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Modelling the impact of climate change and atmospheric N deposition on French forests biodiversity[☆]

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A B S T R A C T

A dynamic coupled biogeochemical–ecological model was used to simulate the effects of nitrogen deposition and climate change on plant communities at three forest sites in France. The three sites had different forest covers (sessile oak, Norway spruce and silver fir), three nitrogen loads ranging from relatively low to high, different climatic regions and different soil types.

Both the availability of vegetation time series and the environmental niches of the understory species allowed to evaluate the model for predicting the composition of the three plant communities. The calibration of the environmental niches was successful, with a model performance consistently reasonably high throughout the three sites.

The model simulations of two climatic and two deposition scenarios showed that climate change may entirely compromise the eventual recovery from eutrophication of the simulated plant communities in response to the reductions in nitrogen deposition. The interplay between climate and deposition was strongly governed by site characteristics and histories in the long term, while forest management remained the main driver of change in the short term.

Keywords:

Atmospheric N deposition
Climate change
Forest ecosystem
ForSAFE-Veg model
Vegetation composition

1. Introduction

Anthropogenic activities have contributed to a significant increase in sulfur and nitrogen emissions into the atmosphere. This has resulted in the acidification and eutrophication of ecosystems (de Schrijver et al., 2008; de Vries et al., 2007), which potentially have significant impacts on forest ecosystems due to their influences on soil biogeochemistry, forest health and biodiversity, among others (Azevedo et al., 2013; Jonard et al., 2012; Sutton et al., 2011).

In an attempt to reduce the impact of long-distance atmospheric pollution, the Geneva Convention on Long-Range Transboundary Air Pollution (CLRTAP) was ratified in 1979 by 34 European countries under the aegis of the European Union and the United Nations (UNECE, 2005). As a consequence, sulfur emissions decreased by approximately 90% in France (CITEPA, 2015), leading to a similar decrease in deposition (Pascaud, 2013), but the reduction in nitrogen emissions was noticeably more modest, with NO_x and NH_y emissions declining by 50% and 4% respectively from 1980 to the present day (CITEPA, 2015).

Extensive studies have examined the impacts of nitrogen on soil biogeochemistry and vegetation composition in different terrestrial ecosystems, from prairies to forest ecosystems (Bobbink et al., 2010; Galloway et al., 2003; van Dobben and de

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Vries, 2010). Results show that high nitrogen inputs may produce significant variations in the nitrogen cycle, and can lead to changes in species richness (Stevens et al., 2004, 2010), community composition (Bobbink et al., 2010; de Vries et al., 2007; Krupa, 2003) or relative species abundance (Gilliam, 2006).

Ecosystem simulation models use existing experimental and empirical knowledge to simulate future ecosystem changes in response to nitrogen reduction and other environmental changes. The first models designed for this purpose were steady-state mass balance models (Hettelingh et al., 2001, 2008). While steady-state models are compatible with the critical loads concept (CLRTAP, 2015; Posch et al., 2004), they are not suitable for simulating temporal changes. In order to estimate atmospheric nitrogen deposition impacts continuously over a long-time period, dynamic biogeochemical–ecological coupled models have been developed (Belyazid, 2006; de Vries et al., 2010; Wallman et al., 2005).

Although the impacts of nitrogen deposition on ecosystems have become a subject of interest in the last few decades, its effects cannot be evaluated outside the actual context of climate change (Belyazid et al., 2011a,b; de Vries and Posch, 2011; Wamelink et al., 2009). Indeed, the response of plant species is strongly affected by climate change since the expected temperature increase could directly induce extensive changes in plant communities (Bertrand et al., 2011; Lenoir et al., 2010). Moreover, soil biogeochemistry can also be strongly impacted by climate since soil temperature, soil organic matter decomposition and soil nitrogen availability are directly influenced by temperature increase (Butler et al., 2012; Guntiñas et al., 2012; Rustad et al., 2001).

Atmospheric nitrogen deposition and climate change are often considered independently from one to another, although they also have combined effects (Bytnerowicz et al., 2007; Serengil et al., 2011). In order to model the evolution of forest ecosystems over time, atmospheric N deposition and climate change have to be taken into account simultaneously.

Against this backdrop, the aim of this study was to analyse the effects of atmospheric nitrogen deposition and climate change, considered separately and together, on three French forest ecosystems. The evolution of the understory vegetation composition from 1800 to 2100 was evaluated using a dynamic coupled biogeochemical–ecological modelling approach. First, the environmental niches and physiological properties of a set of species were calibrated on observed field relevés. Second, the modelled plant relative abundances were evaluated against further measured data. Finally, the model was used to simulate the future evolution of plant communities under different climate and nitrogen deposition scenarios.

2. Material and methods

2.1. Coupled biogeochemical – ecological ForSAFE-Veg model

The simulated trends of soil solution chemistry, light extinction in the tree canopy and hydrology are conveyed to the Veg model, which uses them with physiological plant traits to simulate the composition of the understory vegetation community. Veg model builds on plant-specific ecological niches for

temperature, climate, soil solution pH and soil solution nitrogen to estimate the strength of the probability of occurrence of a given plant. The strength of the respective plants is scaled by their respective colonisation rate, shading height and rooting depth to simulate competition between the different plants potentially present at a site and produce relative abundances for each plant. This model chain simulates the changes in understory plant communities in response to simultaneous environmental changes (see for example Sverdrup et al. 2007), and can be used to derive critical loads of atmospheric nitrogen (Belyazid et al. 2011a,b; McDonnell et al., 2014; Sverdrup and Belyazid, 2015).

2.2. Forest sites

Three forest sites belonging to the French forest monitoring network RENECOFOR (REseau National de suivi à long terme des ECOsystèmes FORestiers) (Ulrich and Lanier, 1996) were selected for this study (Fig. 1). The selection was based on the availability of the data and with the aim of accounting for different environmental and physiological site characteristics and tree cover. The sessile oak (CHS41) and Norway spruce (EPC87)-dominated sites are located in central France in the Atlantic climatic zone, the former in a lowland region and the latter in an elevated zone. The silver fir-dominated site (SP57) is located in the extreme north-east of France, in the climatic continental zone of the Vosges Mountains (Table 1). The environmental parameters used to model the soil biogeochemistry and tree cover of the three sites are described in Gaudio et al. (2015).

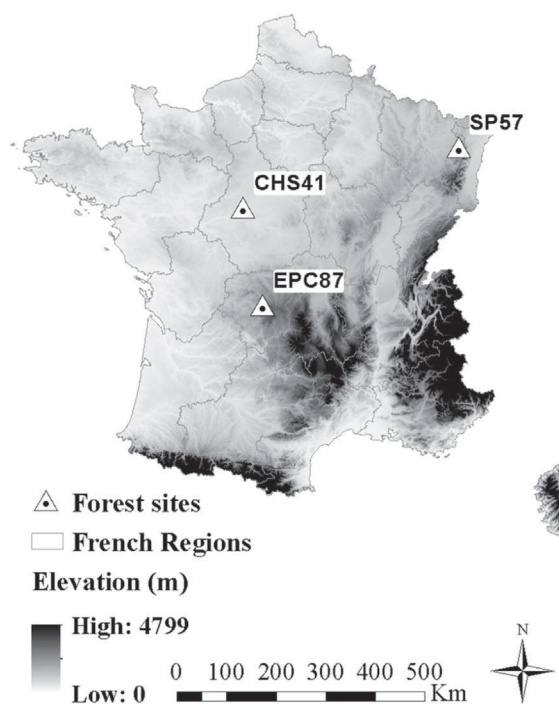


Fig. 1. Location and elevation of the three studied sites CHS41, EPC87 and SP57.

