A model-based scenario analysis of the impact of forest management and environmental change on the understorey of temperate forests in Europe

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Abstract

The temperate forest understorey is rich in terms of vascular plant diversity and plays a vital functional role. Given the sensitivity of this forest layer to forest management and global environmental change and the limited knowledge on its long-term dynamics, there is a need for decision support systems that can guide temperate forest managers to optimize their management in terms of understorey outcomes. In this study, using understorey resurvey data collected from across temperate Europe, we developed Generalized Additive Models (GAM) to predict four understorey properties based on forest management and environmental change data, and implemented this model in a web-based tool as a prototype understorey Decision Support System (DSS). Using seventy-two combined climate change, nitrogen(N) deposition and forest management scenarios, applied to two case study regions in Europe, we predicted temperate forest understorey biodiversity dynamics between 2020 and 2050. A sensitivity analysis subsequently allowed to quantify the relative importance of canopy opening, N deposition and climate change on understorey dynamics. Our study showed that, regardless of regions, understorey richness and the proportion of forest specialists generally decreased among most scenarios, but the proportion of woody species and the understorey vegetation total cover increased.

Climate warming, N deposition, and increases in canopy closure all influenced understorey dynamics. Climate warming will shift composition towards a selection of forest generalists and woody species, but a less open canopy could mitigate this shift by increasing the proportion of forest specialists. The case studies also showed that these responses can be context-dependent, especially in terms of responses to N deposition.

Keywords: Temperate forest, climate change, N deposition, scenario analysis, DSS, sensitivity analysis, regional scale

1 Introduction

The forest understorey layer is the forest stratum composed of vascular plants with a height below ca. 1 m, and is a crucial diversity reservoir in temperate forest ecosystems, containing more than 80% of the vascular plant diversity (Gilliam, 2007). Besides, this layer plays an essential functional role in temperate forests, for instance, by influencing tree regeneration, water cycling, nutrient, and carbon dynamics (Landuyt et al., 2019).

Substantial research efforts have been invested into how the diversity and functioning of the understorey community is being affected by multiple environmental drivers during the last decade (e.g. (Bernhardt-Römermann et al., 2015; Dries Landuyt et al., 2020). These studies have found, for example, that climate warming can cause a “thermophilization” of the understorey community, reflected in declines in cold-adapted species and increases in warm-adapted species (De Frenne et al., 2013; Zellweger et al., 2020a). Moreover, elevated levels of N deposition can lead to acidification and eutrophication at the forest floor (De Schrijver et al., 2011; Schmitz et al., 2019), leading to a replacement of oligotrophic species by eutrophic species (Dirnböck et al., 2014; Verheyen et al., 2012), and often also a decline in species richness (Gilliam, 2006). Besides these global change drivers, also management has been found to influence the understorey. Different forest management practices, ranging from drastic overstorey species conversion to subtle differences in silvicultural systems, have all been shown to affect understorey composition. Verstraeten et al. (2013), for example, found that overstorey conversion from a temperate mixed deciduous forest to spruce plantation may lead to a compositional turnover in the understorey, leading to an increased abundance of light-demanding and acid-tolerant understorey species. Similar effects have been found when comparing alternative silvicultural systems. Selective cutting, for example, has been found to have a negative effect on both the structural and functional plant diversity compared to traditional coppice-with-standards management (Decocq et al., 2004). Finally, also forest management intensity may change the functional composition of the understorey (Patry et al., 2017). Förster et al. (2017), for example, found that understorey species richness may increase in intensively managed forests, mainly because of an increase in canopy openness. In addition to these direct effects, forest management can also affect the availability of resources (mainly light) for the understorey, via its effect on tree cover, and can therefore decouple local resource availability and growing conditions from regional trends, potentially buffering responses of the understorey to global change(Depauw et al., 2020; Dries Landuyt et al., 2020).

Future responses of the understorey to global change, however, are still difficult to predict. Context-dependencies and interactions between different global change drivers and forest management make it often hard to apply the findings above to predict understorey dynamics in a specific setting(Perring, et al., 2018). Especially since previous studies have focussed predominantly on system understanding and inference, and less on improving the predictive ability of their models (Landuyt et al., 2018). This lack of predictive models (in contrast to those available for overstorey modelling (e.g. Bugmann, 2001; Reyer, 2015) makes it extremely hard for forest managers to account for the understorey while taking management decisions. Since numerous forest managers are starting to acknowledge the importance of the understorey and are widely concerned about biodiversity, climate change, and forest regeneration in temperate deciduous forests (Blondeel et al., 2021), there is a clear need for predictive understorey models and, more importantly, decision support systems (DSS). These DSS generally combine a user interface with simulation tools whose outcomes are translated into relevant information for decision-making (Muys et al., 2011). However, understorey DSS are currently not available, mainly due to the limited availability of understorey models with an acceptable predictive performance (Landuyt et al., 2018; Blondeel et al., 2021).

In this study, we present a proof-of-concept prototype understorey DSS and, by applying our DSS, show how forest understorey communities respond to a combination of changes in forest management and changes in environmental conditions. Based on the European scale understorey resurvey database forestREplot (http://www.forestreplot.ugent.be/) , we fitted multiple GAM models to establish empirical links between a set of key understorey properties, including species richness, vegetation cover, the percentage of woody species and the percentage of forest specialists, and a set of environmental predictors, including canopy closure, climate, N deposition and soil data. Next, we developed a web-based tool as a prototype understorey DSS using the fitted GAM model to predict future responses of the understorey to forest management interventions and global change. Using scenario analyses, we predicted understorey dynamics under multiple policy-oriented climate change, N deposition and forest management scenarios from 2020 to 2050, for two case study regions in Europe. Based on a sensitivity analysis, we finally quantify the relative importance of canopy closure, N deposition and climate change on understorey dynamics within both case study regions.

2 Methods

2.1 Model setup

2.1.1Data collection

Understorey data was retrieved from the forestREplot database (https://forestreplot.ugent.be/). From this database, we selected a subset of plots, following Perring et al.(2018), using 40 datasets (1814 plots) containing resurvey data (i.e. vegetation survey conducted at two points in time) distributed across temperate Europe, with an average interval of 38 years between the initial and recent vegetation surveys (Perring, Diekmann, et al., 2018). All plots are considered ancient forest plots that have been forested continuously since 1850 or earlier. Each dataset (containing data on multiple plots within a specific region) in the forestREplot database comes from a relatively homogeneous area in terms of climate and atmospheric N deposition, so we considered all plots within a given dataset to experience similar macroclimatic and atmospheric N deposition conditions. We complemented the data from the forestREplot database with data from the PASTFORWARD database (https://pastforward.ugent.be/) , the latter containing data on 192 temperate forest plots scattered across 19 regions within the Central-Western European temperate deciduous forest biome along spatial environmental gradients of atmospheric N deposition and climate conditions (Maes, et al. 2020). For each plot, both databases hold information on plot size (m^2), survey year, MAT(°C), atmospheric N deposition (kg ha^{-1} $year^{-1}$ of N), mean annual precipitation (MAP, mm) and understorey and overstorey composition both for the original and repeated surveys (Bernhardt-Römermann et al., 2015; Maes, et al., 2020; Perring, et al., 2018). We extracted topsoil pH (0-5 cm) values for all plots from the SoilGrids database with a spatial resolution of 250m (Batjes et al., 2020). We recalculated tree cover percentages using the Fischer correction method to obtain total tree cover values between 0 and 100% (Bernhardt-Römermann et al., 2015). These environmental variables (Figure 1) were used as predictor variables to train and test a set of general additive models to predict understorey composition (see section 2.1.2).

