Forest Ecology and Management 566 (2024) 122091

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Predicting trajectories of temperate forest understorey vegetation responses to global change

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ARTICLE INFO

Keywords:
ForestREplot
Forest understorey
Climate change
Soil pH
Machine learning
Site-scale

ABSTRACT

Predicting forest understorey community responses to global change and forest management is vital given the importance of the understorey for biodiversity conservation and forest functioning. Though substantial effort has gone into disentangling the impact of global change on understorey communities, scarcity of information on site-specific environmental drivers across large temporal-spatial scales has limited our ability to predict global change effects at specific forest sites. In this study, using vegetation resurvey and soil data from 1363 plots across temperate Europe, we applied a machine learning approach (gradient boosting regression, GBR) to model and predict site-specific responses of four understorey properties to global change. We applied our final GBR models at 8 forest sites in Austria to validate the model performance, predict understorey trajectories, and evaluate the effect of alternative scenarios for future nitrogen(N) deposition, climate change and forest management on the projected trajectories. Our results showed that the R^2 value of the four final GBR models on the independent testing dataset ranged between 0.611 and 0.723 and the most important environmental drivers in predicting the trajectory of understorey properties at specific forest sites were soil pH, soil total carbon-to-nitrogen ratio, overstorey shade-casting ability and regional-scale mean annual precipitation. The out-of-sample R^2 value of the four final GBR models on the Austrian data ranged between 0.224 and 0.561. The forecasted trajectories for the Austrian forest sites showed that site-specific understorey responses to near-future climate warming were expected to be weak. Under N deposition decreases, the proportion of woody species was predicted to increase, while species richness and total vegetation cover were predicted to decrease. Furthermore, under a closed canopy, the understorey community was predicted to shift towards more woody species and more forest specialists, albeit with reduced species richness and vegetation cover. Given expected warming and declining N

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https://doi.org/10.1016/j.foreco.2024.122091
Received 18 March 2024; Received in revised form 6 June 2024; Accepted 12 June 2024

pollution pressures, our presented GBR models allow the prediction of trajectories of understorey vegetation responses to global change and management interventions at specific forest sites. Such projections could aid forest management in addressing challenges posed by global change.

1. Introduction

The forest understorey layer harbours more than 80 % of the vascular plant diversity in temperate forests (Gilliam, 2007; Spicer et al., 2020) and plays a crucial functional role in temperate forests by influencing tree regeneration, water cycling, nutrient, and carbon dynamics (Landuyt et al., 2019). However, their biodiversity and functioning are being impacted by a complex set of pressures, including accelerating climate change, high levels of acidifying and eutrophying deposition of reactive nitrogen (N), natural disturbance, and changes in forest management (Bertrand et al., 2011; Gilliam, 2006; Perring et al., 2016; Seidl et al., 2017; Zellweger et al., 2020). Predicting how temperate forest understorey communities will respond to these pressures is crucial for forest management to be able to conserve forest biodiversity and function in an era of global change.

Past studies on the effects of global change on temperate forest understorey communities have shown that these communities are sensitive to multiple global-change drivers, but that responses are often context-dependent, driven by differences in soil characteristics and overstorey structure and composition (Ampoorter et al., 2016; De Frenne et al., 2009; Naaf and Kolk, 2016; Perring et al., 2018b; Verheyen et al., 2012). Climate warming can, for example, cause a shift in understorey composition, favouring warm-adapted species, forest generalists, and woody species (e.g. Blondeel et al., 2020; Govaert et al., 2021; Maes et al., 2020), while the tree layer has the potential to slow down these responses by buffering temperature changes at the forest floor (De Frenne et al., 2013; Zellweger et al., 2020). In addition, alterations in precipitation regimes, potentially leading to drought stress, may steer understorey composition towards a state where only stress-resistant plant species can survive (McDowell et al., 2008). Again, the local tree layer will co-determine the severity of drought stress at the plot level, by regulating throughfall amounts and below canopy vapour pressure deficit (Bachofen et al. 2023; Zhang et al. 2022), and, in turn, affect the composition and structure of understorey communities. Elevated levels of N deposition have been found to increase the dominance of eutrophic species (Dirnböck et al., 2014) and cause understorey species richness loss (Midolo et al., 2019). Again, understorey responses to N deposition will often depend on local soil and canopy characteristics (Perring et al., 2018b).

Many context-dependent understorey responses originate from distinct local abiotic and biotic conditions. The overstorey, for instance, influences light availability, forest floor temperature and humidity and nutrient availability for the understorey, which can modulate understorey responses to several global-change drivers (Hedwall et al., 2021; Márialigeti et al., 2016; Richard et al., 2021). Global-change-induced alterations in the soil, especially topsoil pH and total carbon-to-nitrogen ratio (CN), can affect understorey composition and biodiversity (Zhang et al., 2021). However, these soil properties also strongly depend on overstorey tree species composition (Weigel et al., 2019) due to species-specific differences in leaf litter quality (Maes et al., 2019). Such context-dependencies of understorey community responses to environmental drivers make it important to integrate both regional-scale global-change drivers and site-specific drivers (biotic and abiotic) for predicting forest understorey trajectories.

Although previous empirical studies have enhanced our understanding of general correlative relationships between global-change and understorey responses to these changes, predicting site-specific understorey responses to global-change remains extremely challenging. In contrast to a large number of predictive overstorey models (e.g. Mahnken et al., 2022), reliable predictive understorey models are still scarce (Landuyt et al., 2018). Although some predictive models already exist (in a previous study, we already proposed GAM models to predict regional average trends (Wen et al., 2022)), models that can predict understorey vegetation responses to global change at specific forest sites are lacking, which limits their application in forest understorey decision support systems (Blondeel et al., 2021). Understorey biodiversity and functioning are expected to react in complex non-linear ways to environmental change, so flexible modelling tools are required (De'Ath and

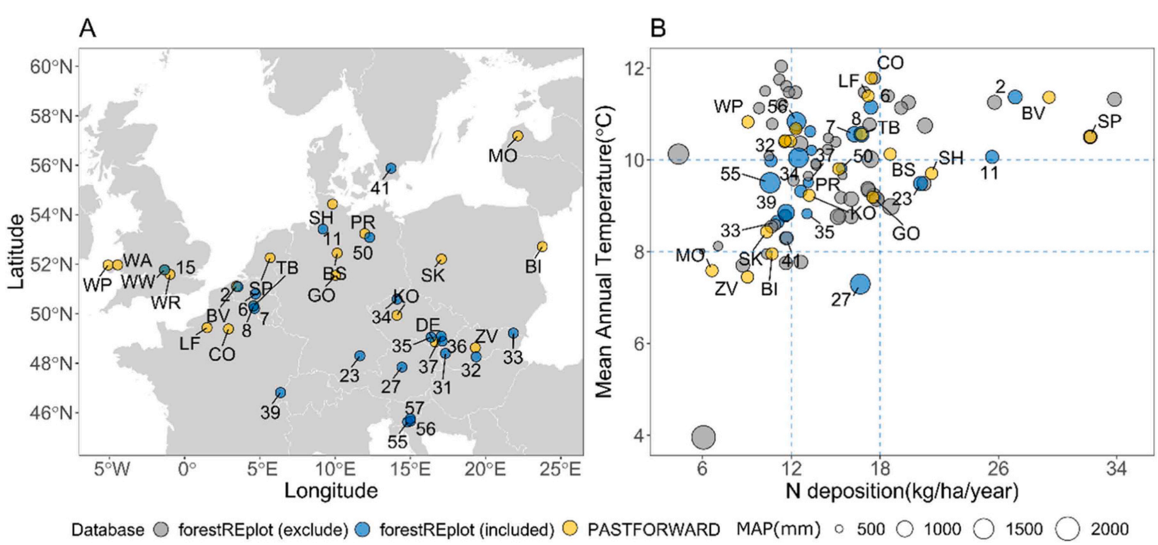

Fig. 1. The geographic location of all datasets in the forestREplot and PASTFORWARD database (A) and the environmental gradients covered by these datasets (B), in terms of mean annual temperature (MAT [°C], averaged over a period of 10 years prior to the year 2017) and mean annual N deposition (N deposition averaged over a period of 10 years prior to the year 2017, [kg N ha^{-1} y^{-1}]) are plotted, with symbol size reflecting the mean annual precipitation (MAP [mm], averaged over a period of 10 years prior to the year 2017). Numbers and codes on the map represent dataset ID as reported in Table S1. Blue dashed lines in panel B delineate the considered environmental zones as explained in the main text.