Table 1

Description of the environmental characteristics for the three selected forest sites.

Site	CHS41	EPC87	SP57
Tree dominant species	<i>Quercus petraea</i> Liebl.	<i>Picea abies</i> Karst.	<i>Abies alba</i> Mill.
Latitude	47.568631	45.799222	48.608705
Longitude	1.259404	1.815031	7.133165
Altitude	127 m	650 m	400 m
Mean P/mean Temp. (annual average 1961–1990)	630 mm/10.3 °C	1211 mm/9.8 °C	1091 mm/7.6 °C
EUNIS habitat	G1.8	G3.F	G3.1
Phytosociological reference	<i>Querccenion robori-petraeae</i>	<i>Luzulo sp. pl. – Fagion sylvaticae</i>	<i>Luzulo luzuloidis-Fagenion sylvaticae</i>
Number of understorey species	31	31	48

2.3. Atmospheric nitrogen deposition and climate change scenarios

2.3.1. Atmospheric nitrogen deposition

Three atmospheric deposition scenarios were considered in this study (Fig. 2). The EMEP model was applied to estimate and rebuild the historical trends of atmospheric deposition from 1880 to 1993. The historical trends were scaled to measured monthly bulk deposition available between 1993 and 2008 (Ulrich et al., 1998). From 2010 to 2100, the three scenarios were as follows: (i) the Current Legislation in Europe (CLE) deposition scenario, defined by European legislation and the Gothenburg protocol; (ii) the Maximum Feasible Reduction scenario (MFR), which corresponds to reduced emissions scaled to what is currently technically possible and (iii) a background (BKG) scenario, corresponding to a stable rate of atmospheric deposition from 1880 to the present day.

Atmospheric nitrogen deposition trends at the three sites reached a peak in the 1980s that corresponds to the maximum nitrogen emissions observed in France (CITEPA, 2015). Based on their geographical location, atmospheric deposition was greater at the fir-dominated site than at the oak site. An important deposition decrease has also been observed since the late 1990s that to a certain extent coincides with the reduction in N emissions of around 50% (CITEPA, 2015). These reductions observed up to the present day were then predicted by the EMEP model for the period from 2010 to 2100. Differences in nitrogen deposition between current legislation and the maximum feasible reduction scenarios varied by a factor two between the sites.

2.3.2. Climate change

In the case of climate change, two temperature increase scenarios were adopted (Fig. 2). For the period from 1959 to 2009, data from a meteorological database provided by SAFRAN (from the National Centre of Meteorological Research, CNRM-GAME/CEN) were used (Quintana-Segui et al., 2008). For the period 2009 to 2100, two climate scenarios from the IPCC Special Reports on Emission Scenarios (Nakicenovic et al., 2000) were used: (i) a “no climate change” scenario in which no temperature increase was predicted and (ii) the A2 “high growth” scenario in which the temperature followed the actual rate of increase. In order to obtain a representative current climate year, a ten-year average of temperature and precipitation between 1997 and 2007 was calculated.

Although there was a difference of around 500 m in the elevations of CHS41 and EPC87, the mean annual temperature of the two sites was fairly similar (just 0.5 °C higher at the oak-dominated site). Overall temperature trends were the same for the A2 high growth scenario at the two sites. However, the climate differed in relation to the precipitation regime. The high elevation spruce site located into the northern part of the Massif Central received twice as much precipitation as CHS41. The main difference in temperature regime was observed for the fir site. This site, located in the continental climate of the Vosges Mountains, had a much lower mean annual temperature than the other sites. A higher

temperature increase was observed for the most continental site, SP57, whereas both CHS41 and EPC87 sites had a similar general mean annual temperature trend with both climate change scenarios.

2.4. Plant species

Floristic surveys have been carried out at five-years interval since 1995. There were eight replicated subareas ($S = 100 \text{ m}^2$) at each of the studied sites: four inside a fenced area and the other four outside the fence (Dobremez et al., 1997). Species abundance was evaluated two times during the growing season using the Braun–Blanquet index classes. These abundances were then converted into a mean annual cover percentage used as a reference for the model calibration (Archaux et al., 2009; Camaret et al., 2004).

Since wildlife density was not systematically available for all the sites, the plant niches were calibrated on the fenced relevés. Only species with a cover greater than 1% for at least one year between 1993 and 2010 were used (29 species at the three sites).

2.5. Similarity index

Species richness is a relevant indicator for comparing plant communities in forest ecosystems, particularly boreal coniferous ones (Bobbink, 2008). For this reason, a similarity index was used to evaluate the model simulations against the observed relevés and project plant community changes under the different studied scenarios. The similarity index used here was the Czekanowski (CzI, Equation (1)) (Bray and Curtis, 1957). CzI, also known as the Sørensen index or the reverse Bray–Curtis index, was selected for three reasons relevant to the present cases: 1) it performs equally well on smaller samples, 2) it is well adapted to symmetrical systems (such as the normalised covers used here), and 3) it does not penalise or overly account for the non-dominant species (Bloom, 1981; Wolda, 1981). $CzI = 1$ indicates a perfect fit, and the smaller the CzI, the less the similarity between the two compared communities (modelled and measured or scenario and reference).

$$CzI = 1 - \frac{\sum_{i=1}^N |P_i - O_i|}{\sum_{i=1}^N (P_i + O_i)} \quad (1)$$

where P_i and O_i are the occurrence of the i th item in the predicted and in the observed sample, respectively.

2.6. Presentation of the Veg module

The 29 plant species recorded at the study sites were parameterised for the Veg module (Table 2). At the origin, the hypothetical niches for light, temperature, soil moisture, soil solution nitrogen and soil solution pH were defined based on expert judgement (Probst et al., 2015) and statistically derived responses from the ecological database EcoPlant (Coudun and Gégout, 2005;

Gegout et al., 2005) for 415 species. The details of the procedure are explained in Probst et al. (2015). The niches were adapted to the structure described in Belyazid (2006), and included the physiological traits of shading height and rooting depth used for plant competition (Table 2).

shade-tolerant species. As it is a heliophilous species that bears fruits abundantly only in full sunlight (Rameau et al., 1989), its response to light intensity was extended to match the requirements of shade-tolerant and heliophilous species. With these adjustments, a greater similarity between the observed and modelled

Table 2

Structure of the Veg table: extract of the list of plant species and environmental factors parameterisation used on the three sites (only a sub-sample of the 29 species used in this study is presented). Parameters: **K+**, **K-** and **w** are relative to plant Nitrogen response; **kCa** is relative to retarding Calcifuge effect, **pHhalf** is relative to plant response to pH; **Wmin**, **Wtop** and **Wmax** are relative to plant response to water availability; **Tmin**, **Ttop** and **Tmax** are relative to plant response to temperature; **Lmin** and **Lmax** are relative to plant light requirements; **years** is a delay time parameter; **h** is the plant shading height. For more details relative to the parameters, see Belyazid et al. (2011a,b) and Probst et al. (2015).

