Title: Responses of competitive understorey species to spatial environmental gradients inaccurately explain temporal changes

Authors: Emiel De Lombaerde[a,*], Kris Verheyen[a], Michael P. Perring[a,b], Markus Bernhardt-Römermann[c], Hans Van Calster[d], Jörg Brunet[e], Markéta Chudomelová[f,g], Guillaume Decocq[h], Martin Diekmann[i], Tomasz Durak[j], Radim Hédl[f], Thilo Heinken[k], Patrick Hommel[l], Bogdan Jaroszewicz[m], Martin Kopecký[n,o], Jonathan Lenoir[h], Martin Macek[n], František Máliš[p,q], Fraser J.G. Mitchell[r], Tobias Naaf[s], Miles Newman[r], Petr Petřík[n], Kamila Reczyńska[t], Wolfgang Schmidt[u], Krzysztof Świerkosz[v], Ondřej Vild[f], Monika Wulf[s], Lander Baeten[a]

*: Corresponding author. Tel.: +32 9 246 90 30

Email address: emiel.delombaerde@ugent.be (E. De Lombaerde)

[a]: Forest & Nature Lab, Campus Gontrode, Faculty of Bioscience Engineering, Ghent University, Geraardsbergsesteenweg 267, 9090 Melle-Gontrode, BELGIUM (mailing address for correspondence)

[b]: School of Biological Sciences, The University of Western Australia, 35 Stirling Highway, Crawley WA 6009 AUSTRALIA

[c]: Institute of Ecology and Evolution, Friedrich Schiller University, Jena, Dornburger Str. 159, 07743 Jena, GERMANY

[d]: Research Institute for Nature and Forest, Kliniekstraat 25, 1070 Brussel, BELGIUM

[e]: Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Box 49, 230 53 Alnarp, SWEDEN

[f]: Department of Vegetation Ecology, Institute of Botany, The Czech Academy of Sciences, Lidická 25/27, CZ-657 20 Brno, CZECH REPUBLIC

[g]: Department of Botany and Zoology, Faculty of Sciences, Masaryk University, Kotlářská 2, CZ-611 37 Brno, CZECH REPUBLIC

[h]: Unité de recherche “Ecologie et Dynamique des Systèmes Anthropisés” (EDYSAN, FRE 3498 CNRS-UPJV), Université de Picardie Jules Verne, 1 rue des Louvels, F-80037 Amiens Cedex 1, FRANCE

[i]: Vegetation Ecology and Conservation Biology, Institute of Ecology, FB 2, University of Bremen, Leobener Str. 5, DE-28359 Bremen, GERMANY

[j]: Department of Ecology, University of Rzeszów, ul. Rejtana 16C, PL-35- 959 Rzeszów, POLAND

[k]: General Botany, Institute of Biochemistry and Biology, University of Potsdam, Maulbeerallee 3, DE-14469 Potsdam, GERMANY

[l]: Wageningen Environmental Research (Alterra), P.O. Box 47, 6700 AA Wageningen, THE NETHERLANDS

[m]: Białowieża Geobotanical Station, Faculty of Biology, University of Warsaw, ul. Sportowa 19, 17-230 Białowieża, POLAND

[n]: Department of GIS and Remote Sensing, Institute of Botany, The Czech Academy of Sciences, Zámek 1, CZ-252 43, Průhonice, CZECH REPUBLIC

[o]: Department of Forest Ecology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, CZ-165 00 Prague 6 – Suchdol, CZECH REPUBLIC

[p]: Technical University in Zvolen, Faculty of Forestry, T. G. Masaryka 24, 960 53 Zvolen, SLOVAKIA

[q]: National Forest Centre, T. G. Masaryka 22, 960 92 Zvolen, SLOVAKIA

[r]: Botany Department and Trinity Centre for Biodiversity Research, School of Natural Sciences, Trinity College, the University of Dublin, College Green, Dublin 2, IRELAND

[s]: Leibniz Centre for Agricultural Landscape Research (ZALF), Eberswalder Straße 84, 15374 Müncheberg, GERMANY

[t]: Department of Botany, Faculty of Biological Sciences, University of Wrocław, Kanonia 6/8, PL-50-328 Wrocław, POLAND

[u]: Department Silviculture and Forest Ecology of the Temperate Zones, Georg-August-University Göttingen, Büsgenweg 1, D-37077 Göttingen, GERMANY

[v]: Museum of Natural History, University of Wrocław, Sienkiewicza 21, PL-50-335 Wroclaw, POLAND

Abstract

Understorey plant communities play a key role in the functioning of forest ecosystems. Under favourable environmental conditions, competitive understorey species may develop high abundances and influence important ecosystem processes such as tree regeneration. Thus, understanding and predicting the response of competitive understorey species as a function of changing environmental conditions is important for forest managers. In the absence of sufficient temporal data to quantify actual vegetation changes, space-for-time (SFT) substitution is often used, i.e. studies that use environmental gradients across space to infer vegetation responses to environmental change over time. Here we assess the validity of such SFT approaches and analysed 36 resurvey studies from ancient forests with low levels of recent disturbances across temperate Europe to assess how six competitive understorey plant species respond to gradients of overstorey cover, soil conditions, atmospheric N deposition and climatic conditions over space *and* time. The combination of historical and contemporary surveys allows (i) to test if observed contemporary patterns across space are consistent at the time of the historical survey, and, crucially, (ii) to assess whether changes in abundance over time given recorded environmental change match expectations from patterns recorded along environmental gradients in space. We found consistent spatial relationships at the two periods: local variation in soil variables and overstorey cover were the best predictors of individual species' cover while interregional variation in coarse-scale variables, i.e. N deposition and climate, was less important. However, we found that our SFT approach could not accurately explain the large variation in abundance changes over time. We thus recommend to be cautious when using SFT substitution to infer species responses to temporal changes.

Keywords: temperate forest; herb layer; tree regeneration; global change; nitrogen deposition; canopy; spatiotemporal resurvey data; cover abundance; chronosequence; forestREplot

Introduction

The importance of understorey plant communities and their key role in the functioning of forest ecosystems are increasingly recognized (Gilliam, 2007; Nilsson & Wardle, 2005; Thrippleton, Bugmann, Kramer-priewasser, & Snell, 2016). One important influence of the understorey is its effect on tree regeneration; each tree in the overstorey has recruited in and passed through this forest layer as a seedling. Through the initial competitive interactions with the regeneration of overstorey tree species, the understorey community acts as a filter and may have long-term impacts on forest overstorey structure and composition (George & Bazzaz, 1999; Royo & Carson, 2006). Opportunistic, fast-growing understorey plant species develop high abundances when resource availability is high, leading to reduced seedling growth and survival, and even complete failure of the tree regeneration (Balandier, Collet, Miller, Reynolds, & Zedaker, 2006; George & Bazzaz, 1999; Royo & Carson, 2006). Thus, it is important for forest managers to understand which (combinations of) environmental factors mainly drive the abundance response of these competitive species.

Understorey species' distribution and abundance are first of all determined by the local-scale environment. The overstorey community can determine the composition and abundance of understorey plants by controlling resources and conditions on the forest floor (Gilliam, 2007; Härdtle, Oheimb, & Westphal, 2003; Li et al., 2012; Nieto-lugilde et al., 2015). Overstorey opening results in increased light availability at the forest floor, but can also improve nutrient and water availability and temperature conditions for understorey plants (Barbier, Gosselin, & Balandier, 2008; Wagner, Fischer, & Huth, 2011). This may lead to a shift in species composition, with a higher cover of light-demanding, competitive species (Degen, Devillez, & Jacquemart, 2005; Kelemen, Mihók, Gálhidy, & Standovár, 2012; Naaf & Wulf, 2007). Understorey species composition and abundance also depend strongly on local soil conditions such as moisture, pH or nutrient availability (Marage & Gégout, 2009; Van Couwenberghe, Collet, Lacombe, & Gégout, 2011; Wagner et al., 2011). In addition to the local site conditions, environmental drivers that vary over broad gradients such as climate and atmospheric nitrogen (N) deposition may be important as well. Coudun and Gégout (2007) found that mean annual temperature predicted the cover of the competitive dominant species *Vaccinium myrtillus*, in addition to soil acidity and nutrient levels. An experiment by De Frenne et al. (2015) reported that tall, competitive plants, increased in response to elevated temperature, especially under high light availability. Studies on atmospheric N depositions have also documented increasing dominance of fast growing, nitrophytes at the expense of oligotrophic and stress tolerant species (Bobbink et al., 2010; Dirnböck et al., 2014; Gilliam et al., 2016). Integrating all these variables acting at the local and regional scale may thus be very important in predicting understorey species cover along environmental gradients.

Environmental conditions in forests are changing over time due to global change and management interventions. Understanding how these environmental changes are causing shifts in the abundances of the species that hamper tree regeneration, preferably requires temporal data (Verheyen et al., 2017). Repeated observations of species abundance are, however, often not available because people have not had the (financial) means or foresight to establish permanent plots or precisely georeference long-term data for particular species or vegetation. Space-for-time (SFT) substitution, which can be broadly defined as using (contemporary) spatial data to infer changes over time, can therefore provide a very useful alternative (Pickett, 1989). In the case of forest understorey vegetation, vegetation inventories covering broad spatial gradients of climate and deposition could be used to understand how competitive understorey species will potentially respond to changing environmental conditions over time (Hedwall & Brunet, 2016). However, opinions on whether the use of SFT substitution is valid differ and the assumption that drivers of spatial gradients also drive temporal changes requires validation (Banet & Trexler, 2013; Blois, Williams, Fitzpatrick, Jackson, & Ferrier, 2013; Johnson & Miyanishi, 2008).

In this study, we performed a literature search to identify which understorey plant species are the most important and frequent competitors of tree seedlings in European temperate forests. We then used the data from 36 vegetation resurvey studies from forests across temperate Europe to assess how these competitive understorey species respond to broad gradients of overstorey cover, soil conditions, atmospheric N deposition and climatic conditions over space *and* time. Each study provides data from historical vegetation records and contemporary resurveys of those records after at least two decades. Our general aim was to assess whether widely available contemporary inventory data can be used to infer likely responses to changing conditions over time. Our main research questions were: (i) which species are considered as most important competitors of tree regeneration in temperate European forests?; (ii) which environmental conditions determine the abundance of these species along spatial gradients and is the relative importance of these drivers consistent across the contemporary and historical vegetation data? and (iii) do species abundance changes over contemporary spatial environmental gradients allow predicting how environmental change over time cause species to actually change their abundances?

