Tree regeneration responds more to shade casting by the overstorey and competition in the understorey than to abundance *per se*

Authors: Emiel De Lombaerde[1,] *, Kris Verheyen[1], Hans Van Calster[2] & Lander Baeten[1]

[1]: Forest & Nature Lab, Campus Gontrode, Faculty of Bioscience Engineering, Ghent University, Geraardsbergsesteenweg 267, 9090 Melle-Gontrode, BELGIUM

[2]: Research Institute for Nature and Forest, Havenlaan 88 bus 73, 1000 Brussel, BELGIUM

*Corresponding author: Emiel.DeLombaerde@UGent.be

Abstract

Manipulating the overstorey is the key tool for forest managers to steer natural regeneration. Opening up the canopy does not only create favourable light conditions for tree seedling growth, but also for (competitive) understorey species. Therefore, a thorough understanding of how changes in the abundance of the overstorey and understorey influence tree regeneration is needed to attain successful regeneration.

To this end, we used the regional Flemish Forest Inventories, which contain vegetation plots that were surveyed at two times and include large variation in species composition and abundance of both overstorey and understorey layers. These plots were classified into poor and rich forest types, which differ in overstorey and understorey species composition and soil fertility. For each forest type, we first investigated the effect of overstorey abundance and shade-casting ability on the understorey herbaceous vegetation cover and its competitive nature. Then, we modelled how both these strata influence the presence-absence as well as the cover of tree regeneration, using the zero-inflated beta distribution.

Our results show that the understorey cover and its competitiveness mainly increase when the abundance and shade-casting ability of the overstorey is reduced. The shade-casting ability of the overstorey and competitiveness of the understorey were more important in determining tree regeneration, especially probability of presence, than the abundance of these layers *per se*. This was consistent for both forest types, although directions and magnitudes of the effects differed. In predictions mimicking several thinning scenarios we found that in the poor forests, reducing overstorey abundance could lead to an increase in seedling cover, whereas in rich forests, the opposite is true and seedling cover will potentially be reduced. Finally, in a single-species analysis focusing on *Quercus*, we found a trade-off between sufficiently reducing overstorey abundance, while at the same retaining parent trees as potential seed sources. These findings can be used to guide forest management decisions in order to attain successful forest regeneration in temperate forests.

Key-words: Forest inventory; herb layer; canopy; competition; forest management; natural regeneration; gap dynamics; forest renewal; logging

1 Introduction

Tree regeneration is of key importance in forest ecosystems, as it provides the next generation of overstorey (canopy) trees. During the past decades, a growing interest in a more extensive forest management based on natural processes, i.e. “close-to-nature management”, has arisen and in many places the dominant regeneration method is shifting from traditional planting to natural regeneration (Ammer et al., 2018; Puettmann et al., 2015). Natural regeneration is less cost-intensive and can provide other advantages such as a better adaptation to microhabitats or higher seedling densities, compared with artificial regeneration (Kolo et al., 2017).

Changing overstorey cover and composition is the key tool for forest managers for controlling forest floor light availability and initialising natural tree regeneration (Schütz, 2004). If too much light reaches the forest floor, opportunistic, fast growing understorey species may start to compete strongly with tree seedlings for the available resources and reduce seedling survival or growth (Balandier et al., 2006; Royo and Carson, 2006). However, under light limitation neither the vegetation nor the tree seedlings will be able to grow well (Pagès and Michalet, 2003). To be successful, optimal light conditions need to be attained, so tree seedlings can establish and grow, but at the same time restricting excessive growth of understorey vegetation (Schütz, 2004; Wagner et al., 2011). Therefore, to attain this indirect facilitation (Pagès et al., 2003) and successful natural regeneration, we need a better understanding of how the overstorey influences tree regeneration directly, by reducing light, and indirectly through the response of the understorey vegetation.

Experimental studies have shown negative effects of the presence of an understorey vs. without understorey (control) on tree regeneration survival, density and growth (e.g. George and Bazzaz, 1999a, 1999b; Royo and Carson, 2008). There are fewer studies that also apply an overstorey treatment and this treatment then often covers only two grades of overstorey openness (e.g. shade vs. no shade; gap vs. no gap) (Pagès et al., 2003; Pagès and Michalet, 2003; Putnam and Reich, 2017). Repeated large-scale observational data, such as national or regional forest inventories, often cover large gradients of environmental conditions and can therefore provide valuable data for studying forest tree regeneration and its relations with environmental conditions. Most studies that have used inventory data to research tree regeneration are from Mediterranean forest, in which other factors, such as temperature stress and moisture availability play a more important role compared with temperate forests (e.g. Bravo et al., 2008; Monteiro-henriques and Fernandes, 2018; Vayreda et al., 2013). Furthermore, only few studies have looked at the combined effects of both understorey and overstorey on tree regeneration (Plieninger et al., 2010; Shen and Nelson, 2018) and none of these studies explore the effects of the overstorey on understorey and regeneration together.

In this study, we make use of the regional Forest Inventory of Flanders, the northern part of Belgium. This dataset contains temperate forest vegetation plots, which were surveyed two times, with an intercensus interval of 10-20 years. The dataset includes large variation in species composition and abundance of both overstorey and understorey layers, allowing to test the effect of both these forest layers on tree regeneration and the consistency of these effects over time. In all analyses, we discriminated between plots in forests on soils with low nutrient availability, i.e. poor forests, and plots on more fertile soils, i.e. rich forests. We modelled the relationship between overstorey (abundance and shade-casting ability) and understorey herbaceous vegetation (cover and competitive signature), and then quantify how changes in these two forest layers influence tree seedling cover. First, we looked at regeneration across multiple species, i.e. grouping the most frequent species per forest type, and then zoomed to the level of an individual tree species and quantified effects for *Quercus spp.*, the most frequent and economically important tree species in the study region. Finally, to better understand the implications of our results for the management of tree regeneration, we predicted changes in tree seedling cover for different thinning scenario's reducing the overstorey. We hypothesise that (i) a higher abundance and shade-casting ability of the overstorey layer will lead to lower cover and reduced competitiveness of the understorey herbaceous vegetation by reducing light availability at the forest floor, (ii) increasing abundance of both over- and understorey as well as increasing competitive (light-reducing) nature of these layers will result in reduced cover of tree seedlings, however, (iii) overstoreys might indirectly affect tree regeneration by reducing understorey growth and thus reducing competition on the forest floor. We evaluated the consistency of our three hypotheses for the poor vs. rich forest types.

2 Material & Methods

2.1 Regional forest inventory data

For this study, we used data from the first and second Flemish Forest Inventory (FFI; Wouters et al., 2008). The FFIs contain data on forest vegetation plots spread across Flanders, i.e. the northern part of Belgium (Fig. 1). Mean annual temperature and precipitation for this region are 10.5 °C and 852 mm, respectively. Flanders has a forest surface area of approximately 146 000 ha (11% of the total area). Forest in Flanders cover a large range in forest and soil types from nutrient poor oak-pine forests on sandy soils to ash-alder on moist, rich loamy soils. For the first FFI, vegetation plots (16 m x 16 m) were systematically selected by laying a 1 km x 1 km grid over the Flemish forest mapping (1978 – 1990). All plots were sampled for the first time during 1997 – 1999 (n = 1383). For the second FFI, the

Agency for Nature and Forest (ANF) shifted from a periodic (a short measuring campaign every ten years) to a continuous inventory (every year one tenth of the sampling population is measured). The plots in the second FFI were revisited between 2009 – 2017. We selected the plots which were surveyed during both inventory campaigns using the exact same location (n = 394); due to changes in the sampling strategy, the location of multiple plots were changed for the second FFI and thus were not suitable for this study. Based on the vegetation composition observed during the first FFI, the temporally paired plots were classified into different forest type groups following Cornelis et al. (2009). We split up the plots into vegetation types 'typically found on nutrient poor soil' (oak-beech and oak-pine forests; referred to as "poor plots") and vegetation types 'generally found on nutrient rich soils' (ash-oak, ash-alder and elm-ash forest; referred to as "rich plots"). A total of 304 poor and 69 rich plot-pairs were retained (Fig. 1). Remaining plots (n = 24) were unassigned as they were situated on very wet soils, e.g. alder swamp, birch-alder and alluvial willow forests, or in calcareous sycamore-ash forest (as classified by Cornelis et al., 2009). Plots in both forest types were primarily situated in even-aged forest (only 5% was uneven-aged) and stand age was on average 55 years in all the plots with only a minor proportion younger than 20 years. The FFI vegetation plot data contains detailed information on the cover of all plant species per plot in the understorey (non-woody and woody plants < 0.5 m, incl. seedlings), the shrub layer (woody plants ≥ 0.5 m and < 6 m), and the tree layer (woody plants ≥ 6 m). The cover class of each species in every layer was estimated using the transformed Braun-Blanquet scale based van der Maarel (1979) (Table A1).

2.2 Tree seedling species

The tree seedling selection was based on the data of the selected poor and rich forest plots. The most frequent and silviculturally important native tree species were selected per forest type (Table A2). These very young seedlings are < 0.5 m and have therefore not yet overgrown the understorey layer. For the poor forest types, *Quercus robur* and *petraea* were grouped as *Quercus* (number of plots in which regeneration is present in at least one survey n = 242); *Betula pendula*, *pubescens* and *spp.* were grouped as *Betula (n = 126)*; *Fagus sylvatica*, *Pinus sylvestris* and *Acer pseudoplatanus* will be refered to as *Fagus (n = 42)*, *Pinus (n=85)* and *Acer (n = 58)*, respectively. For the rich forest type, *Quercus robur* and *petraea* were grouped as *Quercus (n =44)*; *Fraxinus excelsior (n = 35), Acer pseudoplatanus* (n = 27) and *Prunus avium* (n = 22) will also be referred to by their genus. *Quercus* seedlings were most frequently present of all these tree species in both forest types and is the economically most important species in the study region. Therefore, we used *Quercus* as a study species in an individual species analysis (see below). We used the cover of the seedlings in the vegetation surveys as a measure of abundance, i.e. as an alternative to densities. Visually estimated cover of understorey plants has been shown to predict biomass well (Axmanová et al., 2012) and the Braun-Blanquet cover-abundance scale used for the surveys actually combines densities with cover in the lower classes (Table A1). Some basic descriptors of the tree seedling data showed that the cover of the selected species was on average higher in the rich forest plots during the first survey (Table 1). Furthermore, the cover-weighted average shade tolerance per plot based on the species-specific shade tolerance indices of the selected tree species (Niinemets and Valladares, 2006) showed higher average seedling shade tolerance in the rich than in the poor forest plots, both in the past and the recent survey (Table 1).

2.3 Environmental characteristics in the poor and rich forest plots

We calculated variables related to overstorey, understorey and soil to describe the prevailing environmental conditions in the poor and rich plots.

To characterise the overstorey conditions and light availability in each plot we calculated two measures of abundance: (1) total sum of cover of all species in tree and shrub layer; (2) total basal area of all trees with height more than 2 m. The total basal area was not derived from the earlier described 16 m x 16 m vegetation plots, but was derived from dendrometric measurements from concentric nested circular plots (max. radius of 18 m; see Wouters et al., 2008). We also derived the average shade-casting ability (SCA), i.e. a weighted average (by total cover or total basal area) of the species-specific shade-casting indices that range from 1 (low) to 6 (high ability to cast shade of mature trees when growing in a monospecific stand) (Table A3; see also Baeten et al., 2009; Van Calster et al., 2008; Verheyen et al., 2012). In the single-species models for *Quercus*, we added a predictor variable 'parent tree', that is, the sum of cover or total basal area of *Quercus* trees in the stand, to account for the potential seed availability (see 2.4.2).

The sum of cover of the understorey vegetation (tree/shrub species excluded) was calculated from species-specific cover values and has been shown to be a good predictor for the total forest understorey biomass (Axmanová et al., 2012). Furthermore, we calculated the CSR functional signature for each plot following Hunt et al. (2004). These functional signatures give for the present vegetation in a plot the proportion of competitive, stress-tolerant and ruderal signatures. These values were derived from the nineteen possible functional types distinguished in the CSR-triangle (Grime, 2001) and their standard triangular coordinates, which were weighted by species cover. In our study, we use the competitive signature of the community (C-score), as understorey communities with this signature are dominated by acquisitive species which have the ability to rapidly colonize forest gaps or more open forest and have high potential to compete for light with the tree seedlings.

As proxies of the prevailing plot-specific soil properties, we calculated cover-weighted mean Ellenberg indicator values using the individual species' indicator values (tree/shrub species excluded) for soil fertility (EIV_N), soil reaction (EIV_R) and soil moisture (EIV_F) (Diekmann, 2003; Ellenberg et al., 2001). Additionally, we calculated the average litter quality (LQ), which can be interpreted as a proxy for nutrient cycling and availability, as a weighted average of litter quality indices of individual overstorey species (Table A3) (see also Baeten et al., 2009; Van Calster et al., 2008; Verheyen et al., 2012).

There is a clear distinction in site conditions between the rich and poor forest types (Table 1). Even though they are on average equally dense, overstoreys in rich forest have a higher SCA than in poor forests. Understoreys in the rich forest plots also have a much higher total cover and have a higher competitive score (C-score) in the first survey than in the poor forest plots. The average Ellenberg indicator values for soil fertility (EIV_N) and soil reaction (EIV_R) indicate that soils in rich forest types are more productive and have higher base saturation. Rich forest plots have a higher share of species with easier decomposing leaf litter in the overstorey than the poor plots, indicating a higher nutrient turnover and availability. Between the two surveys, both the abundance of the overstorey (total basal area and cover), as well as the cover of the understorey increased in the two forest types (Table 1). The cover of the selected tree seedling species only increased in the poor plots. Finally, in the poor forests, values for EIV_N and EIV_R increased, indicating increases in soil nutrient availability and base saturation (Table 1).

