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The presence of shade-intolerant conifers facilitates the regeneration of *Quercus petraea* in mixed stands

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Abstract

Positive productivity-diversity relationships, pest-effect mitigation and increased resilience and stability maintain an ongoing interest for mixed stands in forestry. However, how mixing species affects forest regeneration is yet to be further explored.

We used data from the French National Forest Inventory (from 2006 to 2016) to model *Quercus petraea* (Matt.) Liebl regeneration cover in pure and mixed *Quercus petraea* stands; we included the effects of abiotic and biotic factors as well as mixture. We hypothesized that the characteristics of the companion species would prevent or facilitate the regeneration of oak.

Quercus petraea regeneration cover in this study responded negatively to total canopy cover and herbivory pressure. Mean July potential evapotranspiration (PET), mean December maximal temperature and soil pH are variables whose spatial variations over a given territory structure regeneration cover; all three of these variables have optimum values. *Quercus petraea* regeneration cover is linked to the proportion of *Quercus petraea* in the canopy layer in all mixed stands, except when the oak is mixed with shade-intolerant conifers: in this case, *Quercus petraea* regeneration is enhanced. The shade tolerance of admixed broadleaved species did not affect the *Quercus petraea* regeneration. This suggests that oak regeneration was facilitated with a shade-intolerant coniferous companion species due to better light transmittance through the crown or the competitive advantage of *Quercus petraea* over coniferous shade-intolerant species.

These results are of interest for oak mixtures since *Quercus petraea* regeneration cover benefits from mixtures with shade-intolerant conifers and is at least equal to that of pure stands.

Keywords

Regeneration, National Forest Inventory, *Quercus petraea*, Modelling, Mixed stands, Shade tolerance, Oak ecology

1. Introduction

Oak forests are widespread in the northern temperate ecotone, and are both ecologically and economically important (Bobiec et al., 2018; Johnson et al., 2019). They provide many ecosystem services such as wood production, aesthetic value and watershed protection (Löf et al., 2016). These forests also play a critical role in maintaining biodiversity as they provide habitats in living trees and deadwood and temperature buffering for many endangered insects (Milberg et al., 2016) and bird species (Felton et al., 2016). However, maintaining oaks in the canopy layer to ensure a sufficient supply of masting trees and including natural regeneration in managed forests are challenging aspects. Poor oak regeneration is widespread throughout its distribution area (Bobiec et al., 2018; Götmark, 2007; Kelly, 2002; Löf et al., 2016), and identifying the factors affecting regeneration is not straightforward. As a mid-shade tolerant species, oak suffers from insufficient light in the understory (Götmark, 2007; Kelly, 2002; Larsen and Johnson, 1998) and lacks the ability to compete with more shade-tolerant species during regeneration (Ligot et al., 2013; Van Couwenberghe et al., 2013), even when the canopy is kept open to favor light-demanding species (Muscolo et al., 2014; Van Couwenberghe et al., 2013). Regeneration failures due to high browsing pressure are also well documented in zones with dense herbivore populations (Kelly, 2002; Kuiters and Slim, 2002; Petersson et al., 2019; Ramirez et al., 2018).

There is a growing interest in tree species mixtures in forestry; indeed, mixed forests often offer advantages. For instance, many studies have documented over-yielding: the mixed stand is more productive than the sum of the expected productivity in the corresponding pure stands (Liang et al., 2016). Tree diversity, trait diversity within the community and evenness in the distribution of the species present are all drivers of the over-yielding observed in mixed forests (del Río et al., 2016; Perot and Picard, 2012; Vallet and Pérot, 2011; Zhang et al., 2012). These three factors are especially interesting for increased productivity on poor sites since certain mixtures result in a greater over-yielding effect, in line with the stress gradient hypothesis (Bertness and Callaway, 1994; Jucker et al., 2016; Toïgo et al., 2015a). This effect could be explained by better crown complementarity between adult trees, optimized light interception and the complimentary use of available resources (Forrester, 2014; Jucker et al., 2015; Ligot et al., 2016, p. 20). Mixing tree species also improve forest stability and resilience against extreme events and global changes (Aussenac et al., 2019; DeClerck et al., 2006; Loreau and de Mazancourt, 2013; Thompson et al., 2009). A richer regeneration layer improves resilience and stability if a species is removed (Yachi and Loreau, 1999). Therefore, it is relevant to study the effects of species mixture on regeneration because mixture is a key component of forest resilience. A diverse regeneration is critical to ensure that the properties of mixed stands carry on to the next generation as the composition of the canopy layer ultimately depends on human interventions and the composition the regeneration layer (Bobiec et al., 2018; De Lombaerde et al., 2019; Tinya et al., 2019).

Light is one of the primary limiting factors of tree growth in temperate forests. Therefore, shade tolerance should be a useful trait to investigate since it is related to the mechanisms described above; shade-intolerant species in the canopy do not capture as much light as shade-tolerant species since they have narrower crowns, a lower leaf density and are typically found in less dense stands (Aiba and Nakashizuka, 2009; Niinemets, 2010). This could lead to a brighter understory that would increase the abundance and the growth of the regeneration of mid-shade tolerant and shade-intolerant species. A synthetic trait like shade tolerance is relevant in a diversity-function study because it may help reveal underlying ecological mechanisms and provide a generic explanation of observed effects.

National Forest Inventory (NFI) data offer an interesting way of studying regeneration because they are distributed over time and space and are representative of the forest resource of the territory, and therefore are usually comprised of a large number of plots. We used French NFI data and developed methods to explore the ecological processes driving forest regeneration in northern temperate forests. Our study focused on sessile oak (*Quercus petraea* (Matt.) Liebl), which accounted for 18% of the living broadleaved stock in France in 2019 (IGN, 2019). This species is widespread and often grows in mixtures with many different companion species with contrasted shade-tolerance traits. We hypothesized that (1) *Q. petraea* regeneration would increase with the proportion of *Q. petraea* in the canopy layer. This hypothesis is based on the increase of abundance of near seed-bearer *Q. petraea* generate an increase of regenerating *Q. petraea*, and serves as a null hypothesis for hypothesis (2). We next hypothesized that (2) companion species mixed with *Q. petraea* may have a beneficial or a detrimental effect on *Q. petraea* regeneration; and (3) that this beneficial effect would be explained by the shade tolerance of the companion species, with an increase in *Q. petraea* regeneration as the shade tolerance of the companion species decreased.

2. Materials and methods

a. General methodology

We used French National Forest Inventory (NFI) data to study *Q. petraea* regeneration in pure and mixed stands at the national scale. We aimed to identify the biotic and abiotic environmental factors influencing *Q. petraea* regeneration cover through a regeneration model. We also studied stand mixture effect on *Q. petraea* regeneration: we included a relationship between the proportion of *Q. petraea* in the canopy and its regeneration cover. In order to identify the companion species capable of facilitating or hindering *Q. petraea* regeneration, we only chose bispecific mixed stands; we then tested if the identity of the companion species modified the relationship between the proportion of *Q. petraea* in the canopy and *Q. petraea* regeneration cover.