We selected four understorey response variables, these being understorey species richness, Fischer-corrected total understorey vegetation cover (%), the proportion of woody species (%) and the proportion of forest specialists (%). The richness and Fischer-corrected vegetation cover were directly estimated from the forestREplot and PASTFORWARD databases. We counted all woody species in a plot and calculated the proportion of woody species as the ratio of the number of woody species to total richness. This proportion of woody species can be a proxy for the amount of woody regeneration in the understorey. We extracted 'woodiness' (two levels: woody versus herbaceous) as a functional trait from the LEDA trait database (Kleyer et al., 2008). We used the proportion of forest specialists (specialist versus non-specialist) as a proxy for number of species with conservation concerns, as these species are linked explicitly to ancient forests. Heinken et al. (2022) have created a list of vascular plant species for 24 geographical regions across 13 countries in Western, Central and Northern Europe to classify forest specialist and generalist species based on their affinity to forests. We tallied the number of times each species was counted as a specialist across all countries (categories “1.1” and “1.2”). If this specialist tally was higher than all other classes combined, it was classified as a specialist and otherwise as a generalist. These four variables (Figure 1) were used as response variables to train and test a set of general additive models (see section 2.1.2). As not all records in the final dataset contained data on all of the selected variables, we eliminated those records with missing data and retained a dataset with 3733 records for modelling, including records from both the initial and recent vegetation surveys conducted in the 2006 selected plots.

2.1.2 GAM model training

We applied general additive models (GAMs) to fit non-linear relationships between the environmental predictor variables and the understorey response variables using R 4.1.1(R Core Team, 2020; Wood, 2017). The separate non-linear effects for multiple environmental variables are added together in the GAM models, and thus produce complex compound effects depending on the input values. The GAM model structure (see Equation 1) included seven independent variables, including five environmental variables (N deposition, MAT, Tree cover, MAP and pH), and two survey-related covariates (Plot size and Survey year). We consistently used the same independent variables in the GAMs for all four response variables, being species richness, the Fisher-corrected understorey vegetation total cover (%), the proportion of woody species (%) and the proportion of forest specialists (%). For each response variable, we selected optimal link functions given the distribution of the data rather than transforming the response variables to make residuals normally distributed. A Poisson distribution for richness was used because these are count values (Oksanen et al., 2019). For the three other response variables, the beta distribution was used because these continuous proportional values are bounded between 0 to 1 (Douma & Weedon, 2019). For model training, we used data from the initial and recent survey as independent records, comparable to a traditional space-for-time approach.

$$Response \sim s(N\_deposition) + s(MAT) + s(Tree\_cover) + s(MAP) + \ s(pH) + s(Plot\_size) + s(Survey\_Year)$$

(Equation 1)

We first did multicollinearity analysis among selected seven independent variables, all VIF values were below 5 which means there is no multicollinearity among independent variables (see online supporting information Table S1). Then, we randomly split the complete dataset without empty records (n=3733) into five equal portions and divided the five equal portions into a training dataset(n=2986) and an independent training dataset (n=747). We first used the training dataset cross-validated the GAMs to select the optimal splining method and the dimension (k) of the included smoothing terms to make robust predictions, while avoiding overfitting. And then we used the testing dataset to test the final model performance when the training procedure via cross-validation was finished. The detailed cross-validation of the GAM model can be found in the online supporting information. Our analysis can be regarded as a machine learning approach, which aims to maximize the predictive performance rather than focus on statistical inference. Hence, spatial autocorrelation, potentially violating statistical model assumptions, was not considered as being problematic in our analysis.

2.1.3 Model performance

After model optimization, the penalty type was set to cubic regression splines, and the number of dimensions (k) was set to 3 (Final model see Equation S1). When reviewing the model fits for the final GAMs (Figure S5), we found relatively low R^2 values overall. These low R^2 values largely reflect the large variation in the observations (see pairwise scatterplots between all four response variables and each of the seven predictor variables in the online supporting information (**Error! Reference source**

not found.S4)). For understorey richness, the proportion of forest specialist and the proportion of woody species, the predictor variables explained 20% of the variation but with relatively even residual variance over the range of fitted values. This means that across the range of environmental values, the mean values of observations roughly match the mean values of predictions. However, for cover, R^2 was found to be low (10%), which resulted in a consistent prediction of the intercept value. Such a consistent prediction of the average cover value across the whole data range means that cover will likely be insufficiently sensitive to a change in environmental condition. Hence, both scatterplots showed that the GAMs cannot accurately predict forest properties in one particular site, but can pick up averaged trends of the species richness, proportion of woody species, and proportion of forest specialists across environmental gradients.

2.1.4 Model predictions

To perform predictions based on the fitted final GAM models (as done in the DSS and for the two cases studies in this manuscript), all predictor variables were set to a specific value, representing a certain environmental change and management scenario. Predictor variables that were less relevant for performing predictions, including 'survey year' and 'plot size', were either set to a fixed value (plot size was set to 100m²) or excluded from the model (survey year) when calculating a certain expected understorey response., While 'survey year' was excluded as a moderator on the expected value by using exclude function from mgcv library (Wood, 2017), it was included when calculating the standard error on the predictions. This means that, for a prediction in the future, 'survey year' will not change the value of the prediction but it will affect the amount of uncertainty associated to the predicted value.

2.2 Development of the understorey DSS

With our fitted models being the underlying machinery, we developed a proof-of-concept forest understorey DSS (named underscore, see https://underscore.shinyapps.io/understorey_tool_project/) with the Shiny and Leaflet libraries from R (Chang, W.,et al., 2020; Cheng, J., et al., 2020; R Core Team, 2020). This web-based shiny application can provide the user with trends of changes in the understorey for a range of environmental scenarios between 2020 and 2050.

2.2.1 Geographic extent and spatial resolution

We set the spatial-environmental boundaries of the DSS to the temperate mixed deciduous forest biome of Central-Western Europe (Figure 2). To identify this biome, we selected the area taken up by the Atlantic Central, Atlantic North, Continental, Nemoral, and Pannonian Environmental Zones by using the climatic stratification of Europe(Metzger et al., 2005). We regionalized these environmental zones into the Nomenclature of Territorial Units for Statistics (NUTS) administrative regions of the European Union (EU) and the United Kingdom(UK), which is a hierarchical system for dividing up the economic territory of the EU and the UK (Eurostat, 2018). We selected the NUTS level 1 for our purpose which separated administrative regions of countries on the level of major socio-economic regions (e.g. federated states in Germany) (Eurostat, 2018). We randomly sampled 30 points within each NUTS region. These sample points were used to calculate regional averages of environmental variables and were used as the current input data for the DSS.