Latin_name	Number of plants 14			mgCa.L ⁻¹ kCa	pH pHhalf	% Water saturation			Yearly average (°C)			μmol(photons).m ⁻² .sec ⁻¹			Group	
	mgN.L ⁻¹		Unitless			Wmin	Wtop	Wmax	Tmin	Ttop	Tmax	Lmin	Lmax	years		h(m)
	K+	K-	w													
Atrichum_undulatum	1.5	1000	1	0	3.4	0.12	0.22	0.48	-1	7	15	60	150	5	0.02	Moss
Dicranum_scoparium	0.9	20	1	0	3.4	0.01	0.1	0.3	-1	7	15	60	200	5	0.03	Moss
Polytrichum_formosum	1.2	100	1	0	3.5	-0.1	0.08	0.32	2	8	16	45	180	5	0.03	Moss
Athyrium_felix_femina	1	1000	1	0	3.8	0.18	0.35	0.62	0	8	15	6.25	40	20	0.3	Fern
Dryopteris_affinis	0.5	10	2	0	3.3	0.19	0.3	0.6	2	10	17	10	50	20	0.3	Fern
Dryopteris_carthusiana	1	10	2	0	3.2	0.18	0.3	0.6	0	8	16	15	50	20	0.3	Fern
Festuca_altissima	1.5	1000	1	0	3.7	0.14	0.22	0.6	-2	5	9	20	50	10	0.3	Grass
Luzula_luzuloides	0.5	10	1	1000	3.4	0.08	0.2	0.55	-1	5	9	40	150	5	0.3	Herb
Oxalis_acetosella	1.2	1000	2	0	3.8	0.18	0.32	0.54	-1	6	14	10	50	2	0.05	Herb
Rubus_fruticosus	0.8	10	2	0	3.2	0.05	0.14	0.4	3	11	22	45	220	10	0.5	Shrub
Rubus_ideaus	1	100	1	0	3.4	0.08	0.15	0.4	2	7	18	80	249.25	3	0.5	Shrub
Vaccinium_myrtillus	0.2	1	1	0	3	-0.1	0.15	0.3	-4	5	11	80	200	10	0.3	Shrub
Abies_alba	1.5	100	1	0	3.7	0.1	0.25	0.475	-4	6	12	50	200	60	0.5	Tree
Picea_abies	0.8	10	1	0	3	0.16	0.25	0.5	-4	7	12	80	150	60	0.5	Tree
...

Calibration of the Veg parameters consisted in adapting the ecological niche limits of each species to forest environmental conditions in France.

3. Calibration and validation of the Veg table

The calibration of the plant niches was based on observed realised niches from 1995. The subsequent relevés from 2000, 2005 and 2010 were used in the evaluation.

3.1. Calibration

To calibrate the plant species responses to drivers with a significant influence, the ecological niches needed to be adapted to French environmental conditions. The step-by-step procedure is described below. In the first instance, species with more than 5% abundance were considered.

Before the calibration, at the CHS41 oak-dominated site in 1995, the predicted abundance of three main species, including *Lonicera periclymenum* L., *Holcus mollis* L. and *Vinca minor* L., was obviously underestimated. Indeed, the limits of species ecological niches were too restrictive in comparison with the site environmental conditions. *Rubus fruticosus* L. was the main observed species on this site and its cover was also incorrectly predicted by the model. As a consequence, calibration focused on this species first, for which the main driver was response to nitrogen. *R. fruticosus* L. is generally found at sites whose soils have a relatively low nitrogen content (Julve, 1998), such as CHS41. However, the response of *R. fruticosus* L. to nitrogen was calibrated to be more abundant in richer soils. A reduction of the nitrogen response niche allowed a better calibration for *R. fruticosus* L., increasing the similarity between the observed and modelled covers quantified through the Czekanowski index. *R. fruticosus* L. was parameterised as a strictly

aboveground vegetation composition was achieved. However, as the model took the competition effect into account, the modelled response of some overestimated species such as *Hedera helix* L. had to be reduced in order to fit with their observed cover. Since the strength of these species was overestimated, the modelled response of more dominant species was lower than expected. As it is a climbing plant, the shade effect of *H. helix* L. was fixed at 1.2 m. Species response is a function of the product of all the controlling factors. Since the strength of one of these drivers was too high, species cover was overestimated. By reducing the *H. helix* L. shade effect to 0.2 m, since it can cover the ground extensively, the cover percentage of *R. fruticosus* L. and *L. periclymenum* L. increased to the observed level. After these adjustments, the similarity index was 0.6. Less abundant species were then calibrated in order to obtain a better Czi value. Ecological niches of *H. mollis* L. and *V. minor* L. were adapted in relation to nitrogen response, light intensity response and temperature. *H. mollis* L. prefers relatively poor soils as regards the nitrogen content (Julve, 1998; Rameau et al., 1989). As a consequence, parameterising *H. mollis* L. as a less tolerant species to nitrogen led to better model predictions. In contrast, the response of *V. minor* L. to nitrogen was calibrated by increasing its ecological niche since it is a common species on nitrogen-rich soils. Thanks to these ecological niche adjustments, a similarity improvement between the observed and modelled species was observed, with Czi increasing from 0.69 to 0.84.

The final steps in the calibration process consisted of adding species with a cover percentage of around 1% one by one. When added to the list of modelled species, each had its niches adapted with regard to ecological requirements. When new species were added to the model, the similarity between the observed and modelled samples decreased slightly to Czi = 0.82 because of greater biodiversity.