Finally, in order to generalize our results and gain in interpretability, we tested whether or not the shade tolerance of the companion species explained the mixture effect on *Q. petraea* regeneration.

b. NFI sampling and NFI data

The French National Forest Inventory (NFI) implements systematic sampling based on a 1 km by 1 km grid laid across the territory. The data cover a broad set of climatic conditions from oceanic to semi-continental, mean annual temperatures ranging from 5.9 to 13.8 °C, and annual precipitation ranging from 566 to 2125 mm. Since 2005, around 6000 equally dispersed temporary plots on this grid have been surveyed each year. Our dataset was comprised of the information recorded from 2006 to 2016.

On each plot, the free canopy cover (i.e. the part of the canopy that has free access to light) for every tree species present with at least one individual with a diameter at breast height (dbh) above 7.5cm is visually assessed within a 25-meter-radius circle around the plot center. With data from these observations, we calculated the proportion of each species as the free cover of that species in the canopy layer over the total free cover in the canopy layer of the plot (equation 1).

$$Prop_{sp_i} = \frac{Free\ Canopy\ Cover_{sp_i}}{Total\ Free\ Canopy\ Cover} \qquad (1)$$

where $Prop_{sp_i}$ is the proportion of species *i*, and $Free\ Canopy\ Cover_{sp_i}$ is the free canopy cover of species *i*. This data was supplemented with a floristic survey within a 15-meter-radius circle around the plot center. This survey included all herbaceous and shrub species as well as tree saplings (dbh< 7.5cm). The abundance of each species was given a value ranging from 0 to 5 with 0 for absence, 1 for a cover between 0 and 5%, 2 for a cover between 5 and 25%, 3 for a cover between 25 and 50%, 4 for a cover between 50 and 75% and 5 for a cover above 75%.

c. Plot selection

We selected plots where the proportion of *Q. petraea* ($Prop_{QuPe}$) trees with a diameter at breast height over 7.5 cm (these trees considered by the NFI) was at least 10%. This allowed us to emphasize factors influencing regeneration over factors influencing species distribution, since only plots containing adult *Q. petraea* were included. To test the effect of the companion species on *Q. petraea* regeneration one at a time, only pure and bispecific mixed stands were included in our model. We selected pure *Q. petraea* stands (with a proportion of 100%) and, to minimize the effect of trees species other than the main companion species, mixed stands where the sum of the proportion of *Q. petraea* and of the main companion species was at least/above 90%. To minimize the effect of tree species other than the main companion species, we kept only the plots where the proportion of the remaining species was lower than the proportion of each of the two main species in the mixture. In order to guarantee that our final sample was representative of the whole range of Q. petraea proportion values, we only retained bispecific mixtures for which the Q. petraea cover proportion amplitude of the NFI plots is at least 70%. We removed the plots identified as “temporarily deforested” in the NFI classification because of the lack of reliable cover data. Finally, to ensure a reliable estimation of the mixture effect, we removed the mixtures represented by less than 20 plots. The final dataset was made up of 1767 pure *Q. petraea* plots, 4899 *Q. petraea*-broadleaved mixed plots with 11 different broadleaved companion species, and 643 *Q. petraea*-conifer mixed plots with seven different coniferous companion species (Table 1, Figure A.1).

d. Regeneration cover variable

We used the NFI floristic survey to calculate our *Q. petraea* regeneration cover variable, defined in this study as the cover proportion of all trees less than 7.5 cm in diameter at breast height. The NFI classifies regeneration cover with values between 0 and 5. For our quantitative approach, we transformed this variable with the mean of each cover class, thus obtaining six values of absolute regeneration cover for each plot: 0, 0.025, 0.125, 0.375, 0.625 and 0.875. Hereafter, $RegeCover_{QuPe}$ refers to the regeneration cover of *Q. petraea*, which is our response variable.

Table 1: Mean of environmental and cover variables (2.5% and 97.5% quantiles in parentheses) per plot type. Shade tolerance values were provided by Niinemets and Valladares (2006), except for Pinus nigra var corsicana which has no shade tolerance value.

Plot type	Companion species	Shade tolerance	Number of plots	Annual mean temperature (°C)	Annual mean precipitation (mm)	Total canopy cover (%)	Mean *Q. petraea* proportion
Q. petraea pure			1767	11 (9.3-12.8)	824 (629-1278)	85 (27-100)	1
Q. petraea - broadleaved species	*Fagus sylvatica* (Fa.sy)	4.56	1889	10.6 (9-12.5)	913 (649-1404)	85 (40-100)	0.57 (0.1-0.9)
	Carpinus betulus (Ca.be)	3.97	1128				
	Quercus robur (Qu.ro)	2.45	766				
	Castanea sativa (Ca.sa)	3.15	470				
	Betula sp (Be.sp)	1.94	246				
	Quercus pubescens (Qu.pu)	2.31	142				
	Fraxinus sp (Fr.sp)	2.66	112				
	Populus tremula (Po.tr)	2.22	50				
	Prunus sp (Pr.sp)	3.33	37				
	Tilia sp (Ti.sp)	3.93	31				
	Robinia pseudoacacia (Ro.ps)	1.72	28				
Q. petraea - coniferous species	*Pinus sylvestris* (Pi.sy)	1.67	347	10.5 (8.4-12)	893 (654-1494)	83 (40-100)	0.47 (0.1-0.9)
	Pseudotsuga menziesii (Ps.me)	2.78	77				
	Abies alba (Ab.al)	4.60	72				
	Pinus pinaster (Pi.pi)	1.89	54				
	Picea abies (Pi.ab)	4.45	40				
	Pinus nigra nigra (Pi.ni)	2.10	33				
	Pinus nigra var corsicana (Pi.co)	X	20				

e. *Covariables*

i. *Stand and cover variables*

We computed the total canopy cover by summing all the free cover from a given plot. The NFI provides topographic variables such as plot aspect, the steepest slope in the plot and the type, depth and percentage of rocks in the soil. The NFI also provides a classification of the vertical structure of the stand based on a visual estimate (this was also the variable used to define deforested plots i.e. when the vertical structure is lacking) and mentions if a cut has occurred in the last 5 years.

ii. *Climate variables*

We used the 30-year climatic values for the period 1981-2010 from the AURHELY Météo France spatial layer to obtain monthly mean, minimum and maximum temperatures (T, in °C) and precipitation (PPT, in mm). We derived monthly potential evapotranspiration from these variables (Piedallu et al., 2013; Piedallu and Gégout, 2007).

iii. *Soil, floristic and bio-indication variables*

We estimated soil water holding capacity (SWHC, in mm) for all the plots from soil texture, percentage of rock and soil depth (Piedallu et al., 2018). We used the floristic survey to infer acidity (pH), carbon to nitrogen ratio (C:N) of the soil organic matter and the base saturation (S:T) of the first layer of the soil by averaging indicator values of each present species (Gégout et al., 2005). The floristic survey was also used to estimate regeneration inhibition by three competitive plants: *Rubus fruticosus*, *Molinia caerulea* and *Pteridium aquilinum*; we created 3 Boolean variables when their respective absolute cover was more than 50%.

