	4.1	4.3	4.4
	Temporal change	0.3	0.5***	0.6	−0.1	0.1	0.3
L - affinity to light	Initial	4.8	4.9	5.1	5.3	5.4	5.5
	Temporal change	−0.3	−0.2***	−0.04	−0.1	0.04	0.2
F - affinity to moisture	Initial	5.2	5.3	5.4	5.4	5.5	5.6
	Temporal change	−0.1	0.1	0.2	−0.1	0.04	0.1

We found a clear and significant shift toward higher N and pH affinities for bryophytes, which we interpret as indicative of community responses to increased substrate N and pH. These results are consistent with other studies finding signatures of eutrophication in European forests due to atmospheric nutrient deposition (Thimonier et al. 1994; Bobbink et al. 1998, 2010; Erisman & de Vries 2000; Lameire et al. 2000; Baeten et al. 2010; McClean et al. 2011; Verstraeten et al. 2013; Bernhardt-Römermann et al. 2015). Our results for vascular plants were less clear, but not inconsistent with the hypothesis of N deposition as a driver of vegetation change. Regional studies have shown high levels of NO_x and SO_x emissions in the study area, with a peak of acidification ~30 yr ago (CITEPA 2003; PRQA 2009), likely representing an ultimate source of our observed

plant community shifts via on-going N accumulation and declining acidification.

Compared to vascular plants, little is known about how bryophytes will respond to N deposition, although responses might depend on the form of added N (Verhoeven et al. 2011) or the ecosystem (*see* Bobbink et al. 2010). We found a shift over time toward more N-demanding and high pH-associated bryophyte species. Interestingly, some species that declined in abundance tend to be associated with acidic and late successional forests (e.g. *Leucobryum glaucum, Eurynchyum striatum, Pleurozium schreberi, Brachythecium velutinum* and *Hylocomium splendens*) while new species or those that increased in abundance were more often associated with rich soils and early or intermediate succession (e.g. *Brachythecium rutabulum, Kindbergia praelonga, Plagiothecium succulentum; see*

Appendix S1). Another study in a similar ecological context with corticolous bryophytes found that more mature stands were associated with acidophilous species while early successional stands were characterized by more broadly tolerant species such as *B. rutabulum* or *K. praelonga* (Bardat & Aubert 2007), consistent with increasing acidity of the organic layer during this kind of forest succession (Aubert et al. 2004). However, if anything, the forests in our study have matured during the period of study, so disturbance is not likely to be responsible for the changes we observed. Although we can only speculate as to the precise mechanisms underlying these changes, recovery from the peak of acid deposition might prompt an apparent 'successional regression' of bryophyte communities with respect to the natural successional sequence.

We also found a small but significant increase of temperature affinities for bryophyte communities, consistent with the hypothesis of climate warming, but no trend was observed for vascular plants (Table 2). Temperature in this region has been steadily rising over the past 40 yr (Fig. 1). Other legacy studies have shown responses of vascular plant communities to climate warming (Le Roux & McGeoch 2008; Bertrand et al. 2011; Savage & Vellend 2015), and at present we cannot say whether vascular plant communities are simply not responding to warming in our region, or whether the responses are too slow or subtle to have been detected given our time frame, sample size and measure of temperature affinity. In either case, bryophyte communities do appear more responsive to warming than vascular plant communities, although we consider this conclusion tentative given the small effect size. Our results showed that neither bryophyte nor vascular plant communities showed temporal shifts in moisture affinities (Table 2), which is consistent with the lack of temporal trend in precipitation in this region during the period of study (Fig. 1).

Changes over time in local-scale plant diversity over the past century have been highly variable (Vellend et al. 2013a,b, 2017). Here we found opposite temporal changes of species richness of bryophytes and vascular plants. While bryophytes experienced a near doubling of local species richness, vascular plant richness declined by almost 40% (Table 1). One implication of this result is that vascular plant diversity (more often studied) cannot be used as a proxy for bryophyte diversity (Möls et al. 2013; Bagella 2014). While the change in vascular plant diversity is consistent with expectations based on N deposition, the increase in bryophyte richness is more difficult to explain. Changes in local richness of the magnitude observed here raise the question of the comparability of the two surveys. However, in this study (unlike many legacy studies) the original surveyor, Jacques Bardat, also took part in the recent survey, which was conducted at the same time of year to control for phenological variation. Observer bias

thus cannot account for these large differences. Another potential source of variance is 'pseudo-turnover', due to imprecise plot re-location (Fischer & Stöcklin 1997). However, the forest structures and composition in our study site are relatively homogeneous at local scales, and moreover, in 2009 and 2012 plots were likely within 20–30 m of original plots, which might introduce some random variance, but not systematic bias in local richness. There are no plausible reasons to suspect that these results stem from methodological artefacts. Thus, we are confident in the robustness of results.

Conclusion

Our study is one of only a few to compare the relative magnitude of temporal community change for bryophytes and vascular plants (Alatalo et al. 2014). We found that bryophyte and vascular plant communities both showed compositional shifts over time, but bryophyte communities showed responses of a markedly higher magnitude, with directional responses likely related to nutrient deposition, and to a lesser degree, warming. These results point to the possibility that the large number of studies of temporal change in vascular plant communities collectively underestimate the magnitude of change in the broader plant community, which includes bryophytes. Our knowledge of long-term changes in communities of bryophytes and other cryptogams (e.g. lichens) is minimal compared to our knowledge of vascular plants (but see Vanneste et al. 2017), despite the major ecosystem-level consequences of cryptogam diversity and composition (Cornelissen et al. 2007). Additional studies in a variety of ecological settings are needed to increase our understanding of these important components of plant communities.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of bryophyte species and number of occurrences per survey.

Appendix S2. List of vascular plant species and number of occurrences per survey.

Appendix S3. Simplified explanations of Ellenberg values.

Appendix S4. Complete model results of LMM.

Appendix S5. Temporal change of bryophyte richness per subplot (microhabitat).