2.4 Data analysis

2.4.1 Modelling understorey variables

To test the first hypothesis, we analysed the effect of the overstorey on the understorey vegetation. We used variables related to the abundance and competitiveness of both the overstorey, i.e. total basal area and SCA, as well as the understorey layer, i.e. sum of cover and C-score, respectively. We separated between abundance and competitiveness because even though two plots can have a similar total basal area, the overstorey may be composed of different species with varying abilities to cast shade, resulting in different light levels at the forest floor. Similarly, understoreys may have comparable cover, but may differ in their ability to compete for resources with the tree regeneration. The variables related to soil conditions (EIV) and nutrient turnover (LQ) were used to characterise the two forest types and are no longer considered in our models. Using linear multilevel models, we modelled the understorey cover in response to the overstorey total basal area and SCA as fixed effects (**Model 1**). We also added the predictor 'Survey' (levels for each survey time FFI1 and FFI2) as a fixed effect to model the time-effect and accounted for the fact that each plot was surveyed two times by adding 'Plot' to the model as a random intercept. Additionally, we added the interactions of the other two fixed effects with survey to the model, capturing how (and if) the change between surveys depends on the predictors. A similar model was built for the understorey C-score as the response (**Model 2**). Both these understorey variables were modelled using a Gaussian distribution, which was truncated at zero for understorey cover. For formula notation of these models we refer to Appendix

B. We also modelled these relations (and those in part 2.4.2) using overstorey cover and the SCA weighted by cover, instead of total basal area; these results are included in the Appendix (Fig. A2). All our model analyses were performed for poor and rich forest types separately. To detect possible multicollinearity between the different predictor variables, variance inflation factors (VIF) were calculated (Zuur et al., 2009). These VIF values were negligible (< 3), indicating low collinearity. All explanatory variables were standardized (subtracting the sample mean and dividing by the standard deviation) prior to the modelling.

2.4.2 Modelling tree seedling cover

The second hypothesis was tested by modelling total tree seedling cover in response to total basal area and SCA of the overstorey, as well as the sum of cover and C-score of the understorey. For this analysis, we summed the cover of the selected tree seedling species per forest type as frequency for single species was low (except for *Quercus* in the poor plots). This sum of cover also approximates a continuous distribution. Visually estimated plant cover data, which is typically zero-inflated, is often analysed using standard statistical methods (e.g. classical linear regression), which has important drawbacks (Damgaard, 2009). Therefore, we applied a multilevel modelling approach using the zero-inflated beta distribution to model the visually estimated tree seedling cover data (e.g. Damgaard, 2014, 2009; Herpigny and Gosselin, 2015; Irvine et al., 2016). This flexible distribution first models the probability of absence (zero-inflation part ZI) and then models the rest of the data with a beta-distribution, i.e. the cover conditional on a tree seedling being present (Ospina and Ferrari, 2010). For both the beta part and the zero-inflated part, the logit link function was used, whereas for the precision parameter, the log link function was used. The model structure for total seedling cover was the same as for Model 1 and 2, but here we also added understorey cover and C-score as fixed effects, and their interactions with survey (**Model 3**). The same model structure (Fig. A1) was used for both the ZI and the beta part of the model, so that the effect of these variables on the unconditional overall cover (which is the probability of presence times the conditional cover) can be modelled.

Additionally, we model the presence-absence and cover of the seedlings for a single species (*Quercus*) using the same structure as Model 3, but added an extra explanatory variable 'parent tree', which is the basal area of conspecific *Quercus* in the overstorey, and the interaction with survey to both the zero-inflation and the beta part of the model. Due to the low frequencies of the other species selected for the previous grouped analyses, single-species models did not converge and could thus not be included in this study. The measurement scale of cover values for a single species is a discretised continuous scale as the Braun-Blanquet cover-abundance scale was used in the inventories (Table A1). This type of data is interval-censored, which means that values are only known to lie within a certain interval (not exact), in this case the asymmetric Braun-Blanquet cover classes. For this reason, an interval-censored model was applied to take into account the distribution of this data in cover classes (Damgaard, 2014, 2009; Herpigny and Gosselin, 2015; Irvine et al., 2016; Pescott et al., 2016).

All models were fitted with the probabilistic programming language Stan through the *brms* package with R version 3.5.0 (Bürkner, 2017; R Core Team, 2018). We used the default priors for these multilevel models and ran four chains of a thousand iterations each, after a warm-up of one thousand iterations. Convergence and mixing of chains was inspected visually using the *bayesplot* package (Gabry and Mahr, 2018). We present posterior means as well as 80 and 95% credible intervals (CI) for relevant model parameters. A Bayesian equivalent for R^2 was calculated for all models using the *bayes_R2* function (Gelman et al., 2017). We calculated R^2 variables for the variance explained by the fixed effects only, i.e. $R^2_{Marginal}$, and for the variance explained by both fixed and random effects, i.e. $R^2_{Conditional}$ (*sensu* Nakagawa and Schielzeth, 2013).

2.4.3 Predicting regeneration in thinning scenarios

To understand and illustrate the implications of our results in terms of management-related changes in the overstorey, we predict changes in total tree seedling cover for different thinning scenarios. The same scenarios were predicted for total seedling cover in poor forest, rich forest and for *Quercus* as a single species.

First, we predicted the understorey cover and C-score for a mature forest plot with a dense overstorey in the initial inventory (survey = 1) with a starting total basal area of 35 m^2/ha, composed of 50% *Quercus* and 50% *Fagus*, making the SCA 4.5 (Table A3). All predictions were made only considering fixed effects. Hereto, we used the fitted models 1 and 2 and drew 1000 posterior samples to generate 1000 predictions of understorey cover and C-score. Then, we used these understorey predictions, together with the same total basal area (35 m^2/ha) and SCA (4.5) to predict total tree seedling cover, using the fitted model 3. We also drew 1000 posterior samples to generate 1000 predictions of tree seedling cover. Note that this approach accounts for the uncertainty of the understorey predictions (1000 samples) in the predictions of seedling cover. We report the median total tree seedling cover, 80 and 95 % prediction intervals (PI). Second, we simulated different thinning scenarios. In a first set of scenarios, we simulate thinning cuts by removing similar proportions of *Quercus* and *Fagus* (resulting in no change in SCA) in this plot by subsequently reducing the total basal area to 25, 15 and 5 m^2. In the second set of scenario's, the same reductions in total basal area was assumed, but now only *Fagus* overstorey trees are removed so that SCA is reduced to 3. Similar steps were followed to make these predictions as was done for the initial situation, using the model fits for the second survey of the inventory data (survey = 2). This means we predict how tree seedling cover may develop in future scenario's, using observed patterns between the surveys, assuming that the changes that have taken place over time have been gradual and directional and will be similar for the future. We also predicted the response of *Quercus* only, starting from the same initial conditions and for the same scenarios using fits from the single-species model. For the scenario where the same proportion of overstorey *Quercus* and *Fagus* trees are cut (SCA remains the same), the parent tree basal area starts from 17.5 and is reduced to 12.5, 7.5 and 2.5 m^2/ha. When only *Fagus* is cut (SCA reduced to 3), parent tree basal area is reduced to 17.5, 15 and 5 m^2/ha.

3 Results

3.1 Effect of overstorey on the understorey community

For the **poor plots**, we found negative effects of total basal area and SCA on understorey cover (Fig. 2a, c; Fig. A1). This means, for instance, that reducing total basal area from 35 to 15 m^2/ha or a reduction in SCA from 4.5 to 3 (see also predictions in part 3.3) in the first survey, leads to an increase in understorey cover with 16% (95% CI = [9.10, 24.11]) and 10% (95% CI = [7.12, 12.89]), respectively. The SCA had a small positive effect on the C-score of the understorey in the first survey, but not in the second (negative interaction effect between SCA and Survey; Fig. 3c; Fig. A1). Reducing SCA from 4.5 to 3 in the first survey, leads to a reduction of C-score of 0.05 (95% CI = [0.02, 0.08]).

For the **rich plots**, we found a negative relationship between the SCA and the understorey cover and the C-score (Fig. 2d and 3d; Fig. A1). Reducing SCA from 4.5 to 3 in the first survey, leads to an increase in understorey cover with 37% (95% CI = [6.42, 67.06]) and an increase in C-score of 0.16 (95% CI = [0.06, 0.25]). Similar results were found for the models using overstorey cover; these are included in the appendix (Fig. A2).

3.2 Effects of overstorey and understorey communities on tree seedlings

For the **poor plots**, we found a negative effect of total basal area on the unconditional overall tree seedling cover for the second survey, but not the first (Fig. 4a). When looking at the 95% CI intervals there were no clear effects for both ZI and beta parts for total basal area (Fig. A1). Reduction of total basal area from 35 to 15 in the recent survey leads to a small increase of unconditional seedling cover of 0.67% ([0.31, 1.1]). SCA had a positive effect on the unconditional cover for the second survey period only (Fig. 4c). This relationship results from a negative effect of SCA on probability of presence (ZI part), but more importantly, the interaction between SCA and the survey period found for the conditional cover (beta part; Fig. A1). A reduction in SCA from 4.5 to 3 for the recent survey results in a decrease of 0.47% (95% CI = [0.11, 0.88]) of unconditional cover. The competitive signature of the understorey (C-score), however, did affect tree seedling cover (Fig. 4g). A negative effect is found for the unconditional cover with increasing C-score (Fig. 4g) due to the negative effect on the presence of seedlings (Fig. A1). An increase in C-score from 0.5 to 0.75 leads to reduction of unconditional cover of 0.41% (95% CI = [0.09, 0.73]) in the recent survey.

For the **rich plots**, we found a negative non-linear relation between C-score and the unconditional tree seedling cover (Fig. 4h). This effect was largely due to the negative effect of C-score on the presence of seedlings (ZI part; Fig. A1). An increase in C-score from 0.50 to 0.75 results in an average decrease in seedling cover of 2.2% (95% CI = [0.43, 4.2]) in the recent survey. Probability of presence however decreases with 45% (95% CI = [9.39, 85.09]) for this change in C-score. The interaction between SCA and the survey period was different from zero for the ZI part, resulting in a positive trend for SCA in the first period and a negative in the second survey period (Fig. A1).

For the **single-species model** with *Quercus*, we found that SCA had a clear negative effect on the unconditional cover of *Quercus*, this due to the negative effect of SCA on the probability of presence of *Quercus* seedlings (Fig. 5a; Fig. A1). For a reduction in SCA from 4.5 to 3, unconditional cover increases with 0.27% (95% CI = [0.14, 0.37]) and probability of presence increases with 24% (95% CI = [15, 32]). The total basal area of *Quercus* overstorey trees, i.e. parent trees, had a positive effect on the unconditional cover (Fig. 5d). This was mainly due to the positive effect of this variable on the probability of presence (Fig. A2). Reducing the basal area of *Quercus* overstorey trees from 35 to 15 results in a decrease in *Quercus* seedling cover with 0.56% (95% CI = [0.16, 1]) and probability of presence decreases with 17% (95% CI = [0.74, 28]). The total basal area of the overstorey did not clearly affect the unconditional cover of *Quercus* seedlings (Fig. 5), but had a negative effect on the probability of presence (Fig. A1). Reducing total basal area of the overstorey from 35 to 15 leads to an increase in probability of presence on average by 6.4%, but could also lead to an increase in the recent survey (95% CI = [-21, 7.5]).

3.3 Predicting regeneration scenarios

Tree seedling cover responded differently in the two forest types and for single species *Quercus* when simulating various regeneration cuttings (Fig. 6). In addition to the predictions, we tested for potential lag effects of the different predictors on the responses used in our analyses (understorey cover, C-score and tree seedling cover; see Appendix C). We did not find any evidence for lag effects. When starting from a **poor forest** stand with total basal area of 35 m^2 and a SCA of 4.5 (Fig. 6a; red prediction), results show that tree seedling cover is likely to increase when reducing overstorey basal area (for each predicted level) by removing the same proportion of each tree species (i.e. SCA remains the same; 80% PI differ from zero and do not overlap for the predictions; Fig. 6a; blue predictions). This increase is mainly caused by the direct effect of the decrease in basal area and by the survey component in model 3, i.e. change in cover independent of the other predictors. When the same decrease in basal area is realised by removing shade-casting species (i.e. SCA decreases), tree seedling cover is also likely to increase (Fig. 6a; green predictions). In this situation however, the increase will be smaller due to the reduction in SCA, resulting from the change in the relation between conditional tree seedlings cover and SCA in the second survey period.

When making predictions for the same scenarios in the **rich forest** plots, we see a negative trend when opening up the overstorey, accompanied by large uncertainties (Fig. 6b). This trend is mainly caused by the increase in understorey cover over time, causing a decrease in seedling cover. When the SCA is reduced by selective cutting, tree seedling cover is even more likely to decrease (Fig. 6b; green predictions). This is due to the indirect effects of decreasing SCA, which causes understorey cover to increase, as well as the competitive signature, which both have negative effects on tree seedling cover.

The predictions for the **single species *Quercus*** show a less clear pattern (Fig. 6c). Changes in *Quercus* seedling cover are due to a combination of variables. Reducing total basal area has a positive effect, but if *Quercus* overstorey trees are cut, this will lead to a lower cover of *Quercus* seedlings. Reducing SCA leads to an increase in mean *Quercus* seedling cover. Understorey cover increased slightly in response to reducing basal area and SCA which had a small positive effect on *Quercus* seedling cover. These predictions were accompanied by large uncertainties; none of the PI differed from zero.