iv. *Herbivory pressure proxy*

In order to obtain a proxy for the pressure exerted by herbivores on *Q. petraea* acorns, seedlings and saplings, we used district-level hunting statistics provided by the French Office of Biodiversity (OFB). A yearly ungulate pressure index was calculated by district from i) hunting bag statistics of *Sus scrofa*, *Capreolus capreolus* and *Cervus elaphus*; ii) their respective basal metabolic rates estimated from the mean body mass of the species to the power of 0.75 (Clarke et al., 2010; Petersson et al., 2019; White and Seymour, 2005); and iii) the surface of the district, the calculation is summarized in equation (2).

$$Herbivory\ index_c = \frac{\sum_j n_{jc} * m_j^{0.75}}{Area_c} \quad (2)$$

Where n_{jc} is the number of species *j* killed in the district *c*, m_j is the mean mass of the species *j*, and $Area_c$ is the area of the district *c* (Petersson et al., 2019). The resulting index was then smoothed with a 3-year moving averaging to reduce inter-annual variability and because we did not know which year the saplings had been browsed.

v. Shade tolerance data

Values for shade tolerance, from 1 (shade intolerant) to 5 (shade tolerant) of the tree species, were provided by Niinemets and Valladares (2006).

f. Modelling framework

Regeneration cover values are constrained between 0 and 1; we therefore modelled them with a logistic model (Wright, 1995). We multiplied this function by a reducer in order to take into account the proportion of *Quercus petraea* in the stand. Without the companion species interaction, this reducer gave a decrease proportional to *Q. petraea* proportion in the stand: a mixed stand with 50% *Q. petraea* would have 50% less regeneration than a pure stand with the same environmental conditions. We chose this linear relationship for its robustness, after carrying out a scatter plot analysis. Finally, an estimated species-specific parameter was included in the reducer to allow us to modify the slope of the linear relationship for mixed stands depending on the companion species.

Equation (3) describes this model:

$$RegeCover_{QuPe} = F_1(X_n) * F_2\left(Prop_{QuPe}, SP_i\right) \quad (3)$$

where F1 is a logistic model, depending on the environmental variable X_n, F2 is the mixture reducer function, $Prop_{QuPe}$ is the proportion of *Quercus petraea* in the canopy, and SP_i is a dummy variable set to 1 only when the companion species of *Q.petraea* was species *i*.

The full expression of the model is written as:

$$RegeCover_{QuPe} = \left(\frac{1}{1-e^{-\left(\beta_0+\sum_n \beta_n \times X_n\right)}}\right) \times \left(1-\left(1-Prop_{QuPe}\right) \times max(0,(\textstyle\sum_i SP_i \times (1-a_i)))\right) + \varepsilon \quad (4)$$

where β_n and a_i are fitted parameters. In equation (4), $\left(1-Prop_{QuPe}\right)$ represents the proportion of the companion species. We then multiplied $\left(1-Prop_{QuPe}\right)$ by ($1-a_i$) to express the effect of the companion species and to make it possible to test the significance of the effect: if a_i is not significantly different from 0, the reducer acts as a proportional relationship between regeneration and *Quercus petraea* proportion. This formulation resulted in a model that could include both pure and mixed stands, which allowed us to fit the model on all the selected plots at once. As the reducer is linear, we added the function "max" so that the model would not produce negative values, and would instead show no regeneration.

The term ε represents the residual errors, following a Gaussian distribution with a mean of 0 and a variance σ^2. Regeneration cover data displayed heteroscedasticity when plotted against total cover and *Q. petraea* proportion. We therefore applied a power variance model to these two variables in order to take this heteroscedasticity into account (Pinheiro and Bates, 2000).

The structure of our cover data was unbalanced, both in terms of the distribution of the different cover categories and the range of cover included in these categories. Consequently, ε displayed a slightly asymmetric distribution, but which we considered to be within a normal range and therefore ignored.

To ensure better robustness and biologically accuracy, we included the environmental variables in three different forms: linear, quadratic and one with exponential decay. We scaled all the quantitative environmental variables in order to simplify the fitting procedure and to obtain comparable parameter estimates.

We selected the environmental variables following an ascending stepwise AIC procedure. In order to select the most parsimonious model, a variable is kept in the model only if it decreases the AIC (Akaike Information Criterion) by at least 2 points with a linear form, or 4 points with quadratic or exponential-decay forms because they have 2 parameters (Akaike, 1974; Burnham and Anderson, 2002). To avoid collinearity between environmental variables, we excluded any variable from the procedure when its Spearman correlation coefficient with a previously selected variable exceeded 0.4.

i. Shade tolerance model

Once we had fitted the full model in equation (4), we used the shade tolerance values of the companion species to test whether shade tolerance structured the estimated species-specific parameters. We used a linear model for that purpose, as described in equation (5):

$a_i = s_0 + s_1 * Tolerance_i + \varepsilon$ (5)

where a_i are the estimated species-specific parameters fitted in equation (4), $Tolerance_i$ is the tolerance of the companion species, and s_0 and s_1 are the parameters of the model. The model was fitted separately for coniferous and broadleaved companion species. We excluded *Pinus nigra var. corsicana* because we lacked the shade tolerance value for this species. ε represents the Gaussian errors with a mean of 0 and variance σ^2. Because species-specific parameters are not estimated with the same precision when fitting equation (4), this variance is weighted by the inverse of the squared standard error of the estimated parameters in order to give more weight to the most accurate parameters.

ii. Statistical procedures

We analyzed the data with the R software 3.6.2 (R Core Team, 2019). We fitted the model in equation (4) with the *gnls* function of the R package 'nlme' according to the generalized least squares method (Pinheiro et al., 2017). We fitted the second model, presented in equation (5), with a linear weighted model. The normalized residuals of the regeneration model in equation (4) were plotted against every variable as well as with the X and Y coordinates, and no patterns diverging from the 0 axis were found.

3. Results

a. *Q. petraea regeneration*

Overall, we observed the presence of *Q. petraea* regeneration in 67% of our plots. Regeneration presence varied among plot types: 75%, 64% and 72% respectively of pure, mixed *Q. petraea*-broadleaved companion species and mixed *Q. petraea*-coniferous companion species stands displayed *Q. petraea* regeneration. The mean Q. *petraea* regeneration cover was 14.5% in pure stands, 7.3% in mixed *Q. petraea*-broadleaved stands and 9.1% in mixed *Q. petraea*-coniferous stands, and varied with companion species (Figure 1). Mean regeneration cover displayed high variability, with a coefficient of variation of 180%.

