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# Modelling the effect of tree species mixing on *Quercus petraea* regeneration with the French National Forest Inventory

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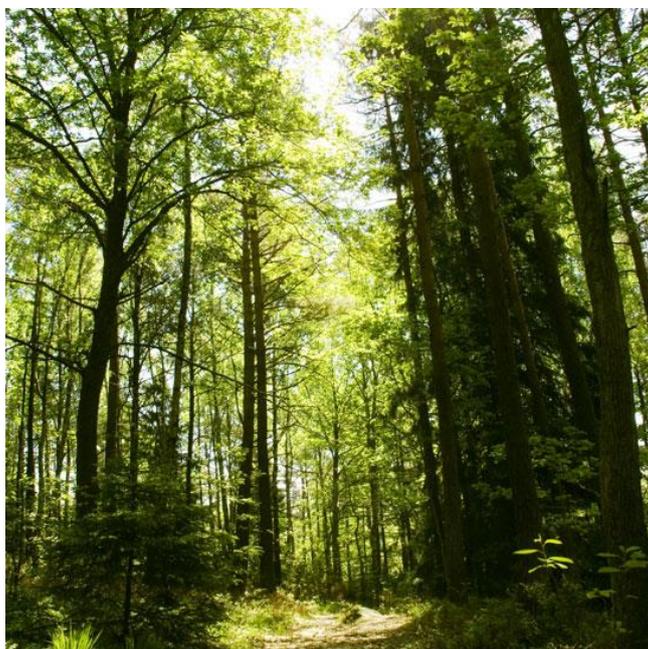
Abstract

The ongoing interest for mixed stands in forestry is supported by positive productivity - diversity relationships, pest effects mitigation and an increased resilience and stability, however how species mixing affect forest regeneration is yet to explore.

We used the years 2006 to 2016 of the French National Forest Inventory to model *Quercus petraea* regeneration cover in pure and mixed *Quercus petraea* stands. This model allowed to indentify environmental variables at play in *Quercus petraea* regeneration and uses them to indentify the effect of the companion species in bispecific mixed stands regardless of the environmental variations. We the modeled this mixture effect as a function of the shade tolerance of the companion species.

Quercus petraea regeneration responds negatively to total canopy cover and herbivory pressure, and the retained biogeoclimatic variables are mean potential evapotranspiration of July, mean maximal temperature of December and soil pH. *Quercus petraea* regeneration is proportionally related to the relative cover of *Quercus petraea* in the canopy layer in mixed stands, but mixed stands with shade intolerant conifers display an enhanced *Quercus petraea* regeneration compared to the other mixed stands, our shade tolerance model did not identify this effect for broadleaved companion species. This suggests a facilitation of regeneration via a better light transmittance through the crown of the companion species or a competitive advantage of *Quercus petraea* saplings against shade intolerant saplings and reinforces the idea that mixing species can contribute to the resilience and stability of the stand.

Résumé

L'intérêt pour les peuplements mixtes dans la sylviculture est soutenu par des relations positives de productivité - diversité, l'atténuation des effets des ravageurs et l''augmentation de la résilience et de la stabilité, mais la manière dont le mélange des espèces affecte la régénération des forêts reste encore à explorer.

Nous avons utilisé les années 2006 à 2016 de l'Inventaire Forestier National Français pour modéliser le couvert de régénération de *Quercus petraea* dans les peuplements purs et mixtes de *Quercus petraea*. Ce modèle a permis d'identifier les variables environnementales en jeu dans la régénération de *Quercus petraea* et les utilise pour identifier l'effet des espèces compagnes dans des peuplements mixtes bispécifiques, indépendamment des variations environnementales. Nous avons modélisé cet effet mélange en fonction de la tolérance à l'ombrage des espèces compagnes.

La régénération de *Quercus petraea* répond négativement au taux de couvert total de la canopée et à la pression d'herbivorie, et les variables biogéoclimatiques retenues sont l'évapotranspiration potentielle moyenne de juillet, la température maximale moyenne de décembre et le pH du sol. La régénération de *Quercus petraea* est proportionnellement liée au couvert relative de *Quercus petraea* dans la canopée, mais les peuplements mixtes avec des espèces compagnes conifères et intolérantes à l'ombrage montrent une régénération de *Quercus petraea* améliorée par rapport aux autres peuplements mixtes, notre modèle utilisant la tolérance à l'ombrage n'a pas identifié cet effet pour les espèces compagnes feuillues. Ce résultat suggère une facilitation de la régénération par une meilleure transmission de la lumière à travers les houppiers de l'espèce compagne ou un avantage compétitif des jeunes arbres de *Quercus petraea* contre les jeunes arbres intolérants à l'ombre et renforce l'idée que le mélange d'espèce contribue à la résilience et la stabilité du peuplement.