Materials and methods

Study species

We performed a formal literature search to identify which understorey species are the most important and frequent competitors of tree seedlings in European deciduous temperate forests (research question 1). We searched for peer-reviewed publications using the bibliographic database of the ISI Web of Knowledge in March 2016 over all available years (1955 to 2016). We used the following search string: Forest* AND tree* AND (seedling* OR sapling* OR regeneration) AND ((understor* OR “ground layer” OR “herb* layer” OR “ground vegetation” OR “ground flora”) AND compet*) OR (vegetation AND management) OR (weed*) OR (neighbo*r* AND compet*). Returns from this search were further inspected, and studies that met the following criteria were retained: (i) experimental studies, field experiments, observational field studies or reviews, (ii) studies from European temperate forests and (iii) a forest understorey species is reported to have had a negative impact on the performance of tree seedlings (e.g. their emergence, survival or growth). Studies were initially filtered by title and then by reading the abstracts to retain those studies with possible relevance to the research question. We then examined relevant studies individually and we searched the reference lists for additional publications. Of the 147 studies that we closely examined, 57 publications matched our criteria. A search using similar combinations of search terms using Google Scholar, reviewing only the first two pages (sorted by relevance), did not yield additional publications. For each understorey species, we counted the number of publications where it was identified to have a negative effect on tree regeneration (Table 1and Appendix A: Table 1). Although we cannot be certain that we found all available studies, we are confident that our set is a representative selection of species that are considered most important competitors of tree regeneration in European temperate forests. Our list of study species was further restricted by including only those that were mentioned to have a negative effect on tree regeneration in at least five publications. Furthermore, species had to be present in more than 100 plots and 10 data sets for both contemporary and historical surveys, that is, retaining species with sufficient data points and spatial coverage. Finally, we excluded species that showed a low cover across almost all plots (percentage cover lower than 15% in over 90% of the plots), because at low cover values they probably have a negligible negative effect on regeneration. Ultimately, six species matched these criteria: *Deschampsia flexuosa, Molinia caerulea, Pteridium aquilinum*, *Rubus fruticosus* agg., *Rubus idaeus* and *Vaccinium myrtillus* (Table 1, bold species).

Data sets

We used the data from 36 independent vegetation resurvey data sets in semi-natural temperate forests across Europe: from Switzerland to southern Sweden (south–north) and from the Ireland to Poland (west–east) (Fig. 1 and Appendix A: Table 2). The data sets included in our analyses cover long/broad gradients of overstorey cover, soil conditions, atmospheric N deposition and climatic conditions. Each data set is composed of multiple non-overlapping (in space) permanent or quasi-permanent plots recorded at two time points. The historical surveys were carried out between 1935 and 1994 and the resurveys between 1987 and 2014. Time intervals between the two surveys ranged between 17 and 75 years (38 years on average). The vast majority of plots in these data sets are described as ancient forest sites (*sensu* Peterken 1996) in which no forest stand replacement had taken place between the surveys (e.g. no clear cutting and replanting with conifers). However, management system changes could have taken place without abrupt changes in tree species composition (e.g. gradual transformation from former coppicing to mature forest). Generally, forest management remained stable or became less intensive between the surveys (Bernhardt-Römermann et al., 2015). All data sets are included in the forestREplot network (www.forestreplot.ugent.be), a global database combining biodiversity resurveys across temperate forests to advance global change research (Verheyen et al., 2017). For further details, see Appendix A (Table 2).

The data sets distinguish between three vegetation layers: the understorey layer (< 0.5-1 m plant height, incl. woody saplings/seedlings), shrub layer (woody plants of minimum height 0.5 to 1 m and maximum height 5 to 14 m) and tree layers. We used cover estimates of each species in each layer as a measure of abundance. Because species cover was recorded in different ways across data sets, cover data were harmonized by converting the different cover recording scales to mid-point percentages of their cover class.

For each species, two subsets of plots were selected: one with the contemporary plots where the species is present (i.e. cover > 0%) and one with the historical plots (Table 1). We also selected species-specific subsets of plot-pairs in which the study species is present at both survey times. The response variable used in our models is the cover percentage of the subject species per plot where it is present.

Explanatory variables

We used coarse-scale variables expressing gradients in climate and atmospheric N deposition to explain variation in cover among data sets. We used mean annual temperature (MAT; °C) and mean annual precipitation (MAP; mm) to characterize the climatic conditions. Climate data were derived from the Climatic Research Unit at a spatial resolution of 0.5 ° covering monthly means for the period 1901–2013 (Harris, Jones, Osborn, & Lister, 2014). For each data set, we calculated MAT and MAP by averaging annual values for the 10 years preceding the historical surveys and the contemporary resurveys. Nitrogen deposition rate ("Ndep"; kg N/ha/year) was quantified using the EMEP database at a 50-km spatial resolution. We calculated a mean N deposition rate for the period equal to the intercensus interval preceding both the historical survey and resurvey for each data set in a similar way as Verheyen et al. (2012) and Bernhardt-Römermann et al. (2015) using the correction factors provided by Duprè et al. (2010). De Schrijver et al. (2011) showed that the modelled EMEP data and locally observed N deposition data are strongly correlated.

To explain variation in species cover between plots within data sets, we derived plot-level variables related to light availability at the forest floor and soil properties for the two surveys separately. As a measure for light availability at the forest floor, we calculated the total cover of tree and shrub layer species (overstorey cover; "OS") based on species-specific cover values using the approach developed by Fischer (2015). This approach takes into account the overlap between the layers by subtracting the product of the cover values from their sum. As proxies of the prevailing plot-specific soil properties, we calculated cover-weighted mean Ellenberg indicator values using the individual species' indicator values for soil fertility (EIV_N), soil reaction (EIV_R) and soil moisture (EIV_F) (Diekmann, 2003; Ellenberg, Weber, Düll, Wirth, & Werner, 2001). The study species were excluded from the EIV calculations to avoid circularity. In this study, we used the product EIV_N x EIV_R, which is known to be a good proxy for the turnover rates of organic matter and soil nutrient availability (humus quality; "Hms") (Godefroid, Massant, & Koedam, 2005; Rogister, 1978).

Data analysis

To quantify which environmental variables determine the dominance of our six study species (research question 2), we related the cover abundance of each species to the plot-level and coarse-scale environmental variables using multilevel models to account for the hierarchical structure of the data. First, only the abundance variation along spatial gradients in the contemporary data sets was modelled; these models are henceforth called "spatial models". Models were fitted with the lmer function in the lme4 package in R 3.4.1 (Bates, Maechler, Bolker, & Walker, 2015; R Core Team, 2017). To linearize the relationship between response and explanatory variables and stabilize residual variance, we used a natural logarithmic transformation on the species cover data (Gelman & Hill, 2007). All explanatory variables, measured at different scales, were standardized prior to analysis which results in the estimation of regression coefficients that are comparable in magnitude (Schielzeth, 2010). The parameter estimates of regression coefficients express how the log-cover values change for a one standard deviation change in the explanatory variables. To detect possible multicollinearity between the different explanatory variables, variance inflation factors (VIF) were calculated according to Zuur et al. (2009). These VIF values were low (< 3), indicating low collinearity.

To obtain the most parsimonious model for each species, we started from the ''beyond optimal model'' (Zuur et al., 2009). This model contained all explanatory variables (Hms, EIV_F, OS, MAT, MAP and Ndep) as fixed effects and a random effect term for 'data set' (Spatial model):

$$\ln(y) = \beta_0 + \beta_1 x + \cdots + random\ part$$

Spatial model

In this model, y is the percentage cover of one of the study species at the contemporary survey, x is one of the six explanatory variables and the $random\ part$ denotes the effect of 'data set' and residual error. Backward elimination of explanatory variables was done using maximum likelihood-fitted models at a 5% level of significance. This procedure was automatized using the StepLmer function (R package lmerTest) with F-tests for parameter estimates calculated using the "Kenward-Roger" approximation. For *M. caerulea*, a quadratic term for $\mathrm{EIV_F}$ was added after observing a bell shaped pattern in the model residuals. For each species, the most parsimonious model was refitted with restricted maximum likelihood. The goodness of fit for these models were estimated by calculating pseudo R^2 values following the method of Nakagawa and Schielzeth (2013). R^2_{marginal} expresses variance explained by fixed effects and $R^2_{\mathrm{conditional}}$ expresses variance explained by both fixed and random effects.

To determine whether the relative importance of the explanatory variables of species abundance was consistent across the contemporary and historical vegetation data, we applied the same set of explanatory variables identified in the most parsimonious spatial models above to the historical survey data. This means we modelled the historical survey cover data of each species in response to the historical survey values of only those explanatory variables that were retained in the models for the contemporary data. By comparing parameter estimates and goodness-of-fit estimates for the models using the historical and resurvey data, we explored to what degree explanatory variables of present-day patterns in cover abundance, especially those retained in the model selection, are also relevant to explain patterns in the old data.