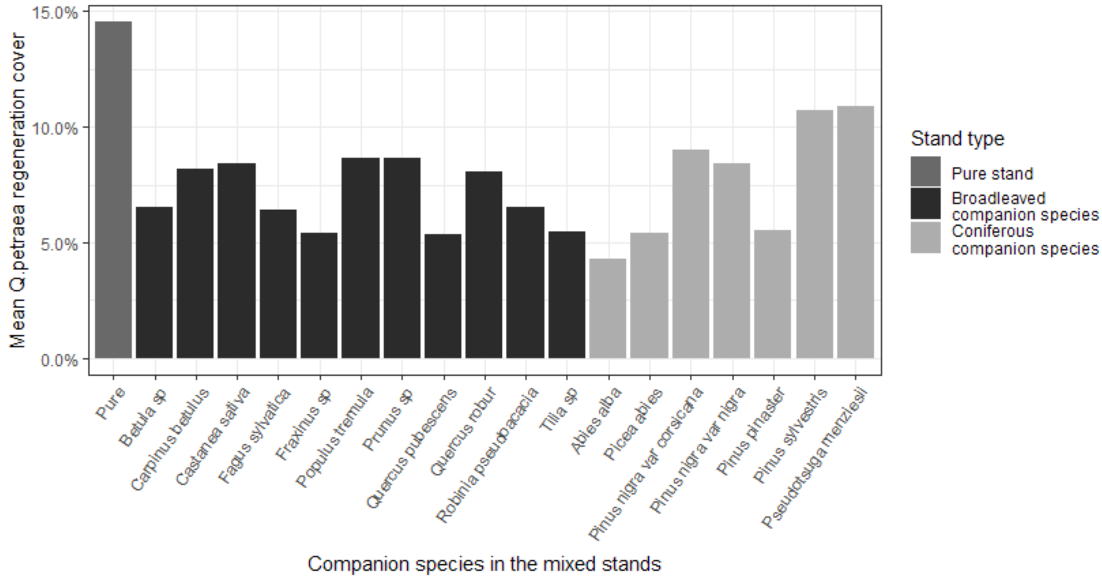

Figure 1: Mean Q. petraea regeneration cover as a function of the companion species in the mixed Q. petraea stands.

b. *Estimated parameters of the regeneration model*

In our model, 11 environmental variables explain the regeneration cover of *Quercus petraea* (Table 2). Regeneration cover decreases with increasing total canopy cover of the stand (Figure A.2, A), and to a lesser extent, is higher in coppice-with-standards stands. The presence of an absolute cover of *Molinia caerulea* equal to or greater than 50% had a negative effect on *Q. petraea* regeneration, but with a p-value only significant at the 10% type-1 error threshold.

The best fitting form for the herbivory index was exponential decay. The negative effect on regeneration of an herbivory index between 0 and 50 (the mean value of the index) was drastic with regeneration cover divided by two over this interval, but the effect stabilized after that (Figure A.2, B).

The other selected parameters are associated with bio-geo-climatic variables: PET_7 (Mean evapotranspiration potential in July), $Tmax_{12}$ (mean December maximal temperature) and the bio-indicated soil pH. These three variables all had a quadratic form, with an optimum occurring within the range of values, i.e. a PET_7 of 134 mm, a $Tmax_{12}$ of 5.9°C and a pH of 4.7 (Figure A.2, C, D, E). The presence of a carbonated soil, the percentage of rocky outcrop and Northern exposure and Eastern exposure had a slightly negative effect in terms of magnitude on *Q. petraea* regeneration cover via a simple linear relationship (Table 2).
The species-specific parameters of the Corsican pine (*Pinus nigra var corsicana*), Scots pine (*Pinus sylvestris*), maritime pine (*Pinus pinaster*), Douglas fir (*Pseudotsuga menziesii*) and chestnut (*Castanea sativa*) were significantly positive. This result implies that the relationship between *Q. petraea* regeneration cover and the proportion of *Q. petraea* in the canopy was more beneficial to regeneration than a proportional relationship in mixed stands with these companion species (Figure 2). No companion species had a significantly negative species-specific parameter thus no companion species had a detrimental effect on *Q. petraea* regeneration.

Table 2: Coefficients (Estimate), standard errors (Std.error) and p-values of the estimated parameters in the selected regeneration model. The variables associated with environmental function parameters are all scaled except for the Boolean variables (Coppice-with-standards stand, Molinia caerulea, $Soil_{carbonated}$, and the companion species variables). Significant companion species parameters are in bold. Means, standard deviations and ranges for the continuous variables are available in Table A.1. For a detailed explanation of the form associated with the environmental variables, see Table A.1. For a representation of the response curves of the continuous variables, see Figure A.2.

	Variable	**Estimate**	**Std. Error**	**p-value**
F1 part of the model: environmental variables	Intercept	-1.97	0.0693	$<10^{-4}$
	Total canopy cover	-0.0624	0.0322	0.052
	Total canopy cover ²	0.0608	0.0111	$<10^{-4}$
	Coppice with standards stand	0.18	0.0435	$<10^{-4}$
	Molinia caerulea	-0.311	0.162	0.055
	Herbivory index_1	0.117	0.0472	0.013
	Herbivory index_2	-1.67	0.313	$<10^{-4}$
	PET_7	0.463	0.0327	$<10^{-4}$
	$PET_7{}^2$	-0.159	0.0215	$<10^{-4}$
	$Tmax_{12}$	-0.2	0.0315	$<10^{-4}$

	$Tmax_{12}{}^2$	-0.19	0.0288	$<10^{-4}$
	pH	-0.173	0.0285	$<10^{-4}$
	pH^2	-0.144	0.0241	$<10^{-4}$
	$Soil_{carbonated}$	-0.303	0.161	0.060
	Rocky outcrop	-0.0827	0.0265	$<10^{-4}$
	North-South exposure	-0.112	0.0432	$<10^{-4}$
	East-West exposure	-0.0922	0.0401	0.021
F2 part of the model: companion species parameters	***Pinus nigra var corsicana***	**0.635**	**0.0968**	$\mathbf{<10^{-4}}$
	Pinus sylvestris	**0.467**	**0.0471**	$\mathbf{<10^{-4}}$
	Pinus pinaster	**0.331**	**0.115**	$\mathbf{<10^{-4}}$
	Tilia sp	0.3	0.252	0.235
	Pseudotsuga menziesii	**0.251**	**0.0661**	$\mathbf{<10^{-4}}$
	Castanea sativa	**0.171**	**0.0403**	$\mathbf{<10^{-4}}$
	Pinus nigra var nigra	0.166	0.237	0.484
	Betula sp	0.152	0.102	0.137
	Picea abies	0.0704	0.103	0.496
	Fagus sylvatica	0.0346	0.0241	0.152
	Carpinus betulus	0.0227	0.0521	0.663
	Quercus robur	0.0201	0.0314	0.522
	Abies alba	0.00696	0.0817	0.932
	Quercus pubescens	-0.0117	0.101	0.908
	Robinia pseudoacacia	-0.0173	0.207	0.933
	Fraxinus sp	-0.112	0.103	0.275
	Prunus sp	-0.244	0.317	0.441
	Populus tremula	-0.246	0.321	0.443
Model statistics	Degrees of freedom	7274		
	Power of the *Q. petraea* proportion variance function	0.627		
	Power of the Total cover variance function	0.130		

c. *Mixture effect on regeneration as a function of the companion species*

We used the values of these species-specific parameters (Table 2) to predict how mixture would affect *Q. petraea* regeneration cover for each companion species mixed with *Q. petraea*. When a species-specific parameter is non-significant, the relationship between *Q. petraea* regeneration and *Q. petraea* proportion is close to a proportional relationship (Figure 2). However, for *Pinus nigra var corsicana, Pinus sylvestris, Pinus pinaster, Pseudotsuga menziesii* and *Castanea sativa,* which had positively significant parameters, mixed stands with these species and a canopy proportion of 50% *Q. petraea* respectively displayed 81%, 73%, 67%, 63% and 59% of the regeneration cover in a pure *Q. petraea* stand with the same environmental conditions (Figure 2).