2.2.2. Definition of current environmental conditions

For each NUTS region, we included data on the current MAT, MAP, N deposition, and topsoil pH (0-5cm) in the DSS. We used the CRU TS3.4 (Harris et al., 2014) climate database to calculate the long-term climate between 1980-2015. We recalculated this monthly average surface temperature and precipitation data into MAT and MAP values and used them as current values. This climate dataset was also used to complement the understorey resurvey data with climate data, data that was used for model training (Perring et al., 2018; Maes et al., 2020). We used the recent N deposition data for the year 2018 from the European Monitoring and Evaluation Program on air pollution data (EMEP, 2019) to estimate the current average annual N deposition at a spatial resolution of 1 degree by 1 degree.

We refrained from using long-term cumulative N deposition data, because such values currently do not have a clear policy implication while annual deposition values do (Dirnböck et al., 2018). We integrated the available data on dry and wet oxidized and reduced N from the EMEP MSC-W model (“DDEP_OXN_m2Grid”, “WDEP_OXN_m2Grid”, “WDEP_RDN_m2Grid”, “DDEP_RXN_m2Grid”), and recalculated the data into an average N deposition in kg N·ha^{-1}·yr^{-1} as current values across the NUTS regions. We included information on topsoil acidity (pH 0-5 cm) using the 250m resolution spatial data from the SoilGrids database (Batjes et al., 2020). Given that there are no policy targets associated to MAP and topsoil pH, these two variables are treated as constant through time in the DSS and hence not considered as dynamic inputs that can be modified by the users.

2.2.3. Definition of future environmental conditions

For the definition of future global change scenarios in the DSS, we build upon the work of Dirnböck et al.(2018), who evaluated forest plant species trajectories under current legislation emission scenarios of N deposition in combination with climate change scenarios (Representative Carbon Pathways, RCP). We allowed three types of model inputs to vary, being N deposition, climate, and canopy closure. The latter as a proxy for forest management intensity. We used existing policy scenarios for N deposition from the First Clean Air Outlook(COM(2018)446) (European Commission, 2021) including a business-as-usual (BAU) scenario and a current legislation (CLE) scenario. The BAU scenario propagates the same annual rate of N deposition from 2018 until 2050. Data on the CLE scenario for N deposition are available on the Greenhouse Gas – Air Pollution Interactions and Synergies portal (GAINS: https://gains.iiasa.ac.at/models/) presented by the Clean Air Outlook. We selected the European N deposition EMEP 28km SVG gridded data, with the scenario specified as “EU Outlook 2017 – ver Dec. 2018” and “REF_post2014_CLE_v.Dec.2018” (see also Dirnböck et al., 2018). After recalculating the unit of N deposition by applying the conversion factor of 1 keq N $ha^{-1}yr^{-1}$ being equal to 14 kg N $ha^{-1}yr^{-1}$, we used 30 sample points per NUTS region to calculate an average N deposition of CLE.

Four climate change scenarios were used based on Shared Socioeconomic Pathways (SSPs). SSPs are a set of carbon emission scenarios driven by different socioeconomic assumptions for the future, including SSP1, SSP2, SSP3, SSP4 and SSP5 (IPCC, 2018). The SSP scenarios come with a narrative to describe the socio-economic pathway that leads to a specific emissions amount. SSP4 was not included in the DSS, because of the lack of available data for this scenario on the WorldClim database. The data of future climate under these four scenarios is available from the Couple Model Inter comparison Project Phase 6 (CMIP6, O'Neill et al., 2016). We selected 10 minutes gridded data for the period 2041-2060 (centered around the final year included in the DSS predictions (2050)) of the IPSL-CM6A-LR model (among nine available models) in WorldClim v2.1(Boucher et al., 2018). We used 30 sample points per NUTS region to calculate an average MAT for the period between 2041 and2060, for each SSP scenario. Fischer-corrected tree cover(continuous values from 0%-100%) were used as the value of canopy closure (Bernhardt-Römermann et al., 2015) which represent forest management intensity. In the DSS, we included 3 different canopy closure values: 25% and 100% cover indicative for open and closed forest conditions, respectively, and 75% cover as an intermediate value between both extremes (Meeussen et al., 2021). These options were made available for both the starting and ending conditions. As main outputs, the underSCORE DSS provides trends for four understorey properties, including species richness, the Fisher-corrected understorey vegetation total cover (%), the proportion of woody species (%) and the proportion of forest specialists (%).

2.2.4. Graphical user interface

The interface of the DSS, shown in Figure 2, includes three panels: the first panel allows users to select a region of interest on the map to start the simulation procedure. When choosing a region of interest, the current environment values (MAT, MAP, N deposition, pH) for the region will be shown on the map. In the left panel, users can adjust the current environmental conditions and select future change scenarios for the period 2020-2050. Predicted understorey trends for the selected region and global change scenario will be displayed in the right panel.

2.3 Scenario analysis

Based on our built GAM model, we projected scenario analysis and sensitivity analysis in two case study regions, to show how forest understorey communities respond to a combination of changes in forest management and changes in environmental conditions in the future.

2.3.1 Case study areas

We selected Flanders (NUTS code BE2) and Slovakia (NUTS code SK) as our case study regions. Flanders is located in the north of Belgium, with 13.625 km^2 area and a 6.6 million population, is a highly industrialized and densely populated area with a total forest cover of 11%, being one of the least forested regions of Europe (EU, 2021). Slovakia is located in Central Europe, with 49.034 km^2 area and a ca. 5.3 million population, with a high total forest cover of 45.3 % (EU, 2021). In Flanders, the current MAT is 10.6℃ , the current annual N deposition value is 19.3 kg ha^{-1} $year^{-1}$, and the current MAP is 832 mm. In Slovakia, the current MAT is 8.1 ℃, the current annual N deposition value is 10.2 kg ha^{-1} $year^{-1}$, and the current MAP is 756 mm. We extracted top soil pH data from the SoilGrids database (Batjes et al., 2020) , where the average soil pH value of Flanders is 5.5, and the average soil pH value of Slovakia is 5.8.

2.3.2 Scenario analysis

To predict the understorey dynamics under management interventions and multiple environmental changes between 2020 and 2050 in the two selected case study regions, we carried out a full scenario analysis, including 2 N deposition scenarios, 4 climate change scenarios and 9 forest management scenarios, which in combination give rise to 72 (2x4x9) individual scenarios to be analyzed. The scenarios information for two case study areas can be found in the Table 1.