Finally, we test if species abundance changes over contemporary spatial environmental gradients allow predicting how environmental change over time cause species to change their abundances (research question 3; see Appendix B for detailed information on our approach). First, we modelled observed changes in species abundance over time, by fitting regression models for each species using the subset of plots in which a species was present at both survey times for each species (Temporal model). For each plot-pair, temporal change was characterized as the natural logarithm of the ratio between the contemporary resurvey and the historical survey. We did this for the response variable (percentage cover), and for all the explanatory variables used in the spatial models. Similar as for the spatial models, we used a multilevel modelling approach with random effects for ‘data set’.

$$\ln\left(\frac{y_r}{y_i}\right) = \beta_0^T + \beta_1^T \ln\left(\frac{x_r}{x_i}\right) + \cdots + random\ part$$

Temporal model

In this model, y_r and y_i are the percentage cover of one of the study species at the contemporary and historical survey resp., x_r and x_i are one of the six explanatory variables at the contemporary and historical survey resp. and $random\ part$ denotes the effect of ‘data set’. The intercept β_0^T catches the average temporal change in abundance not accounted for by the used explanatory variables. Second, these temporal models then allowed making predictions of abundance change over time in response to a particular change in environmental conditions. For each predictor variable separately, we predicted the change in species cover (as log ratio) for a realistic change in the predictor (also as log ratio): here we used the observed mean change in the predictor between the two survey times, $\overline{r_x} = \frac{\overline{x_r - x_i}}{x_i}$ (Table 2).

$$\widehat{y^T} = \widehat{\ln\left(\frac{y_r}{y_i}\right)} = \beta_0^T + \beta_1^T \ln\overline{\left(\frac{x_r}{x_i}\right)} = \beta_0^T + \beta_1^T \ln(1 + \overline{r_x})$$

Temporal prediction

Additionally, predictions were made for the mean change in abundance in the absence of environmental change,

$$\widehat{y^{T}} = \beta_0^{T}$$

'No change' prediction

Third, we made similar predictions of temporal change in abundance in response to the same environmental change in each predictor $\overline{r_x}$, but based on the species' abundance patterns along spatial gradients, that is, using the contemporary spatial models:

$$\widehat{y^{SFT}} = \beta_1 \ln(1 + \overline{r_x})$$

Space-for-time prediction

In this way, we were able to compare the predicted change in the species' abundances for the actual temporal vs. the spatial model, based on the same change $\overline{r_x}$ in an environmental predictor x. See Appendix B for a more detailed explanation on the predictions using our SFT approach and how these are comparable to the predictions using the temporal models. For the temporal models, 95% confidence intervals were calculated using direct model output, i.e. the mean and standard error of each parameter. For the predictions based on the spatial models, 95% confidence intervals were calculated following an informal Bayesian approach (Gelman & Hill, 2007). For each prediction, we drew 1000 random samples from a normal distribution for the mean and standard error of each model parameter. For each of these samples we were able to calculate the log ratios and compute the confidence intervals around the predictions.

Results

Spatial models

Results of the most parsimonious spatial models using resurvey data (x-axis in Fig. 2) show that local variation in the proxies for soil conditions (moisture and humus quality) and overstorey cover to a lesser extent were the best predictors of individual species' cover. Even though covering a broad range in climatic conditions, MAT and MAP were not even retained in the spatial models. Only the interregional variation in N deposition rate had a significant but weak negative impact on the cover of *R. idaeus*. We found that humus quality had a significant and negative effect on all species except for *R. fruticosus* agg. and *R. idaeus*. Soil moisture (EIV_F) had a varying effect on species cover; we observed a negative effect on *D. flexuosa*, whereas the cover of *M. caerulea* had a bell-shaped, quadratic response for EIV_F with a maximum between mean Ellenberg values of 6 and 7. Overstorey cover was found to have a negative effect on the cover abundance of *D. flexuosa*, *M. caerulea*, *R. fruticosus* agg. and *R.* idaeus, although the magnitude of the effect was relatively small. A more detailed summary of parameter estimates, significance tests and goodness-of-fit estimations for each species model can be found in Appendix A (Tables 3-8). Overall, the contemporary spatial models fitted the data well, indicated by the $R^2_{conditional}$ values ranging from 0.24 up to 0.55 (Fig. 2; Appendix A: Tables 3-8). On average 32% of the total variability was explained by the random 'data set' effect, reflected by the differences between corresponding $R^2_{marginal}$ and $R^2_{conditional}$ estimations. For *R. fruticosus* agg. and *R. idaeus*, only 3% and 4% of variability respectively was explained by the fixed effects ($R^2_{marginal}$=0.03 and 0.04, respectively; Appendix A: Tables 3-8).

Relations between the species' cover abundance and the explanatory variables that were found to be significant in the spatial models using resurvey data were mainly consistent when linking the historical survey abundance data to the historical survey predictor values (Fig. 2; Appendix A: Fig. 1). For all retained explanatory variables, except for overstorey cover and EIV_F for *D. flexuosa* and humus quality for *P. aquilinum*, the confidence intervals of the parameter estimates overlapped with the 1:1 line, indicating that the effects of the predictors were consistent in the spatial models for both surveys. For *D. flexuosa* these effects differed in both magnitude and direction, whereas for *P. aquilinum* only marginally in magnitude. Both $R^2_{marginal}$ and $R^2_{conditional}$ estimates were similar between the models fitted with resurvey and historical data (Fig. 2; Appendix A: Tables 3-8).

Temporal vs. space-for-time approach

The models fitted using contemporary spatial data could not accurately explain variation in abundance response of our six study species to changes in the different explanatory variables over time. None of the mean changes in explanatory variables (Table 2), for both temporal models or SFT approach, lead to a significant change in cover, except for the SFT prediction for a mean change in N dep rate for *R. idaeus* (Fig. 3). This shows that even though the effect of a certain predictor variable may be large, a realistic change over time may not cause a significant change in plot-scale species' cover abundance, as was the case here. Similar results were found when making predictions for more extreme change in the explanatory variables, i.e. predictions for the 20% percentile and 80% percentile of the observed change in the plot-pairs between historical and contemporary resurveys (Appendix A: Fig. 2). The SFT approach cannot account for the changes in species' cover over time in absence of environmental change, i.e. β_0^T in the temporal models ('No change'; Fig. 3). The confidence intervals of many predictions using our SFT approach did not overlap with the mean prediction using the temporal models. Additionally, uncertainty of the predictions using temporal data was always substantially larger than the predictions using our SFT approach (except for N deposition rate). For these reasons, predictions made using our SFT approach could not match the predictions based on actual temporal data.

Discussion

Being able to predict how competitive understorey species respond to different environmental drivers can be of key importance in attaining tree regeneration success. In this study, we first identified which understorey species are most important competitors of tree regeneration in European temperate forests. Using a large set of observational data along contemporary spatial gradients in environmental conditions, we then showed that local-scale variables related to light and soil conditions were most important in predicting the abundance of competitive species' abundance. Variation in coarse-scale variables such as climate and nitrogen deposition were less important. Finally, we showed, however, that these contemporary spatial relations could not accurately explain the large variation in species' abundance response over time.

Previous studies that analysed the response of individual understorey species cover to overstorey openness observed strong effects (Gaudio, Balandier, & Marquier, 2008; Ricard & Messier, 1996; Van Couwenberghe et al., 2011). In our study, we found, however, that overstorey cover had only a relatively small and negative effect or no significant effect on cover abundance. This might be because *D. flexuosa, P. aquilinum, R. fruticosus and V. myrtillus* have been shown to be able to tolerate shaded conditions; they may, even under lower light levels, be able to maintain productivity and, especially in the case of *R. fruticosus* agg., remain dominant in the understorey (Balandier et al., 2013; den Ouden, 2000; Van Couwenberghe et al., 2011). Furthermore, the vast majority of plots used in this study are described as ancient forest sites (sensu Peterken, 1996) in which no forest stand replacement had taken place between the surveys (e.g. no large cuttings). Studies using spatial data linking species' abundance to light availability on the forest floor that also include more intensely managed and disturbed forests (e.g. Van Couwenberghe et al., 2011) may therefore show stronger effects to overstorey openness.

In contrast to overstorey cover, the variables used as proxies for soil nutrient availability (humus quality) and soil moisture (EIV_F) showed stronger effects on cover abundance. All species except for *R. fruticosus* agg. and *R. idaeus* developed higher cover on sites with low humus quality, which indicates their association as acidophytes with oligotrophic site conditions. This is largely in agreement with previous studies (Coudun & Gégout, 2007; Taylor, Rowland, & Jones, 2001; Van Couwenberghe et al., 2011). It should be noted that *R. fruticosus* agg. is a polymorphic grouping of numerous apomictic microspecies that are phylogenetically very close to each other and difficult to differentiate. It prefers to grow on acid soils, but can grow on a wide variety of soil types (Ellenberg et al., 2001). This can explain why proxies related to soil conditions did not have a significant effect on the cover of *R. fruticosus* agg. The EIV for soil moisture had a negative effect on the abundance of *D. flexuosa* and we found a bell-shaped, quadratic relation between cover of *M. caerulea* and the EIV for soil moisture with a maximum at high soil moisture content. This concurs with previous studies which indicated that abundance of *M. caerulea* is primarily determined by soil water saturation, soil aeration, and nutrient availability (Ellenberg et al., 2001; Taylor et al., 2001).

This data set, covering a large geographical range, gave us a unique opportunity to test the effect of coarse-scale environmental variables on the cover of understorey species. In our results, neither variables related to climate (MAT and MAP) or atmospheric N deposition rate were important in explaining variation in the cover of the study species. Species may simply be indifferent to variation in temperature or precipitation, e.g. *D. flexuosa*, *R. idaeus* and *M. caerulea* (Ellenberg et al., 2001). Previous studies have shown that forests with dense overstoreys can potentially buffer the effects of N deposition as well as macroclimate warming on understorey plant communities (De Frenne et al., 2013; Hedwall, Skoglund, & Linder, 2015; Verheyen et al., 2012). This can help to explain why these variables did not have a significant effect in our study. Spatio-temporal resolution of the data on the broad-scale drivers used in this study is relatively coarse and may fail to capture the variation in cover abundance on the local scale. A more detailed characterisation of the environment and measurements on a finer (micro)climatic scale could better explain variation in cover (Lenoir et al., 2013).

Other (a)biotic factors not included in this study may improve the amount of explained variability for the understorey species' cover. Past land-use can possibly have a strong, underestimated effect on the composition and abundance of temperate forest understoreys (Dupouey, Dambrine, Laffite,

& Moares, 2002; Perring et al., 2016; Randin, Jaccard, Vittoz, Yoccoz, & Guisan, 2009). This includes both real changes in land use (e.g. forests on agricultural land) as well as historical transitions in forest management (e.g. coppice to high forest). As the vast majority of the plots included in our study were located in ancient forests, only the latter could be an important factor in this study. Past forest management may have an influence on the composition of understories and abundance of species at present (den Ouden, 2000; Kopecký, Hédl, & Szabó, 2013). Also using data from forestREplot, Perring et al. (2018) have shown that understorey community trajectories were clearly influenced by interactions between management legacies from over 200 years ago and environmental change. Yet, detailed data on management history is often lacking and hard to come by. Large herbivores also have a large impact on the abundance of understorey species (Kirby & Thomas, 2000; Rooney, 2001; Vild et al., 2017). Reductions in the cover of species such as *Rubus* spp. are a common result in grazed woods (Kirby & Thomas, 2000), e.g. under selective browsing by roe deer (*Capreolus capreolus*; Boulanger et al., 2017; Moser, Schütz, & Hindenlang, 2006). Including detailed information on large herbivores may thus improve models predicting abundance cover. Abundance of these competitive species can also be influenced by the presence of other competitors. Hester et al. (1991) found that abundance of *V. myrtillus* decreased where *D. flexuosa* was present. *Deschampsia flexuosa*, in turn, was outcompeted by *Agrostis capillaris*, however less successfully under shaded conditions. Due to this competitive hierarchy (cf. Boulanger et al., 2017), as a result of asymmetric competition, cover of the 'weaker' competitor may decrease even though conditions are favourable. The presence of particular understorey plant species may therefore be important in determining cover abundance response of understorey species to environmental change.