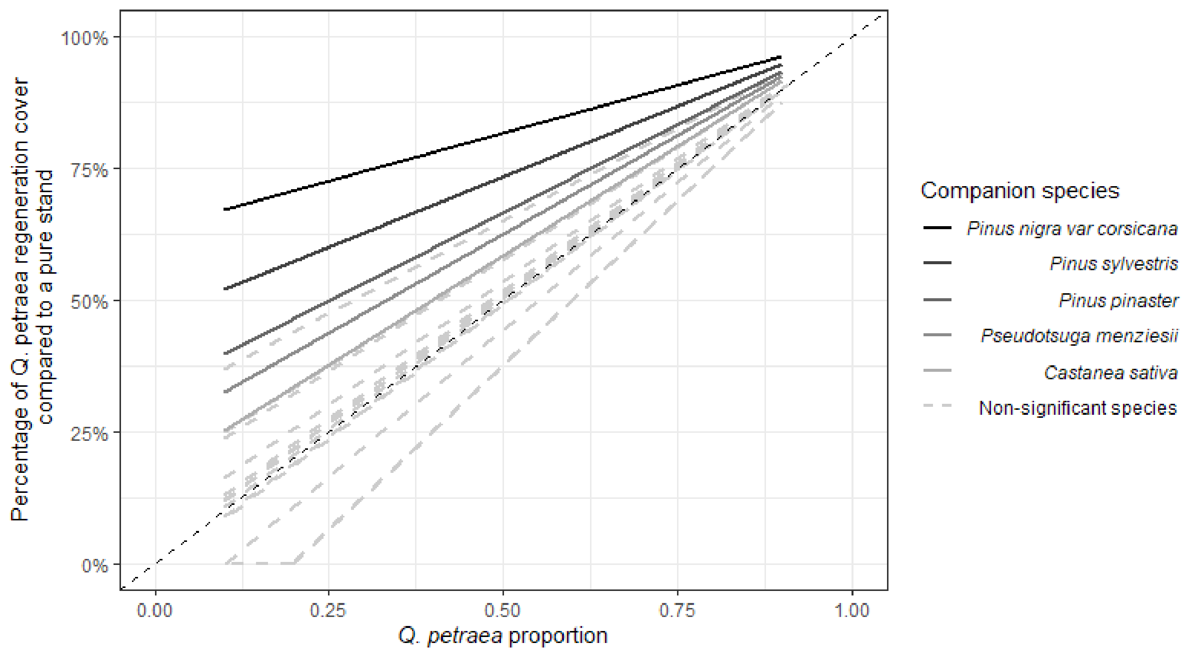

Figure 2: Percentage of Q. petraea regeneration cover in a mixed stand compared to a pure stand in the same environmental conditions as a function of companion species identity and Q. petraea canopy proportion, according to the regeneration model (i.e. the value of the reducer function F2). Solid lines represent the species with significant species-specific parameters. The segments stop at the minimal and maximal Q. petraea proportion observed in the dataset for each companion species.

d. *Mixture effect as a function of companion-species shade tolerance*

The linear model for the coniferous companion species (p-value<10^{-4}, R^2 = 0.941) detected a significant relationship between the value of the species-specific parameter described in Table 2 and the shade tolerance of the associated companion species; this was not the case for the broadleaved companion species (Table 3, Figure 3).

Table 3: Estimates, standard errors and p-values of the estimated parameters, and the R^2 of the linear regression presented in equation (5). We fitted the model for the coniferous and the broadleaved companion species separately.

Coniferous companions	**Estimate**	**Std. Error**	**p-value**	**R^2**
Intercept	0.686	0.0531	$<10^{-4}$	0.941
Shade tolerance	-0.147	0.0185	$<10^{-4}$	
Broadleaved companions	**Estimate**	**Std. Error**	**p-value**	**R^2**
Intercept	0.0603	0.0839	0.491	0.00251
Shade tolerance	-0.00341	0.0228	0.884	