For each case study, we used the GAMs model to predict, for all four response variables and 72 scenarios, a trend between 2020 and 2050. For these predictions, regional means of annual precipitation (MAP) and soil pH were treated as constants. Next, we calculated the change of each predicted response variable as the difference of each understory property value between 2020 and 2050 (Equation 2 and Equation 3, with response variable i and scenario j). This scenario analysis hence resulted in one absolute change values for all response variables and for all 72 scenarios.

$$\triangle \hat{Y}_{i\cdot \mathrm{j}} = \hat{Y}_{i\cdot \mathrm{j}\cdot 2050} - \hat{Y}_{i\cdot \mathrm{j}\cdot 2020}$$

Equation 2

$$SE_{\triangle \hat{Y}_{i\cdot \mathrm{j}}} = \sqrt{SE^2_{\hat{Y}_{i\cdot \mathrm{j}\cdot 2050}} + SE^2_{\hat{Y}_{i\cdot \mathrm{j}\cdot 2020}}}$$

Equation 3

2.3.3 Sensitivity analysis

To analyze the sensitivity of the model to changes in its predictor variables, we fitted linear regression models relating both changes and starting conditions in forest management and environmental drivers to the predicted changes in understorey response variables, for both case studies separately. The obtain standardized regression coefficients (SRC) denote the relative importance of each predictor variable, representing the sensitivity of all response variables to multiple environmental changes and forest management interventions. As predictor variables, we included N deposition decrease, annual temperature increase (climate warming), the initial canopy closure, and canopy closure trend. We didn't include the current N deposition load because that can be regarded as a constant within each case study region. As response variables, we included change in species richness, change in understorey vegetation total cover (%), change in proportion of woody species (%), and change in proportion of forest specialists (%). N deposition decrease (as N deposition is expected to decrease under the proposed Clean Air Outlook policy scenario) was defined as the difference between the future N deposition and the current N deposition. Difference in MAT was defined as the difference between future MAT and current MAT and denoted here as 'Climate warming', as it is expected to increase in all future scenarios, including the most stringent SSP1 scenario. Canopy closure trend was defined as the difference between canopy openness in 2050 and the current canopy openness. As mentioned in section 2.2.3, we had three possible current canopy conditions (25%,75% and 100%), and three possible 2050 canopy conditions (25%, 75% and 100%).

We first standardized the independent variables and response variables, and then fitted linear regression models for the four response variables separately. Next, we selected the optimal model using a multilevel model selection approach based on AIC by applying the dredge function from the MuMIn library in R 4.1.1 (Barton & Barton, 2020; R Core Team, 2020) to get the standardized regression coefficient for each independent variable.

3 Results

3.1 Understory biodiversity dynamics between 2020 and 2050

We found significant negative changes in understorey species richness for 70 out of 72 scenarios in Flanders. The forecasted change in understorey richness ranged between -2.46 and 0.095 species. In Slovakia, all scenarios decreased understorey richness ranging between -10.52 and -5.82 species, a more substantial change compared to Flanders (Figure 3). N deposition barely influenced understorey species richness in Flanders, but significantly changed understorey richness in Slovakia. The understorey species richness decreased under warming (from SSP1 to SSP5), across the majority of canopy scenarios, regardless of region. (Figure 3)

In Flanders, the understorey vegetation total cover ranged between 71% and 81% and is expected to increase across all 72 scenarios. The forecasted change in understorey vegetation total cover in Flanders ranged between 4.1% and 12.8%. In Slovakia, the total cover ranged between 68% and 78%, and is expected to increase in 64 out of 72 scenarios. The forecasted changes in understorey vegetation total cover of Slovakia ranged from -1.9% to 8.0%. The understorey vegetation total cover increased when warming occurred under all canopy scenarios in both regions. In Flanders, understorey vegetation total cover is expected to increase slightly with decreasing N deposition. In

Slovakia, however, understorey vegetation total cover is expected to decrease mildly with decreasing N deposition (Figure 4).

We observed significant positive changes in the proportion of woody species for 66 out of 72 scenarios in Flanders. The forecasted change in the proportion of woody species ranged between -4.4% and 27.9%. In Slovakia, the proportion of woody species is expected to increase under 67 scenarios, and is expected to decrease under the other 5 scenarios. The forecasted change in the proportion of woody species ranged between -5.4% and 33.3%. Independent of the region, the proportion of woody species is expected to sharply increase when warming occurs under closed canopy conditions. The proportion of woody species hardly responded to changes in N deposition in Flanders. However, in Slovakia, with N deposition decreasing, changes in the proportion of woody species significantly increased (Figure 5).

In Flanders, the proportion of forest specialists is expected to decrease across 56 out of 72 scenarios, with the change in the proportion of forest specialists ranging between -23.9% and 9.5%. In Slovakia, the proportion of forest specialists is expected to decrease across 60 out of 72 scenarios, with the forecasted changes in the proportion of forest specialists ranging between -27.8% and 6.8%. In both regions, climate warming will shift the composition towards a higher share of forest generalists. A closure of the canopy over time (e.g. O to I, O to C) in combination with lower N deposition rates (CLE) are expected to benefit forest specialists (Figure 6).

3.2 Sensitivity analysis

The standardized regression coefficients (SRC) that quantify the relative importance of all environmental drivers in determining changes in the understorey for the two selected case study areas are shown in Table 2. The sensitivity analysis showed that N deposition decrease was the most important driver (absolute value of SRC > 0.6) for changes in understorey species richness in Slovakia, with an SRC of 0.62. However, no significant effect of N deposition decrease on understorey richness was found in Flanders. Climate warming was observed to be the most influential indicator for changes in understorey vegetation cover, with positive effects in both regions, with an SRC of 0.75 for Flanders and an SRC of 0.82 for Slovakia. Both in Flanders and Slovakia, the closure of the canopy over time was found to be the most influential indicator for changes in the proportion of woody species, with an SRC of 1.08 for Flanders and an SRC of 0.95 for Slovakia, indicating that a closure of the canopy over time leads to a higher proportion of woody species. Also for the proportion of forest specialists, changes in canopy openness was found to be the strongest predictor, with an SRC of 0.95 for Flanders and an SRC of 0.97 for Slovakia, indicating that a decrease in canopy openness over time increases the proportion of forest specialists (Table 2) and vice versa.

4 Discussion

In this study, we used a GAM model-based scenario analysis combined with a sensitivity analysis to project how understorey dynamics can be altered by global change in temperate deciduous forests. We found that climate warming, N deposition, and canopy opening all influenced understorey dynamics. Although changes in understorey richness and the total cover were not huge, the predicted changes were mainly affected by climate warming (both richness and total cover) and the interaction between changes in canopy opening and initial canopy openness (for richness only). The proportion of woody species increased a lot with climate warming and an increase in canopy closure. The proportion of forest specialist decreased with climate warming, but an increase in canopy closure may reverse this expected reduction. The forecasted changing trends were generally similar across both regions, but differed in term of the response to N deposition.

4.1 Strengths and weaknesses of the proposed approach

An important step in environmental decision support is to predict the consequences of different management alternatives for achieving societal goals (Reichert et al., 2015). Ecological modelling and scenario analysis can be used to support this step**.** An essential aspect of making ecological models useful for environmental management is to align model inputs and outputs with management decisions (Schuwirth et al., 2019). In our GAM model, input indicators, such as MAT, N deposition, and canopy opening, are related to management and policy priorities, while the output indicators, four understorey properties, are related to the foci (e.g. biodiversity loss, forest regeneration) from decision-makers in temperate deciduous forests (Blondeel et al., 2021). Similarly, the two global environmental change drivers we selected for scenario development, climate change and N deposition, can be considered the dominant drivers that will shape future environmental conditions with clearly defined future targets that are focused upon by policy makers. Finally, the forest management scenarios are closely related to the actions taken by local managers in the field. This combination of policy and manager-oriented scenarios can be considered as a main strength of our DSS.