There is no scientific consensus in ecological research on whether or not space-for-time (SFT) substitution is a valid method in predicting change over time. Conclusions from previous studies range from strong support (Banet & Trexler, 2013; Blois et al., 2013; Rolo, Olivier, Guldemond, &

van Aarde, 2016; Walker, Wardle, Bardgett, & Clarkson, 2010) to strong rejection (França et al., 2016; Isaac, Girardello, Brereton, & Roy, 2011; Johnson & Miyanishi, 2008). In our study, we show that managers and researchers have to be cautious when using spatial data to infer abundance changes of forest understorey species over time. The spatial models fitted using the historical plot data showed a similar relationship between the species cover and the explanatory variables as the models fitted using the resurvey data. This suggests that the contemporary spatial relations we found are consistent at other moments in time and can be used to predict cover abundance over spatial gradients at different points in time. However, by comparing the real observed temporal changes in species abundance in response to environmental change with the predicted changes in abundance based on a SFT, we found that the latter approach could not accurately predict how environmental change over time may cause species to change their abundances. This is mainly due to the fact that understorey species changed considerably in abundance even if changes in the predictors (included in our study) were fairly small. An explanation for these discrepancies is that understorey plant species may not be in equilibrium with the current environment. Observed cover abundance may be lagging behind present environmental conditions and instead reflect past habitat conditions (Bertrand et al., 2011; Dahlgren, Eriksson, Bolmgren, Strindell, & Ehrlen, 2006). This may be due to buffering effect of the overstorey or due to the fact that plants are able to persist under unfavourable conditions (Bertrand et al., 2016) and their lifespan can be as long as several decades (Ehrlén & Lehtilä, 2002). Lauenroth and Sala (1992) showed that the main reason their SFT approach did not match temporal models was due to a temporal lag in the time required for the studied vegetation to capitalize on the amount of precipitation at a given time. Such a time-lagged response may also be reflected in the Ellenberg indicator values. The use of direct measurements such as soil pH or soil moisture content (cf. Raduła, Szymura, & Szymura, 2018) instead of indirect values may therefore improve our models. Another reason SFT substitution fails is hysteresis: the rate of changes in species' cover-abundance is not the same when the environment shifts from shade to light (fast changes) or when it shifts from light to shade (slow changes). For example, *R. fruticosus* agg. can rapidly establish and spread in a clearing, but it will take several decades after canopy closure before it significantly declines. Additionally, sources of unwanted variability or bias in the used resurvey data may also arise because of relocation errors due to the use of quasi-permanent plots, observer biases and differences in recording seasons (Kapfer et al., 2017; Milberg, Bergstedt, Fridman, Odell, & Westerberg, 2008). These re-sampling errors may add a random error to the temporal change in vegetation, observer-related differences in composition (identification bias) and quantitative properties (abundance bias) among vegetation samples and may result in over- or under-estimation of species abundance. Furthermore, plant species may shift in their responses, either across geographical gradients (Diekmann & Lawesson, 1999; Wasof et al., 2013) or shift their niches over time (Pearman, Guisan, Broennimann, & Randin, 2008). This variation may result in inaccuracy of the temporal models and in the mismatch between our SFT approach and temporal models.

We investigated whether space-for-time substitution allows predicting how species that are considered important competitors for tree regeneration will respond to changing environmental conditions. However, the used data set restricted us from directly modelling tree regeneration in relation to these understorey species and environmental factors. In future research, given adequate data on tree seedlings (e.g. cover or counts) is available, these relationships could be modelled directly, for instance with structural equation modelling (SEM; Grace, Anderson, Olff, & Scheiner, 2010). Furthermore, the data used in this study mainly covered ancient forests with low levels of disturbance. Repeating our analyses on an extended data set that also includes more open-canopy forests could give further insights into how understorey species and tree regeneration change abundance under different environmental contexts. Due to the large scale of the data, we were also restricted to using indirect or coarse variables to characterise environmental conditions. In spite of these shortcomings related to data availability, phytosociological vegetation (re)survey data of this sort represents a valuable source of information to improve our understanding of how vegetation changes in relation to environmental gradients over space and time. Quantifying how ecosystems and communities vary along environmental gradients using observational data is a relevant method that complements the knowledge gained from experiments and modelling studies (Verheyen et al., 2017). We showed in our analyses that spatial (re)survey data can prove valuable in determining which environmental variables affect competitive understorey species cover. Our results suggest, however, that forest ecologists and managers should be cautious when using inventory data across large spatial gradients to predict the impacts of global change. More studies, similar to ours, that simultaneously examine variation in community composition over space, time, and along environmental gradients may clarify under what circumstances using space-for-time substitution, as a tool in ecology, is valid.

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Appendix A. Supplementary data

Appendix B. Detailed information on the temporal vs. space-for-time approach

Supplementary data associated with this article can be found, in the online version, at XXXXX.

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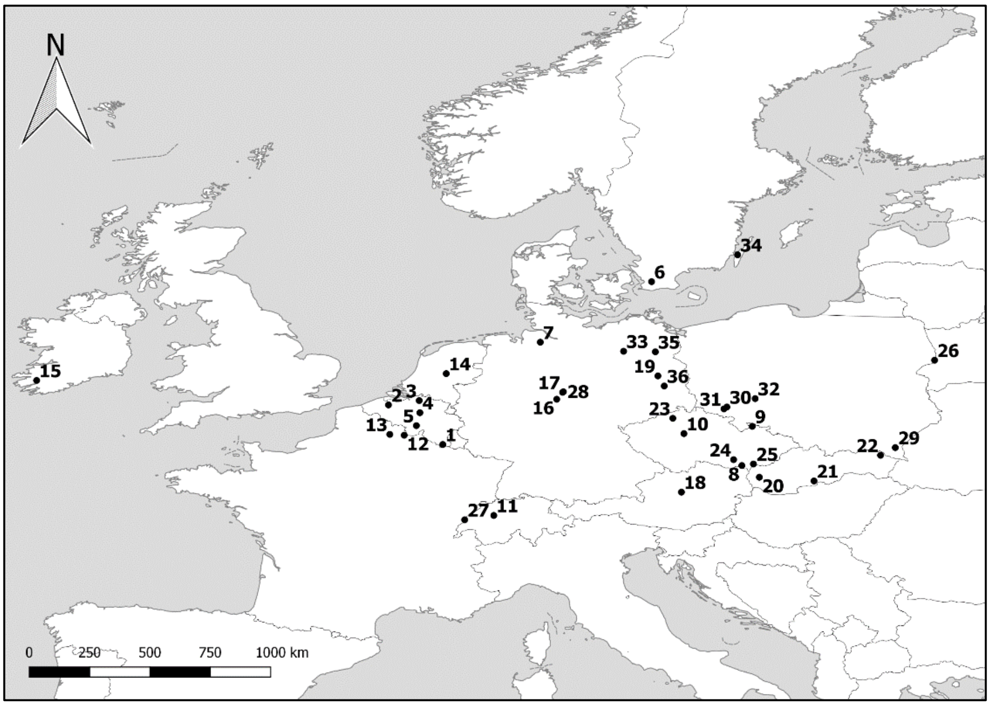
Figure captions

Fig. 1: Map showing the location of the 36 data sets included in this study (the numbers refer to data set IDs in Table S2). All data sets are included in the forestREplot network, a global database of understorey resurvey plots from temperate forests.

Fig. 2: Results of species-specific models predicting the cover abundance of six understorey plant species in response to spatial gradients in local-scale and large-scale explanatory variables. Points representation of the estimated effects (+/- 95% CI) of the explanatory variables for the spatial models using contemporary resurvey data (x-axis) and historical survey data (y-axis); only the explanatory variables that were retained after model selection are shown. The line represents the 1:1 line of no difference. Different shapes represent the six study species and colours the different explanatory variables. In parentheses $R^2_{\text{conditional}}$ values for historical and resurvey models are given, respectively.

Fig. 3: Predicted cover abundance change of six understorey plant species in response to temporal changes in several environmental explanatory variables. Predictions were based on species abundance changes along spatial environmental gradients (contemporary spatial models) and on actually observed temporal changes in abundance. For each explanatory variable separately, we predicted the change in species cover (as log ratio) to the observed mean change in that predictor

between the two survey times. Additionally, predictions of cover change were made in the absence of environmental change (No change). The dotted line represents these predictions using the temporal models. Explanatory variables that were retained in the most parsimonious contemporary spatial models are annotated in grey. The lines indicate the 95% confidence intervals around the predictions. Red: temporal predictions; Blue: predictions using SFT approach. Humus quality (Hms), Ellenberg F value (EIVF), Overstorey cover (OS), Mean annual temperature (MAT), Mean annual precipitation (MAP) and mean N deposition rate (Ndep).