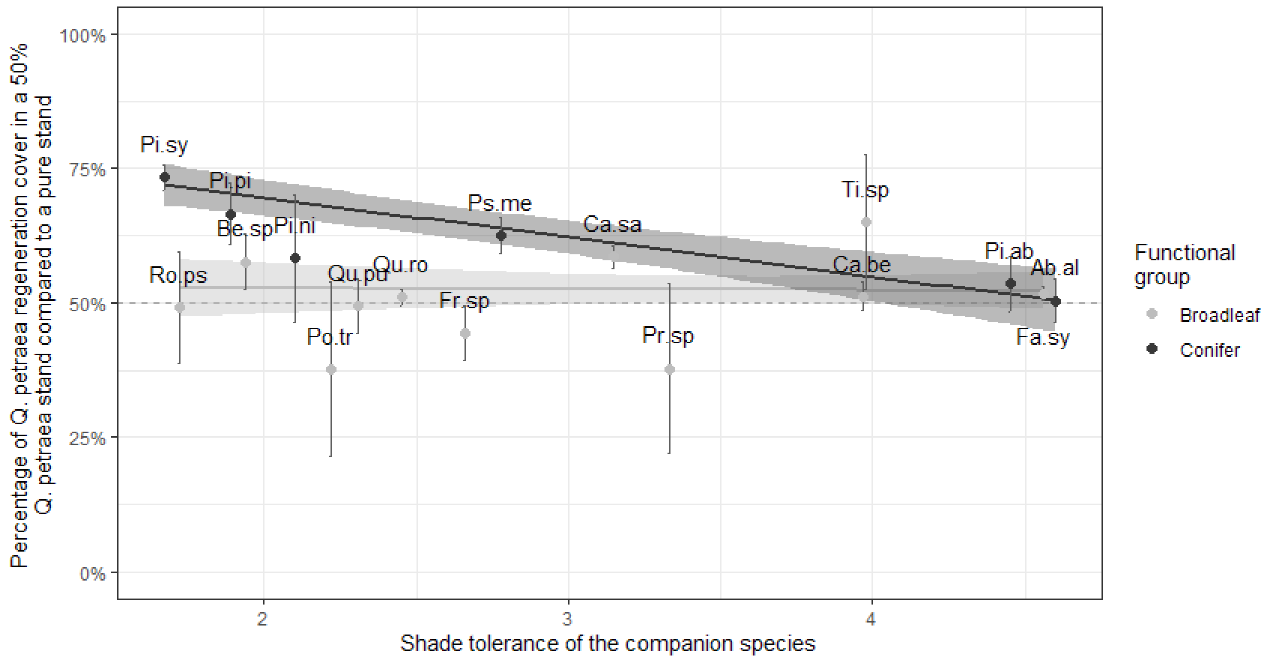

Figure 3: Proportion of Q. petraea regeneration cover in a 50%-50% mixed stand compared to a pure stand as a function of companion-species shade tolerance and functional group, according to the regeneration model (i.e. the value of the reducer function F2 at 50% Q. petraea proportion). The vertical segment shows the prediction ± the standard error of the associated parameter from Table 2. The linear shade tolerance model for each of the two functional groups is represented by a straight line, while the shaded ribbon shows the confidence interval. Abbreviations for companion species are given in Table 1. Pinus nigra var corsicana is not shown because its shade-tolerance value was lacking.

4. Discussion

To study the influence of environmental factors and species mixture on *Q. petraea* regeneration at the national scale, we built a regeneration model based on French NFI regeneration and cover data that explicitly considered both of these effects. The selected environmental factors allowed us to compare the mixtures independently of environmental conditions and also provided us with interpretable ecological variables. The species mixture part of the model revealed mixtures where *Q. petraea* regeneration was higher than expected; this effect concerned shade-intolerant coniferous companion species only.

a. *Biotic and abiotic environmental drivers of Q. petraea regeneration*

As for many intermediate shade-tolerant species, light condition plays a major role in *Q. petraea* regeneration. Our results confirmed previous findings since, in our study, total canopy cover was negatively correlated with *Q. petraea* regeneration cover (Ádám et al., 2013; Annighöfer et al., 2015; Jarvis, 1964; Larsen and Johnson, 1998). However, the relationship between total canopy cover and regeneration was not linear: first, a drastic decrease occurred between 0 and 50% total canopy cover, then the curve stabilized. This may be due to the ability of *Q. petraea* to adapt its light acquisition strategy, to a certain extent, when growing in heavy shade, by allocating more carbon and resources to leaf and shoot development (Jarvis, 1964; Larsen and Johnson, 1998; Rodríguez-Calcerrada et al., 2008). We can interpret the positive effect of 'coppice-with-standards stand' (a vertical structure variable) as an extension of this interpretation, since vertical heterogeneity can increase light availability and light heterogeneity. This relationship is still unclear, however, because the variable also depends on heterogeneity in stand composition and diameter at breast height (Ligot et al., 2016).

The presence of an important *Molinia caerulea* cover was the only understory variable the model identified, but magnitude and significance were low. This was surprising since some understory species can have a significant influence on regeneration via competition for light and soil water and nutrient resources. The effect of competitive vegetation on regeneration interacts with many environmental variables, for example, light availability and site productivity, which affect both regeneration and the diversity and cover of competitive vegetation (De Lombaerde et al., 2019; Gaudio et al., 2011; Ward et al., 2018). These effects are hard to disentangle for a large plot sample like ours. Indeed, clearly identifying vegetation interference variables will require dedicated plot selection and analysis and an understanding of the environmental factors affecting both regeneration and competitive vegetation.

Q. petraea saplings are subject to browsing by ungulates, sometimes to the point where regeneration can be compromised. Our results support these findings since *Q. petraea* regeneration cover was negatively linked to our herbivory index, exponentially decreasing with increasing herbivory (Kelly, 2002; Kuiters and Slim, 2002; Petersson et al., 2019). The regeneration cover we modelled mostly consisted of *Q. petraea* saplings, and deer have a larger impact on already established saplings by browsing their leaves and shoots, especially the newly-grown, more palatable ones; this limits overall sapling growth and competitiveness, acorns could also be predated by wild boars, thus reducing regeneration (Götmark et al., 2005; Mårell et al., 2018; Ramirez et al., 2018).

It should be noted, however, that we calculated our herbivory index at the district scale. Therefore, our index does not accurately represent the spatial heterogeneity of the actual browsing pressure. Browsing effect on regeneration would be more accurately assessed with finer scale data, and by including interactions among other factors: for example, the presence or absence of other palatable species (Jensen et al., 2012), the presence of deadwood acting as a physical barrier (Borkowski et al., 2017; Hagge et al., 2019), interactions with humans (Miller et al., 2009), the distance to the closest forest edge and, of course, trees species in the mixture (Bernard et al., 2017; Boulanger et al., 2009), as was the case in our study.

Bio-geo-climatic variables can encompass many processes. The two selected variables, mean July PET and mean December maximum temperature, were mean values over 30 years. Therefore, they provide spatial information on *Q. petraea* regeneration distribution and preferences. The increase in *Q. petraea* regeneration with July PET up to the optimum peak can be attributed to more light availability (as solar radiation is included in PET calculations) and warmer and more productive forests, while the decrease after the optimum peak can be linked to an insufficient water balance and a higher probability of drought (Piedallu and Gégout, 2007). Soil pH was also an explanatory variable, with a concave-shaped response curve that reached its optimum at 4.8. This result corroborates the findings of other authors, who set the optimum pH for even-aged *Q. petraea* stands from acidic to neutral soils (Bergès et al., 2005). Following this reasoning, our negative results for carbonated soil seem logical.

b. Companion species effect on Q. petraea regeneration in mixed stands

We showed that *Q. petraea* proportion had a proportional relationship with *Q. petraea* regeneration cover, and that this relationship could be modified in a mixed stand with certain companion species. Previous regeneration studies had positively linked oak regeneration to the proportion of adult oaks in the overstory; oak dispersal capacity is low, resulting in higher sapling and acorn density near adult oaks (Ádám et al., 2013; Annighöfer et al., 2015; Battaglia et al., 2008; Fei and Steiner, 2008; Tinya et al., 2019). We therefore used the simple proportional relationship as our null hypothesis to test for a companion-species effect on *Q. petraea* regeneration. We found that the relationship was modified and that certain companion species had a positive effect on oak regeneration. This was the case for the following companion species: *Pinus nigra var corsicana, Pinus sylvestris, Pinus pinaster, Pseudotsuga* *menziesii* and *Castanea sativa*. We also demonstrated that the shade tolerance value of the coniferous companion species structured the extent of the positive effect on *Q. petraea* regeneration but that this effect was not detected for the broadleaved companion. We also noted that no companion had any detrimental effect on Q. petraea regeneration cover, regardless of the species; we observed satisfactory *Q. petraea* regeneration in every mixed stand. This lack of a negative effect on regeneration added to the positive effects mixture is known to have on mature stands (see Introduction) leads to an overall positive effect. This was surprising since species like the shade tolerant beech *Fagus sylvatica* can outcompete and outgrow oaks (Ligot et al., 2013; Van Couwenberghe et al., 2013). There are two possible explanations for this lack of detrimental effect for *Fagus sylvatica*. First, our data did not reflect the vertical stratification, growth and vigor of the regeneration; therefore, *Q. petraea* regeneration was recorded even if *F. sylvatica* trees might potentially outcompete the oak regeneration as the stand aged. Second, foresters tend to eliminate *F. sylvatica* saplings to promote oak saplings, and observational data such as those provided by the NFI do not take this into account.