To construct our DSS and the underlying models, we applied a space-for-time approach. The validity of this approach has been debated in the literature, with conclusions ranging from strong support (Blois et al., 2013) to strong rejection (Damgaard, 2019). The main assumption behind a space-for-time approach is that spatial and temporal patterns of biodiversity response to environment are equivalent (Pickett, 1989), however, biodiversity changes may be lagging behind environmental changes (Bertrand et al., 2016) leading to the fact that space-for-time approaches often fail to accurately predict biodiversity change as a response to environmental change over time. On the other hand, a space-for-time model usually has less uncertainties than a temporal model (De Lombaerde et al., 2018). Moreover, space-for-time approaches often make use of a broader range of environmental variables for model training, limiting the need for extrapolation beyond the dataset limits when predicting into the future as aimed for in our study.

The rather low predictive performance of our GAM models, suggesting that our models can not accurately predict changes in understorey composition for a specific stand, can be considered the main weakness of our DSS. However, the predicted mean trends remain meaningful when interpreted on the regional scale. This low predictive performance was expected because we did, for instance, not consider local variation in edaphic conditions, land-use history, the local understorey species pool and forest age. Although including these additional predictor variables would probably increase model performance significantly, it would also increase data needs substantially, not only for setting up scenarios, but also for setting current environmental conditions by the end-users of the DSS.

4.2 Global change effects on understorey dynamics

In two regions, understorey richness and total cover are not the primary expected changes, hence understorey alpha diversity and productivity are likely not threatened in the future. However, we can expect major compositional shifts in extreme scenarios, where climate warming will benefit woody species and forest generalists, but a closed canopy could mitigate this shift by slowing down the decrease in forest specialists, such findings provide us with a perspective that increasing canopy closure is key for understorey conservation in forest management. Increases in the proportion of woody species with warming was expected, as previous studies already reported that the understorey can shift to more woody species as a response to warming (Blondeel et al., 2020; Govaert et al., 2021). Warming is an important driver of tree regeneration (and hence woody species in the understorey), which has been found to influence temperate deciduous tree seedling performance positively by both increasing survival and growth (e.g Carón et al., 2015; De Lombaerde et al., 2020). Additionally, in a long-term warming experiment, Govaert et al., (2021) found that competitive generalists performed better at the cost of forest specialists, as the forest specialist (e.g. *Anemone nemorosa*) was found to be negatively affected by warming at the expense of the fast-growing generalists (e.g. *Rubus fructicosus*). Indeed, across wide spatiotemporal gradients, forest generalists with large ranges are now taking over at the expense of small-ranged forest specialists leading to a homogenization pattern in forest understories (Staude et al., 2020). However, increasing canopy tree cover can reduce warming rates inside forests (De Frenne et al., 2019; Zellweger et al., 2020b) and, hence, mitigate this shift, leading to a more stable number of forest specialists over time.

We additionally found that there were obvious differences between the two case study regions, especially in terms of the responses to N deposition decrease. The influence of N deposition decrease on understory richness was only found in Slovakia, and not in Flanders. This might be caused by the initial high N deposition in Flanders. Bernhardt‐Römermann et al., (2015) analyzed temporal understorey diversity changes across European temperate forests, and found that the initial level of N deposition determined the subsequent diversity changes. If the initial level of N deposition was high, the understorey richness changes was lower. High N deposition benefits nutrient-demanding species (often large-ranged species), which replace small-ranged species, so that species turnover leads to no net loss in local alpha diversity (Staude et al., 2021). Another alternative explanation is that the effects of N-deposition in high deposition regions are no longer noticeable because the most sensitive species are already lost (Walter et al., 2017). A reduction of N-deposition will not bring back the species that have been lost from the regional species pool, given the slow colonizing capacity of forest specialists (Verheyen et al., 2003). Additionally, Dirnböck et al., (2018) who assessed benefits of the CLE scenario on understorey vegetation also found that the decrease in N deposition under the CLE scenario was not enough to result in species recovery from eutrophication and suggested that N emission reduction targets needed to be considerably more ambitious in high N deposition regions. In relation to our case studies, we can conclude that the N reduction target under the CLE scenario for Flanders is probably too restricted to yield species recovery. In regions with a high current N deposition rate, there is clearly a need for more stringent targets, to provide opportunities for lost species to recover.

4.3 Outlook

A DSS should be generally applicable for multiple professional groups, e.g. scientists, educators, forest managers, policy makers and consultants (Blondeel et al., 2021). Our online DSS is currently more oriented towards policy-makers that operate on a regional scale, rather than being oriented towards day-to-day practitioners that are responsible for the management of specific forest sites. Practitioners are likely more interested in a DSS that could underpin decision-making at a local stand-scale. Site-specific factors, such as forest structure and tree species composition as well as soil properties (e.g. soil pH, C/N ratio, soil moisture,..) , are known to significantly influence understorey composition and diversity (Weigel et al., 2019; Zellweger et al., 2015). Future work should focus on integrating these site specific data which will help to obtain more accurate site-specific predictions under global change.

Author statement

HB, DL, KV outlined the goal of the study. BW performed statistical analyses; HB performed model selection and developed the online DSS; BW, with contributions from HB, DL and KV, wrote the manuscript. All authors contributed to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