Fabricius, 2000). Machine learning tools are an example of such a flexible modelling tool and can extract non-linear and complex patterns from data without a priori system understanding of biological phenomena required (Bzdok et al. 2017). Over the years, machine learning approaches have gained importance in ecological research and have been used to predict biodiversity patterns and dynamics at multiple scales (Cai et al., 2023; Park et al., 2020; Sabatini et al., 2022). However, their performance in modelling site-specific understorey community responses to global change has not been explored. Limited information on site-specific environmental conditions (e.g. soil characteristics) in regional-scale datasets prevented such efforts in the past.

In this study, we use field-collected soil data and understorey vegetation resurvey data from 1363 temperate forest plots across central-western Europe, integrate both regional-scale and site-specific drivers and apply a machine-learning approach to (1) develop plot-level predictive models of the trajectories of temperate forest understorey properties (i.e. species richness, total vegetation cover, proportion of woody species, proportion of forest specialists) in response to global change and forest management. We then apply these predictive models to (2) identify important environmental factors driving understorey properties, and (3) predict trajectories of understorey vegetation responses to climate change, N deposition and forest management at eight specific forest sites in Austria.

2. Methods

2.1. Data collection

2.1.1. Datasets

For our purpose of predicting trajectories of forest understorey properties in response to global-change drivers and forest management, we used data for 1363 plots from 40 individual resurvey studies in temperate forests across Western and Central Europe deposited in the forestREplot database (https://forestreplot.ugent.be/) and the PASTFORWARD project (https://pastforward.ugent.be/) to build and test models. We considered the understorey to comprise woody and herbaceous vascular plants with a height below 1 m (Gilliam, 2007). Of these 1363 plots, 1171 plots (21 resurvey datasets) were selected from the forestREplot database and 192 plots (19 resurvey datasets) were selected from the PASTFORWARD project. We selected 1171 plots from the forestREplot database based on two criteria. First, we classified all datasets in the forestREplot database in nine different environmental zones based on three classes of N deposition rates following the classification used in Blondeel, (2019): low (<12 kg N ha^{-1} y^{-1}), medium (12–18 kg N ha^{-1} y^{-1}), and high (>18 kg N ha^{-1} y^{-1}), and three classes of mean annual temperature (MAT): low (<8 ℃), medium (8–10 ℃) and high (>10 ℃). We selected at least one dataset from each environmental zone in the forestREplot database. Second, we only selected datasets that had field-collected soil data available or datasets that we could complement ourselves with soil data by revisiting the plots in the year 2022 or 2023, given our focus on the site-specific drivers (Fig. 1). Since the datasets classified as "high N / low MAT", and the datasets classified as "low N /low MAT" did not have field-collected soil data or the possibility of soil sampling, we ended up with 1171 plots from the forestREplot distributed in seven environmental zones. We then complemented the resulting 1171 plots from the forestREplot database with 192 plots (19 datasets) to ensure maximum representation of European N deposition and MAT gradients (Fig. 1). The 192 plots were collected within the frame of the PASTFORWARD project which contains data on understorey community composition, field-collected soil data and overstorey data distributed across the Central-Western European temperate forest biome (Maes et al., 2020). Each of the 1363 plots analysed here holds information on plot size (m^2), survey year, understorey and overstorey species composition and structure, topsoil pH and CN. Initial vegetation surveys (hereafter referred to as 'initial surveys') were carried out between the year 1928 and 2003, while the most recent surveys (hereafter referred to as 'resurveys') took place between the year 1999 and 2017. Time intervals between two surveys in the 1363 plots analysed here ranged between 12 and 83 years (37.88 ± 12.47[1 SD] years on average); such intervals are considered sufficient to detect directional change in the understory (De Frenne et al., 2013). For further details of the datasets, see Appendix S1.

2.1.2. Understorey properties

We focussed on changes in four understorey properties, including species richness, Fischer-corrected total vegetation cover, proportion of woody species, and proportion of forest specialists, since these aspects (i.e. biodiversity, forest regeneration) have been found to be of most concern for forest managers (Blondeel et al., 2021). Species richness was calculated as the number of all vascular plant species occurring in the understorey layer within a plot. The total vegetation cover was calculated per plot based on species-specific cover values for all species occurring in the understorey layer, following the Fischer method to account for overlap (Fischer, 2015). The proportion of woody species was calculated as the ratio of the number of woody species to total species richness within a plot, which 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). The proportion of forest specialists can be a proxy for understorey species of conservation concern, as these species are linked explicitly to forests. Based on the forest specialist species list created by Heinken et al. (2022), we tallied the number of times each species was counted as a specialist (categories "1.1" and "1.2" in the aforementioned forest specialist species list) across all countries. We then classified a species as a forest specialist if the total tally of this species listed as a specialist was higher than the tally of this species listed as other categories combined; If this was not the case, the species was classified as a generalist (Wen et al., 2022). The proportion of forest specialists was calculated as the ratio of the number of forest specialist species to total species richness within a plot. We calculated these variables for all plots and survey dates. We then calculated absolute changes in these responses over time by subtracting the value of the understorey property at the initial survey from the value of that property at the resurvey. Understorey properties in the resurvey and absolute changes of understorey properties over time were used as response variables for modelling, while understorey properties in the initial survey were used as predictor (explanatory) variables (see Section 2.2).

2.1.3. Regional-scale global-change drivers

We estimated regional-scale global-change drivers from open-source databases. Climate data, including MAT (℃) and mean annual precipitation (MAP, mm), were derived from CRU TS4.06 (https://data.ceda.ac.uk/badc/cru/data/cru_ts/cru_ts_4.06) (Harris et al., 2014) based on plot coordinates and survey dates. Per plot, we calculated average MAT and MAP for a period of 10 years before the initial survey and a period of 10 years before the resurvey, representing climatic conditions for the initial survey and the resurvey, respectively. Absolute changes in climatic conditions between survey dates were calculated by subtracting the value of the initial survey from the value of the resurvey. Trend data of atmospheric N deposition (wet and dry deposition of reduced and oxidized N) for the years 2000–2017 were extracted from EMEP (www.emep.int), and extrapolated to the years 1900–2000 based on N deposition for the year 2000 (kg N ha^{-1} y^{-1}) and correction factors published by Duprè et al. (2010). We then calculated the average annual N deposition for a period of 10 years before the initial survey and a period of 10 years before the resurvey, representing average N deposition conditions for the initial survey and the resurvey, respectively. The absolute change of N deposition between the two survey dates was calculated by subtracting the value of the initial from the value of the resurvey. MAT, MAP and N deposition at initial surveys (hereafter referred to as 'initial MAT', 'initial MAP', 'initial N deposition') and absolute change between two survey dates of these three variables

Table 1
List of predictor variables and response variables included in the final GBR models. Mean and Range [Min, Max] represent the mean and [minimum (min) and maximum (max)] range values of the variables in the datasets that were used in models.