N
34
6
7
33
35
26
14
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250
500
750
1000 km

Fig. 1

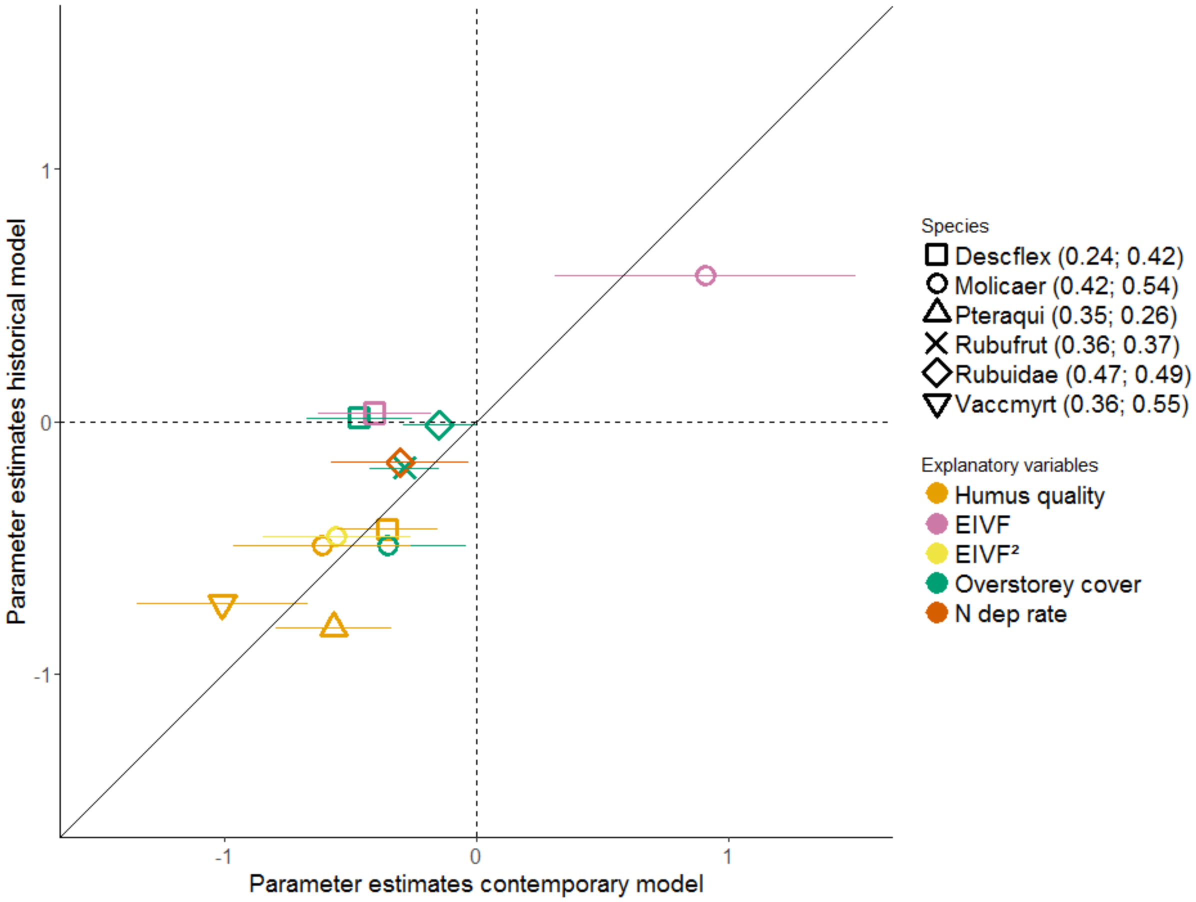
Parameter estimates historical model
1
0
-1
-1
0
1
Parameter estimates contemporary model
Species
Descflex (0.24; 0.42)
Molicaer (0.42; 0.54)
Pteraqui (0.35; 0.26)
Rubufrut (0.36; 0.37)
Rubuidae (0.47; 0.49)
Vaccmyrt (0.36; 0.55)
Explanatory variables
Humus quality
EIVF
EIVF²
Overstorey cover
N dep rate

Fig.2 (colour)

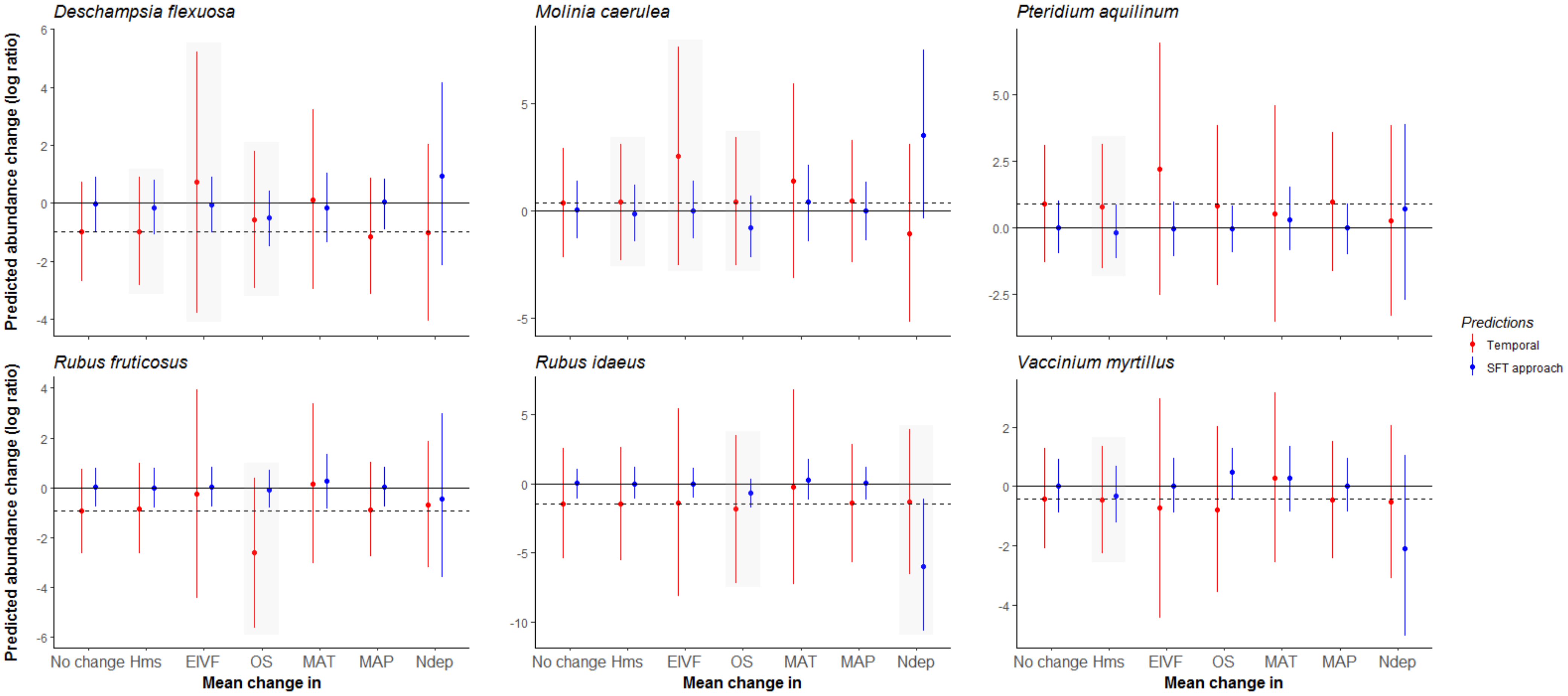
Deschampsia flexuosa
Molinia caerulea
Pteridium aquilinum
Rubus fruticosus
Rubus idaeus
Vaccinium myrtillus
Predicted abundance change (log ratio)
Predicted abundance change (log ratio)
6
4
2
0
-2
-4
5
0
-5
5.0
2.5
0.0
-2.5
4
2
0
-2
-4
-6
5
0
-5
-10
2
0
-2
-4
No change
Hms
EIVF
OS
MAT
MAP
Ndep
Mean change in
Predictions
Temporal
SFT approach

Fig.3 (colour)

Table 1: Results of a literature review, showing the understorey species that are reported in > 5 publications as having negative effects on tree regeneration. Species in bold were selected for this study based on their presence and abundance in our data.

Species	# Publications	# Resurvey plots [# data sets]	# Historical plots [# data sets]
***Rubus fruticosus* agg.**	20	651 [27]	502 [24]
Deschampsia flexuosa	12	246 [21]	274 [19]
Rubus idaeus	8	403 [29]	365 [21]
Pteridium aquilinum	8	228 [19]	228 [21]
Molinia caerulea	7	139 [16]	135 [16]
Agrostis capillaris	7	87 [11]	78 [14]
Deschampsia cespitosa	7	359 [27]	406 [29]
Vaccinium myrtillus	6	266 [20]	310 [20]
Calamagrostis epigeios	6	96 [9]	62 [9]

Table 2: Overview of the environmental conditions in the plots used in this study and how they changed over time. Mean values of all used explanatory variables over the contemporary and historical plots in which at least one study species is present are given. Mean changes between surveys are calculated for the subset of plots in which at least one species is present at both survey times. Values between brackets are the 20th and 80th percentiles of the range of change over time.

	Historical	**Contemporary**	**Mean change (20th, 80th) (%)**
Hms (EIV_N x EIV_R)	23.16	24.11	12.01 (-12.26, 38.66)
EIV_F	5.20	5.33	1.22 (-4.10, 7.47)
OS (%)	75.18	74.10	-0.73 (-17.15, 20.09)
MAT (°C)	8.65	9.90	15.30 (10.66, 20.49)
MAP (mm)	806.13	810.13	2.55 (-1.26, 7.29)
Ndep (kg/ha/year)	8.47	17.68	214.87 (-10.45, 505.81)

Appendix A: Supplementary data

Table 1: Species that are reported in scientific literature to be competitive towards tree seedlings in temperate European forests. Ranking according to number of publications.

Species or genus	Publications	# Publications
Rubus fruticosus agg.	(1–20)	20
Deschampsia flexuosa	(2, 3, 10, 21–29)	12
Rubus idaeus	(2, 9, 10, 14, 23, 30–32)	9
Pteridium aquilinum	(2, 8, 13, 21, 33–36)	8
Molinia caerulea	(2, 3, 21, 27, 30, 33, 37)	7
Agrostis capillaris	(2, 10, 38–42)	7
Deschampsia cespitosa	(2, 23, 24, 27, 43–45)	7
Vaccinium myrtillus	(2, 3, 21, 26, 46, 47)	6
Calamagrostis epigeios	(2, 3, 10, 20, 21, 27)	6
Epilobium angustifolium	(2, 9, 10, 48)	4
Calluna vulgaris	(2, 3, 33)	3
Holcus lanatus	(28, 38, 39)	3
Lolium perenne	(2, 28, 49)	3
Carex brizoides	(2, 27, 50)	3
Juncus effusus	(2, 3, 10)	3
Festuca rubra	(39, 42, 51)	3
Calamagrostis villosa	(27, 46, 48)	2
Cytisus scoparius	(2, 38)	3
Urtica dioica	(2, 9)	2
Cirsium vulgare	(2, 28)	2
Epilobium ciliatum	(2, 28)	2
Poa annua	(2, 28)	2
Holcus mollis	(10, 38)	2
Agrostis stolonifera	(43, 45)	2
Dactylis glomerata	(39, 52)	2
Robinia pseudoacacia	(2, 53)	2
Betula pubescens	(2, 41)	2
Sambucus nigra	(2, 23)	2
Calamagrostis arundinacea	(48)	1
Brachypodium pinnatum	(54)	1
Fagus sylvatica	(55)	1
Allium ursinum	(56)	1
Senecio ovatus	(56)	1
Persicaria maculosa	(28)	1
Rumex obtusifolius	(28)	1
Arrhenatherum elatius	(39)	1
Carex sylvatica	(3)	1
Carex digitata	(3)	1
Vaccinium vitis-idaea	(21)	1
Vaccinium uliginosum	(21)	1
Trientalis europaea	(21)	1
Poa pratensis	(51)	1
Agrostis canina	(51)	1
Poa trivialis	(28)	1

Table 1: continued.