Figures

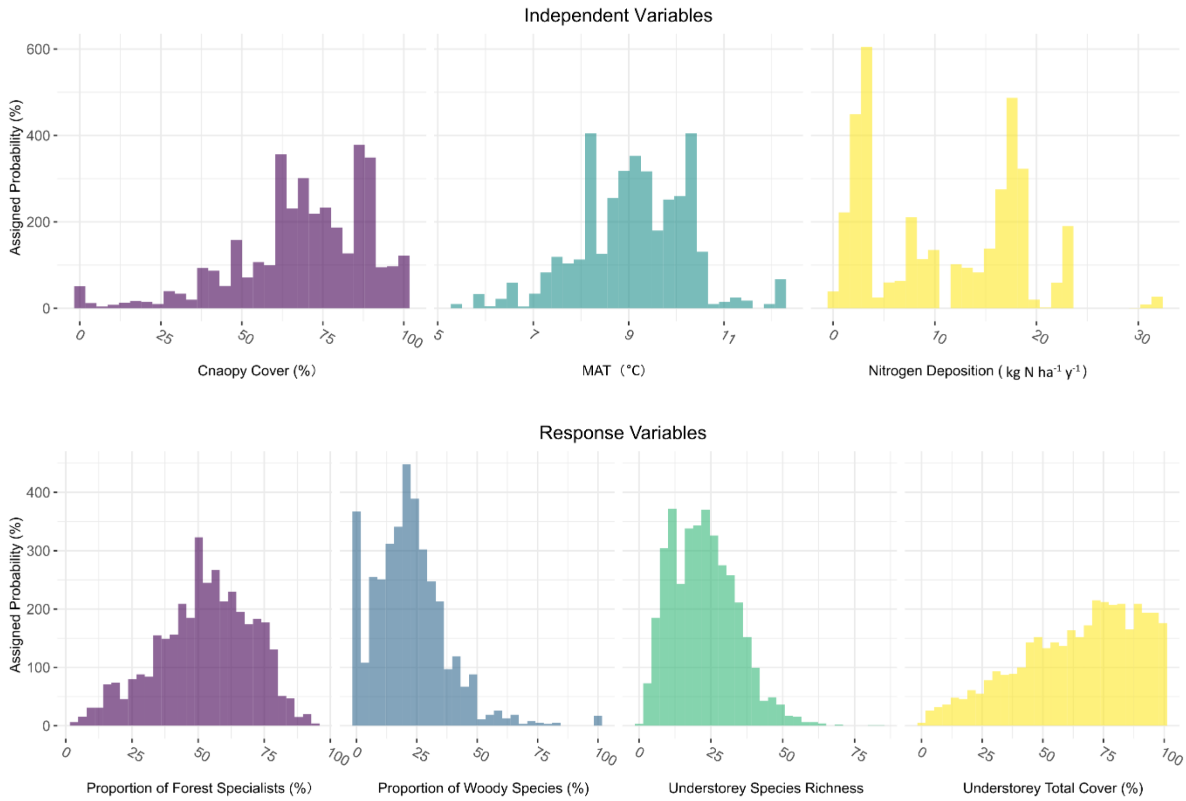

Figure 1. Graphical overview of the spread of understorey community properties and regional environmental conditions included in the forestREplot database.

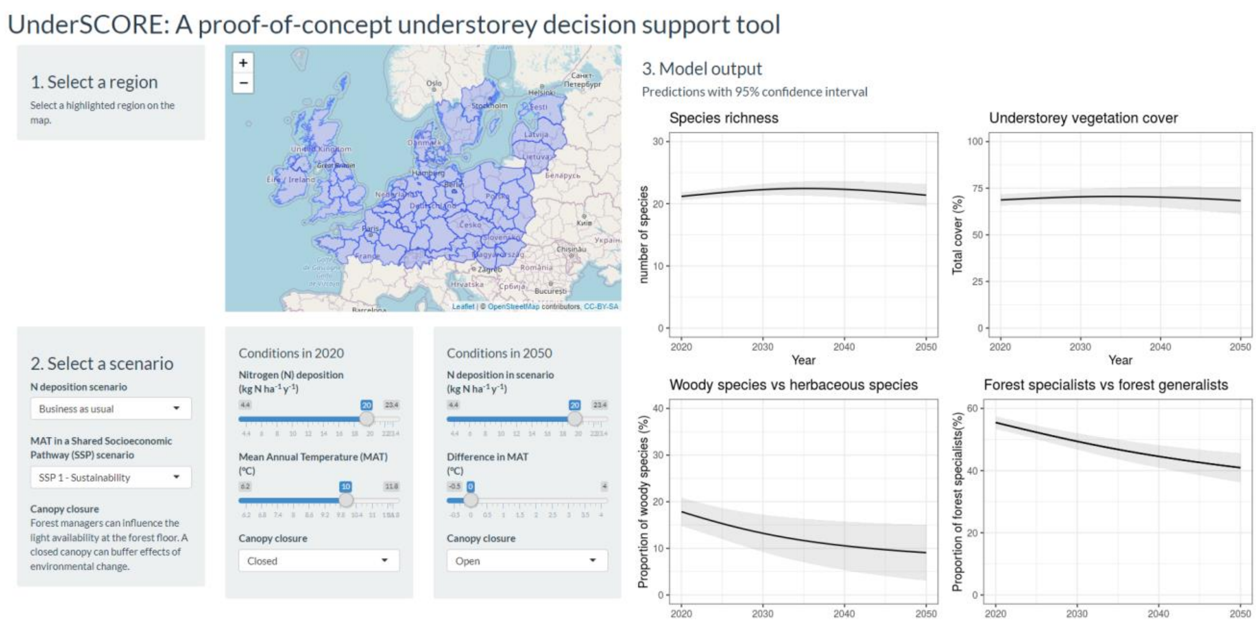

Figure 2. Screenshot of the underSCORE DSS showing the map with all included EU-NUTS administrative regions and the scenario panel at the left, and the predicted trends at the right.

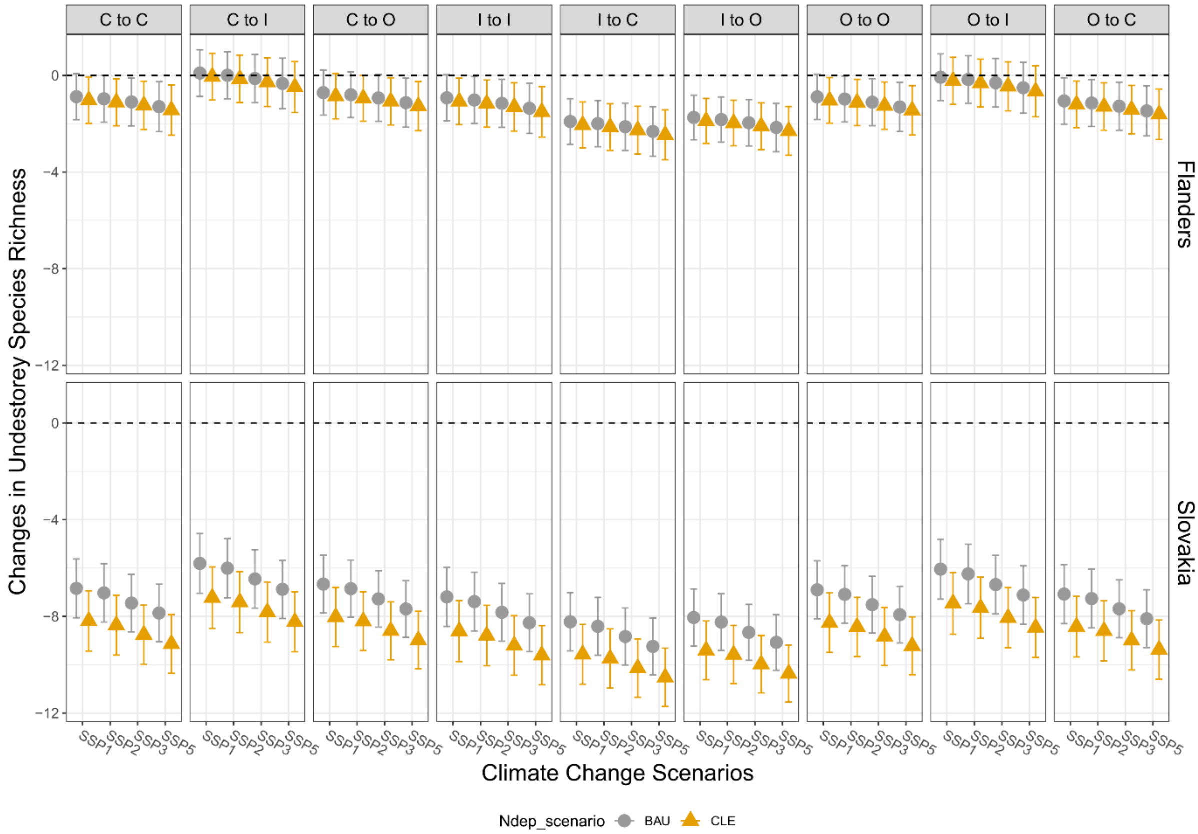

Figure 3. Understorey richness changes under different scenarios in Flanders and Slovakia. BAU and CLE are N deposition scenarios, representing the business as usual and current legislation EU scenarios, respectively. SSP1, SSP2, SSP3, SSP5 are four climate change scenarios. Panel titles represent expected canopy dynamics between 2020 and 2050, with "C" representing a closed canopy (100% cover), "I" an intermediately open canopy (75%), and "O" an open canopy (25%).