Category	Types	Abbreviation	Variable description	Mean	Range [Min, Max]	Unit
Predictors	Regional-scale	Initial MAT	Mean annual temperature, averaged over a period of 10 years prior to the initial survey date.	8.50	[6.02,10.22]	°C
	Regional-scale	ΔMAT	Absolute change of MAT between resurvey and initial survey.	1.13	[0.35, 1.74]	°C
	Regional-scale	Initial MAP	Mean annual precipitation, averaged over a period of 10 years prior to the initial survey date.	846.10	[510.90,1486.70]	mm
	Regional-scale	ΔMAP	Absolute change of MAP between resurvey and initial survey.	11.37	[-78.50, 152.85]	mm
	Regional-scale	Initial N deposition	Mean annual N deposition, averaged over a period of 10 years prior to the initial survey date.	16.43	[0, 60.58]	kg N ha^{-1} y^{-1}
	Regional-scale	ΔN deposition	Absolute change of N deposition between resurvey and initial survey.	0.03	[-25.49, 19.53]	kg N ha^{-1} y^{-1}
	Site-specific	Initial Tree Cover	Fischer -corrected total tree cover from initial survey	0.68	[0,1]	-
	Site-specific	Δ Tree Cover	Absolute change of tree cover between resurvey and initial survey	-0.03	[-0.80,0.88]	-
	Site-specific	Initial SCA	Cover-weighted averaged SCA from initial survey	3.23	[0,5]	-
	Site-specific	ΔSCA	Absolute change of SCA between resurvey and initial survey	0.30	[-4.06,5]	-
	Site-specific	Initial LQ	Cover-weighted averaged LQ from initial survey	1.81	[0,5]	-
	Site-specific	Δ LQ	Absolute change of LQ between resurvey and initial survey	0.05	[-5,3.38]	-
	Site-specific	Soil pH	Topsoil pH-H_2O (calibrated or original depending on pH estimation method (see Section 2.1.4).	5.16	[3.69,8.19]	-
	Site-specific	Soil CN	Topsoil total Carbon to total Nitrogen ratio.	14.29	[6.948,23.79]	-
	Covariate	Plot size	The size of plot, calibrated into three categories in the modelling (Section 2.2.1)	298.30	[49,2500]	m^2
	Understorey properties	Initial species richness	The number of all species that occurred in the understorey layer within the plot in the initial survey	24.68	[1,72]	
		Initial total vegetation cover	The Fischer-corrected total vegetation cover was calculated per plot based on species-specific cover values for all species that occurred in the understorey layer in the initial survey	0.72	[0.01,1]	-
		Initial proportion of woody species	The ratio of the number of woody species to total species richness in the understorey layer within the plot in the initial survey	0.10	[0,1]	-
		Initial proportion of forest specialists	The ratio of the number of forest specialist species to total species in the initial survey	0.52	[0,1]	
Responses	Understorey properties	Resurvey species richness	The number of all species that occurred in the understorey layer within the plot in the resurvey	27.29	[0105]	-
		Resurvey total vegetation cover	The Fischer-corrected total vegetation cover was calculated per plot based on species-specific cover values for all species that occurred in the understorey layer in the resurvey	0.60	[0,1]	-
		Resurvey proportion of woody species	The ratio of the number of woody species to total species richness in the understorey layer within the plot in the resurvey	0.14	[0,1]	-
		Resurvey proportion of forest specialist	The ratio of the number of forest specialist species to total species in the resurvey	0.53	[0,1]	-

(hereafter referred to as 'ΔMAT', 'ΔMAP', 'Δ N deposition'), were used as predictor variables for modelling (see Section 2.2).

2.1.4. Site-specific biotic and abiotic drivers

Local forest management, through its impact on tree cover, can influence resource availability (mainly light) and growing conditions at the forest floor, and thus understorey biodiversity and functioning. We included three variables to represent management and resource availability, which were tree cover, overstorey shade-casting ability and litter quality. Tree cover was calculated as the total cover of all species (both tree and shrub) that occurred in the overstorey layer (plant height >1 m) based on species-specific cover values, again following the Fischer method to account for overlap (Fischer, 2015). Plot-level shade-casting ability (SCA) of the canopy layer was calculated as the cover-weighted mean of species-specific shade-casting ability scores, ranging between 1 (low shade-casting ability) and 5 (high shade-casting ability). Plot-level overstorey litter quality (LQ) scores were calculated in the same way, ranging between 1 (slow litter decomposition) and 5 (fast litter decomposition). SCA and LQ scores were adapted from Depauw et al. (2020), the two scores for tree and shrub species that occurred in the overstorey layer can be found in Appendix S2. All three aforementioned variables were calculated for all plots and two survey dates. Absolute changes between survey dates were calculated by subtracting the value of the initial survey from the value of the resurvey. Tree cover, SCA scores and LQ scores at initial surveys (hereafter referred to as 'initial Tree Cover, 'initial SCA', 'initial LQ') and absolute change between survey dates of the three variables (hereafter referred to as 'ΔTree Cover', 'ΔSCA', 'ΔLQ') were used as predictor variables for modelling (see Section 2.2).

We complemented the available vegetation data with two soil variables, topsoil pH and soil CN. Each of the 1363 plots holds field-collected soil pH and soil CN data for at least one survey date, including 183 plots (from the forestREplot database) with soil data for both survey dates, 136 plots (from the forestREplot database) with soil data for the initial survey only, and 1044 plots (i.e. 852 plots from the forestREplot database and 192 plots from the PASTFORWARD project) with soil data for the resurvey only. For the 183 plots that hold soil data for both survey dates, the absolute change in soil pH between both survey dates ranged between -1.75 and 1.63 (0.03 ± 0.49(SD)), the absolute change in soil CN ratio between both survey dates ranged between -15.15 and 5.17 (on average -1.15 ± 4.7(SD)). We then performed a paired t-test to investigate changes over time and found no significant difference between the two survey dates in terms of pH (p-value= 0.789) and CN (p-value= 0.153) (Figure S2) which showed that there is no directional change of soil pH and CN overall. Hence, soil properties were assumed to remain relatively stable across years. As a consequence, we only used one soil dataset per plot (soil data collected during the resurvey, or soil data collected during the initial survey when resurvey soil data were not available, or soil data collected in 2022/2023 if no historic soil data were available). Following this rule, the final soil dataset (n=1363) included 1171 plots from the forestREplot database (i.e. 1035 plots with soil data collected during the resurvey and 136 plots with soil data collected during the initial survey) and 192 plots from the PASTFORWARD project with soil data collected during the resurvey. Soil acidity was determined using a suspension of soil in water (pH-H_2O), or in a potassium chloride solution (pH-KCl), or a calcium chloride solution (pH-$CaCl_2$). 412 plots hold data on both pH-H_2O and pH-KCl, 21 plots hold data on both pH-H_2O and pH-$CaCl_2$, 325 plots hold data on pH-KCl, 97 plots hold data on pH-$CaCl_2$, and 508 plots hold data on pH-H_2O. For all plots, we transformed pH data to pH-H_2O values based on linear regression models, calibrated based on plot data that containing multiple estimates of soil acidity with different approaches (more detailed information can be found in Appendix S3). Finally, pH-H_2O and soil CN data were used as predictor variables for modelling (see Section 2.2).

2.2. Model setup

In a fully data-driven way, we trained a range of models for two types of response variables (resurvey understorey properties and the absolute change of understorey properties between surveys), and by using two distinct modelling techniques: Generalized Additive Models (GAM) and Gradient Boosting Regression (GBR) models, using the same set of predictor variables for each understorey property (Table S5). The best-performing model for each understorey property was the one that predicted resurvey understorey properties using GBR (final GBR models). We thus focussed our further analyses using the GBR models. The results of other tested models and model performance comparisons can be found in Appendix S4.

2.2.1. Response variables and predictor variables

In the final GBR models, we considered four response variables (four understorey properties in resurvey), including (i) resurvey species richness, (ii) resurvey total vegetation cover, (iii) resurvey proportion of woody species and (iv) resurvey proportion of forest specialists. Two types of predictor variables were included, regional-scale global-change drivers and site-specific biotic and abiotic drivers (Table 1). Regional-scale global-change drivers included (i) initial N deposition and Δ N deposition, (ii) initial MAT and ΔMAT, and (iii) initial MAP and ΔMAP. Site-specific biotic and abiotic drivers included (i) initial Tree Cover and ΔTree Cover, (ii) initial SCA and ΔSCA, (iii) initial LQ and ΔLQ, and (iv) soil pH and CN. We also considered understorey properties at the initial survey (being initial species richness, initial total vegetation cover, initial proportion of woody species, and initial proportion of forest specialist, depending on the modelled understorey property), as predictor variables to account for the regression to the mean phenomenon (Mazalla and Diekmann, 2022). We included a discrete plot size variable as an additional predictor variable for modelling resurvey species richness, given the non-linear scale dependence of plot-level richness measurements (Dengler et al., 2020; Gotelli and Colwell, 2001). Plot size discretization was based on the distribution of the data, with the midpoint values for each discrete class set to the first quartile (100 m^2), the mean (298.3 m^2), and the third quartile (500 m^2) of the data, classifying plot size into three groups: plot sizes smaller than 200 m^2 were assigned to the 100 m^2 class, plot sizes range between 200 m^2 and 400 m^2were assigned to the 300 m^2 class, and plot sizes above 400 m^2 were assigned to the 500 m^2 class.