The same method was applied to calibrate the other sites EPC87

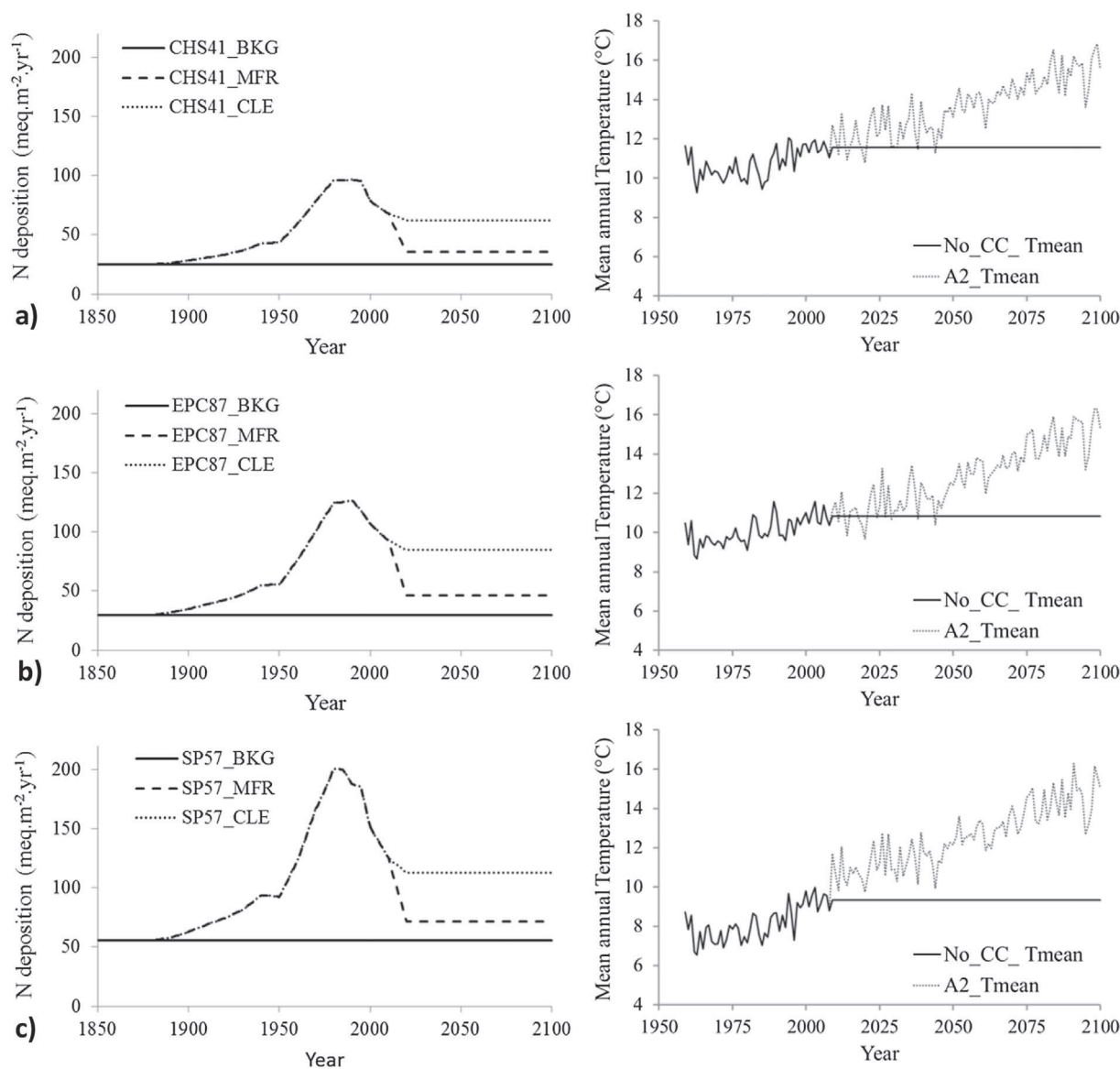


Fig. 2. Nitrogen atmospheric deposition (left) and climate change (right) scenarios for the three studied sites: a) sessile oak (CHS41), b) Norway spruce (EPC87), c) silver fir (SP57). Total atmospheric nitrogen deposition for the period 1800 to 2010 was a) 9050 meq.m⁻², b) 11450 meq.m⁻² and c) 19136 meq.m⁻² for the three sites respectively.

and SP57. Similar results were obtained regarding the evolution of the similarity index, calibrating the dominant species initially and then adding those that were less abundant. The most delicate part of this work was to calibrate species that were common to two or three sites. This was the case for *R. fruticosus* L., *Thuidium tamariscinum* Hedw. and *Polytrichum formosum* Hedw. Owing to the differences in site conditions, the ecological niches of these species were calibrated by making a compromise to obtain the best calibration results for the three sites. As a consequence, the calibration results of these common species were not the best possible ones for each single site, but the final homogenised calibration was the most convenient for the three sites.

3.2. Model evaluation

Model calibration was undertaken using observed data for the year 1995, and the validation was performed by comparing observed and predicted species covers from 2000 to 2010 (Fig. 3). The Czi similarity indices computed in 2000 and 2005 for the three

sites confirmed the fairly good calibration results observed in 1995. Indeed, the similarity rate between the observed and model covers for 2000 and 2005 was around 75% for the oak and the spruce-dominated sites, and even higher for the fir site (82%). Except for some species with low cover, the model was able to simulate species cover evolution faithfully over the years. In 2010, a much lower accuracy was observed for *R. fruticosus* L. and *Polytrichum formosum* Hedw., with these species each being common to two of the three sites. As explained for the calibration in 1995, the homogenisation of these species' ecological niches reduced the model's accuracy. In addition to this calibration process effect, there were obvious discrepancies between the observed and predicted covers for some species. Between 2005 and 2010, a high increase (>25%) of *Quercus petraea* Liebl. was observed in the herb layer, as well as a significant decrease in *R. fruticosus* L. cover. Changes in forest management, such as intermediate cuts or tough climatic events in the years prior to the survey, may lie at the origin of the evolution in these observed covers. Species layer changes (from herb to shrub layer) may also explain these differences.