4 Discussion

Initialising natural regeneration by manipulation of the overstorey requires thorough knowledge of how understorey plant communities and tree seedlings will respond. Using data from the regional Flemish Forest inventory, our results show that understorey plant cover and its competitive signature were mainly negatively affected by the abundance and SCA of the overstorey. Furthermore, we found evidence that the signatures of the overstorey (SCA) and understorey (C-score) were more important in determining tree regeneration, than the abundance of these layers *per se*. We made predictions to illustrate practical implications of our findings and we found that in poor forest types, opening up the overstorey can potentially lead to increased seedling cover, whereas in rich forests this might result in a decrease. Below we discuss these findings and their implications for forest management in more depth.

Overstorey abundance, both total basal area and total cover, as well as its ability to cast shade were found to have negative effects on the understorey cover in both forest types. These relationship are as we expected as understorey biomass production in forests mainly limited by light availability (e.g. Axmanová et al., 2011), which is controlled by the overstorey abundance and its structure (Barbier et al., 2008; Wagner et al., 2011). The competitive signature was not clearly affected by the abundance of the overstorey, but was influenced by its SCA. In the rich plots, changes toward overstorey species with higher SCA (late successional species) lead to a decrease in proportion of competitive understorey species. In the poor forest type, however, the impact of overstorey abundance on the competitive signature was less apparent and even slightly positive, contrary to what one might expect. This effect is likely due to a gradient from forests on extremely poor, sandy soils (dominated by *Pinus*) to forests on soils with a higher loam content with a higher proportion of trees with higher SCA (e.g. *Quercus* or *Fagus*) in which understorey competition levels are known to be higher (Honnay et al., 2002; Willoughby et al., 2009). These results show that the retention of the overstorey and selection for higher shade-casting species can reduce understorey biomass, in both poor as well as rich forest types, and supress competitive species in rich forest types.

Both the overstorey and understorey community influenced tree regeneration in our study area. We found that not the abundance of these layers *per se*, but their composition were more important in determining tree regeneration. In temperate forest, overstorey abundance is expected to have negative direct effects on tree regeneration by reducing light availability (Busing, 1994; Klopcic and Boncina, 2012; Nilsson et al., 2002). In the poor forest plots, the probability that tree seedlings were present was reduced with increasing proportion of overstorey species that cast deep shade (e.g. *Fagus*) and total basal area had a negative effect on unconditional seedling cover despite not affecting the probability of presence or conditional cover clearly. Surprisingly, we found a positive relationship between SCA and tree seedling cover for the second survey period. This may also be due to the gradient in soil conditions in the poor forest plots (see earlier). In the rich plots, our models also showed opposite effects of SCA on probability of presence in each survey, however, with large uncertainties. The different effects in the two forest types and the absence of clear overstorey effects on seedling cover may be due to the fact that the studied seedling species were more tolerant to shade in the rich forest plots. These relationships imply that forest managers should be careful when selectively removing or retaining overstorey trees, as changing the composition of the overstorey may have direct consequences for tree regeneration. Similarly, our results show that when managing understorey vegetation to improve regeneration, it is also important to take the composition into account. Many studies have shown that understorey vegetation in temperate forest can strongly reduce tree seedling regeneration (Balandier et al., 2006; George and Bazzaz, 1999a, 1999b; Royo and Carson, 2008). In our study, we found that an increasing proportion of competitive understorey species (*sensu* Grime, 2001) resulted in lower probability of presence for tree seedlings in both poor and rich forest types. Due to this strong effect on probability of presence, unconditional total cover is also negatively influenced by the competitive signature. This suggests that control of the understorey vegetation to promote tree regeneration will be most effective when applied in communities with a high competitive signature and not just high cover. Our findings provide further insight in how understoreys may affect tree regeneration, which is not only of relevance for forest managers, but also for forest modellers, as it has been shown that interactions between the herbaceous layer and tree regeneration significantly affect the projections of forest structure and composition at large time scales (decades to centuries) (e.g. Landuyt et al., 2018; Thrippleton et al., 2016).

The fact that we did not find clear effects for total basal area and total understorey cover on both tree seedling probability of presence and conditional cover in neither forest types was unexpected. This may be because (i) there are simply no effects, (ii) these factors do not have unidirectional effects on tree regeneration and can imply a complex balance of positive (facilitation) and negative (competition) effects (Callaway and Walker, 1997; Putnam and Reich, 2017) under different conditions which are difficult to detect and (iii) this might a result of pooling different tree seedling species for analysis. Due to insufficient data points to analyse all tree seedling species separately, we were restricted in our analysis to pooled seedling cover per forest types and the single-species analysis of *Quercus* using the poor forest plots. This pooling of species with different traits such as shade-tolerance (Niinemets and Valladares, 2006), may obscure and cancel out effects: e.g. the 80% CI for understorey cover for the ZI part differs from zero and suggests a negative relation between understory cover and tree seedling presence-absence. The lack of clear overstorey effects on seedlings in rich forest plots can, however, be explained by their shade-tolerant nature. Nonetheless, our results give valuable insights in how cover of the most important seedling species is driven by overstorey and understorey using inventory data in our study area (see also Kolo et al., 2017; Vayreda et al., 2013).

The single-species model shows that *Quercus* seedling occurrence is mainly influenced by overstorey variables. Interestingly, both total basal area and SCA decreased occurrence, whereas increasing abundance of conspecific trees, i.e. a proxy for seed sources, had a positive effect. This concurs with Klopcic and Boncina (2012), who also found this relationship for total basal area and basal area of parent trees for seedlings of silver fir, sycamore, Norway spruce and European beech in Slovenia. Monteiro-henriques and Fernandes (2018) also report positive effects of presence of conspecific parent trees for several *Quercus* taxa including *Quercus robur* in forests in Portugal. The magnitude of the effects on *Quercus* cover were small and mainly determined by the zero-inflation part of the model and were thus affecting presence-absence of seedlings. We believe, however, that a change from for example 1% to 0% cover, i.e. absence of Quercus regeneration, is an important; indeed it shows a difference between regeneration presence and failure. Our results suggest that in order to promote *Quercus* regeneration, thinning of heterospecific trees and retaining potential seed trees can prove to be a successful measure.

Between surveys, the total cover of the understorey increased in both forest types and the tree seedling cover increased in the poor forests, independently of the predictors used in our models. These increases may be due to other local- or large-scale drivers not included in this study that have been reported as important for understorey and tree regeneration dynamics. Browsing by large herbivores is often reported as a strong determinant of tree regeneration, by directly inflicting damage to tree seedlings or indirectly by altering understoreys (Kirby, 2001; Kuijper et al., 2010; Royo and Carson, 2006). In our study area, densities of herbivores are not problematic compared to other regions. However, as herbivore densities have been increasing across Europe the past decades (Fuller and Gill, 2001; Milner et al., 2006), this may also become a more prominent driver of tree regeneration in Flanders. Changes in large-scale drivers such as climate change and nitrogen depositions may affect forests in Flanders. Global warming may already have affected tree regeneration over the past decades. The average temperature in Belgium is now +2.3 °C higher than in the pre-industrial age (end 19th century) ("https://www.klimaat.be/", 2019). Together with increased nitrogen inputs through atmospheric depositions these changes may lead to changes in tree seedling recruitment and growth (Fisichelli et al., 2014, 2012; Wheeler et al., 2017). Such effects are hard to detect in our study area due to their large scale. Furthermore, forest understorey plant responses, including tree seedlings', to macroclimatic changes (climate or N dep) may be buffered in forests and effects may vary depending on microclimatic conditions created by e.g. overstoreys (De Frenne et al., 2013; Verheyen et al., 2012; Zellweger et al., 2018). Including such drivers could improve the amount of variability explained in our models.

The simulations of regeneration cuttings based on our models show contrasting results for poor and rich forest types. Our predictions are accompanied with large uncertainties originating from both the variation introduced when predicting the impact of the overstorey on the understorey vegetation as well as the variation in the prediction of tree regeneration responses to overstorey and understorey variables. For the poor forests, we found that, starting from a mature stand, sufficiently thinning the overstorey can promote tree regeneration. Based on our findings, tree regeneration is likely to profit more from the increased light when opening up the overstorey than it will suffer negative effects from the denser understorey cover that is likely to develop. Pages et al. (2003) and Pages and Michalet (2003) found similar trends for regeneration of multiple temperate tree seedlings in their experiments in forests on mesic soils. Other studies, however, have shown that under nutrient poor site conditions when increasing light availability, belowground competition for soil resources (nutrients, water) can become more important than aboveground competition for light (Balandier et al., 2006; Provendier and Balandier, 2008). For the same scenarios in rich forest, we found that tree regeneration is hardly present initially and is likely to decrease to zero cover when opening up the overstorey. In such cases, selectively controlling competitive understorey vegetation or supplementary artificial regeneration (through planting) may be advised (Nilsson et al., 2002; Shen and Nelson, 2018). The predictions for *Quercus* again suggest that stimulating seedling cover can be a compromise between reducing overstorey abundance and retaining sufficient parent trees as potential seed sources. However, we should be cautious in drawing conclusions from these predictions, as they are accompanied by large uncertainties and do not show a clear trend.

To attain successful natural regeneration, a good understanding of how environmental factors influence tree seedlings is needed. Past research has shown that both overstoreys and understoreys can have strong impacts on tree regeneration and intervening in these layers is key for managers to stimulate tree regeneration. In our study, we found that retaining overstorey trees can potentially reduce the cover of the understorey. The signature of both forest layers, i.e. C-score and shade-casting ability, turned out to be most determining for tree regeneration, mostly by influencing seedling probability of presence. Similar variables affect tree regeneration in both forest types, but the direction and magnitude of the effects varied. These results imply that selective management of shade-casting species and not just reducing or retaining abundance of both layer may prove successful in promoting natural regeneration in temperate forests.

Acknowledgement

The research of EDL and KV is supported by the ERC Consolidator Grant 614839 – PASTFORWARD. We kindly thank the Agency for Nature and Forest (ANF) and Leen Govaere to give us the opportunity to use and provide the data of the Flemish Forest Inventories. We thank two anonymous referees for their helpful comments.

Conflict of interest

The authors have no conflicts of interest to declare.

Tables

Table 1. Differences in overstorey, understorey, tree seedling and environmental variables between the two forest types per survey (Poor vs. Rich). Poor and rich forest types refer to both soil fertility and species composition. The last two columns tests the significance of differences between surveys per forest type (FFI vs. FFI2). Comparisons were tested with T-tests (paired for comparisons between surveys).

Survey	FFI1			FFI2			FFI1 vs. FFI2	
Forest type	Poor	Rich	Poor vs. Rich	Poor	Rich	Poor vs. Rich	Poor	Rich
	Mean [SD]	Mean [SD]	Statistic	Mean [SD]	Mean [SD]	Statistic	Statistic	Statistic
Overstorey								
Total basal area (m^2/ha)	27.6 [10.9]	25.4 [11.2]	1.5^{NS}	32.2 [11.9]	32.4 [11.4]	-0.1^{NS}	-5***	-3.7***
Overstorey cover (%)	112.6 [38.9]	118 [46.2]	-0.9^{NS}	152.7 [49.8]	141.7 [56.5]	1.5^{NS}	-11.1***	-2.7**
SCA basal area	2.7 [1]	3.5 [0.7]	-7.4***	2.8 [1]	3.6 [0.7]	-8***	-0.6^{NS}	-0.9^{NS}
SCA cover	2.9 [1]	3.6 [0.7]	-7.6***	3 [1]	3.7 [0.7]	-7.5***	-1.5^{NS}	-0.8^{NS}
Understorey								
Understorey cover (%)	43.9 [39.9]	102.4 [50.1]	-9.2***	60.5 [45.3]	129.7 [76.9]	-7.3***	-4.8***	-2.5*
C-score	0.46 [0.16]	0.54 [0.23]	-2.6*	0.47 [0.14]	0.50 [0.21]	-1.2^{NS}	-0.4^{NS}	1.1^{NS}
S-score	0.47 [0.18]	0.27 [0.18]	8.4***	0.47 [0.13]	0.30 [0.16]	8.5***	-0.3^{NS}	-1^{NS}
R-score	0.07 [0.11]	0.20 [0.14]	-6.9***	0.06 [0.08]	0.21 [0.15]	-7.9***	1.2^{NS}	-0.4^{NS}
Tree seedlings								
Total seedling cover (%)	1.2 [1.2]	2.1 [3.6]	-2.1*	1.8 [2.3]	3.8 [9.7]	-1.8^{NS}	-4***	-1.4^{NS}
Seedling shade tolerance	2.51 [0.58]	2.88 [0.41]	-4.9***	2.6 [0.71]	2.84 [0.39]	-3.4**	-1.4^{NS}	0.5^{NS}
Environment								
Soil fertility (EIV_N)	4.1 [1.5]	6.7 [1.3]	-15***	4.6 [1.7]	6.6 [1.2]	-11.6***	-3.8***	0.4^{NS}
Soil reaction (EIV_R)	3.3 [1.1]	6.5 [0.7]	-29.9***	3.6 [1.3]	6.3 [0.8]	-22.6***	-3**	0.9^{NS}
Soil moisture (EIV_F)	5.8 [0.9]	5.9 [0.7]	-1.1^{NS}	5.9 [0.8]	6 [0.8]	-1^{NS}	-1.5^{NS}	-0.7^{NS}
LQ basal area	2.2 [0.8]	3.1 [1.2]	-5.7***	2.2 [0.8]	3.1 [1.2]	-6.4***	0.7^{NS}	-0.1^{NS}
LQ cover	2.2 [0.7]	3 [0.9]	-7.2***	2.1 [0.7]	3.2 [1]	-8.6***	1.5^{NS}	-1.3^{NS}

Significance: ^{NS}, not significant;*P < 0.05;**P < 0.01;***P < 0.001. SCA: shade-casting ability; LQ: litter quality. FFI1&2: first and second survey time.