2.2.2. Model training

We applied a GBR algorithm to fit separate models for the four response variables using the package scikit-learn in Python 3.7 (Pefregosa et al., 2011). GBR is a tree-based ensemble algorithm that constructs a predictive model from an ensemble of a series of weak predictive models (Friedman, 2001; Friedman, 2002). We randomly split the complete dataset without missing records (n =1178) into a training dataset (80 %, n=942) and a testing dataset (20 %, n=236). First, we scaled all features (predictors) based on the mean and standard deviation of the training set using the *StandardScaler* function and then applied those transformations to the test set (and to the Austrian dataset, see Section 2.3) to avoid any contamination of the test dataset. Second, we used the standardized training dataset to fine-tune the algorithm's hyperparameter set. We first plotted the validation curve for each hyperparameter to check the influence of a single hyperparameter on the training score and the validation score to finetune the search range of each hyperparameter (to reduce calculation time when searching for the most optimal hyperparameter set later on). We also inspected the learning curve, showing training and validation scores for varying training dataset sizes, to define the optimal size of the training dataset, to avoid overfitting or underfitting. We then used the *RandomizedsearchCV* function and the *GradientBoostingRegressor* function with five-fold cross-validation, including early stopping regularization, to find the most optimal hyperparameter set. During five-fold cross--validation, 80 % of the training set was used for training (n=753, while the learning curve showed that the validation score reached a plateau after n=700) and 20 % of the training set was used for validation. The early stopping regularization mechanism terminated the iterative search process when no further improvements of the validation score were detected (validation score increase < 0.001 across 100 iterations).

After optimizing the hyperparameter set, models were fitted on the full training dataset (n=942) using the previously defined optimal hyperparameter set (see Appendix S4 Table S6 for an overview of the applied hyperparameters) and then tested on the testing dataset. The coefficient of determination (R^2) (Equation S1) was used to evaluate the model performance. We then calculated feature importance, which indicates the relative importance of all predictor variables in the final GBR models, using the *feature_importances_* function. This importance was calculated as the sum of the reduction in impurity produced when a node was split using that feature in all trees of the final ensemble model (Pefregosa et al., 2011).

2.3. Predicting trajectories of understorey response to global change

We selected 8 forest sites located in Austria from the forestREplot database (dataset 27 in Fig. 1) since only these plots in the database hold vegetation data at more than two points in time, which allows us to evaluate the model's performance for predicting trajectories of change. These Austrian plots hold vegetation data for the years 1993, 2005, 2008, 2010, 2014, and 2017, and soil data collected in 1993. N deposition decreased from 19.35 kg N ha^{-1} y^{-1} to 16.66 kg N ha^{-1} y^{-1} and MAT increased from 6.3 ℃ to 7.4 ℃ between 1993 and 2017 at these Austrian plots.

We hindcasted and forecasted the trajectories of forest understorey responses to climate change, N deposition, and forest management at the Austrian sites by applying the final GBR models. We applied our final GBR models at each of these sites to hindcast all four understorey properties for the years 2005, 2008, 2010, 2014, and 2017 using 1993 vegetation data as the initial state/predictor in the models. To assess model performance on the Austrian data, we calculated the out-of-sample R^2 (Equation S3) (Hawinkel et al., 2024), and Pearson's r (Equation S4) by comparing model predictions to observations (n=32) (more details can be found in Appendix S4).

To project understorey vegetation responses to global change for the year 2030, we carried out a scenario analysis, including two N deposition scenarios, two climate change scenarios, and three tree cover scenarios, leading to twelve alternative scenarios. The two N deposition scenarios were a business-as-usual (BAU) and a current legislation scenario (CLE). The BAU scenario simply assumes no further change in N deposition rates since 2017, which was calculated as the average N deposition over a period of 10 years prior to the year 2017 based on data extracted from EMEP. The CLE was presented by the Clean Air Outlook of the European Commission and extracted from the Greenhouse Gas-Air Pollution Interactions and Synergies portal (GAINS, https://gains.iiasa.ac.at/models/gains_models4.html). We selected the European N

Table 2
Performance of the final GBR models that predict forest understorey trajectories based on the gradient boosting regression algorithm. R^2_{train} was calculated on the training dataset (n = 942), R^2_{test} was calculated on the test dataset (n = 236), and R^2_{full} calculated on the full dataset (n = 1178). $R^2_{Austrain}$ is the out-of-sample R^2 of the final GBR models on the Austrian subset. Pearson's r values represent coefficients of correlation between predictions and observations for the Austrian subset.

Response Variables	R^2_{train}	R^2_{test}	R^2_{full}	$R^2_{Austrain}$	Pearson's r
Resurvey species richness	0.823	0.657	0.786	0.464	0.451
Resurvey total vegetation cover	0.751	0.639	0.797	0.390	0.664
Resurvey proportion of woody species	0.817	0.723	0.797	0.224	0.188
Resurvey proportion of forest specialists	0.729	0.611	0.707	0.561	0.770

deposition EMEP 0.3° × 0.2° longitude-latitude grid data (available on map view under tab "Air quality and impacts-map of total nitrogen deposition", with the scenario specified as "Clean Air Outlook 2-NAPCP_2030 and NAPCP_2050". We recalculated the given unit of "eq N ha yr^{-1}" by applying the conversion factor of 1 keq N ha^{-1} y^{-1} equals 14 kg N ha^{-1} y^{-1} (GAINS, https://gains.iiasa.ac.at/gains/impacts.EUN/index.menu?page=1524). N deposition of the BAU scenario was set as 19.35 kg N ha^{-1} y^{-1} and N deposition of the CLE scenario was set as 6.83 kg N ha^{-1} y^{-1}.

The two climate change scenarios were based on two contrasting Shared Socio-economic Pathways (SSP1 and SSP5), extracted from WorldClim v2.1 (https://www.worldclim.org/data/cmip6/cmip6climate.html). We selected 10 minutes gridded data for mean annual temperature from the IPSL-CM6A-LR model, as this is a European (French) model that is linked to the ORCHIDEE dynamic global vegetation model. We considered this a good match for our temperate European forest focus. We selected the period of 2021–2040, as the future scenario of year 2030. The MAT in 2030 under SSP1 was set to 9.2 °C, while 2030 MAT under SSP5 was set to 9.4 °C. The three forest management scenarios were represented by different tree cover values: 25 % tree cover representing an open condition, 50 % tree cover representing an intermediate condition, and 100 % tree cover representing a closed condition.

For all 12 scenarios, we projected understorey properties for the year 2030, using our final GBR models. 1993 vegetation data were used as the initial state, ΔN, ΔMAT and ΔTree cover was set based on the considered scenarios, while LQ, SCA, MAP, soil pH, and soil CN were assumed to