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Acknowledgement

I.Introduction

Oak is a widespread, ecologically and economically important tree genus of the northern temperate forests (Bobiec et al., 2018; Johnson et al., 2019). It provides many ecosystem services such as wood production, aesthetics value and watershed protection (Löf et al., 2016). It Also has a critical role in the maintenance of biodiversity as it provides habitats via living and deadwood to many endangered insects (Milberg et al., 2016), and bird species (Felton et al., 2016). However, the maintenance of oaks in the canopy layer to insure a sufficient supply of masting trees and natural regeneration in managed forest faces many challenges. Poor oak regeneration had been widely observed at almost every site of its distribution area (Bobiec et al., 2018; Götmark, 2007; Kelly, 2002; Löf et al., 2016), and disentangling the factors causing this lack of regeneration is not straightforward. As a mid shade tolerant species, oak suffers from insufficient light in the understorey (Götmark, 2007; Kelly, 2002), lack of competitive abilities against more shade tolerant regenerating species (Ligot et al., 2013; Van Couwenberghe et al., 2013), even in a context of a canopy opening designed 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 and are a major concern 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 forestry for tree species mixtures, as these types of forests often present interesting properties, as for instance overyielding. This property leads to a more productive stand in regard to the expected productivity, calculated by just pondering the productivity in pure stand of the species by their relative abundance in the mixed stand. Tree diversity, traits diversity within the community and evenness of the species abundance are all drivers of the overyielding observed in mixed forest (Perot and Picard, 2012; del Río et al., 2016; Vallet and Pérot, 2011; Zhang et al., 2012). This property is especially interesting for increasing productivity in low productivity sites as they display the greater overyielding effects for some mixtures, in line with the stress gradient hypothesis (Bertness and Callaway, 1994; Jucker et al., 2016; Toïgo et al., 2015a). These effects could be explained by a better crown complementarity between adult trees, an optimized light interception and a complimentary use of the available resources (Forrester, 2014; Jucker et al., 2015; Ligot et al., 2016). Mixing trees species is also a promising way of improving forest stability and resilience against extreme events and global changes (DeClerck et al., 2006; Loreau and de Mazancourt, 2013; Spiecker, 2003; Thompson et al., 2009). This resilience and stability improvement can be explained for instance by a richer regeneration layer, leading to more stability if a species is removed (Yachi and Loreau, 1999), the mitigation of the spread of a pest because its target species is less abundant or different response times between species to a stress, leading to a reduced competition during the recovery of the stress (Jactel et al., 2017; Morin et al., 2014; Thompson et al., 2009). Thus, studying the effects of species mixing on regeneration is relevant because it is a key component of forest resilience, and natural regeneration is critical to ensure that the properties of mixed stands are kept in the forest since the next generation canopy layer is partly determined by 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 forest. Therefore shade tolerance appears to be a useful trait to sum up the mechanisms described above, as shade intolerant species do not capture as much light as shade tolerant species, and have narrower crowns (Aiba and Nakashizuka, 2009; Niinemets, 2010). Using this synthetic trait is

relevant in a diversity-function study because it allows to point out the underlying ecological mechanisms and provides generic and interpolable explanation of the observed effect.

Regeneration studies often rely on controlled plantations, regeneration surveys along an environmental or disturbance gradient (Fei and Steiner, 2008; Gaudio et al., 2011), or relative growth measures with different light or herbivore exclosure treatments in times (Bernard et al., 2017; Ligot et al., 2013). National forest Inventory (NFI) data offers a different approach because they are distributed over time and space for representativeness of the forest resource of the territory instead of following prior ecological hypothesis. There are a limited number of studies of regeneration in contrast with the number of available NFI data. These data are very valuable because they allow regeneration distribution to be studied at the landscape scale with a large selection of plots, or test finer hypothesis with a strict selection of plots. The limited use of NFI data to study regeneration can be explained by the lack of information of the regeneration layer, which is less surveyed than the adult trees layer, and the lack of revisited plots that allow to study the relative growth between saplings and competitive vegetation.