Figures

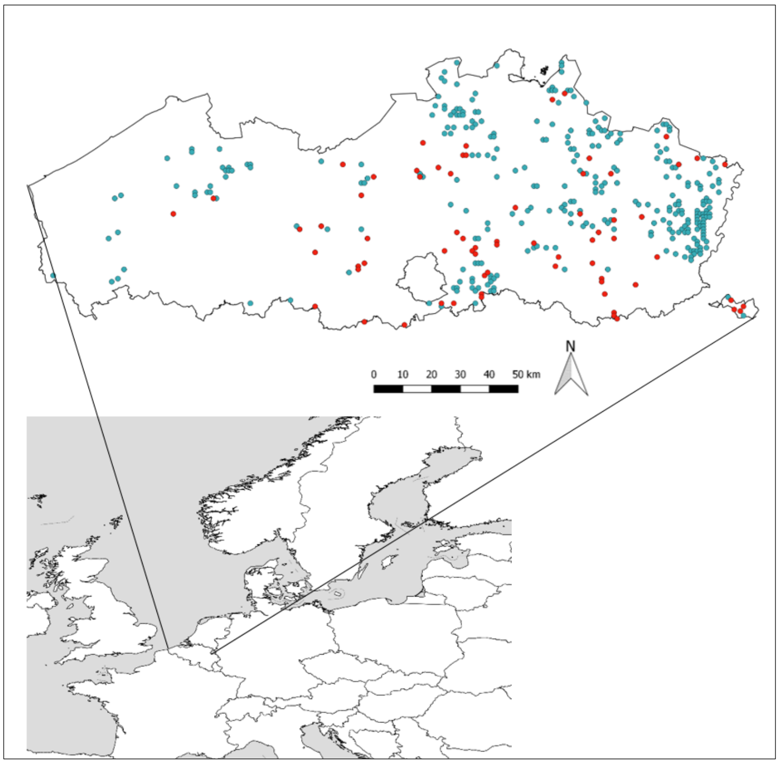


Fig. 1. Map of the location of the forest inventory plots used in this study. The Flemish Forest Inventory only covers the northern part of Belgium (region of Flanders; N 51.037, E 4.241). Blue and red points represent poor and rich forest plots, respectively.

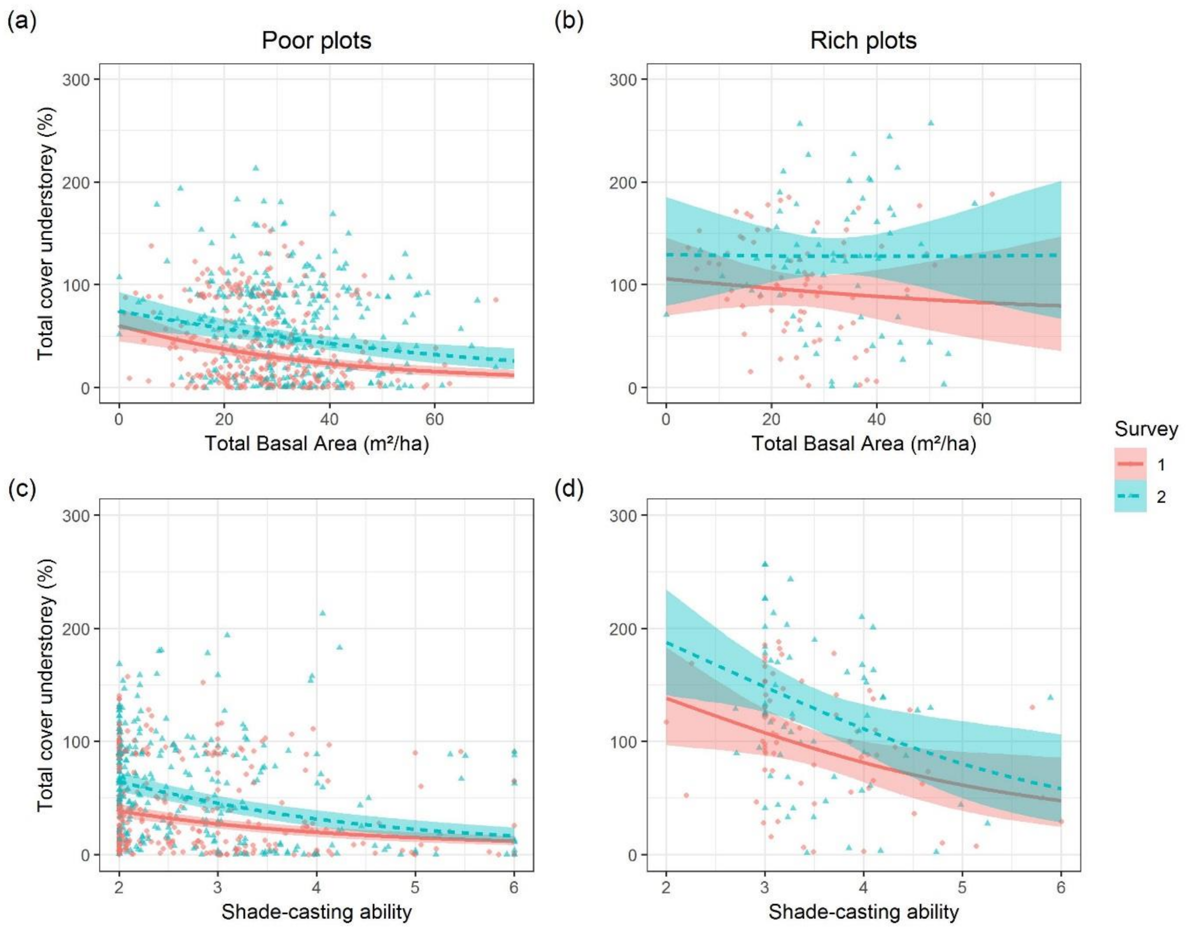


Fig. 2. Response of the total cover of the understorey herbaceous vegetation to the total basal area (a, b) and the shade-casting ability (c, d) of the overstorey canopy in the poor and rich plots. Poor and rich plots refer to both soil fertility and species composition. Points represent raw data. Model fits are based on model 1 and are showed as posterior means (lines) and 95% credible intervals (shaded area); fits are shown for average values of all other predictors. For the poor plots $R_{marginal}$ is 0.13 (95%CI = [0.09, 0.18]) and $R_{conditional}$ is 0.67 (95%CI = [0.63, 0.7]); and for the rich plots $R_{marginal}$ is 0.17 (95%CI = [0.07, 0.26]) and $R_{conditional}$ is 0.5 (95%CI = [0.32, 0.63]). Red dots & full lines: Survey = 1; Bleu triangles &dashed lines: Survey = 2.

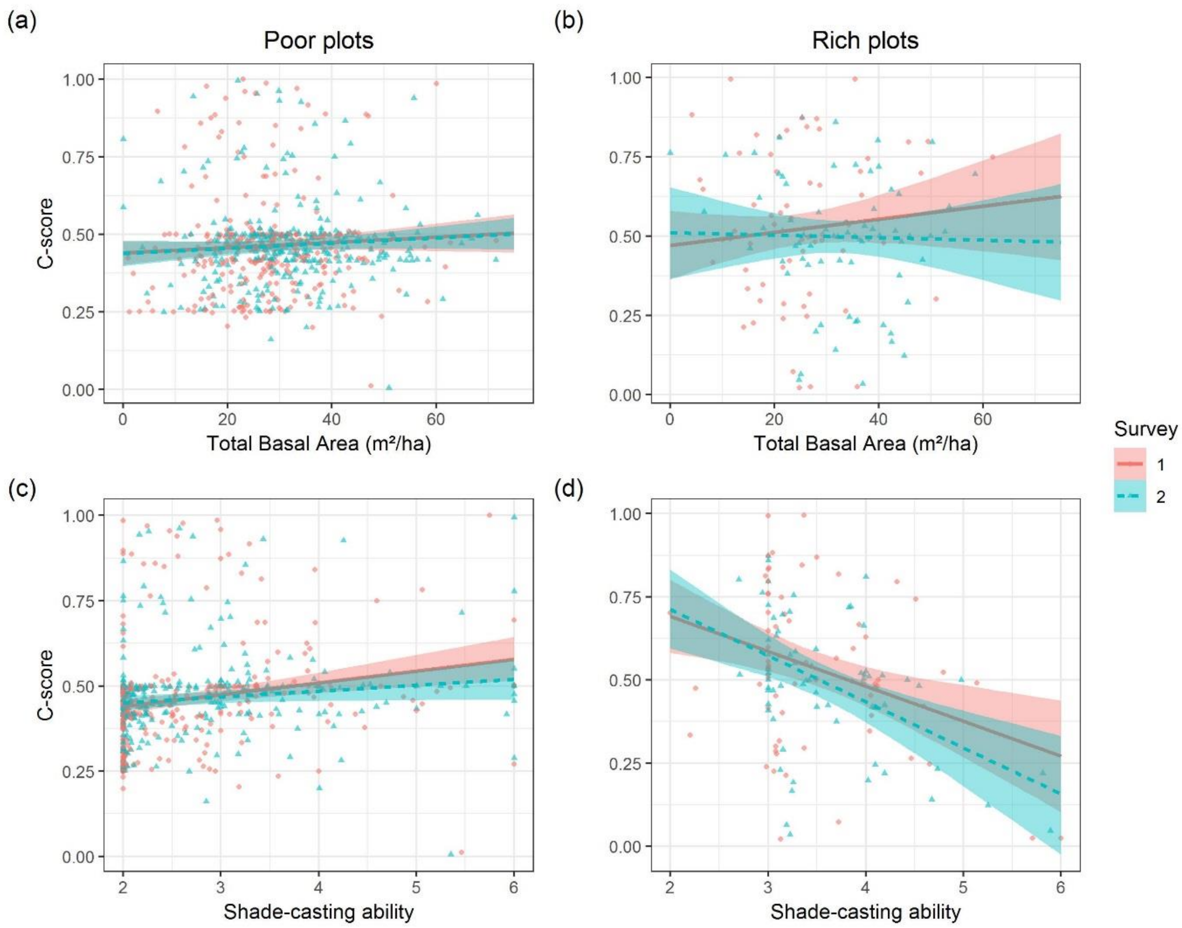
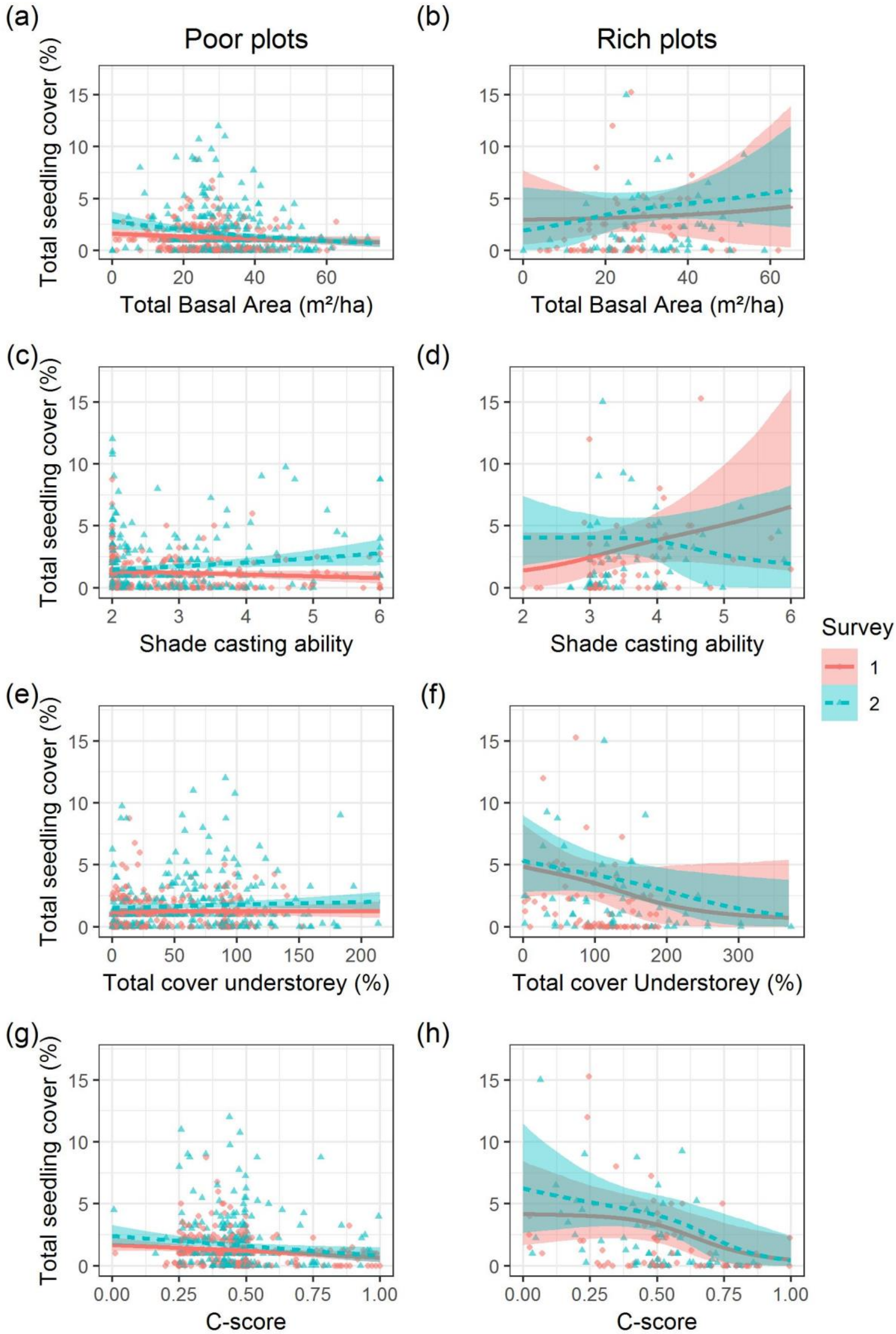