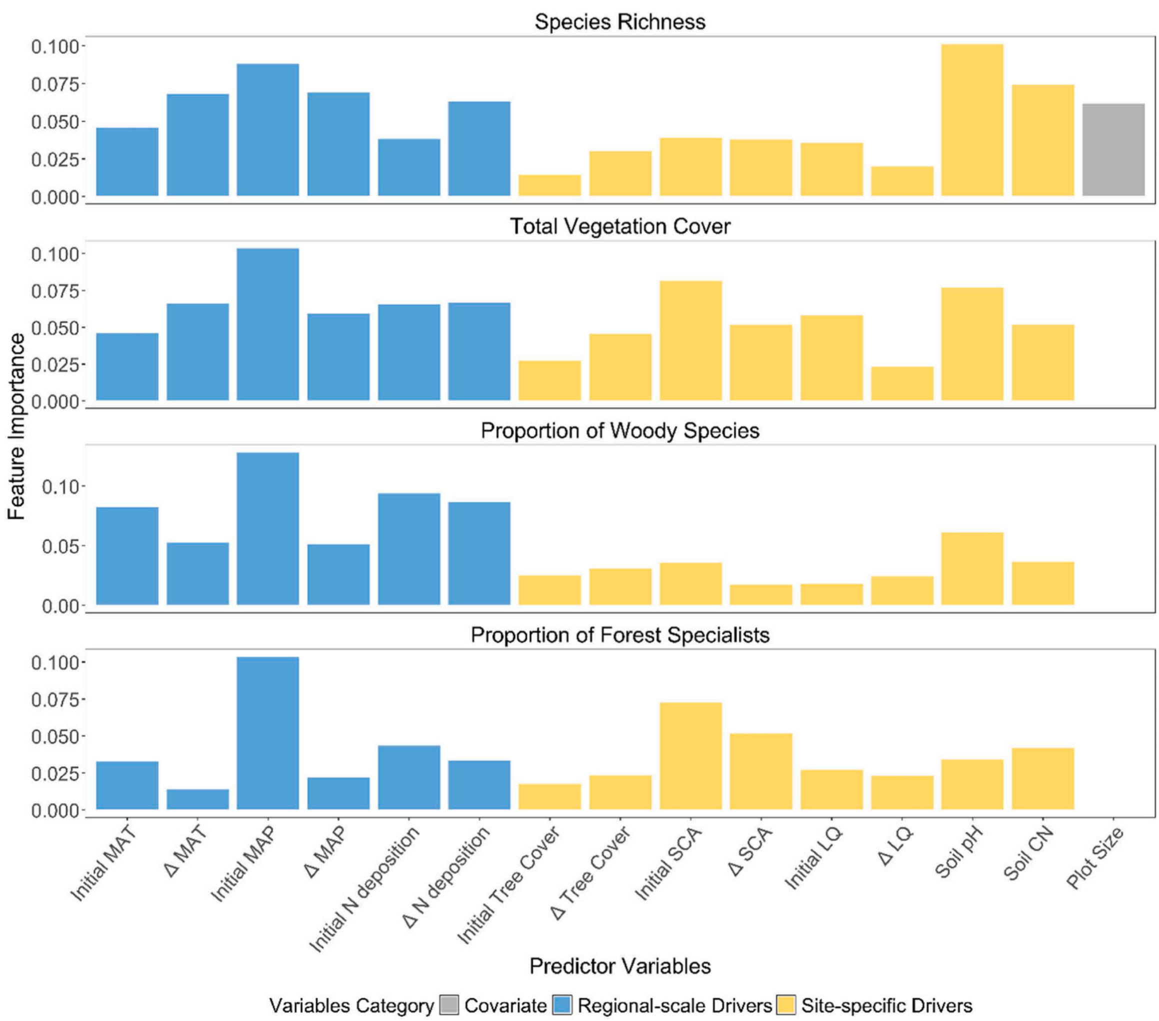

Fig. 2. The feature importance of predictor variables in final GBR models that predict the understorey trajectory, for all four properties, species richness, total vegetation cover, proportion of woody species, and proportion of forest specialists. The initial understorey property is the most important driver in all models but excluded from the figure, with values of 0.207 for the initial species richness, 0.171 for the initial total vegetation cover, 0.251 for the initial proportion of woody species, and 0.454 for the initial proportion of forest specialists. Abbreviations refer to mean annual temperature (MAT), Nitrogen deposition (N), mean annual precipitation (MAP), overstorey shade casting ability score (SCA), and litter quality score (LQ), soil total carbon to nitrogen ratio (Soil CN). 'Δ' refers to absolute changes in the respective drivers between the resurveys and initial survey. Plot Size was counted into three categories, 100 m^2, 300 m^2, and 500 m^2, in the modelling.

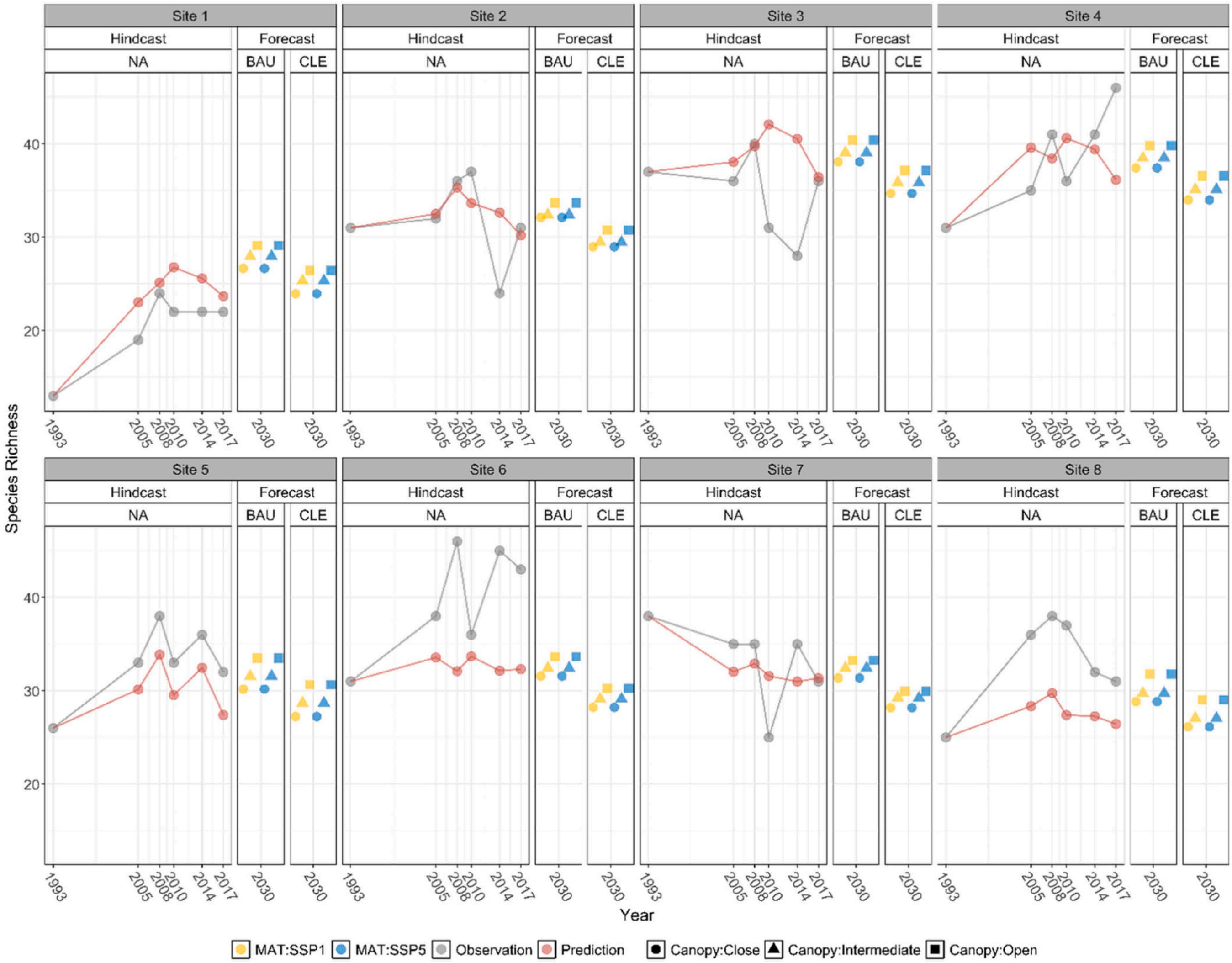

Fig. 3. Trajectories of understorey species richness between 1993 and 2030 for 8 forest sites in Austria. For the year 2005–2017, we hindcast species richness for each year with observed environmental changes. NA refers to no applicable scenario since there is no scenario applied in the hindcasting. For the year 2030, we forecasted species richness for two Nitrogen deposition scenarios: BAU (Business as Usual) and CLE (Clean air outlook of Europe), for two climate scenarios: SSP1 and SSP5, and for three canopy openness scenarios: open (25 %), intermediate (50 %) and closed (100 %).

remain constant over the full simulation period (1993–2030).