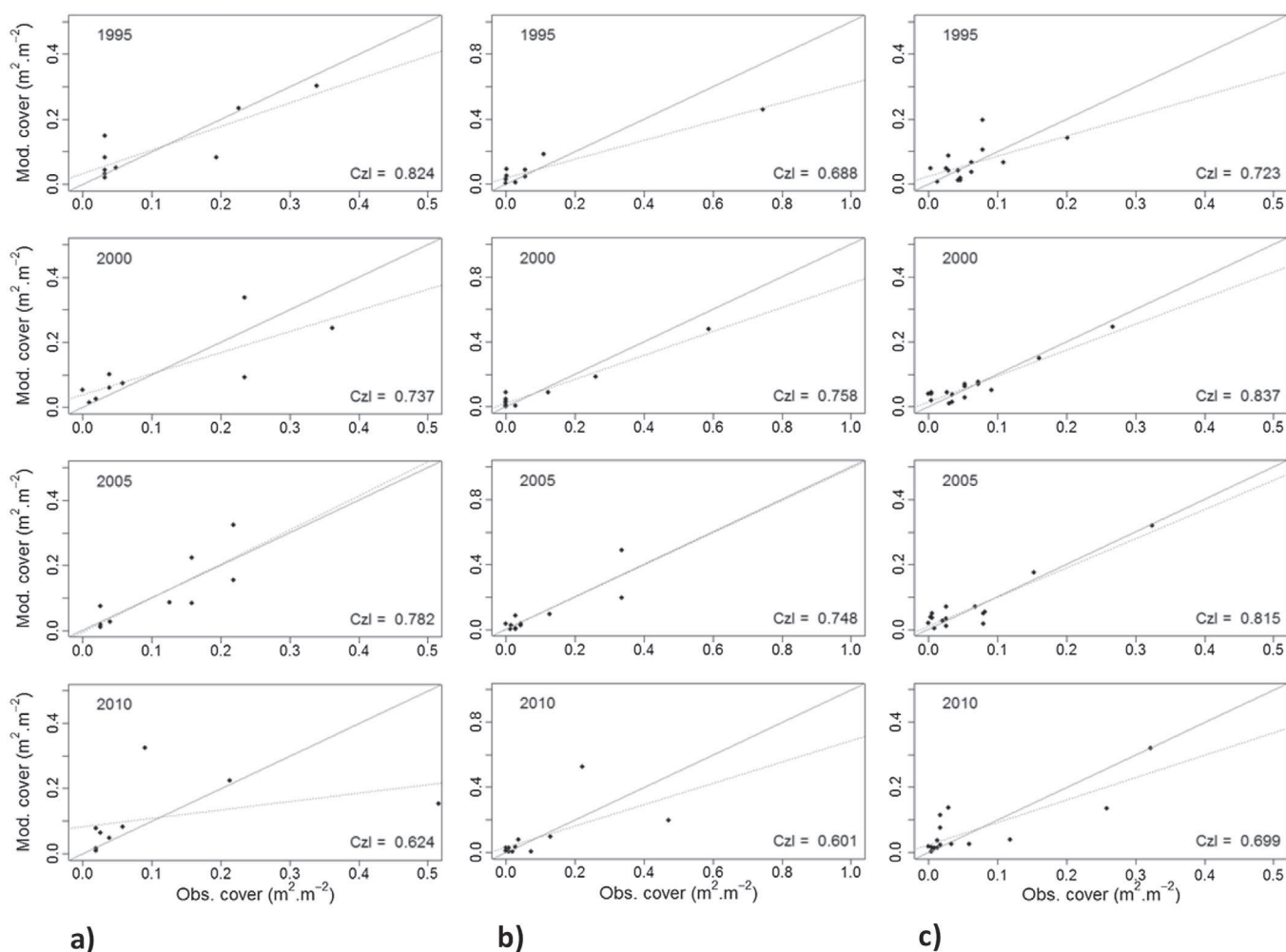


Fig. 3. Calibration of the species for the three studied sites: a) sessile oak (CHS41), b) Norway spruce (EPC87) and c) silver fir (SP57). Calibration was performed on the year 1995 and validation on the years 2000–2010. Czi is the value of the Czekanowski similarity index between observed and modelled cover percentages.

The EPC87 site dominated by *Picea abies* Karst had the lowest similarity indices of the three sites. Compared with the first Czekanowski indices obtained at the beginning of the calibration work (of about 0.5), 75% similarity achieved by the model after the calibration process for the years 2000 and 2005 was fairly good. The difference in performance with the other sites was linked to species composition. Indeed mosses, whose various species have a broad ecological range making them harder to calibrate, represented half of the understory species on this site.

Finally, in order to quantify the evolution in similarity over the years for the observed results on the one hand and for modelled results on the other, similarity indices were calculated between two consecutive years of the survey. The observed similarity between the two years of the survey was always below (–20%) the modelled similarity.

4. Results

Species cover was simulated from 1800 to 2100 under the environmental scenarios described in paragraph 2.3: two for nitrogen deposition and two for climate and then a combination of both. The results presented in Fig. 4 show the evolution in the species response to those scenarios, analysed through changes in the abundance similarity (Czi) between a given reference scenario

(“no climate change” for climate and “BKG background” for nitrogen) and the different scenarios used alone or in combination. The impacts of the environmental changes were therefore analysed at the vegetation community scale and not through the individual species response. As a consequence, the response of species sensitive to nitrogen deposition can drive the similarity change for the biodiversity of the entire site.

4.1. Species composition trends under nitrogen scenarios

The graphs in Fig. 4a, b and c show important variations in the evolution of the plants' abundance similarity in relation to the considered atmospheric nitrogen deposition scenario. A general decreasing trend was predicted, even though the general trend of similarity rate was site specific. If the response of the vegetation similarity to the two scenarios MFR and CLE went in the same direction for the three sites, a greater similarity with the reference scenario was predicted for the MFR scenario. The difference between the scenarios was tenuous, except for the oak site where a more significant change of diversity was predicted if N deposition followed current legislation (CLE scenario) (Fig. 4a). Species response under the CLE scenario overall followed the general trend observed in recent years. A reasonable stability in species abundance over the years was apparent at the *Picea abies* Karst. site