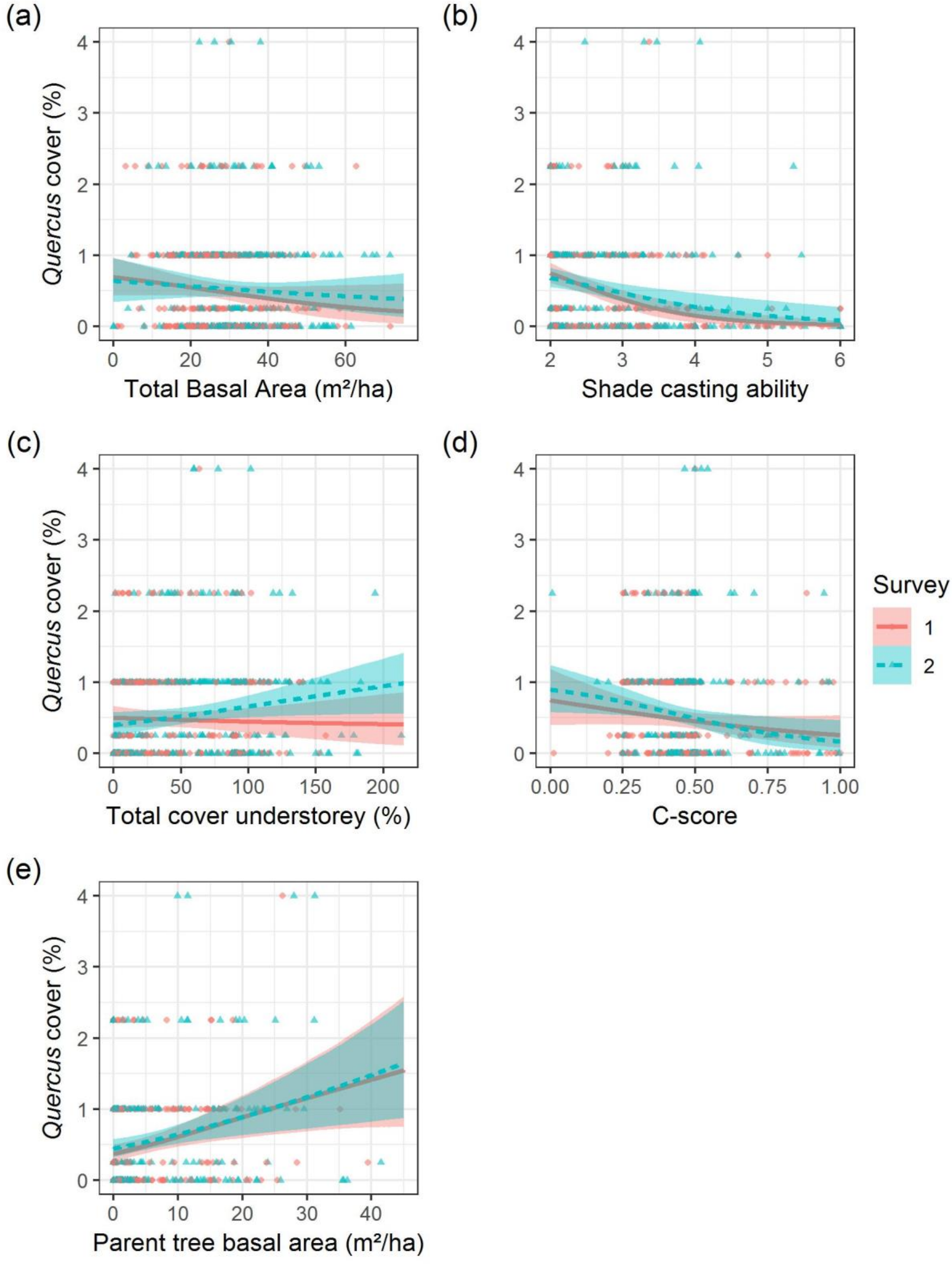
Fig. 3. Response of the competitive signature of the overstorey to the total basal area (a, b) and the shade-casting ability (c, d) of the overstorey canopy in the poor and rich plots. Poor and rich plots refer to both soil fertility and species composition. Points represent raw data. Model fits are based on model 2 are and are showed as posterior means (lines) and 95% credible intervals (shaded area); fits are shown for average values of all other predictors. For the poor plots $R_{marginal}$ is 0.04 (95%CI = [0.01, 0.08]) and $R_{conditional}$ is 0.74 (95%CI = [0.7, 0.77]); and for the rich plots $R_{marginal}$ is 0.18 (95%CI = [0.07, 0.29]) and $R_{conditional}$ is 0.65 (95%CI = [0.53, 0.74]). Red dots & full lines: Survey = 1; Bleu triangles &dashed lines: Survey = 2.



(a)
Poor plots
Total seedling cover (%)
Total Basal Area (m²/ha)
(b)
Rich plots
Total Basal Area (m²/ha)
(c)
Shade casting ability
(d)
Shade casting ability
Survey
1
2
(e)
Total cover understorey (%)
(f)
Total cover Understorey (%)
(g)
C-score
(h)
C-score

517

Fig. 4. Response of the total tree seedling cover to the total basal area (a, b) and the shade-casting ability (c, d) of the overstorey canopy; and to the total cover (e, f) and the competitive signature (g, h) of the understorey vegetation in the poor and rich plots. Poor and rich plots refer to both soil fertility and species composition. Points represent raw data. Model fits are based on model 3 are and are showed as posterior means (lines) and 95% credible intervals (shaded area); fits are shown for average values of all other predictors. For the poor plots $R_{marginal}$ is 0.06 (95%CI = [0.03, 0.09]) and $R_{conditional}$ 0.22 (95%CI = [0.09, 0.33]); and for the rich plots $R_{marginal}$ is 0.09 (95%CI = [0.04, 0.15]) and $R_{conditional}$ is 0.10 (95%CI = [0.05, 0.18]). Red dots & full lines: Survey = 1; Bleu triangles &dashed lines: Survey = 2.



(a)
Quercus cover (%)
Total Basal Area (m²/ha)
(b)
Shade casting ability
(c)
Total cover understorey (%)
(d)
C-score
(e)
Parent tree basal area (m²/ha)
Survey
1
2

Fig. 5. Response of the interval-censored *Quercus* seedling cover in the poor forest plots to the total basal area (a) and the shade-casting ability of the overstorey canopy (b); and to the total cover (c) and the competitive signature (d) of the understorey vegetation; and to the total basal area of parent trees (e). Points represent midpoints of the cover classes. Model fits are based on model 3 with parent tree added as extra predictor in both ZI and beta part of the model and are showed as posterior means (lines) and 95% credible intervals (shaded area); fits are shown for average values of all other predictors. $R_{marginal}$ is 0.25 (95%CI = [0.18, 0.31]) and $R_{conditional}$ is 0.40 (95%CI = [0.32, 0.47]); Red dots & full lines: Survey = 1; Bleu triangles &dashed lines: Survey = 2.

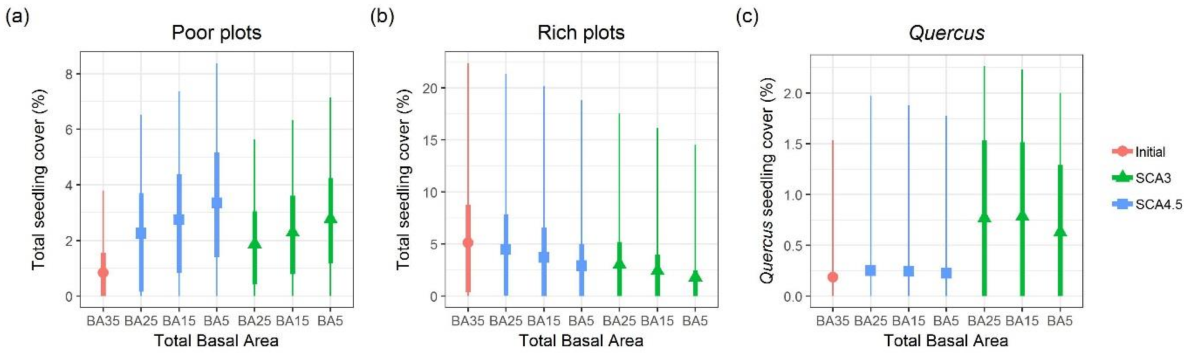


Fig. 6. Predictions simulating thinning cuts to initialise tree regeneration in both forest types and for Quercus alone. Poor and rich plots refer to both soil fertility and species composition. Three thinning intensities are predicted: starting from a basal area of 35 (red; dots), i.e. mature overstorey, and thinning to a basal area of 25, 15 or 5 m^2/ha, with change in the composition of the overstorey and thus SCA (green; triangles) or without (blue; squares) change in composition. Points are mean predictions, thick lines are 80% PI and thin lines represent 95% PI. The y-axis scale for each figure varies.

References

Ammer, C., Fichtner, A., Fischer, A., Gossner, M.M., Meyer, P., Seidl, R., Thomas, F.M., Annighöfer, P., Kreyling, J., Ohse, B., Berger, U., Feldmann, E., Häberle, K.H., Heer, K., Heinrichs, S., Huth, F., Krämer-Klement, K., Mölder, A., Müller, J., Mund, M., Opgenoorth, L., Schall, P., Scherer-Lorenzen, M., Seidel, D., Vogt, J., Wagner, S., 2018. Key ecological research questions for Central European forests. Basic Appl. Ecol. 32, 3–25. https://doi.org/10.1016/j.baae.2018.07.006

Axmanová, I., Tichý, L., Fajmonová, Z., Hájková, P., Hettenbergerová, E., Li, C.F., Merunková, K., Nejezchlebová, M., Otýpková, Z., Vymazalová, M., Zelený, D., 2012. Estimation of herbaceous biomass from species composition and cover. Appl. Veg. Sci. 15, 580–589. https://doi.org/10.1111/j.1654-109X.2012.01191.x

Axmanová, I., Zelený, D., Li, C.F., Chytrý, M., 2011. Environmental factors influencing herb layer productivity in Central European oak forests: Insights from soil and biomass analyses and a phytometer experiment. Plant Soil 342, 183–194. https://doi.org/10.1007/s11104-010-0683-9

Baeten, L., Bauwens, B., De Schrijver, A., De Keersmaeker, L., Van Calster, H., Vandekerkhove, K., Roelandt, B., Beeckman, H., Verheyen, K., 2009. Herb layer changes (1954-2000) related to the conversion of coppice-with-standards forest and soil acidification. Appl. Veg. Sci. 12, 187–197. https://doi.org/10.1111/j.1654-109X.2009.01013.x

Balandier, P., Collet, C., Miller, J.H., Reynolds, P.E., Zedaker, S.M., 2006. Designing forest vegetation management strategies based on the mechanisms and dynamics of crop tree competition by neighbouring vegetation. Forestry 79, 3–27. https://doi.org/10.1093/forestry/cpi056

Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understory vegetation diversity and mechanisms involved-A critical review for temperate and boreal forests. For. Ecol. Manage. 254, 1–15. https://doi.org/10.1016/j.foreco.2007.09.038

Bravo, F., Pando, V., Ordóñez, C., Lizarralde, I., 2008. Modelling ingrowth in mediterranean pine forests : A case study from scots pine (*Pinus sylvestris* L.) and mediterranean maritime pine (Pinus pinaster Ait.) stands in Spain. Investig. Agrar. Sist. y Recur. For. 17, 250–260. https://doi.org/10.5424/srf/2008173-01039

Bürkner, P.-C., 2017. **brms** : An *R* Package for Bayesian Multilevel Models Using *Stan*. J. Stat. Softw. 80. https://doi.org/10.18637/jss.v080.i01

Busing, R.T., 1994. Canopy cover and tree regeneration in old-growth cove forests of the Appalachian mountains. Vegetatio 115, 19–27. https://doi.org/10.1007/BF00119383

Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: A synthetic approach to interactions in plant communities. Ecology 78, 1958–1965. https://doi.org/10.1890/0012-9658(1997)078[1958:CAFASA]2.0.CO;2

Cornelis, J., Hermy, M., Roelandt, B., De Keersmaeker, L., Vandekerkhove, K., 2009. Bosplantengemeenschappen in Vlaanderen, een typologie van bossen gebaseerd op de kruidlaag. INBO.M.2009.5. Agentschap voor Natuur en Bos en Instituut voor Natuur- en Bosonderzoek, Brussels.