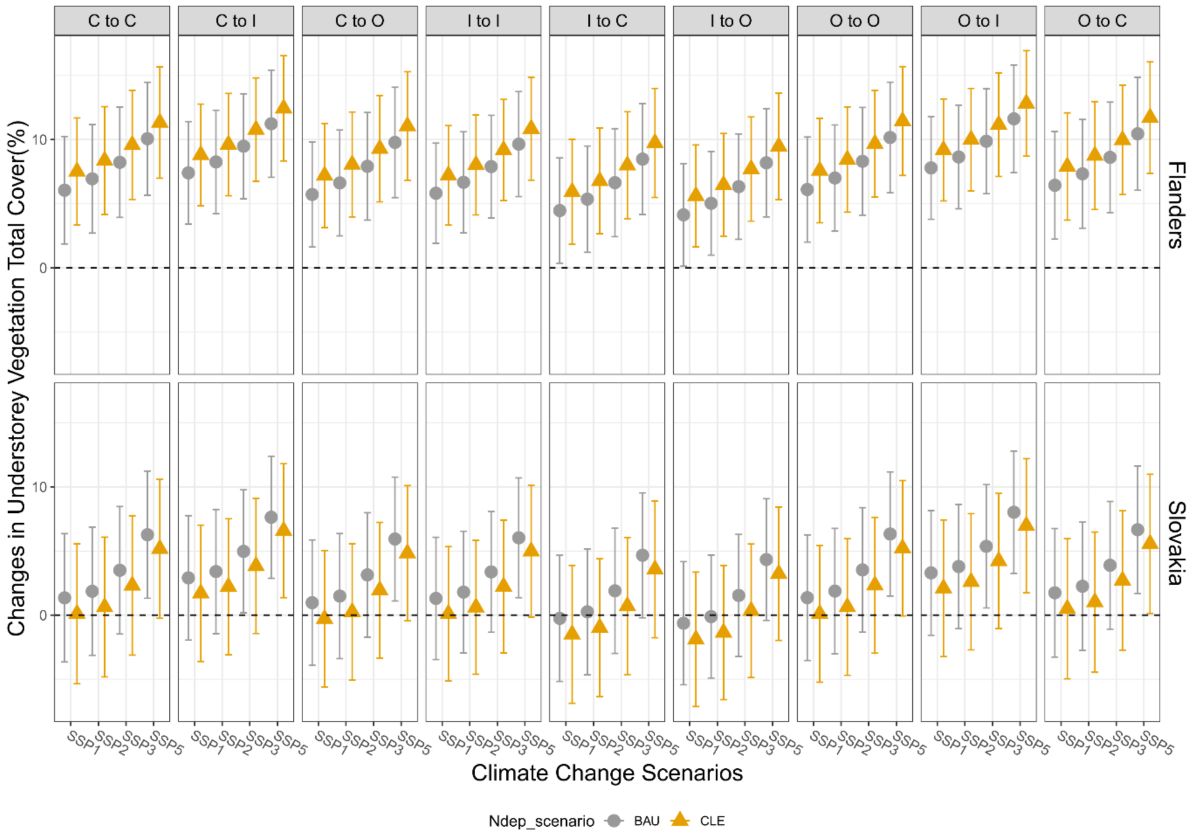

Figure 4. Understorey vegetation total cover changes under different scenarios in Flanders and Slovakia. BAU and CLE are N deposition scenarios, BAU and CLE are N deposition scenarios, representing the business as usual and current legislation EU scenarios, respectively. SSP1, SSP2, SSP3, SSP5 are four climate change scenarios. Panel titles represent expected canopy dynamics between 2020 and 2050, with “C” representing a closed canopy (100% cover), “I” an intermediately open canopy (75%), and “O” an open canopy (25%).

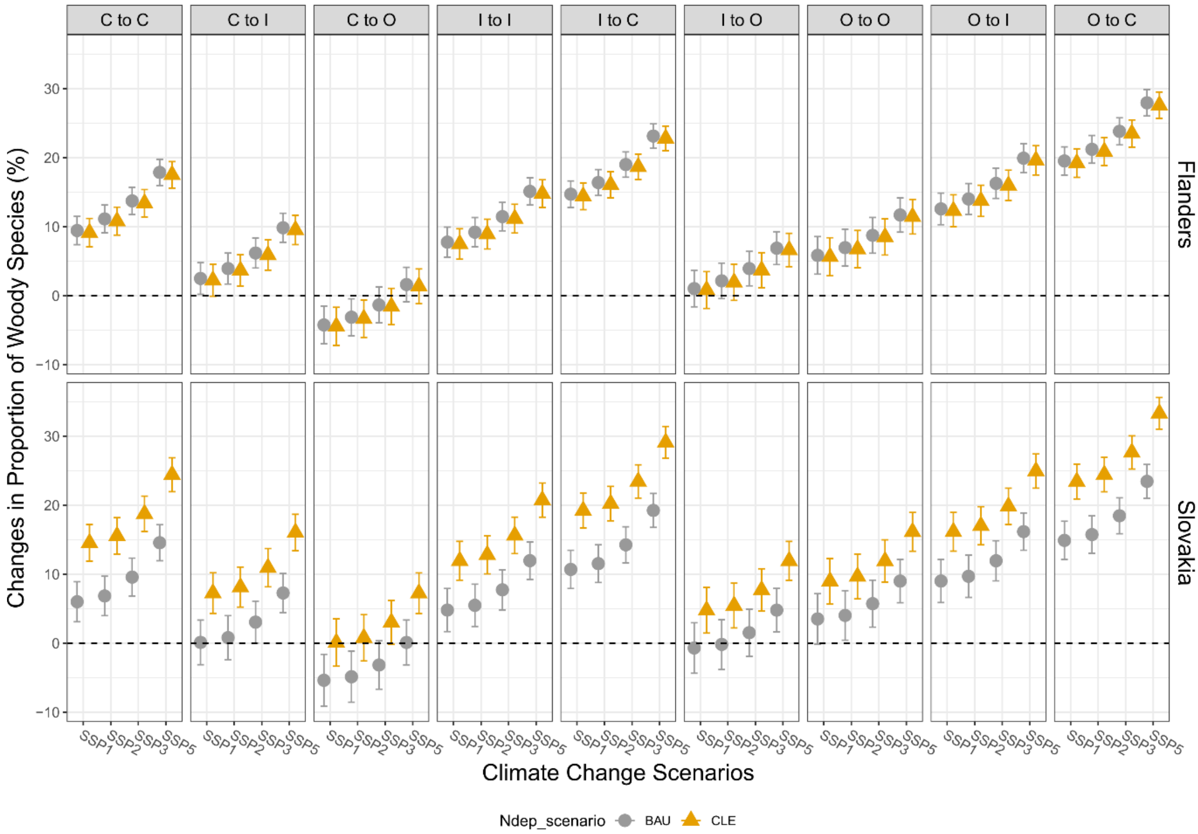

Figure 5. Understorey Woody species proportion changes under different scenarios in Flanders and Slovakia. BAU and CLE are N deposition scenarios, representing the business as usual and current legislation EU scenarios, respectively. SSP1, SSP2, SSP3, SSP5 are four climate change scenarios. Panel titles represent expected canopy dynamics between 2020 and 2050, with “C” representing a closed canopy (100% cover), “I” an intermediately open canopy (75%), and O an open canopy (25%).