Brachypodium sylvaticum	(2)	1
Chenopodium album	(2)	1
Galium aparine	(2)	1
Conyza canadensis	(2)	1
Rumex crispus	(2)	1
Ulex europaeus	(2)	1
Impatiens glandulifera	(2)	1
Elytrigia repens	(2)	1
Dryopteris filix-mas	(2)	1
Polygonum aviculare	(2)	1
Sinapis arvensis	(2)	1
Rorippa sylvestris	(2)	1
Convolvulus arvensis	(2)	1
Galium aparine	(2)	1
Sonchus arvensis	(2)	1
Cirsium arvense	(2)	1
Artemisia vulgaris	(2)	1
Tripleurospermum maritimum	(2)	1
Clematis vitalba	(2)	1
Phytolacca americana	(2)	1
Adenostyles alliariae	(2)	1
Filipendula ulmaria	(2)	1
Rubus caesius	(2)	1
Amorpha fruticosa	(2)	1
Cynodon dactylon	(2)	1
Sorghum halepense	(2)	1
Hedera helix	(2)	1
Solidago canadensis/gigantea	(2)	1
Athyrium filix-femina	(2)	1
Rubus hirtus	(2)	1
Heracleum mantegazzianum	(2)	1
Arbutus unedo	(2)	1
Erica arborea	(2)	1
Empetrum nigrum	(2)	1
Thlaspi arvense	(2)	1
Equisetum arvense	(2)	1

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Table 2: Details of the 36 data sets included in this study. The ID of data set refers to the location on the map in Fig. 1

ID	Country	Study region	Lat (°N)	Long (°E)	Study area (ha)	Plot size (range; m²)	Initial survey year	Recent survey year
1	B	Gaume	49.6	5.6	1000	50-400	1953-1963	2008
2	B	Binnen-Vlaanderen	51.1	3.5	30000	100-200	1977-1983	2009
3	B	Zoerselbos	51.3	4.7	30	100	1982	2008
4	B	Meerdaalwoud	50.8	4.7	1319	125-225	1954	2000
5	B	Tournibus	50.3	4.6	228	100	1967	2005
6	S	Dalby	55.7	13.3	36	1 (16 canopy)	1935	2010
7	D	Elbe-Weser	53.4	9.2	750000	100-400	1986-1989	2008
8	CZ	Milovice Wood	48.8	16.7	2100	500	1953	2006
9	CZ	Rychlebské hory Mts.	50.3	17.1	4800	315	1941-1943	1998-1999
10	CZ	Milíčovský les	50.0	14.5	93	50-625	1986	2008
11	CH	Switzerland	47.0	7.5	1500000	100-400	1940-1965	1998
12	F	Hirson	50.0	4.1	> 1000	500-800	1956-1965	1996-1999
13	F	Andigny	50.0	3.6	> 3000	500-800	1957-1963	1995-1996
14	NL	Speulderbos	52.3	5.7	1000	100-250	1957-1959	1987-1988
15	IRL	Killarney National Park	52.0	-9.6	350	8	1991	2011
16	D	Göttingen, Carici-Fag.	51.3	9.8	4000	30-400	1955-1960	2011-2012
17	D	Göttingen, Hordelymo-Fag.	51.6	10.0	4000	75-400	1955-1967	2009
18	A	Zöbelboden	47.8	14.4	90	100-100	1993	2005-2010
19	D	Brandenburg	52.2	13.6	295	100-400	1963-1965	2012
20	SK	Slovakia, South-West	48.4	17.3	25000	500	1966-1972	2007
21	SK	Slovakia, Central	48.3	19.4	70000	500	1964-1973	2005-2007
22	SK	Slovakia, North-East	49.2	21.9	40000	500	1965-1974	2006
23	CZ	České středohoří	50.6	14.1	8700	500	1965	2012
24	CZ	Krumlov Wood	49.1	16.4	3300	400	1964-1968	2012
25	CZ	Hodonínská Dúbrava	48.9	17.1	3600	400	1965	2012
26	PL	Białowieża	52.8	23.9	4747	100-200	1966	2012
27	F/CH	Jura	46.8	6.4	2268600	200-400	1989	2007

Table 2: Continued information

28	D	Göttingen, Hünstollen	51.6	10.0	56	100-250	1992	2012
29	PL	Sanocko-Turczańskie Mountains	49.5	22.4	25000	100-400	1972-1973	2005-2007
30	PL	Bazaltowa Mt	51.0	16.1	110	200-400	1992-1994	2010-2014
31	PL	Buki Sudeckie beech forest	50.9	16.0	174.42	100-160	1990	2014
32	PL	Trzebnickie Hills	51.3	17.2	25	200	1962	2011-2012
33	D	Prignitz	53.1	12.3	282340	400	1954-1960	2014
34	S	Öland	56.7	16.5	134700	225	1988	2014
35	D	Brandenburg Nord	53.0	13.5	700000	200-800	1963-1964	2014
36	D	Brandenburg Süd	51.8	13.8	500000	400	1960-1966	2014

Table 2: Continued information on each study region.

ID	**Altitude (range; m a.s.l.)**	**Soil texture**	**Bedrock type**	**Dominant tree species**
1	267-372	sand, loamy sand, sandy loam	sandstone (with variable calcareous content)	*Fagus sylvatica, Quercus spp.*
2	5-79	sand, sandy loam, loam	NA	*Populus spp., Quercus robur, Fraxinus excelsior, Acer pseudoplatanus*
3	20-20	sand	NA	*Quercus robur, Pinus sylvestris*
4	62-104	loam	Tertiary sandy formations	*Quercus robur, Acer pseudoplatanus*
5	226-274	loam	sandstone, shale, siltstone	*Quercus spp., Carpinus betulus, Fraxinus excelsior*
6	50-75	loamy clay	chalk	*Fraxinus excelsior, Ulmus glabra, Quercus robur, Fagus sylvatica*
7	14-54	loam	NA	*Carpinus betulus, Fraxinus excelsior, Quercus robur*
8	220-320	clay to silt	loess	*Quercus robur, Carpinus betulus, Acer campestre*
9	380-730	loam	gneiss, granite	*Fagus sylvatica*
10	270-300	loam	eolic, fluvial sediments	*Quercus robur, Quercus petraea, Tilia cordata, Carpinus betulus*
11	400-780	brown (forest) soil	chalk	*Fagus sylvatica, Fraxinus excelsior, Quercus spp.*
12	150-330	gravels (alluvia) to deep loess	schists	*Quercus spp., Fagus sylvatica*
13	145-175	loess, sand	chalk, Thanetian sand	*Quercus robur, Alnus glutinosa*
14	60-60	sand to loamy sand (fine to medium)	NA	*Fagus sylvatica, Quercus robur*

Table 2: Continued.

15	30-120	brown earth-shallow peat	old red sandstone	*Quercus petraea*
16	200-420	clay, silt	limestone	*Fagus sylvatica*
17	290-420	clay, silt	limestone	*Fagus sylvatica*
18	623-846	sandy loam, high coarse fraction	dolomite (Hauptdolomit)	*Fagus sylvatica*
19	50-60	Niedermoortorf, Anmoorgley	NA	*Alnus glutinosa, Carpinus betulus, Pinus sylvestris, Fraxinus excelsior*
20	203-418	loam, clay, silt on gley soils	granodiorite, loess loam	*Quercus petraea*
21	226-595	loam	andesite, loess loam	*Quercus petraea*
22	310-618	clay-loam, loam	flysch slates	*Fagus sylvatica*
23	220-620	variable	basalt	*Quercus petraea, Fagus sylvatica, Tilia cordata, Carpinus betulus, Acer spp.*
24	210-400	loam (sandy loam)	granite, granodiorite	*Quercus petraea, Tilia cordata, Carpinus betulus*
25	165-231	sand	eolic sand	*Quercus robur, Tilia cordata*
26	159-172	sand with admixture of clay and silt	NA	*Carpinus betulus*
27	550-1320	NA	calcareous	*Abies alba*
28	327-422	clay, silt	limestone, red clay	*Fagus sylvatica*
29	400-650	clay	Carpathian flysch, alternating marine deposits of claystones, shales, sandstones	*Fagus sylvatica*
30	300-360	rubble, clay	Basalt, greenstone	*Quercus petraea*
31	440-525	clay	shale pericytes	*Fagus sylvatica*

Table 2: Continued.

32	140-230	sand	Quarternary deposits	*Abies alba*
33	26-112	sand, loam	glacial deposits (Pleistocene), glaco-fluvial sands (Holocene)	*Quercus robur, Fagus sylvatica, Alnus glutinosa, Carpinus betulus, Fraxinus excelsior*
34	4-35	variable	Slate, limestone	*Quercus robur, Acer platanoides, Fraxinus excelsior, Ulmus spp.*
35	15-115	sand	glacial deposits	*Quercus spp.*
36	25-155	sand	glacial deposits	*Quercus spp., Pinus sylvestris*

Table 3-8: Parameter estimates and test statistics of spatial models fitted using recent and initial plot data from summary output in R statistics using “Kenward-Roger” approximation. R² values were calculated following the method of Nakagawa and Schielzeth (2013).