3. Results

3.1. Model performance of the final GBR models and important factors driving understorey properties

All models fitted reasonably well, with R^2 values of 0.657, 0.639, 0.723 and 0.611 on the testing dataset, for species richness, total vegetation cover, proportion of woody species, and proportion of forest specialists, respectively (Table 2). Out-of-sample R^2 values of models validated against the Austrian subset ranged between 0.224 and 0.561 (Table 2). Pearson's r values of models validated against the Austrian dataset ranged between 0.188 and 0.770, with the best model performance for the proportion of forest specialists (Table 2, Figure S4).

When reviewing the feature importance of all predictor variables across the final GBR models (Fig. 2), we found that soil pH, initial MAP, and soil CN were the most important variables explaining species richness. Initial MAP, initial SCA and soil pH were found to be the most important variables explaining total vegetation cover. Initial MAT, initial MAP and ΔN deposition were found to be the most important variables explaining the proportion of woody species, while initial MAP, initial SCA, and ΔSCA were the most important drivers explaining the proportion of forest specialists.

3.2. Understorey trajectories between 1993 and 2030

Species richness in the Austrian sites was predicted to increase from 1993 to 2030 (Fig. 3), following the observed trend in the data up to 2017. Projected species richness responses to climate warming were found to be weak (Fig. 3). Decreasing N deposition led to decreases in species richness but canopy opening led to further increases towards 2030 (Fig. 3).

Understorey total vegetation cover in the Austrian sites was predicted to decrease from 1993 to 2030, following the observed trend in the data up to 2017 (Fig. 4). Projected total vegetation cover responses to climate warming were found to be weak (Fig. 4). Decreasing N deposition led to a further decrease in total vegetation cover towards 2030, while canopy opening was projected to lead to an increase in total vegetation cover (Fig. 4).

The proportion of woody species in the Austrian sites was predicted to increase from 1993 to 2030, following the observed trend in the data up to 2017 (Fig. 5). Projected proportion of woody species responses to climate warming were found to be weak (Fig. 5). While decreasing N

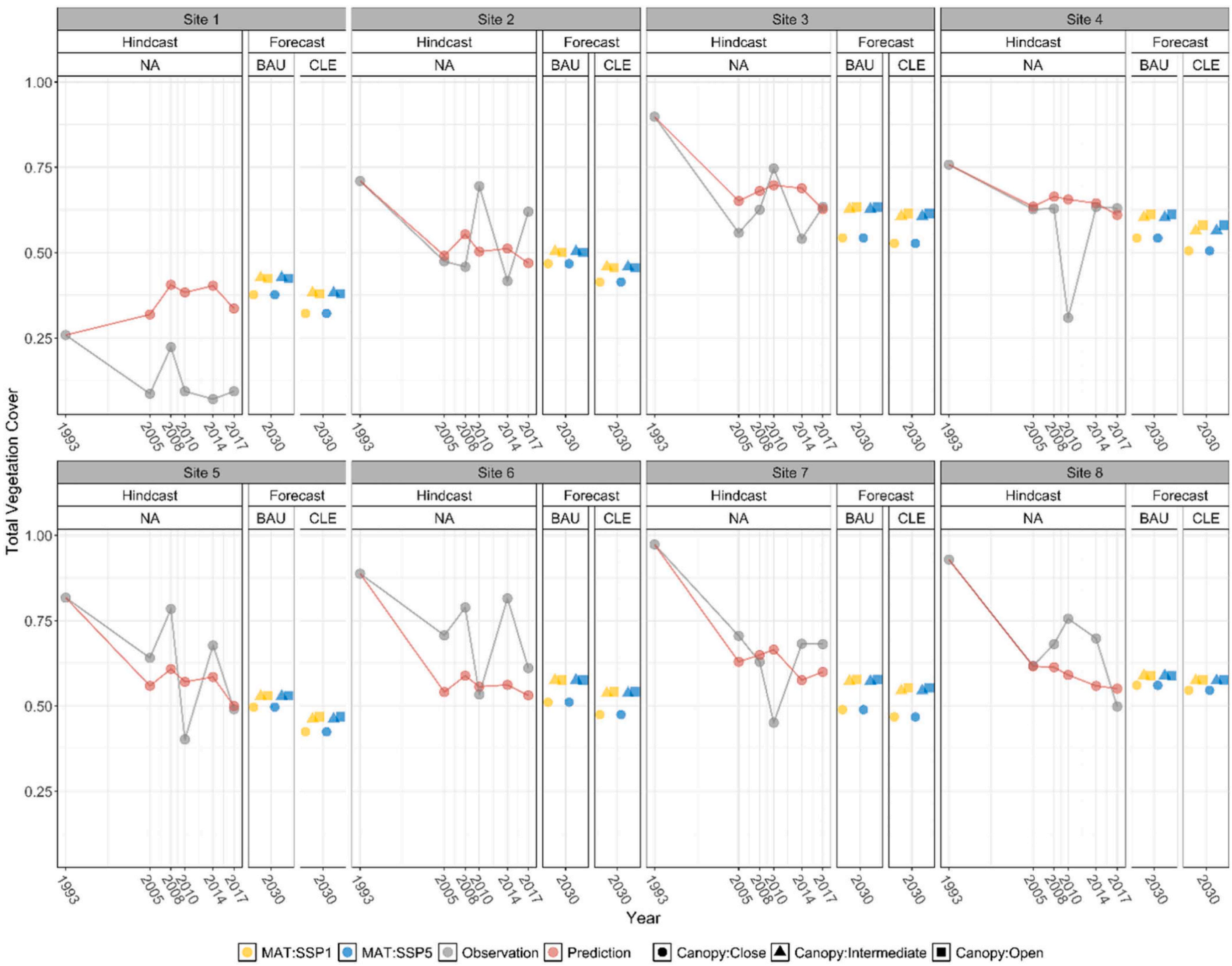

Fig. 4. Trajectories of understorey total vegetation cover between 1993 and 2030 for 8 forest sites in Austria. For the years 2005–2017, we hindcasted total vegetation cover for each year with observed environmental changes. NA refers to no applicable scenario since there is no scenario applied in the hindcasting. For the year 2030, we forecasted total vegetation cover for two Nitrogen deposition scenarios: BAU (Business as Usual) and CLE (Clean air outlook of Europe), for two climate scenarios: SSP1 and SSP5, and for three canopy openness scenarios: open (25 %), intermediate (50 %) and closed (100 %).

deposition led to a further increase in the proportion of woody species towards 2030, canopy opening was projected to lead to a decrease in the proportion of woody species (Fig. 5).

The proportion of forest specialists in the Austrian sites was predicted to increase from 1993 to 2030, while observations showed decreases or increases in this metric from 1993 to 2017, depending on the site (Fig. 6). Canopy opening led to a decrease in the proportion of forest specialists towards 2030 (Fig. 6). Projected responses of the proportion of forest specialists to climate warming were found to be weak, while projected responses to decreasing N deposition were site-specific, showing both decreases and increases (Fig. 6).

4. Discussion

4.1. Global-change and site-specific abiotic and biotic drivers affect understorey dynamics

We found that understorey properties were sensitive to both regional-scale and site-specific drivers. In particular, the relative feature importance results showed that soil pH, soil CN, and SCA (as a proxy of light availability at the forest floor) were the most important site-specific drivers for predicting understorey properties at the plot level. This is consistent with other studies suggesting that initial local conditions determined understorey change over time (e.g. Naaf and Kolk, 2016) and understorey vegetation were more sensitive to light availability and overstorey structure than climate warming (e.g. Chelli et al., 2021; De Pauw et al., 2022). Several studies have shown that soil acidification can be a main contributor to long-term vegetation change in European forests (e.g. Baeten et al., 2009; Van Calster et al., 2008), while soil organic matter and soil N content have been shown to significantly influence understorey species richness and cover (Laughlin et al., 2007). Changes in canopy cover and composition affect light availability, microclimate temperature, humidity and litter quality, and may potentially buffer responses of the understorey to global-change drivers such as N deposition and climate warming (Chevaux et al., 2022; Naqinezhad et al., 2022). The relatively low importance of climatic variables might be explained by this buffering effect of the forest canopy, which is especially pronounced for warming effects (Lenoir et al., 2017; Zellweger et al., 2020).