The beneficial effect on regeneration of several shade-intolerant coniferous companion species suggests better light transmission through the crown of the companion species. This is especially relevant in situations where the canopy is closed or nearly closed. Shade-intolerant species have a less optimized crown architecture (narrower and a less dense) in terms of light interception (Aiba and Nakashizuka, 2009) than do shade-tolerant species since they grow faster and higher. Trees exhibiting this architecture have higher light transmittance, leading to a brighter environment in the regeneration layer, *Pinus* species, that are preponderant in the significant companion species we found, are a notable example of this particular crown architecture (Ligot et al., 2013, p. 200; Messier et al., 1998; Perot et al., 2017). In mixed stands, especially with shade-intolerant species, understory light and light heterogeneity are enhanced (Ligot et al., 2016; Messier et al., 1998). We only identified a significant effect for coniferous, not broadleaved, companion species. This may be because the effect of broadleaved species in mixtures is also smaller with productivity (Toïgo et al., 2018), and may have been impossible to detect with our data.

Furthermore, conifers and broadleaves with the same shade tolerance still differ greatly in crown shape and other traits that could explain the difference in significance of effect on regeneration we found between the two functional groups (Pretzsch and Schütze, 2009). For example, broadleaves are known to have more crown plasticity than conifers; they will often more efficiently fill canopy gaps between adult trees, leading to a darker understory environment (Jucker et al., 2015; Purves et al., 2007). Other significant relationships could also be involved. For example, belowground interactions and root system complimentary may decrease intra- or interspecific competition for a limited water supply, thus resulting in a positive effect of certain mixtures. A drought tolerant companion species could also reduce the overall water demand of the stand, thus leaving more water and a wetter soil for oak seedlings and saplings (Forrester, 2014).

The positive effect on oak regeneration we identified in mixtures with coniferous shade-intolerant species may also be explained by competition in the regeneration layer. Shade-tolerant species can grow even in heavy shade, meaning they will eventually outcompete *Q. petraea* by capturing the available light in the understory. Conversely, a shade-intolerant companion species will cast less shade, thus enabling *Q. petraea* to better compete for the available light and to grow taller than the saplings of the companion species, thus reducing the light available to them and inhibiting their further growth (De Lombaerde et al., 2019; Klopčič et al., 2015; Leuschner et al., 2001; Ligot et al., 2013). However, this effect is hard to investigate with French NFI data because each plot survey is unique (the plots are not permanent), so no temporal data is available to study relative growth and competition among saplings. Moreover, NFI cover data does not include a vertical classification, only absolute cover.

5. Conclusion

We identified several environmental variables influencing *Q. petraea* regeneration in accordance with the current knowledge of *Q. petraea* ecology. By including them in our model, we were able to estimate the companion-species effect independently from environmental conditions. Four out of seven coniferous companion species (Corsican pine, Scots pine, maritime pine, Douglas fir) and one out of eleven broadleaved companion species (chestnut) had a positive effect on *Q. petraea* regeneration. No companion species had a negative effect. For the coniferous companions, their positive effect on oak regeneration was strongly correlated with their level of shade tolerance; no such correlation was found for the broadleaved companion species.

Mixed stands present numerous advantages, such as significantly increased productivity on naturally less productive sites and enhanced resilience to global changes (DeClerck et al., 2006; Toïgo et al., 2015a, 2015b). However, ensuring the regeneration of the overstory species in mixed stands can be challenging since the co-occurring species differ in tolerance levels and ecological preferences. Our results imply that the companion species can have a significant positive effect on regeneration. Future studies on regeneration in mixed stands should assess the regeneration of both species in the mixture to account for competitive interactions between the regenerating species; for example, regenerating pine in a mixture can be very difficult due to its shade intolerance.