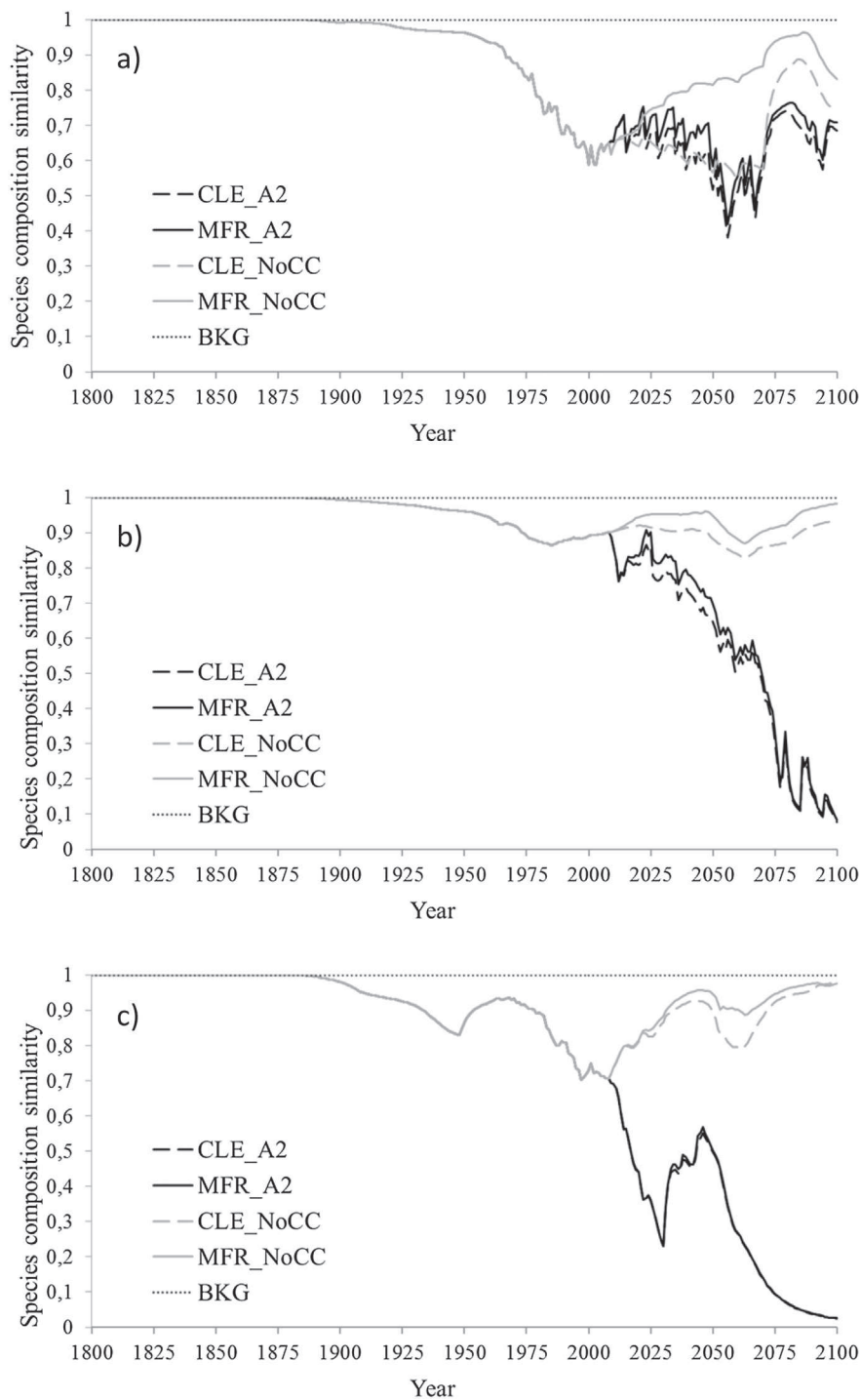


Fig. 4. Evolution in the similarity index between a standard reference (“no climate change” for climate and “BKG” for nitrogen deposition) and the four possible combinations between the MFR or the CLE scenario for N deposition, and the “no climate change” or the A2-“high growth” scenario for climate change. The results are presented for the three sites: a) CHS41, b) EPC87 and c) SP57.

(Fig. 4b). These statements concern general trend predictions. However, short-term fluctuations in vegetation species response could be observed for both scenarios with periods of similarity loss or gain. Such short-term fluctuations were particularly evident at the oak site (CHS41) and the fir site (SP57), for a ten-year period (2020–2075, Fig. 4a) and for longer periods (1950 and 2030, Fig. 4c) respectively, for both deposition scenarios.

4.2. Species composition trends under climate change scenarios

As observed for nitrogen deposition, changes in abundance similarity were also observed when considering climate change scenarios. By 2010, a general decrease in species abundance similarity for the three sites was observed under the A2 – high-growth scenario (Fig. 4). Indeed, this decrease was moderate for the oak-

dominated site (CHS41, Fig. 4a), particularly where it stabilised by 2040 when the temperature increase was more rapid and higher. In contrast, by this date the decrease in similarity was much greater and steeper at the coniferous sites (particularly at the SP57 site). The long-term decrease in species similarity under the influence of temperature increase was interrupted by short periods of an increase in species community similarity for the three sites. These periods were observed every ten years by 2020 for the oak site and were longer with a peak at around 2050 for the coniferous sites (site SP57, Fig. 4c). Two different trends in species response to climate change were therefore observed for the three sites: a general decrease in species community similarity over a long timescale relative to the “no climate change” scenario, interspersed by a regular moderate similarity increase/decrease over short periods of time.

4.3. Species composition trends under a combination of climate and nitrogen scenarios

When combining nitrogen and climate change scenarios, the general trends were preserved. However, smaller differences between the effects of nitrogen deposition scenarios on biodiversity change were observed at the oak site when combined with climate change scenarios. This was also true for the other sites. Indeed, the main general trend in similarity evolution was driven by climate change scenario for all the sites, since the whole plant community trend followed that of the climate scenario.

The secondary trends over short timescales already described for the three sites in the case of the nitrogen and climate scenario

separately were still observed for the scenario using a combination of the two. Although the general trend at the oak site showed a loss of similarity overall when taking climate change into account, an opposite pattern could also be observed, such as in 2070 and 2085. By 2000, these short-term fluctuations were closest to those observed for the nitrogen scenario. Over this short timescale, species abundance seemed to reach the standard plant composition. The same observation was made for the fir site in around 2030.

4.4. Species cover trends under a combination of climate and nitrogen scenarios

In addition to the evolution of plant community similarity under global changes, specific plant response to the four combinations of scenarios was considered. The results are presented for two important understory species at the oak site CHS41 (Fig. 5a, b) and at the fir site SP57 (Fig. 5c, d).

Hedera helix L. cover changed according to the different N deposition. This species was favoured in 2010 under current legislation (CLE) since its cover increased greatly (Fig. 5a). As found with the evolution of the community regarding the similarity criteria (Fig. 4a), this species was favoured under climate change (A2 scenario) in the same way as the CLE response. The same trend could be observed for *Oxalis acetosella* L. as it was favoured in 2010 and by 2060 under current legislation (CLE). However, unlike to *Hedera helix* L., *O. acetosella* L. and *Abies alba* Mill. cover is drastically reduced under climate change (A2 scenario), whatever the N deposition scenario (Fig. 5c, d). In contrast, by 2010, *Holcus mollis* L. cover appeared to be favoured under the low N deposition scenario