Deschampsia flexuosa								
Recent					**Old**			
Variable	Estimate	SE	t value	Pr(>|t|)	Estimate	SE	t value	Pr(>|t|)
Intercept	0.92	0.24	3.78	0.001	1.41	0.21	6.57	< 0.001
Humus quality	-0.35	0.10	-3.57	< 0.001	-0.43	0.11	-3.96	< 0.001
Soil moisture (EIV_F)	-0.40	0.11	-3.55	< 0.001	0.03	0.10	0.32	0.751
Overstorey cover	-0.46	0.10	-4.39	< 0.001	0.21	0.12	1.74	< 0.05
Random intercept (StDev)		R²			Random intercept (StDev)		R²	
Region	Residual	Marginal	Conditional		Region	Residual	Marginal	Conditional
0.86	1.72	0.13	0.42		0.4955	2.21	0.06	0.24

Molinia caerulea								
Recent					**Old**			
Variable	Estimate	SE	t-value	Pr(>|t|)	Estimate	SE	t-value	Pr(>|t|)
Intercept	-0.61	0.18	-3.40	0.002	2.27	0.38	5.79	< 0.001
Humus quality	-1.03048	0.11447	-8.911	< 0.001	-0.49	0.19	-2.46	0.016
Soil moisture (EIV_F)	0.91	0.3	3.00	0.003	0.58	0.25	2.20	0.03
Soil moisture²	-0.55	0.15	-3.76	< 0.001	-0.46	0.16	-2.78	0.006
Overstorey cover	-0.35	0.16	-2.21	0.03	-0.49	0.17	-2.93	0.004
Random intercept (StDev)		R²			Random intercept (StDev)		R²	
Region	Residual	Marginal	Conditional		Region	Residual	Marginal	Conditional
2.00	2.20	0.13	0.54		1.12	2.53	0.16	0.42

Pteridium aquilinum

Recent					**Old**			
Variable	Estimate	SE	t-value	Pr(>|t|)	Estimate	SE	t-value	Pr(>|t|)
Intercept	1.52	0.19	7.73	< 0.001	1.36	0.20	6.74	< 0.001
Humus quality	-0.57	0.12	-4.77	< 0.001	-0.82	0.11	-7.05	< 0.001

Random intercept (StDev)		R²		Random intercept (StDev)		R²	
Region	Residual	Marginal	Conditional	Region	Residual	Marginal	Conditional
0.37	1.99	0.12	0.26	0.44	2.07	0.21	0.35

***Rubus fruticosus* agg.**

Recent					**Old**			
Variable	Estimate	SE	t-value	Pr(>|t|)	Estimate	SE	t-value	Pr(>|t|)
Intercept	0.71	0.22	3.20	0.004	0.74	0.23	3.17	0.005
Overstorey cover	-0.28	0.07	-4.13	< 0.001	-0.19	0.07	-2.72	0.007

Random intercept (StDev)		R²		Random intercept (StDev)		R²	
Region	Residual	Marginal	Conditional	Region	Residual	Marginal	Conditional
1.10	2.21	0.03	0.37	0.97	1.78	0.01	0.36

Rubus idaeus

Recent					**Old**			
Variable	Estimate	SE	t-value	Pr(>|t|)	Estimate	SE	t-value	Pr(>|t|)
Intercept	0.30	0.23	1.30	ns	0.23	0.24	0.90	ns
Overstorey cover	-0.15	0.07	-2.05	0.04	-0.01	0.06	-0.26	ns
Mean N dep	-0.30	0.14	-2.21	0.03	-0.16	0.24	-0.67	ns

Random intercept (StDev)		R^2		Random intercept (StDev)		R^2	
Region	Residual	Marginal	Conditional	Region	Residual	Marginal	Conditional
1.13	1.31	0.04	0.49	0.89	1.02	0.01	0.47

Vaccinium myrtillus

Recent					**Old**			
Variable	Estimate	SE	t-value	Pr(>|t|)	Estimate	SE	t-value	Pr(>|t|)
Intercept	1.25	0.26	4.75	< 0.001	1.30	0.21	6.07	< 0.001
Humus quality	-1.01	0.17	-5.80	< 0.001	-0.72	0.17	-4.24	< 0.001

Random intercept (StDev)		R^2		Random intercept (StDev)		R^2	
Region	Residual	Marginal	Conditional	Region	Residual	Marginal	Conditional
0.92	1.76	0.27	0.55	0.62	2.00	0.17	0.36

Fig. 1: Results of species-specific models predicting the cover abundance of six understorey plant species in response to spatial gradients in local-scale and large-scale explanatory variables. Points representation of the estimated effects (+/- 2SE) of the explanatory variables for the spatial models using contemporary resurvey data (x-axis) and historical survey data (y-axis). The line represents the 1:1 line of no difference. Different shapes represent the six study species and colours the different explanatory variables.

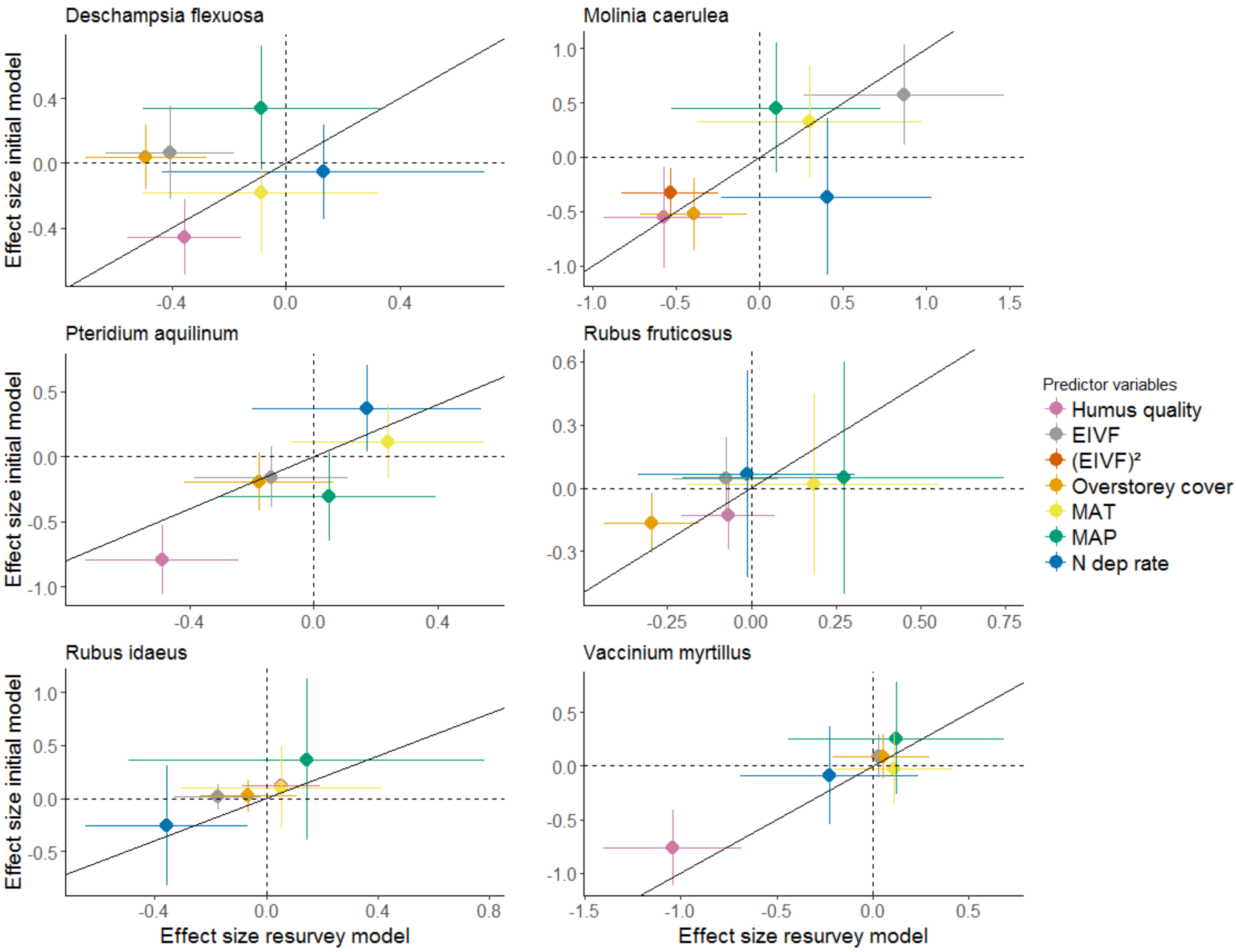
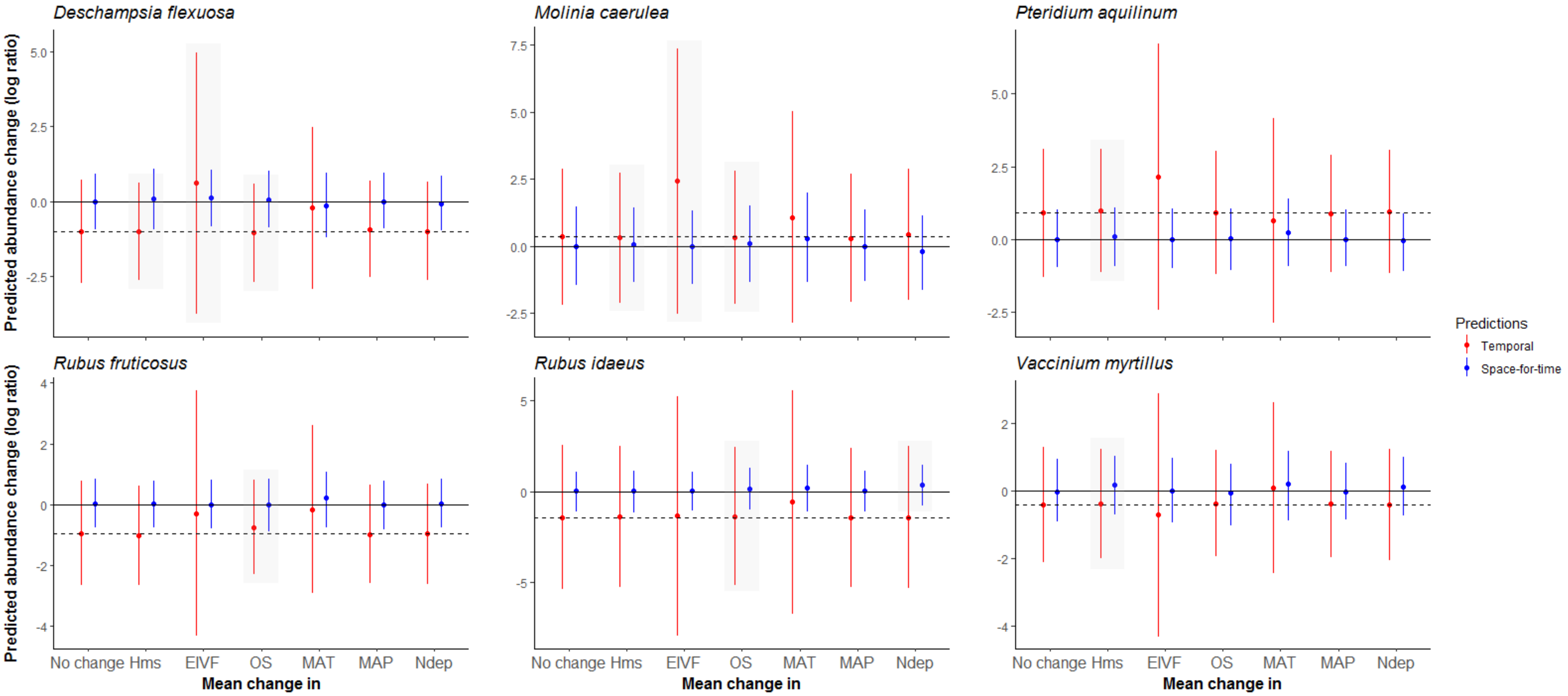
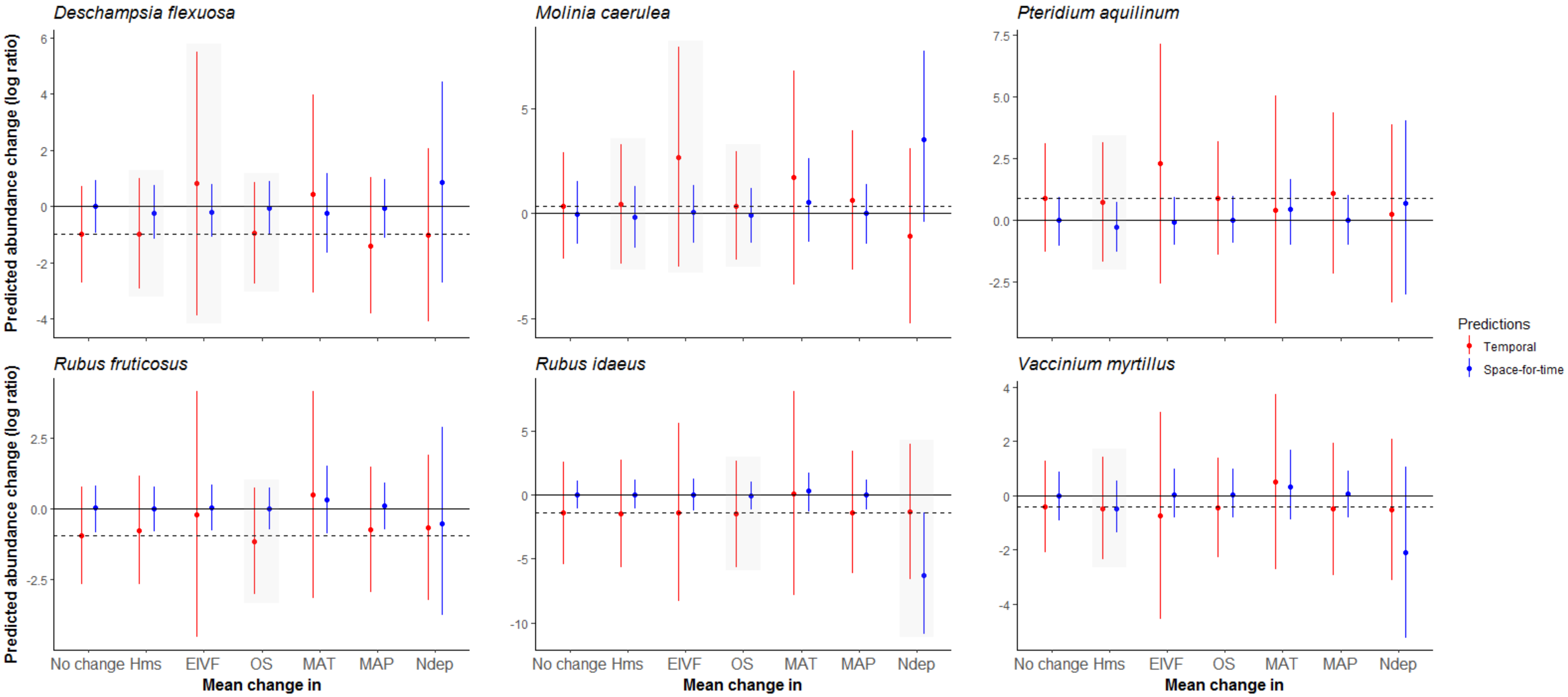