Damgaard, C., 2014. Estimating mean plant cover from different types of cover data : a coherent statistical framework. Ecosphere 5, 1–7. https://doi.org/10.1890/ES13-00300.1

Damgaard, C., 2009. On the distribution of plant abundance data. Ecol. Inform. 4, 76–82. https://doi.org/10.1016/j.ecoinf.2009.02.002

De Frenne, P., Rodríguez-Sánchez, F., Coomes, D.A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Römermann, M., Brown, C.D., Brunet, J., Cornelis, J., Decocq, G.M., Dierschke, H., Eriksson, O., Gilliam, F.S., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M. a, Kelly, D.L., Kirby, K.J., Mitchell, F.J.G., Naaf, T., Newman, M., Peterken, G., Petrík, P., Schultz, J., Sonnier, G., Van Calster, H., Waller, D.M., Walther, G.-R., White, P.S., Woods, K.D., Wulf, M., Graae, B.J., Verheyen, K., 2013. Microclimate moderates plant responses to macroclimate warming. Proc. Natl. Acad. Sci. U. S. A. 110, 18561–18565. https://doi.org/10.1073/pnas.1311190110

Diekmann, M., 2003. Species indicator values as an important tool in applied plant ecology - a review. Basic Appl. Ecol. 4, 493–506. https://doi.org/10.1078/1439-1791-00185

Ellenberg, H., 1996. Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. Ulmer, Stuttgart.

Ellenberg, H., Weber, H., Düll, R., Wirth, V., Werner, W., 2001. Zeigerwerte von Pflanzen in Mitteleuropa., 3rd ed, Scripta Geobotanica. Goltze, Göttingen.

Fisichelli, N., Frelich, L.E., Reich, P.B., 2012. Sapling growth responses to warmer temperatures "cooled" by browse pressure. Glob. Chang. Biol. 18, 3455–3463. https://doi.org/10.1111/j.1365-2486.2012.02785.x

Fisichelli, N., Wright, A., Rice, K., Mau, A., Buschena, C., Reich, P.B., 2014. First-year seedlings and climate change: Species-specific responses of 15 North American tree species. Oikos 123, 1331–1340. https://doi.org/10.1111/oik.01349

Fuller, R.J., Gill, R.M.A., 2001. Ecological impacts of increasing numbers of deer in British woodland. Forestry 74, 193–199. https://doi.org/10.1093/forestry/74.3.193

Gabry, J., Mahr, T., 2018. Bayesplot: plotting for Bayesian models. R package version 1.6.0.

Gelman, A., Goodrich, B., Gabry, J., Ali, I., 2017. R-squared for Bayesian regression models. Unpubl. via http//www. stat. columbia. edu/~ gelman/research/unpublished.

Gelman, A., Hill, J., 2007. Data Analysis Using Regression and Multilevel/Hierarchical Models. Cambridge University Press, New York.

George, L.O., Bazzaz, F.A., 1999a. The fern understory as an ecological filter: growth and survival of canopy-tree seedlings. Ecology 80, 846–856. https://doi.org/10.1890/0012-9658(1999)080[0833:TFUAAE]2.0.CO;2

George, L.O., Bazzaz, F.A., 1999b. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. Ecology 80, 833–845. https://doi.org/10.1890/0012-9658(1999)080[0833:TFUAAE]2.0.CO;2

Grime, J.P., 2001. Plant strategies, vegetation processes, and ecosystem properties, 2nd ed. JohnWiley and Sons, Chichester,UK.

Hermy, M., 1985. Ecologie en fytosociologie van oude en jonge bossen in binnen-Vlaanderen. PhD Thesis.

Herpigny, B., Gosselin, F., 2015. Analyzing plant cover class data quantitatively: Customized zero-inflated cumulative beta distributions show promising results. Ecol. Inform. 26, 18–26. https://doi.org/10.1016/j.ecoinf.2014.12.002

Honnay, O., Bossuyt, B., Verheyen, K., Butaye, J., Jacquemyn, H., Hermy, M., 2002. Ecological perspectives for the restoration of plant. Biodivers. Conserv. 11, 213–242. https://doi.org/10.1023/A:1014531011060

Hunt, R., Hodgson, J.G., Thompson, K., Bungener, P., Dunnett, N.P., Askew, A.P., 2004. A new practical tool for deriving a functional signature for herbaceous vegetation. Appl. Veg. Sci. 7, 163–170. https://doi.org/10.1658/1402-2001(2004)007[0163:anptfd]2.0.co;2

Irvine, K.M., Rodhouse, T.J., Keren, I.N., 2016. Extending Ordinal Regression with a Latent Zero-Augmented Beta Distribution. J. Agric. Biol. Environ. Stat. 21, 619–640. https://doi.org/10.1007/s13253-016-0265-2

Kirby, K.J., 2001. The impact of deer on the ground flora of British broadleaved woodland. Forestry 74, 219–229. https://doi.org/10.1093/forestry/74.3.219

klimaat.be [WWW Document], 2019. URL https://www.klimaat.be/nl-be/klimaatverandering/belgie/waarnemingen-belgie (accessed 2.28.19).

Klopcic, M., Boncina, A., 2012. Recruitment of tree species in mixed selection and irregular shelterwood forest stands. Ann. For. Sci. 69, 915–925. https://doi.org/10.1080/10401334.2013.830514

Kolo, H., Ankerst, D., Knoke, T., 2017. Predicting natural forest regeneration: a statistical model based on inventory data. Eur. J. For. Res. 136, 1–16. https://doi.org/10.1007/s10342-017-1080-1

Kuijper, D.P.J., Cromsigt, J.P.G.M., Jedrzejewska, B., Miścicki, S., Churski, M., Jedrzejewski, W., Kweczlich, I., 2010. Bottom-up versus top-down control of tree regeneration in the Białowieża Primeval Forest, Poland. J. Ecol. 98, 888–899. https://doi.org/10.1111/j.1365-2745.2010.01656.x

Landuyt, D., Perring, M.P., Seidl, R., Taubert, F., Verbeeck, H., Verheyen, K., 2018. Modelling understorey dynamics in temperate forests under global change–Challenges and perspectives. Perspect. Plant Ecol. Evol. Syst. 31, 44–54. https://doi.org/10.1016/j.ppees.2018.01.002

Milner, J.M., Bonenfant, C., Mysterud, A., Gaillard, J.-M., Csányi, S., Stenseth, N.C., 2006. Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. J. Appl. Ecol. 43, 721–734. https://doi.org/10.1111/j.1365-2664.2006.01183.x

Monteiro-henriques, T., Fernandes, P.M., 2018. Regeneration of Native Forest Species in Mainland Portugal : Identifying Main Drivers. Forests 9, 1–22. https://doi.org/10.3390/f9110694

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate

Northern Hemisphere trees and shrubs. Ecol. Monogr. 76, 521–547. https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2

Nilsson, U., Gemmel, P., Johansson, U., Karlsson, M., Welander, T., 2002. Natural regeneration of Norway spruce , Scots pine and birch under Norway spruce shelterwoods of varying densities on a mesic-dry site in southern Sweden. For. Ecol. Manage. 161, 133–145. https://doi.org/10.1016/S0378-1127(01)00497-2

Ospina, R., Ferrari, S.L.P., 2010. Inflated beta distributions. Stat. Pap. 51, 111–126. https://doi.org/10.1007/s00362-008-0125-4

Pagès, J.P., Michalet, R., 2003. A test of the indirect facilitation model in a temperate hardwood forest of the northern French Alps. J. Ecol. 91, 932–940. https://doi.org/10.1046/j.1365-2745.2003.00825.x

Pagès, J.P., Pache, G., Joud, D., Magnan, N., Michalet, R., 2003. Direct and indirect effects of shade on four forest tree seedlings in the French Alps. Ecology 84, 2741–2750. https://doi.org/10.1890/02-0138

Pescott, O., Jitlal, M., Smart, S., Walker, K., Roy, D., Freeman, S., 2016. A comparison of models for interval-censored plant cover data, with applications to monitoring schemes. PeerJ Prepr. 4. https://doi.org/10.7287/peerj.preprints.2532v1

Plieninger, T., Rolo, V., Moreno, G., 2010. Large-Scale Patterns of Quercus ilex , Quercus suber , and Quercus pyrenaica Regeneration in Central- Western Spain. Ecosystems 13, 644–660. https://doi.org/10.1007/s10021-010-9345-2

Provendier, D., Balandier, P., 2008. Compared effects of competition by grasses (Graminoids) and broom (*Cytisus scoparius*) on growth and functional traits of beech saplings (*Fagus sylvatica*). Ann. For. Sci. 65, 510(1–9). https://doi.org/Artn 510\nDoi 10.1051/Forest:2008028

Puettmann, K.J., Wilson, S.M., Baker, S.C., Donoso, P.J., Drössler, L., Amente, G., Harvey, B.D., Knoke, T., Lu, Y., Nocentini, S., Putz, F.E., Yoshida, T., Bauhus, J., 2015. Silvicultural alternatives to conventional even-aged forest management - what limits global adoption? For. Ecosyst. 2. https://doi.org/10.1186/s40663-015-0031-x

Putnam, R.C., Reich, P.B., 2017. Climate and competition affect growth and survival of transplanted sugar maple seedlings along a 1700-km gradient. Ecol. Monogr. 87, 130–157. https://doi.org/10.1002/ecm.1237

R Core Team, 2018. R: A language and environment for statistical computing.

Royo, A.A., Carson, W.P., 2008. Direct and indirect effects of a dense understory on tree seedling recruitment in temperate forests: habitat-mediated predation versus competition. Can. J. For. Res. 38, 1634–1645. https://doi.org/10.1139/X07-247

Royo, A.A., Carson, W.P., 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Can. J. For. Res. 36, 1345–1362. https://doi.org/10.1139/x06-025

Schütz, J.-P., 2004. Opportunistic methods of controlling vegetation, inspired by natural plant succession dynamics with special reference to natural outmixing tendencies in a gap regeneration. Ann. Des Sci. For. 61, 149–156. https://doi.org/10.1051/forest:2004006

Shen, C., Nelson, A.S., 2018. Natural conifer regeneration patterns in temperate forests across the Inland Northwest , USA. Ann. For. Sci. 75, 1–16. https://doi.org/10.1007/s13595-018-0724-8

Thrippleton, T., Bugmann, H., Kramer-Priewasser, K., Snell, R.S., 2016. Herbaceous Understorey : An Overlooked Player in Forest Landscape Dynamics? Ecosystems 19, 1240–1254. https://doi.org/10.1007/s10021-016-9999-5

Van Calster, H., Baeten, L., Verheyen, K., De Keersmaeker, L., Dekeyser, S., Rogister, J.E., Hermy, M., 2008. Diverging effects of overstorey conversion scenarios on the understorey vegetation in a former coppice-with-standards forest. For. Ecol. Manage. 256, 519–528.

https://doi.org/10.1016/j.foreco.2008.04.042

van der Maarel, E., 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. Vegetatio 39, 97–114. https://doi.org/10.1007/bf00052021

Vayreda, J., Gracia, M., Martinez-vilalta, J., Retana, J., Vall, C., 2013. Patterns and drivers of regeneration of tree species in forests of peninsular Spain. J. Biogeogr. 40, 1252–1265. https://doi.org/10.1111/jbi.12105

Verheyen, K., Baeten, L., De Frenne, P., Bernhardt-Römermann, M., Brunet, J., Cornelis, J., Decocq, G., Dierschke, H., Eriksson, O., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Kirby, K., Naaf, T., Peterken, G., Petřík, P., Pfadenhauer, J., Van Calster, H., Walther, G.-R., Wulf, M., Verstraeten, G., 2012. Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. J. Ecol. 100, 352–365. https://doi.org/10.1111/j.1365-2745.2011.01928.x

Wagner, S., Fischer, H., Huth, F., 2011. Canopy effects on vegetation caused by harvesting and regeneration treatments. Eur. J. For. Res. 130, 17–40. https://doi.org/10.1007/s10342-010-0378-z

Wheeler, J.A., Frey, S.D., Stinson, K.A., 2017. Tree seedling responses to multiple environmental stresses: Interactive effects of soil warming, nitrogen fertilization, and plant invasion. For. Ecol. Manage. 403, 44–51. https://doi.org/10.1016/j.foreco.2017.08.010

Willoughby, I., Balandier, P., Bentsen, N.S., Mccarthy, N., Claridge, J., Eds, 2009. Forest vegetation management in Europe: Current practice and future requirements.

Wouters, J., Quataert, P., Onkelinx, T., Bauwens, D., 2008. Ontwerp en handleiding voor de tweede regionale bosinventarisatie van het Vlaamse Gewest. Brussel.

Zellweger, F., Frenne, P. De, Lenoir, J., Rocchini, D., Coomes, D., 2018. Advances in microclimate ecology arising from remote sensing. Trends Ecol. Evol. xx, 1–15.

https://doi.org/10.1016/j.tree.2018.12.012

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effect Models and Extensions in Ecology with R. Springer, New York, USA. https://doi.org/10.1007/978-0-387-87458-6

Appendix A. Supplementary tables and figures

Table A1. The nine classes of the transformed Braun-Blanquet scale based on van der Maarel (1979).

Braun-Blanquet Class	# Individuals	Cover class (%)	Cover (%)
r	very few (1-2)	0 - 0.5	0.25
+	few (3-20)	0.5 - 1.5	1
1	numerous (20-100)	1.5 - 3	2.25
2m	very numerous (uncountable)	3 - 5	4
2a	any	5 - 12.5	8.75
2b	any	12.5 - 25	18.75
3	any	25 - 50	37.5
4	any	50 - 75	62.5
5	any	75 - 100	87.5

Table A2. The number of plots where a tree seedling species is present for both surveys (FFI1 & FFI2) and number of plots where seedlings are present in at least one survey (unique plots) in the poor and rich forests. Poor and rich plots refer to both soil fertility and species composition. Species marked in grey were selected for our analyses based on frequency and silvicultural importance per forest type.