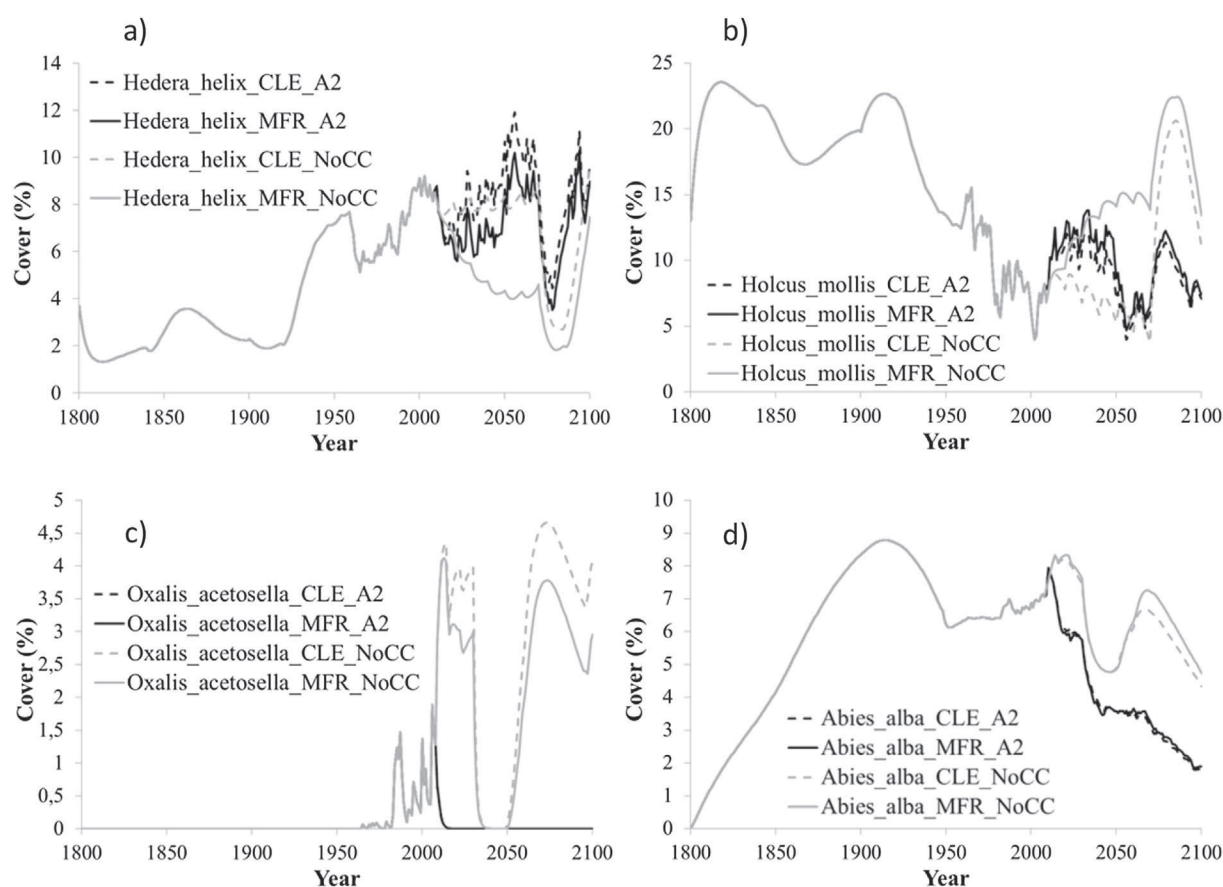


Fig. 5. Evolution of plant cover (%) under combinations of N deposition and climate change scenarios: a) *Hedera helix* L. and b) *Holcus mollis* L. for the oak site CHS41, c) *Oxalis acetosella* L. and d) *Abies alba* Mill. for the fir site SP57.

(MFR, Fig. 5b), as well as *Abies alba* Mill. (Fig. 5d). The response to climate change scenario A2 went in the same direction but was more tenuous. The response of *Holcus mollis* L. cover to the four scenarios in combination followed the trend observed for the similarity of the species community. *Hedera helix* L. followed the exact opposite trend, as it seemed to be stimulated by CLE and climate change, and was reduced by MFR low N-deposition rates. The long-term evolution in the cover of these four abundant understory species was disturbed by short-term episodes showing a dramatic decrease or increase (Fig. 5a, b, c, d).

5. Discussion

5.1. Long-term trends in biodiversity: the role of nitrogen deposition and temperature

The divergence in plant similarity from the reference population closely mirrored the trend of atmospheric N deposition at the three studied sites. This mirroring effect was mediated by the response of soil solution nitrogen to deposition, as shown in Gaudio et al. (2015). Depending on the species' nitrogen affinity, changes in N concentrations in the soil solution can either increase or decrease the cover of that species. For example, *Hedera helix* L. and *O. acetosella* L. responded positively to higher N availability due to elevated N deposition (Fig. 5a, c), in accordance with the observed realised niches (see for example Rameau et al., 1989). On the other hand, the cover of *Holcus mollis* L. declined with elevated N deposition, reflecting its observed low N affinity (Fig. 5b).

Unexpectedly, in the absence of climate change, the similarity index showed a strong recovery, mirroring the reductions in deposition, particularly under the MFR scenario. Although the simulated recovery was gradual and significantly delayed following the reduction in deposition, it was expected to be substantial by the end of the century. Even more interestingly, the sites with the higher historical deposition (EPC87 and SP57) showed as much potential for recovery as the site with low deposition (CHS41). This may be due to the plant species being used for the simulations, which only included plants currently observed at the respective sites. As the sites have been exposed to elevated N deposition for over a century, it is highly probable that the present plant community is already adapted to elevated N loads.

It was also obvious that climate change had a strong impact on plant species, since a significant loss of similarity occurred under the A2 scenario compared to the situation with no climate change. As with N deposition, species were either positively or negatively impacted by temperature increase, resulting in changes in their spatial distribution and composition. The significant decrease in community similarity observed for the coniferous sites had to be linked to a high temperature increase rate (see Fig. 2). This impact on vegetation species could be direct or indirect, as they could act on species temperature requirements or soil biogeochemistry. Inorganic N concentration in soil solution simulated by ForSAFE was significantly lower under the "no climate change scenario" than under A2 (Gaudio et al., 2015). At higher temperatures (under climate scenario A2), faster rates of organic matter decomposition and mineralisation could accelerate the nitrogen cycle, with the consequence of increasing N concentrations in the soil solution (Butler et al., 2012; Guntiñas et al., 2012). This was the case for *Holcus mollis* L. (Fig. 5b), whose cover under climate change followed the same trend as under high N deposition (CLE). Moreover, it can lead to less water drainage due to higher evapotranspiration from trees, as well as a decrease in the precipitation regime, favouring the systematic increase of N concentration with temperature (Weemstra et al., 2013).

However, there were differences between the sites. For example,

the greatest long-term impact of N deposition either under normal temperature conditions or under climate change was observed for the oak site CHS41. This site actually received the lowest rate of N deposition between 1800 and 2010 (see Fig. 2), and had the highest mean annual temperature (see Table 1). An adaptation of the observed plant community to relatively warm conditions, as well as a disruptive N niche exceedance, could lead to this evolution in similarity. In contrast to the CHS41 plant community, species observed on the two other sites had been exposed more to atmospheric N. Thus, their plant communities had already adapted to higher N deposition rates that may explain the lower effect of CLE. Moreover, the low differences observed between MFR and CLE scenarios without climate change in the case of EPC87 indicated a relative stability in species composition similarity over the long term, but could also be explained by the fact that the difference in deposition between CLE and MFR was relatively small. Half of the species observed and modelled at this site were mosses. In comparison with other vegetation groups, mosses have a weaker response to N pressure (Stevens et al., 2010). For a given N deposition scenario, when considering the combined effect of N deposition and temperature increase, the significant decrease in species similarity observed under climate change could be linked to a higher influence of temperature increase on this group. As the moss layer is generally favoured under a *Picea abies* Karst. canopy thanks to the creation of a microclimate (Augusto et al., 2003), a general temperature increase in the stand environment may affect the moss layer and lead to a greater loss of similarity.

5.2. Short-term trends in biodiversity: the role of forest management and disturbance

In addition to the combined effects of nitrogen deposition and climate change, the general trend of a decrease in similarity was disrupted in regular short periods at all sites, irrespective of the general patterns of nitrogen deposition or climate change influences. These discontinuities corresponded primarily to anthropic forest management actions in the stands, such as clearcutting and thinning, or storms. This was particularly evident for sites CHS41 and SP57, where the number of herbaceous species was higher. At both sites, the similarity index was highest following the prescribed clearcutting in 2070 and 2030 respectively. The abrupt effects of clearcutting, involving opening up the canopy and dramatically disrupting the soil solution chemistry, can overshadow N deposition and climate effects in the short term. Forest management therefore had a short-term resilient effect on plant community, with the consequence of completely modifying the general trend of plant community similarity for a few years.