Fig.2: Predicted cover abundance change of six understorey plant species in response to temporal changes in several environmental explanatory variables. Predictions were based on species abundance changes along spatial environmental gradients (contemporary spatial models) and on actually observed temporal changes in abundance. For each explanatory variable separately, we predicted the change in species cover (as log ratio) to **(A)** the 20% percentile and **(B)** 80% percentile of the observed change in the plot-pairs between historical and contemporary resurveys. Additionally, predictions of cover change were made in the absence of environmental change (No change). The dotted line represents these predictions using the temporal models. Explanatory variables that were retained in the most parsimonious contemporary spatial models are annotated in grey. The lines indicate the 95% confidence intervals around the predictions. Red: temporal predictions; Blue: predictions using SFT approach. Humus quality (Hms), Ellenberg F value (EIVF), Overstorey cover (OS), Mean annual temperature (MAT), Mean annual precipitation (MAP) and mean N deposition rate (Ndep).

(A)



957 **(B)**


Deschampsia flexuosa
Molinia caerulea
Pteridium aquilinum
Rubus fruticosus
Rubus idaeus
Vaccinium myrtillus
Predicted abundance change (log ratio)
Mean change in
No change
Hms
EIVF
OS
MAT
MAP
Ndep
Predictions
Temporal
Space-for-time

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Appendix B: Detailed information on the temporal vs. space-for-time approach

We test if species abundance changes over contemporary spatial environmental gradients allow predicting how environmental change over time cause species to change their abundances (research question 3). First, we modelled observed changes in species abundance over time, by fitting regression models for each species using the subset of plots in which a species was present at both survey times for each species (Temporal model). For each plot-pair, temporal change was characterized as the natural logarithm of the ratio between the contemporary resurvey and the historical survey. We did this for the response variable (percentage cover), and for all the explanatory variables used in the spatial models. Similar as for the spatial models, we used a multilevel modelling approach with random effects for 'data set'.

$$\ln\left(\frac{y_r}{y_i}\right) = \beta_0^T + \beta_1^T \ln\left(\frac{x_r}{x_i}\right) + \cdots + random\,part$$

Temporal model

In this model, y_r and y_i are the percentage cover of one of the study species at the contemporary and historical survey resp., x_r and x_i are one of the six explanatory variables at the contemporary and historical survey resp. and $random\,part$ denotes the effect of 'data set' and residual error. The intercept β_0^T catches the average temporal change in abundance not accounted for by the used explanatory variables.

Second, these temporal models then allowed making predictions of abundance change over time in response to a particular change in environmental conditions. For each predictor variable separately, we predicted the change in species cover (as log ratio) for a realistic change in the predictor (also as log ratio): here we used the observed mean change in the predictor between the two survey times, $\overline{r_x} = \frac{\overline{x_r - x_\iota}}{x_\iota}$ (Table).

$$\widehat{y^T} = \widehat{\ln\left(\frac{y_r}{y_\iota}\right)} = \beta_0^T \ + \beta_1^T \ \ln\overline{\left(\frac{x_r}{x_\iota}\right)} = \beta_0^T \ + \beta_1^T \ \ln(1 + \overline{r_x})$$

Temporal prediction

Additionally, predictions were made for the mean change in abundance in the absence of environmental change:

$$\widehat{y^T} = \beta_0^T$$

'No change' prediction

Third, we made similar predictions of temporal change in abundance in response to environmental change, but based on the species' abundance patterns along spatial gradients, that is, using the following contemporary spatial model:

$$\ln(y) = \beta_0 + \beta_1 \ln(x_1) + \cdots + \beta_6 \ln(x_6) + random\ part$$

Spatial model

Using the parameter estimates of the spatial model, we predicted the cover abundance for the mean of each predictor value ($\overline{x_{1,\ldots,6}}$) over all the contemporary plots in which at least one species is present:

$$\widehat{\ln(y_\iota)} = \beta_0 + \beta_1 \ln(\overline{x_1}) + \cdots + \beta_6 \ln(\overline{x_6})$$

Equation [2]

Similarly, we made a second prediction of the species cover, but one of the predictor variables, here $\overline{x_1}$, was increased by the same mean change in that predictor between the two surveys as in the temporal predictions, i.e. $\overline{r_{x_1}} = \overline{r_x}$. All other predictor variables were kept at their mean values as in Equation [2].

$$\widehat{\ln(y_r)} = \beta_0 + \beta_1 \ln\left(\overline{x_1}\left(1 + \overline{r_{x_1}}\right)\right) + \beta_2 \ln(\overline{x_2}) + \cdots + \beta_6 \ln(\overline{x_6})$$

Equation [3]

Equation [2] and [3] were then combined in a log ratio:

$$\widehat{y^{SFT}} = \widehat{\ln\left(\frac{y_r}{y_\iota}\right)} = \widehat{\ln(y_r)} - \widehat{\ln(y_\iota)}$$

$$= \left[\beta_0 + \beta_1 \ln\left(\overline{x_1}\left(1 + \overline{r_{x_1}}\right)\right) + \beta_2 \ln(\overline{x_2}) + \cdots + \beta_6 \ln(\overline{x_6})\right] - \left[\beta_0 + \beta_1 \ln(\overline{x_1}) + \beta_2 \ln(\overline{x_2}) + \cdots + \beta_6 \ln(\overline{x_6})\right]$$

$$= \beta_1 \ln\left(1 + \overline{r_{x_1}}\right)$$

Space-for-time prediction

In this way, we were able to compare the predicted change in the species' abundances for the actual temporal vs. the spatial model, based on the same change $\overline{r_x}$ in an environmental predictor x.