Mean annual precipitation (MAP) was found to be very important in predicting understorey properties, among tested regional-scale drivers. Previously, less attention has been paid to precipitation compared to climate warming. However, variations in precipitation can affect ecosystem structure and function by altering the frequency, severity and

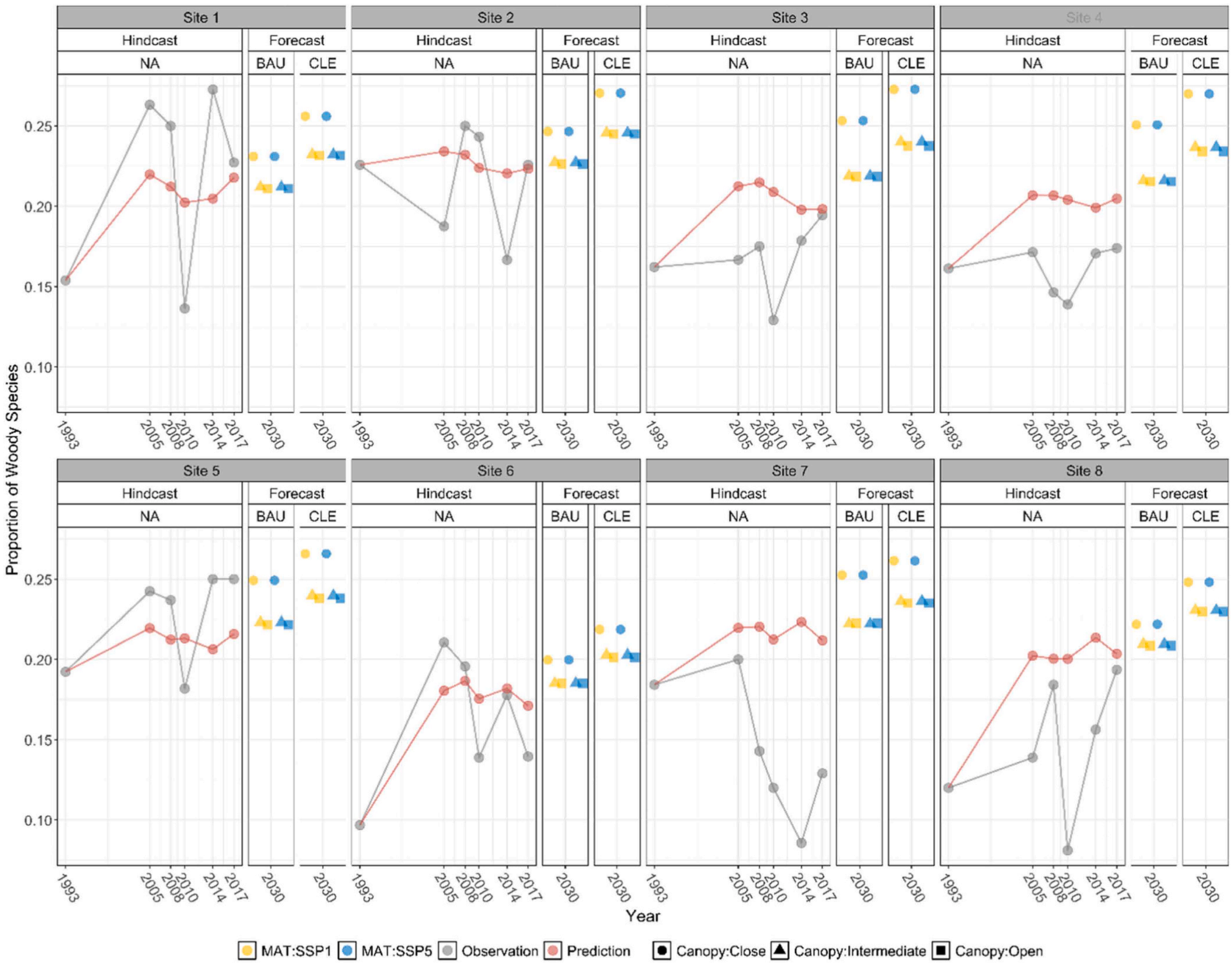

Fig. 5. Trajectories of proportion of woody species between 1993 and 2030 for 8 forest sites in Austria. For the years 2005–2017, we hindcasted the proportion of woody species for each year with observed environmental changes. NA refers to no applicable scenario since there is no scenario applied in the hindcasting. For the year 2030, we forecasted the proportion of woody species for two Nitrogen deposition scenarios: BAU (Business as Usual) and CLE (Clean air outlook of Europe), for two climate scenarios: SSP1 and SSP5, and for three canopy openness scenarios: open (25 %), intermediate (50 %) and closed (100 %).

timing of drought stress in the understorey (Gu et al., 2016). Short-term precipitation treatments have confirmed that variation in precipitation can impact the understorey's functional composition (e.g. Felsmann et al., 2018; Hoeppner and Dukes, 2012). Otsu et al. (2023) also found that long-term increases in precipitation would alter understorey composition towards fewer forest generalist species.

Although N deposition has been declining since the 1980s in Europe (Engardt et al., 2017), it remains unclear how long legacy effects from historically elevated N may linger and affect the understorey community. Some studies reported that understorey herbs are in a slow recovery, either following decreased nitrogen input after the cessation of experimental treatments or from decreasing atmospheric N deposition (e.g. Stevens, 2016; Strengbom et al., 2001). Dirnböck et al., (2018) and Wen et al., (2022) have projected understorey vegetation responses to future declining N deposition targets and found that decreasing rates of N deposition under current legislation scenarios (CLE) do not reduce the N load enough to allow species recovery from eutrophication at the European scale. In our scenario analysis for the Austrian sites, we showed that species richness and total vegetation cover were found to decrease with declining N deposition, suggesting no recovery in terms of species richness and total vegetation cover in the short term. This might be explained by ecosystem hysteresis or legacy effects of past exceedance of critical loads (Gilliam et al., 2019).

Overall, the projections of the four understorey properties in 2030 were not sensitive to climate warming at the Austrian sites. This can be explained by the lower importance of initial MAT and ΔMAT in the models, and the relatively small (0.2 °C) differences between the SSP1 and SSP5 scenarios. At the Austrian sites, a closed canopy could shift the understorey community towards a higher proportion of woody species and a higher proportion of forest specialists but with fewer species and a lower vegetation cover compared to an open canopy. This is in line with previous studies showing that forest canopies can play a key role in moderating the response of understorey vegetation to global change (Bhatta and Vetaas, 2016; De Lombaerde et al., 2022; Yu and Sun, 2013). These findings indicate that thoughtful forest canopy management will be key to protecting understorey biodiversity and functioning in the future.

4.2. *Strengths and limitations of proposed site-specific predictive models*

First, previous studies have suggested that plot-level predictive models of understorey biodiversity should not only incorporate regional-scale global-change drivers but also local-scale predictors representing a range of environmental gradients (e.g. Janssen et al., 2018;