On the fir site SP57, a high increase in similarity was observed by 2030, corresponding to the period of the prescribed clearcutting. At species scale, an important decrease in shade-tolerant species cover occurred in 2030, such as for *Abies alba* Mill. and *O. acetosella* L. (Fig. 5c, d). These species, whose cover increased with N deposition or climate change, recovered the relative abundance they had before the N increase. Over a short period, forest management caused changes to species community dynamics, thus partially compensating for the overall effects of change.

5.3. Influence of site characteristics

Although N deposition and climate had an impact on species composition, the environmental characteristics (geographic location, pedoclimatic conditions) of the sites determined the original plant community in terms of their original floristic composition and dominant tree species.

The smaller loss in similarity predicted for the oak site in

comparison with the spruce site (Fig. 4) for the combination of N deposition and climate change, had to be related to the higher mean annual air temperature due to its lowland geographic situation in the Atlantic zone. Indeed, lowland communities have a greater tolerance to temperature increase thanks to the larger proportion of thermophilous and cosmopolitan species (Bertrand et al., 2011; Thuiller et al., 2005). By contrast, the greater decrease in similarity observed for the two coniferous sites could be explained by the dominance of mosses, which are sensitive to warmer climates and the narrow habitat tolerance of the mountain flora (Bertrand et al., 2011; Thuiller et al., 2005). Indeed, the richness of moss species in understory vegetation observed under fir and spruce canopies (Augusto et al., 2003) is due to these dominant tree species, which promote moss cover and reduce herb cover by creating a moister and cooler microclimate under the canopy (Mikola, 1985; Saetre et al., 1997). Changes in temperature and precipitation regime under the A2 scenario limited the microclimate effect of the conifer canopy and contributed to the significant loss of species similarity under climate change.

Brief similarity recovery effects were observed at the oak site under the climate and nitrogen scenarios (particularly CLE). Dominant tree species may also have had an indirect short-term impact on species response to combined N and climate change through forest management. Indeed, more regular low intensity cuts were performed at the oak site CHS41 than at the spruce site. These management practices slightly modified site conditions, such as the incident light reaching the ground. This had an impact on the response of understory species by favouring oak seedlings for example, and caused a recovery of similarity to values observed before the scenario impacts. For the coniferous sites, the management practices (cut in 2036 and 2030) had led to a considerable decrease in similarities for the fir site (SP57) but had much less of an impact for the spruce site (EPC87). Indeed, the moss species, of which the species community at the two sites was mainly comprised, may not react in the same way to changes in canopy opening.

6. Limitations and perspectives

In order to calibrate the ecological model Veg, some hypotheses had to be proposed concerning species response to environmental factors. The first limitation introduced into the model calibration work concerned observed data. Floristic surveys undertaken every five years evaluate species abundance-dominance on the Braun-Blanquet scale (Delpech et al., 1985). However, this method uses classes to mark the cover percentage of species represented by one index. As a consequence, the species abundance evaluation may be underestimated or overestimated if species cover is close to the boundaries between two classes for example. This limitation can be seen between the field observation and the data in the database. Another uncertainty can also be introduced into observed data when comparing modelled and observed species covers. Indeed, observed covers are obtained by reconvertng the Braun-Blanquet indices of abundance into cover percentages by taking median values of each class (Archaux et al., 2009). This succession of cover conversions from the original data to the observed data used in this work, although necessary, introduced some uncertainty into the observed data that may cause a loss of accuracy in the model calibration.

The availability of observed data constituted another limitation of the modelling approach. As presented in paragraph 3, the model was calibrated on the year 1995 for the three sites so that this calibration could be validated with observed data for the other years. However, some species observed in 1995 were not as dominant as in other years (Fig. 3). This might explain why for some

species, similarity differences were observed between calibration and validation years.

Concerning the analysis of results, the Czekanowski similarity index involved a comparison of species response under the combination of N deposition and climate change scenarios with species response under a reference scenario. Due to the index characteristics, single species responses have a cumulative effect on community evolution, even when an antagonist effect is expected. Indeed, when one species is favoured by climate change while the abundance of another is reduced, a neutral balance effect on the community is expected. However, as the cover of the first species is increasing and the cover of the second one is decreasing, the overall result is that both covers are different from their level before climate change. As a consequence, a loss of similarity is observed. So, one limitation of this index is that while seeing an effect of environmental changes on the species community response, it is not possible to determine whether species are being favoured or reduced by these changes.

The selection of species for modelling may also represent a limitation of the modelling approach. Indeed, observed data for a given species were sampled on each site by distinguishing its cover in each layer in which it was present. The observed vegetation layers were the moss layer, the herb layer, the low and high shrub layers, and the low and high tree layers. As the biogeochemical-ecological model ForSAFE-Veg modelled the evolution of understory species, only covers of species that were present in the moss and the herb layers were considered. This meant that species were taken into account up to a 30 cm height, which corresponded to the upper limit of the herb layer for the RENECOFOR network. For this reason, trees were no longer integrated into the modelling work as they were above 30 cm. This could explain part of the model validation dissimilarity observed for the oak site in 2010. In the present study, layer changes of species were not taken into account, probably introducing another bias into the results.

Finally, the last limitation encountered in this study could be the impact of wildlife browsing. As explained in paragraph 2.4, it was not possible to take the impact of animals on vegetation into account as data relative to wildlife density were not available at that time. However, populations of wild ungulates (deer, roe deer and wild boar) have increased at least fourfold in the last 25 years (Saint-Andrieux et al., 2013). Considering the evolution of species in the inner subareas could lead to the introduction of an experiment bias as one natural condition impacting species growth was missing. The next step in this work would be to collect data on wildlife intensity in order to model species evolution that is closer to natural conditions.

7. Conclusions

This study adds to the growing body of empirical and modelled evidence showing that although nitrogen deposition can have a strong effect on plant communities in forest ecosystems, climatic changes have the potential to be the main driver of change this century. However, this conclusion should be viewed with some caution since this study showed that, in relative terms, the site with the lowest accumulated N deposition, the sessile oak forest, had the weakest response to climate change and the most pronounced and enduring response to N deposition. This reflected the currently predominant hypothesis that nitrogen-poor ecosystems are most vulnerable to N deposition while N rich ecosystems are likely to have already adapted to elevated nitrogen loads.

The calibration and evaluation of the Veg model boosted confidence in its performance and reinforced the relevance of the concept behind the model. The latter builds on the premise that it is possible to reproduce realised niches and intra-community

competition by combining fundamental niches and physiological properties of the plants. Based on unique sets of species-specific fundamental niches and traits, the model is able to reproduce different realised niches over a wide nitrogen load gradient. This in turn points to the potential for expanding the geographical application of the model.

This study and its conclusions would not have been possible without the availability of high-quality and consistent empirical data at the study sites, covering biogeochemical indicators as well as forest floor plant communities. The results presented here again stress the need for long-term integrated monitoring to be maintained, not only for its intrinsic informative value, but also as an irreplaceable basis for constructing and anchoring predictive models.

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