	Poor			Rich		
Species	# Plots		#Unique plots	# Plots		#Unique plots
	FFI1	FFI2	Both FFI	FFI1	FFI2	Both FFI
Acer campestre	0	6	6	3	4	5
Acer pseudoplatanus	42	42	58	17	20	27
Acer species	0	2	2	0	1	1
Alnus glutinosa	1	0	1	3	4	7
Betula pendula	43	39	72	0	0	0
Betula pubescens	40	12	50	0	0	0
Betula species	0	29	29	0	2	2
Carpinus betulus	4	7	10	3	5	6
Cornus species	0	1	1	0	0	0
Corylus avellana	11	26	31	6	14	16
Crataegus monogyna	8	5	11	14	20	25
Fagus sylvatica	14	35	42	4	8	8
Frangula alnus	134	131	180	0	1	1
Fraxinus excelsior	9	17	21	25	29	35
Fraxinus species	0	1	1	0	2	2
Ilex aquifolium	36	84	92	1	12	12
Pinus sylvestris	52	57	84	0	0	0
Populus canescens	0	1	1	0	2	2
Populus tremula	3	4	6	2	1	2
Prunus avium	18	17	28	12	15	22
Prunus padus	2	2	3	2	6	6
Quercus petraea	3	4	5	3	2	3
Quercus robur	190	184	240	21	31	42
Salix aurita	1	0	1	0	0	0
Salix caprea	2	1	3	0	0	0
Salix cinerea	0	1	1	0	0	0
Salix species	0	1	1	0	1	1
Sambucus nigra	28	17	31	34	25	34
Sambucus racemosa	2	2	3	0	0	0
Sorbus aucuparia	212	185	238	11	11	16
Taxus baccata	4	13	15	1	2	2
Tilia species	0	1	1	0	1	1
Ulmus glabra	0	1	1	0	2	2
Viburnum opulus	6	2	6	4	8	11
Cornus mas	0	0	0	2	0	2

Cornus sanguinea	0	0	0	5	7	9
Crataegus species	0	0	0	0	1	1
Euonymus europaeus	0	0	0	0	1	1
Prunus spinosa	0	0	0	0	1	1
Salix alba	0	0	0	0	1	1
Sorbus species	0	0	0	0	1	1
Tilia cordata	0	0	0	0	1	1
Ulmus minor	0	0	0	3	1	3
Ulmus species	0	0	0	0	1	1

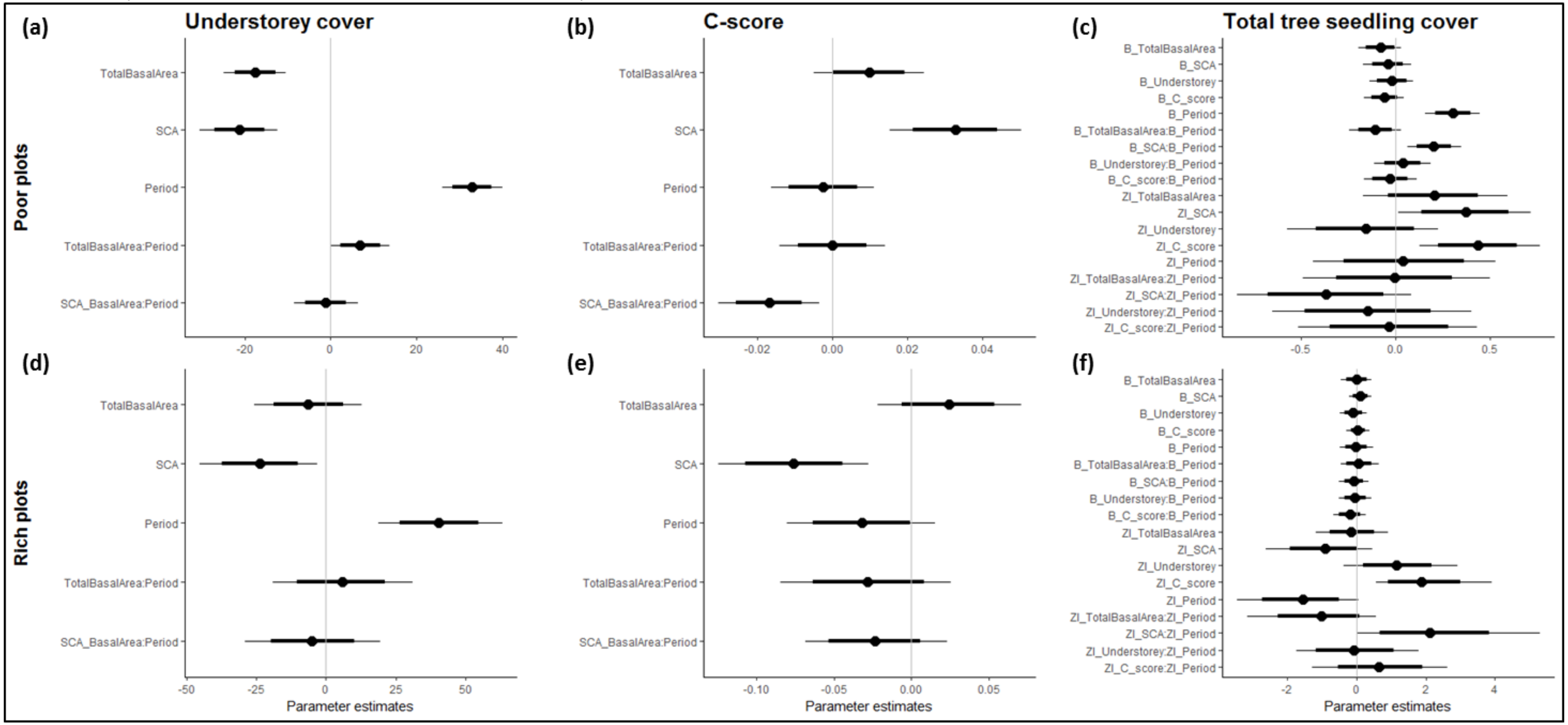
Table A3. Species-specific shade tolerance indices (± Standard errors) for the seedling species selected in this study from Niinemets and Valladares (2010). The tolerance scales range from 0 (no tolerance) to 5 (maximal tolerance).

Tree seedling species	Shade tolerance
Acer pseudoplatanus	3.73 ± 0.21
Betula pendula	2.03 ± 0.09
Betula pubescens	1.85 ± 0.07
Fagus sylvatica	4.56 ± 0.11
Fraxinus excelsior	2.66 ± 0.13
Pinus sylvestris	1.67 ± 0.33
Prunus avium	3.33 ± 0.33
Quercus petraea	2.73 ± 0.27
Quercus robur	2.45 ± 0.28

Table A4. Overview of the litter quality (LQ) index scores (1: very low decomposition rate; 5: very high decomposition rate) (adapted from Hermy, 1985) and the shade-casting ability (SCA) scores (1: very low shade-casting ability; 6: very high shade-casting ability) (adapted from Ellenberg, 1996) used for the calculation of the cover weighted average of the litter quality and shade-casting ability of the canopy for each vegetation plot.

Species	**SCA**	**LQ**	**Species**	**SCA**	**LQ**
Acer campestre	4	4	*Populus tremula*	3	2
Acer platanoides	5	3	*Prunus avium*	4	4
Acer pseudoplatanus	5	3	*Prunus padus*	4	4
Alnus glutinosa	4	4	*Quercus petraea*	3	1
Alnus incana	5	3	*Quercus petraea/robur*	3	1
Betula pendula	2	2	*Quercus robur/petraea*	3	1
Betula pubescens	2	2	*Quercus robur*	3	1
Betula species	2	2	*Quercus rubra*	4	1
Carpinus betulus	6	3	*Quercus species*	3	1
Castanea sativa	4	2	*Robinia pseudoacacia*	4	4
Cornus mas	3	5	*Salix alba*	3	5
Cornus sanguinea	3	5	*Salix caprea*	2	3
Corylus avellana	4	3	*Salix spp. (small leaves)*	3	5
Fagus sylvatica	6	1	*Salix spp. (broad leaves)*	2	3
Frangula dodonei		5	*Sambucus nigra*	4	5
Fraxinus excelsior	4	5	*Sorbus aucuparia*	3	3
Larix decidua	2	1	*Sorbus domestica*	3	3
Larix kaempferi	2	1	*Sorbus torminalis*	3	3
Larix species	2	1	*Sorbus aria*	3	3
Picea abies	5	1	*Taxus baccata*	6	1
Pinus sylvestris	2	3	*Tilia cordata*	5	4
Pinus nigra	2	3	*Tilia cordata/platyphyllos*	5	4
Pinus nigra laricio	2	3	*Tilia platyphyllos*	5	4
Pinus species	2	3	*Tilia species*	5	4
Populus alba	3	4	*Ulmus glabra*	5	5
Populus canadensis	3	3	*Ulmus laevis*	4	5
Populus x canadensis	3	3	*Ulmus minor*	4	5
Populus canescens	3	4	*Ulmus procera*	4	5
Populus species	3	4	*Ulmus species*	4	5

Fig. A1. Parameter estimates for the three models for (a, b, c) the poor and (d, e, f) rich forest types and (g) the single-species model for *Quercus*. Poor and rich plots refer to both soil fertility and species composition. Means, 80 (thick lines) and 95 % (thin lines) credible intervals are given for the standardized fixed effects (logit-scaled). For the zero-inflated beta models, parameter estimates are split up into the beta part (B) and zero-inflation part (ZI). The beta part expresses the increase in the tree seedling cover per increase in one standard deviation of the predictor. The ZI part expresses the increase in chance for absence per increase in one standard deviation of the predictor.