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8. Appendix

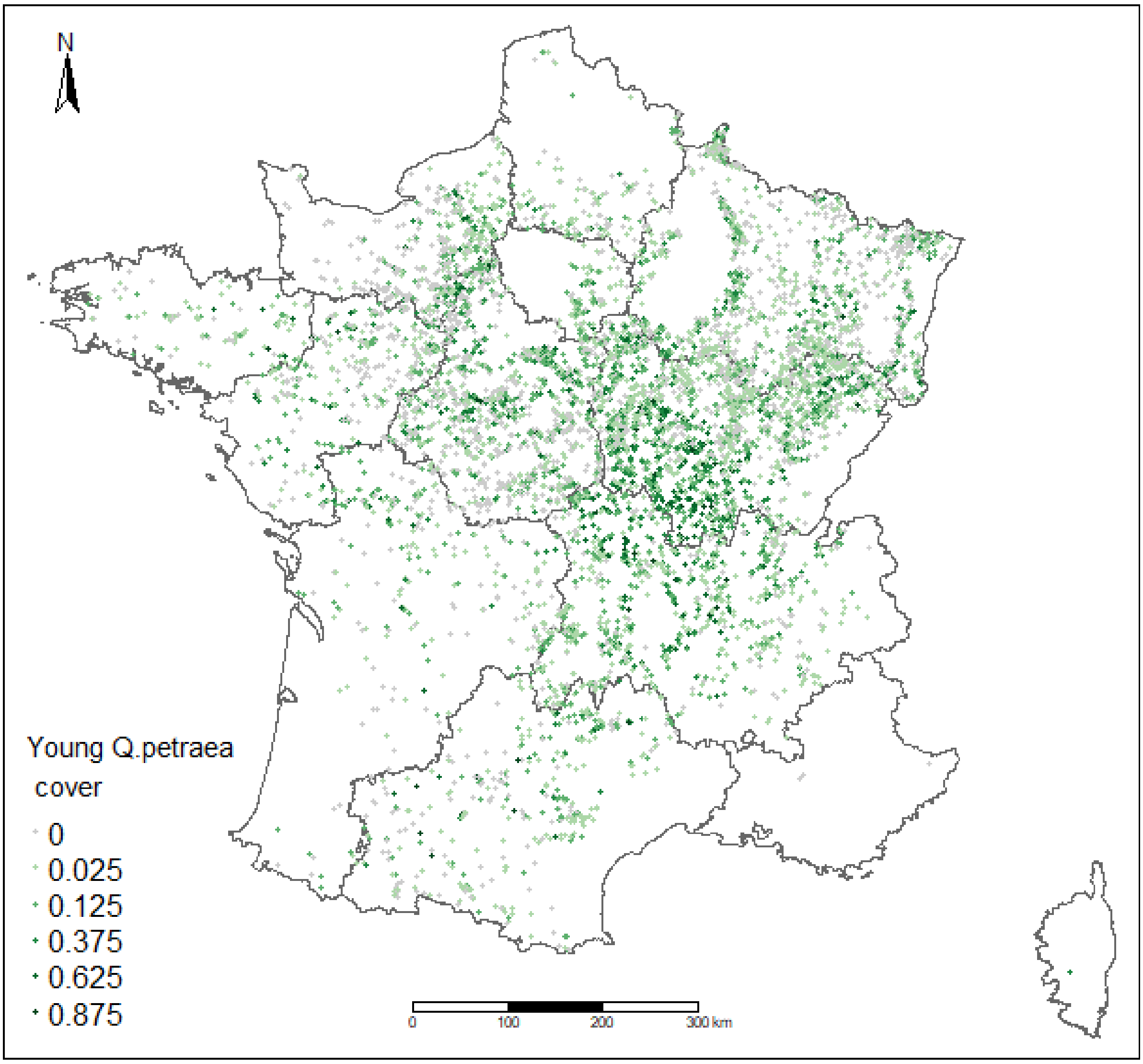
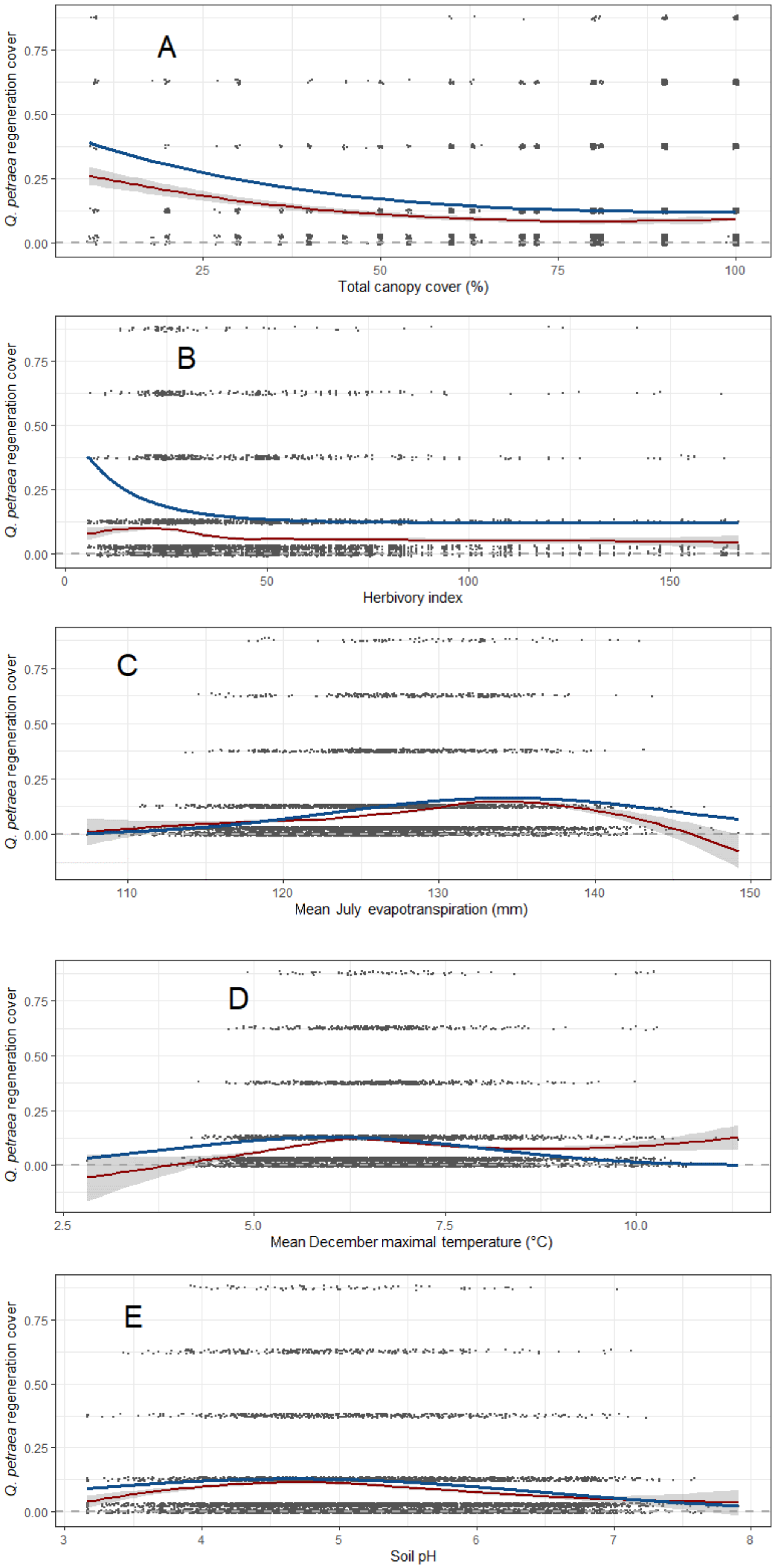


Figure A.1: Map of the cover percentage of regenerating Q. petraea of the final selection of plots

Table A.1: Mean, standard deviation, range and the selected form of fitting procedure for the continuous variables in the regeneration model prior to centering and scaling. Note that we rescaled the variables according to the equation $X_{unscaled} = X_{scaled}$ Standard deviation + Mean*

Variable	Mean	Standard deviation	Range	Selected form
Total canopy cover (%)	85.09	16.86	9 - 100	$a_n * X_n + a_{n2} * X_n{}^2$
PET_7 (mm)	125.9	5.851	107.5 - 149.2	$a_n * X_n + a_{n2} * X_n{}^2$
$Tmax_{12}$ (°C)	6.612	1.164	2.821 - 11.33	$a_n * X_n + a_{n2} * X_n{}^2$
pH	5.209	0.9031	3.17 - 7.907	$a_n * X_n + a_{n2} * X_n{}^2$
Herbivory index	49.8	29.04	5.518 - 166.8	$a_{n1} * exp(a_{n2} * X_n)$
Rocky outcrop (%/10)	0.3047	1.124	0 - 10	$a_n * X_n$
North-South exposure	-0.007146	0.4973	-1 - 1	$a_n * X_n$
East-West exposure	-0.0198	0.504	-1 - 1	$a_n * X_n$

Figure A.2 (next page): Q. petraea regeneration cover as a function of an environmental parameter in the dataset (grey points), smoothed by a LOESS curve (in red) and predicted by the environmental function of the model (blue line) while the other parameters were set either to the mean or to the Booleans reference level for a pure stand. (A) for total canopy cover, (B) for herbivory index, (C) for mean evapotranspiration potential in July, (D) for mean December maximal temperature, and (E) for soil pH.


A
B
C
D
E
Q. petraea regeneration cover
0.00
0.25
0.50
0.75
Total canopy cover (%)
25
50
75
100
Herbivory index
0
50
100
150
Mean July evapotranspiration (mm)
110
120
130
140
150
Mean December maximal temperature (°C)
2.5
5.0
7.5
10.0
Soil pH
3
4
5
6
7
8