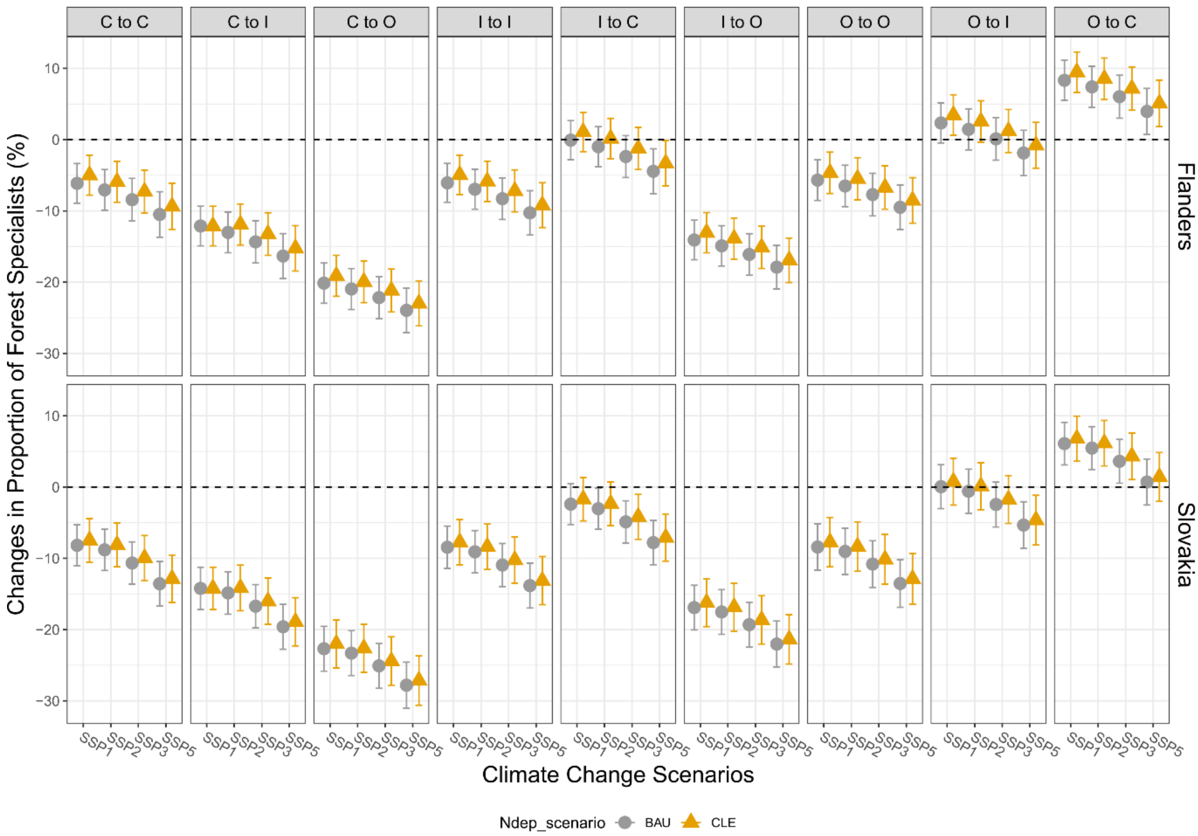

Figure 6. Understorey forest specialist species proportion changes under different scenarios in Flanders and Slovakia. BAU and CLE are N deposition scenarios, BAU and CLE are N deposition scenarios, representing the business as usual and current legislation EU scenarios, respectively. SSP1, SSP2, SSP3, SSP5 are four climate change scenarios. Panel titles represent expected canopy dynamics between 2020 and 2050, with “C” representing a closed canopy (100% cover), “I” an intermediately open canopy (75%), and “O” an open canopy (25%).

Tables

Table1. Annual N deposition under two N deposition scenarios, MAT under four climate change scenarios, and canopy closure under forest management scenarios (column headings) for the two case areas (row headings).

Areas	**Annual N deposition (kg ha-1 year-1)**		**Mean annual temperature (MAT) (℃)**				**Canopy closure of forest management scenarios (start condition)**			**Canopy closure of forest management scenarios (end condition)**		
	Business as usual	**Current legislation**	**SSP1**	**SSP2**	**SSP3**	**SSP5**	**Open**	**Intermediate**	**Closed**	**Open**	**Intermediate**	**Closed**
Flanders	19.30	17.1178	12.08304	12.30506	12.63691	13.14018	25%	75%	100%	25%	75%	100%
Slovakia	10.20	7.703684	10.30073	10.45817	10.91309	11.6152						

Table2. Standardized regression coefficients showing the importance of forest management interventions and multiple environmental drivers (row headings) for determining changes in several understorey properties (column headings), for the two case studies separately. Background colours refer to the following value ranges: grey for -0.6 < SRC <-0.3, white for -0.3 < SRC < 0.3, light orange for 0.3 < SRC < 0.6, bright orange for 0.6 < SRC < 0.9, dark orange for SRC > 0.9. ***, ** and * denote p values <0.001, <0.01 and <0.05, respectively.

Input drivers	Delta Richness		Delta understorey vegetation total cover		Delta woody proportion		Delta forest specialist proportion	
	Flanders	Slovakia	Flanders	Slovakia	Flanders	Slovakia	Flanders	Slovakia
Climate warming	-0.25*	-0.36***	0.75***	0.82***	0.35***	0.36***	-0.18***	-0.24***
N deposition decrease		0.63***	-0.35***	0.25***		-0.45***	-0.06***	-0.04***
Canopy closure trend × Initial canopy closure	-0.44**	-0.35***	-0.26***	-0.21**	0.07*	0.06*	0.04**	0.03**
Canopy closure trend	0.03	0.02	0.18*	0.18*	1.07***	0.95***	0.95***	0.97***
Initial canopy closure	0.11	0.09	0.03	0.05	0.22***	0.23***	-0.05*	-0.01
Canopy closure trend × Climate warming					0.07*	0.08**		
Canopy closure trend × N deposition decrease						-0.10***		
Initial canopy closure× Climate warming					0.05	0.06		
Initial canopy closure× N deposition decrease						-0.07*		
Climate warming × N deposition decrease						-0.04		

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