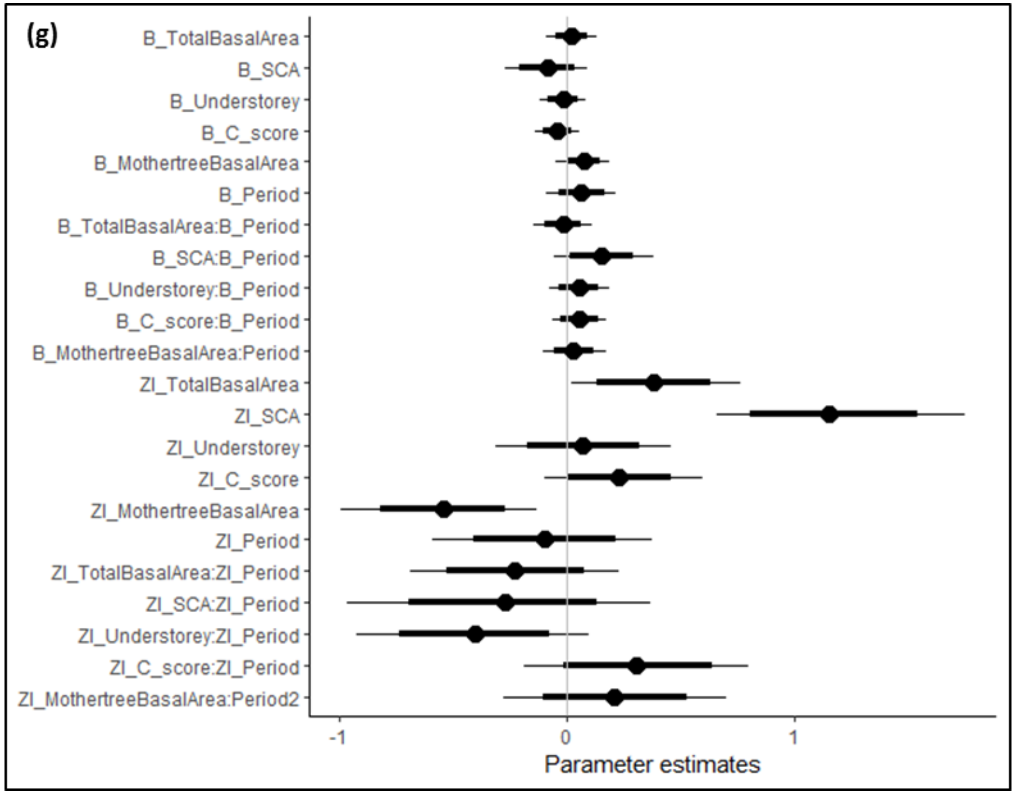
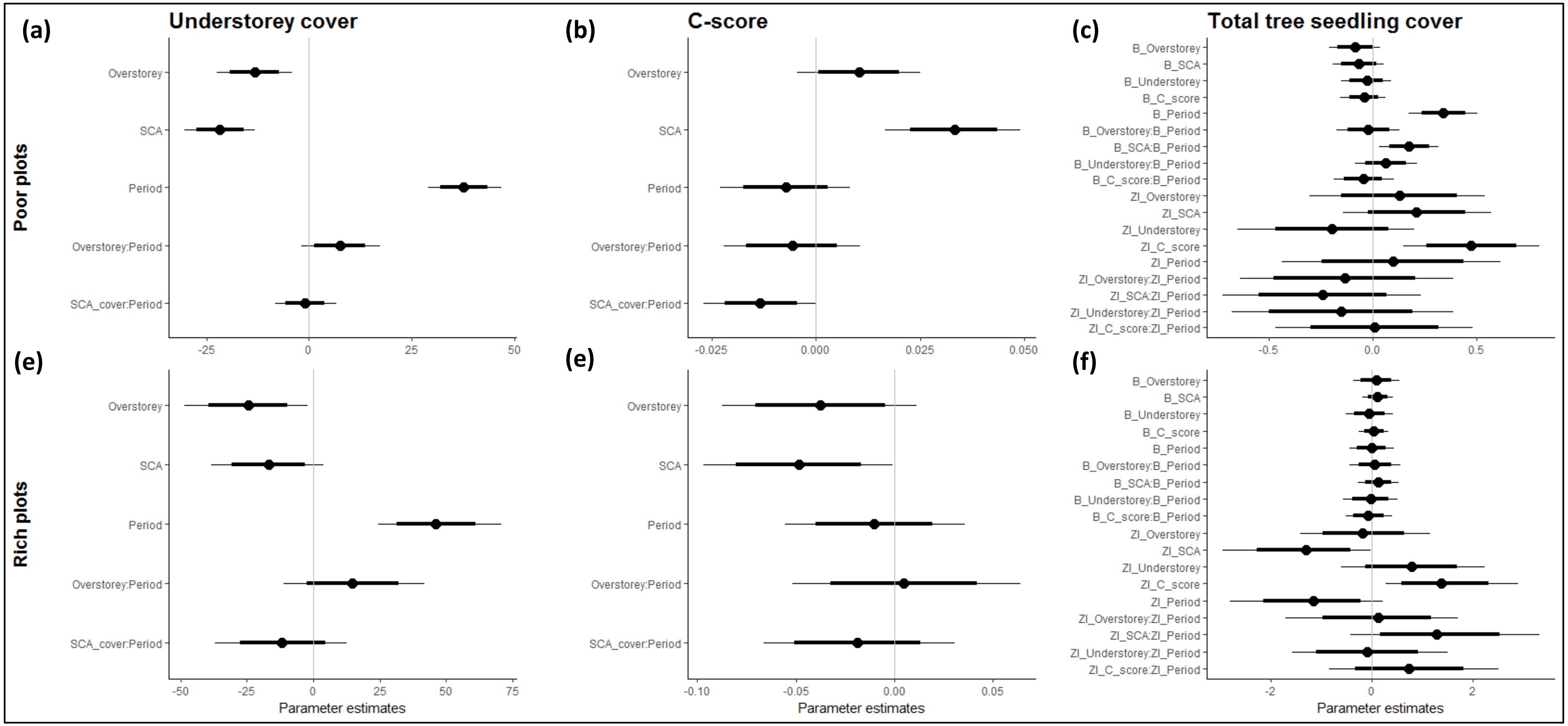
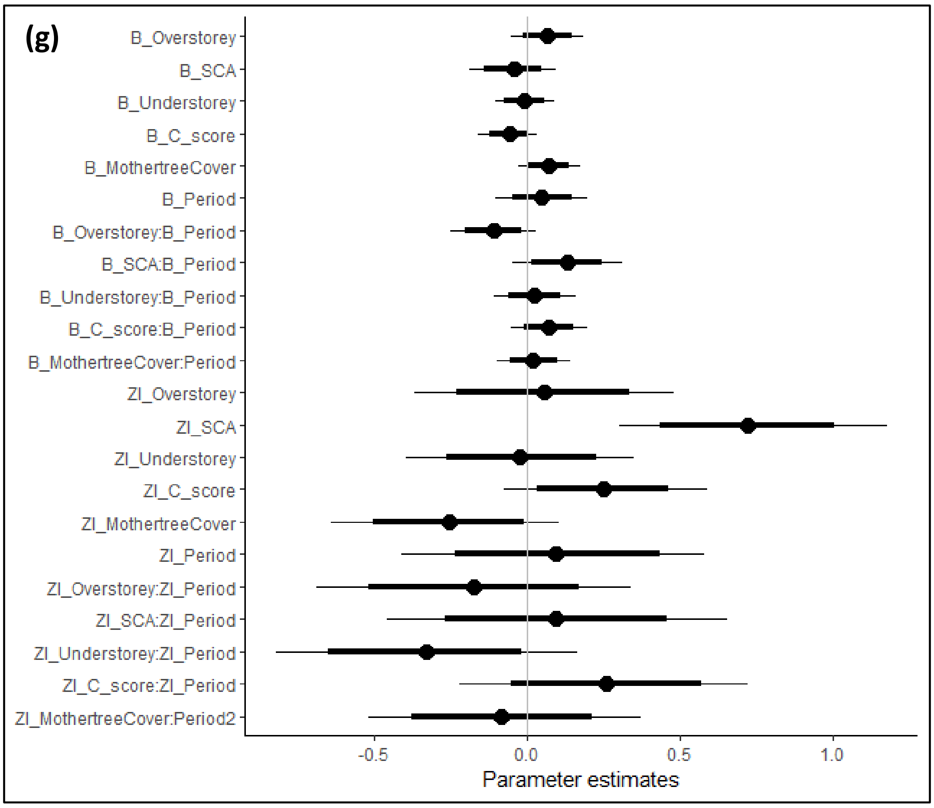

(g)
B_TotalBasalArea
B_SCA
B_Understorey
B_C_score
B_MothertreeBasalArea
B_Period
B_TotalBasalArea:B_Period
B_SCA:B_Period
B_Understorey:B_Period
B_C_score:B_Period
B_MothertreeBasalArea:Period
ZI_TotalBasalArea
ZI_SCA
ZI_Understorey
ZI_C_score
ZI_MothertreeBasalArea
ZI_Period
ZI_TotalBasalArea:ZI_Period
ZI_SCA:ZI_Period
ZI_Understorey:ZI_Period
ZI_C_score:ZI_Period
ZI_MothertreeBasalArea:Period2
-1
0
1
Parameter estimates

Fig. A2. Parameter estimates for the three models for (a, b, c) the poor and (d, e, f) rich forest types and (g) the single-species model for *Quercus*. Poor and rich plots refer to both soil fertility and species composition. Here, overstorey cover and SCA weighted by overstorey cover were used instead of total basal area. Means, 80 (thick lines) and 95 % (thin lines) credible intervals are given for the standardized fixed effects. For the zero-inflated beta models, parameter estimates are split up into the beta part (B) and zero-inflation part (ZI; logit-scale). The beta part expresses the increase in the tree seedling cover per increase in one standard deviation of the predictor. The ZI part expresses the increase in chance for absence per increase in one standard deviation of the predictor.




(g)
B_Overstorey
B_SCA
B_Understorey
B_C_score
B_MothertreeCover
B_Period
B_Overstorey:B_Period
B_SCA:B_Period
B_Understorey:B_Period
B_C_score:B_Period
B_MothertreeCover:Period
ZI_Overstorey
ZI_SCA
ZI_Understorey
ZI_C_score
ZI_MothertreeCover
ZI_Period
ZI_Overstorey:ZI_Period
ZI_SCA:ZI_Period
ZI_Understorey:ZI_Period
ZI_C_score:ZI_Period
ZI_MothertreeCover:Period2
-0.5
0.0
0.5
1.0
Parameter estimates

References Appendix A

Ellenberg, H., 1996. Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. Ulmer, Stuttgart.

Hermy, M., 1985. Ecologie en fytosociologie van oude en jonge bossen in binnen-Vlaanderen. PhD Thesis.

Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecol. Monogr. 76, 521–547. https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2

van der Maarel, E., 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. Vegetatio 39, 97–114. https://doi.org/10.1007/bf00052021

Appendix B. Statistical models

Full notation of the models used in this study. In all models, i indexes Survey and j indexes Plot. SCA = shade-casting ability.

Models 1 and 2 are linear multilevel models using a Gaussian distribution. For Model 1, the distribution was truncated with lower bound zero.

$$Understorey\ cover_{ij} = \beta_0 + \alpha_j + \beta_1 Total\ basal\ area_{ij} + \beta_2 SCA_{ij} + \beta_3 Survey_i + \beta_4 Total\ basal\ area_{ij}{:}Survey_i + \beta_5 SCA_{ij}{:}Survey_i + \epsilon_{ij}$$

with,

$\alpha_j \sim \mathrm{N}(0, \sigma_\alpha^2)$ Random effect 'Plot'

$\epsilon_{ij} \sim \mathrm{N}(0, \sigma^2)$ Noise term **(Model 1)**

$$C\text{-}score_{ij} = \beta_0 + \alpha_j + \beta_1 Total\ basal\ area_{ij} + \beta_2 SCA_{ij} + \beta_3 Survey_i + \beta_4 Total\ basal\ area_{ij}{:}Survey_i + \beta_5 SCA_{ij}{:}Survey_i + \epsilon_{ij}$$

with,

$\alpha_j \sim \mathrm{N}(0, \sigma_\alpha^2)$ Random effect 'Plot'

$\epsilon_{ij} \sim \mathrm{N}(0, \sigma^2)$ Noise term **(Model 2)**

Model 3 is a mixed-effect zero-inflated beta distribution model. For both the beta part and the zero-inflation part, the logit link function was used, whereas for the precision parameter, the log link function was used.

$$g(\mu_{ij}) = \beta_0 + \alpha_j + \beta_1 Total\ basal\ area_{ij} + \beta_2 SCA_{ij} + \beta_3 Understorey\ cover_{ij} + \beta_4 C\text{-}score_{ij} + \beta_5 Survey_i + \beta_6 Total\ basal\ area_{ij}{:}Survey_i + \beta_7 SCA_{ij}{:}Survey_i + \beta_8 Understorey\ cover_{ij}{:}Survey_i + \beta_9 C\text{-}score_{ij}{:}Survey_i$$

(Model 3: Beta part)

with,

$\mu_{ij} = \mathbf{E}(Y_{ij})$ Expected value

$g(p) = log\frac{p}{1-p}$ Logit link

$Y_{ij} \sim \mathrm{Beta}(\mu_{ij}, \varphi) = \frac{1}{B(\mu_{ij}\varphi, (1-\mu_{ij})\varphi)} Y^{\mu_{ij}\varphi-1}(1-Y)^{(1-\mu_{ij})\varphi-1}$ if $Y_{ij} \in]0,1[$ Beta distribution

$\alpha_j \sim \mathrm{N}(0, \sigma_\alpha^2)$ Random effect 'Plot'

With *B*(), the beta function.

$$g(z_{ij}) = \beta_0 + \alpha_j + \beta_1 Total\ basal\ area_{ij} + \beta_2 SCA_{ij} + \beta_3 Understorey\ cover_{ij} + \beta_4 C\text{-}score_{ij} + \beta_5 Survey_i + \beta_6 Total\ basal\ area_{ij}{:}Survey_i + \beta_7 SCA_{ij}{:}Survey_i + \beta_8 Understorey\ cover_{ij}{:}Survey_i + \beta_9 C\text{-}score_{ij}{:}Survey_i$$

(Model 3: zero-inflated part)

with,

$g_{ij} = \mathbf{E}(Y_{ij})$ Expected value

$g(p) = log\frac{p}{1-p}$ Logit link

$Y_{ij} \sim \mathrm{Bernoulli}(z_{ij}) = \begin{cases} z_{ij} & \text{if } Y_{ij} \in]0,1] \\ 1 - z_{ij} & \text{if } Y_{ij} = 0 \end{cases}$ Bernoulli distribution

$\alpha_j \sim \mathrm{N}(0, \sigma_\alpha^2)$ Random effect 'Plot'

The zero-inflated part and beta-part are connected through:

$$Y_{ij} \sim \text{zero-inflated-beta}(\mu_{ij}, \varphi_{ij}, z_{ij}) = \begin{cases} z_{ij}\mathrm{Beta}(\mu_{ij}, \varphi) & \text{if } Y_{ij} \in]0,1] \\ 1 - z_{ij} & \text{if } Y_{ij} = 0 \end{cases}$$

Appendix C. Testing lag effects

We tested for potential lag effects of the predictors on the used response variables in our analyses, i.e. understorey cover, C-score and tree seedling cover. To test this for each forest type, we fitted the models as described in our methods and appendix B for the three responses measured at the second survey, but now using the predictors measured either at first or the second survey, as opposed to using the predictor data from both surveys for the plot-pairs as we did in our main analyses. As we only used data from one survey time in these analyses, the predictor for ‘Survey’, the interactions with ‘Survey’ and the random effect ‘Plot’ were not included in the models. Then we calculated the Bayesian equivalent for R^2 for all these models using the *bayes_R2* function (Gelman et al., 2017) to explore if the past state of the predictors (at survey 1) can better predict the contemporary responses (from survey 2) compared with the state of the predictors at the second survey. Results show that, for both forest types and for all responses, the contemporary predictor set could better (or similar) predict the contemporary responses than the past predictor set (Table C1). We did thus not find evidence for lag effects.

Table C1. Bayesian R^2 values with 95% credible intervals for the different models that fitted the three responses, i.e. understorey cover, C-score and tree seedling cover, using the predictors measured either at first or the second survey. Poor and rich plots refer to both soil fertility and species composition.

Poor forest type				Rich forest type			
Response	Predictors	R^2	95% CI	Response	Predictors	R^2	95% CI
Understorey cover ~	Survey 2	0.10	[0.05, 0.16]	Understorey cover ~	Survey 2	0.10	[0.01, 0.22]
	Survey 1	0.06	[0.02, 0.11]		Survey 1	0.10	[0.01, 0.23]
C-score ~	Survey 2	0.04	[0.01, 0.08]	C-score ~	Survey 2	0.21	[0.06, 0.35]
	Survey 1	0.03	[0, 0.07]		Survey 1	0.22	[0.07, 0.36]
Tree seedling cover ~	Survey 2	0.04	[0.02, 0.08]	Tree seedling cover ~	Survey 2	0.06	[0.02, 0.13]
	Survey 1	0.02	[0, 0.05]		Survey 1	0.05	[0.01, 0.12]

CI: credibility interval