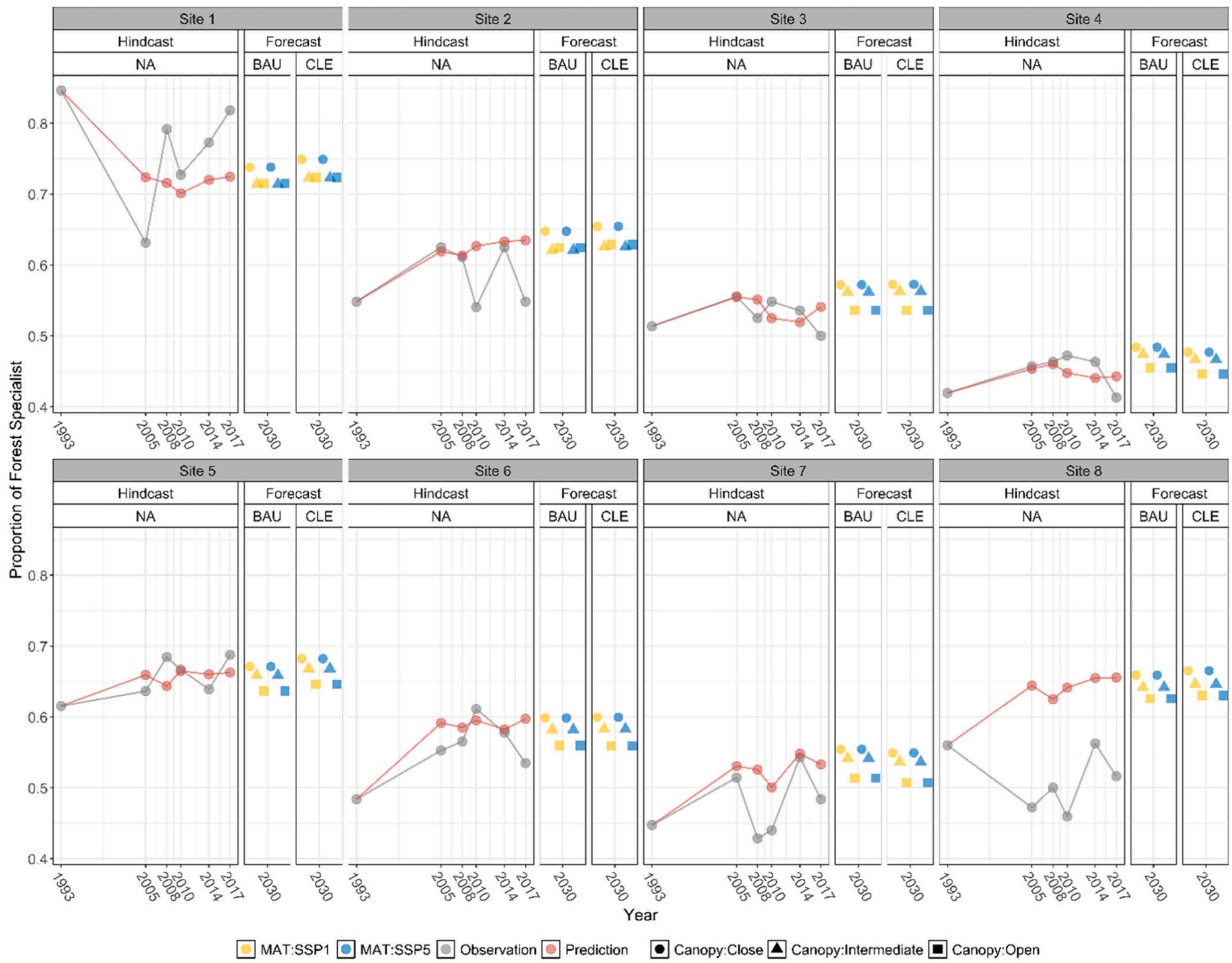

Fig. 6. Trajectories of proportion of forest specialists between 1993 and 2030 for 8 forest sites in Austria. For the year 2005–2017, we hindcasted proportion of forest specialists for each year with observed environmental changes. NA refers to no applicable scenario since there is no scenario applied in the hindcasting. For the year 2030, we forecasted proportion of forest specialists for two Nitrogen deposition scenarios: BAU (Business as Usual) and CLE (Clean air outlook of Europe), for two climate scenarios: SSP1 and SSP5, and for three canopy openness scenarios: open (25 %), intermediate (50 %) and closed (100 %).

Zellweger et al., 2015). In our GBR models, we included regional-scale drivers together with site-specific drivers, which led to a relatively high predictive model performance compared to our previous regional-scale models (without site-specific drivers) that predicted averaged trends of understorey change (Wen et al., 2022). Second, benefiting from the machine learning approach, predictive performance increased on average by 47.45 % compared to the tested GAM models (Table S10).

While our models exhibited a good predictive ability to forecast understorey properties under global change and forest management for specific forest sites (Figs. 3–6), they also have some limitations that should be considered in future studies. Given that the datasets from the forestREplot database are not representative (probabilistic) samples of European temperate forests, this might have introduced a bias in the final models. Second, since historical N deposition data are not available from the EMEP database, we estimated past N deposition using decadal correction factors (Duprè et al., 2010). More precise historical N deposition data are likely needed to further improve the models. Third, there was still a small discrepancy between the performance evaluated based on the training dataset and the performance evaluated based on the test dataset (Table 2). This might be because our dataset is still quite small for a machine learning application, and hence prone to overfitting, although we used a regularization technique to avoid this (Jabbar and Khan, 2015). Although increasing the number of data points can be considered a straightforward solution to overcome this issue in the future, extending ecological datasets such as the one applied in this study with additional site-specific data is challenging and labour-intensive. Advances in remote sensing might open up new opportunities in the future to enrich large datasets with additional local-scale drivers (e.g. canopy height, canopy cover) (Newnham et al., 2015). Moreover, the models' performance on the Austrian subset was not as good as on the training and testing dataset, especially for the model that predicts the proportion of woody species. This indicates that models should be used with caution, especially for some of the considered understorey properties. Nevertheless, GBR model performance was found to be much better than the performance of GAM models (Table S10). A potential reason for the lower model performance on the Austrian dataset might be the rather short time intervals between survey dates (between 12 and 24 years), time intervals that were only comparable to those of a small subset of training dataset. Finally, we only used one machine learning algorithm rather than ensemble predictions of multiple machine learning algorithms. With multiple machine learning algorithms, a larger dataset, and a more complete characterization of the abiotic and biotic environment (e.g. microclimate data), it might be possible to further improve the predictive ability of the models (Araújo and New, 2007).

5. Conclusion

Our study applied a machine learning approach to predict temperate forest understorey trajectories in response to global-change and site-specific drivers. Our findings illustrate that a machine learning approach is promising to grasp complex relationships between local environmental conditions, regional-scale global-change and understorey dynamics. It allows forecasting trajectories of different understorey properties, based on a relatively small dataset. The presented GBR models could allow forest managers to predict understorey responses to global change with high forecast precision at specific forest sites, which could aid in adjusting management interventions to address challenges posed by global change. Future work could focus on evaluating the accuracy and general applicability of such models and integrating these with decision support systems that could be used by forest managers and planners to support decision-making in an uncertain future.

CRediT authorship contribution statement

Markéta Chudomelová: Writing – review & editing. **Kris Verheyen:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Markus Bernhardt-Römermann:** Writing – review & editing. **Bingbin Wen:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Thomas A. Nagel:** Writing – review & editing. **Keith Kirby:** Writing – review & editing. **Jörg Brunet:** Writing – review & editing. **Tobias Naaf:** Writing – review & editing. **Jonathan Lenoir:** Writing – review & editing. **Monika Wulf:** Writing – review & editing. **Ondřej Vild:** Writing – review & editing. **Leen Depauw:** Writing – review & editing. **Martin Kopecký:** Writing – review & editing. **Michael P. Perring:** Writing – review & editing. **František Máliš:** Writing – review & editing. **Lander Baeten:** Writing – review & editing. **Dries Landuyt:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Thomas Dirnböck:** Writing – review & editing. **Haben Blondeel:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Hans Van Calster:** Writing – review & editing. **Radim Hédl:** Writing – review & editing. **Luc De Keersmaeker:** Writing – review & editing. **Martin Macek:** Writing – review & editing. **Sybryn L. Maes:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We thank the European Research Council (ERC) for funding this research through the UnderScore project (ERC Proof of Concept Grant:861957) and the PASTFORWARD project (ERC Consolidator Grant:614839). BW is supported by the China Scholarship Council (CSC) on a PhD research fellowship. DL is supported by the Research Foundation-Flanders (FWO) on a postdoctoral fellowship. LD was supported by FWO (1221523 N). RH and MC were supported by the Czech Science Foundation (No. 21–11487S) and the long-term development project of the Czech Academy of Sciences (RVO 67985939). MK and MM were supported by the Czech Academy of Sciences (RVO 67985939). MC was supported by the postdoctoral fellowship L200052302. We thank all collaborators from the forestREplot network for providing data support in this study. Thanks to Lingfeng Li and Loïc Gillerot who helped in the preparation of fieldwork. Thanks to Kris Ceunen, Tosca Vanroy, Robbe De Beelde, and Jari Vandendriessche who helped in the fieldwork. Thanks to Luc Willems, Greet De Bruyn, Maarten Volckaert, Sophie Schepens, and Mathieu Schatteman who helped to analyse soil samples. We also express our gratitude to the editor and four anonymous reviewers for their constructive comments on an earlier version of the manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122091.

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