Our study focuses on sessile oak (*Quercus petraea* (Matt.) liebl), which accounts of 17% of the living broadleaved stock and 40% of the oaks living stock in France in 2019 (IGN, 2019). This species is widespread and present in a lot of different mixtures with species that have contrasted shade tolerances.

The aim of our study is to identify environmental variables structuring *Q. petraea* regeneration at the national scale, and use them to compare *Q. petraea* regeneration in mixtures with various companion species all other things being equal. We hypothesize that (1) *Q. petraea* regeneration increases with the proportion of *Q. petraea* in the canopy layer (2) certain companion species mixed with *Q. petraea* have a beneficial effect on its regeneration (3) this beneficial effect can 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 decreases.

Our study uses the French National Forest Inventory (NFI) because it allows us to have a national scale approach, thanks to an important number of plots, on regeneration that is representative of the french forests. The use of the French NFI to study regeneration is original and could highlight novel methods and opportunities to explore the ecological processes driving forest regeneration in northern temperate forests

II. Materials and methods

a. General methodology

We used the French National Forest Inventory (NFI) to study *Q. petraea* regeneration in pure and mixed stands at a national scale. This allows to cover a broad set of abiotic conditions from oceanic to semi-continental climate with a mean annual temperature ranging from 5.9 to 13.8 °C and annual precipitation ranging from 566 to 2125 mm. We aimed to identify biotic and abiotic environmental variables impacting *Q. petraea* regeneration cover by creating a regeneration model. We also wanted to study the mixture effect of the stand on *Q. petraea* regeneration by adding mixed stands in the model in order to include a relationship between the relative cover of *Q. petraea* in the canopy and its regeneration. In order to identify companion species capable of facilitating or altering *Q. petraea* regeneration, we only chose bispecific mixed stands and tested if the identity of the companion species can modify the relationship between *Q. petraea* cover in the canopy and its regeneration. We also wanted to

test if the effect of the companion species on *Q. petraea* regeneration can be explained by their shade tolerances to gain in interpretability and genericity, by modelling the value of the parameter describing the companion species effect on regeneration as a function of the shade tolerance of this species.

b. NFI sampling and NFI data

The French National Forest Inventory (NFI) is a systematic sampling forest land cover with a 1km by 1km grid laid across the territory. Since 2004, around 6000 equally dispersed plots on this grid are surveyed each year. Our dataset is comprised of the plots from the years 2006 to 2016 of the NFI.

On each plot, the free canopy cover (only trees that have free access to light) for every trees species with a diameter at breast height (dbh) over 7.5cm is visually assessed within a 25 meter radius circle around the plot center. We calculated from these observations the canopy proportion of every species as the relative free cover. These observations are completed with a floristic survey done in a 15 meter radius circle around the plot center. This survey includes every herbaceous, bush species and saplings (dbh< 7.5cm) of the trees species. The abundance of these species is assessed with a code ranging from 0 to 5 inspired by the Braun-Blanquet code (Westhoff and Van Der Maarel, 1978). 0 means absence, 1 means an absolute cover ranging between 0 and 5%, 2 a cover between 5 and 25 %, 3 a cover between 25 and 50%, 4 a cover between 50 and 75% and 5 a cover over 75%.

c. Plot selection

To conduct this study, we selected plots where adults *Q. petraea* (dbh>7.5cm) represented at least 10% of the free cover. This choice allows to emphasize on the factors influencing regeneration over species distribution factors, because only plots with adults *Q. petraea* are included. Since the model is designed to study the effect of the companion species on *Q. petraea* regeneration, only pure and bispecific mixed stands were selected, in order to test the effect of the companion species one at a time. We selected stands with a *Q. petraea* relative cover of 100% for pure stands, and stands where the sum of *Q. petraea* relative cover and the relative cover of the main companion species is over 90% for mixed stands. To minimize the effect of trees species other than the main companion species, we checked that the relative cover of the remaining species are lower than the relative cover of the two main species of the mixture. In order to have a representative view of the mixing effect as a function of *Q. petraea* relative cover, we kept mixtures that are close to cover the full range of available *Q. petraea* relative cover values by selecting the one that displays at least 70% *Q. petraea* relative cover difference between their higher and lower relative cover value. The plots identified as "temporarily deforested" according to the NFI classification were removed because of the lack of reliable cover data. Finally, we also removed mixtures represented by less than 20 plots. The final dataset comprises 1767 pure *Q. petraea* plots, 4899 *Q. petraea*-broadleaf mixed plots with 11 different companion species and 643 *Q. petraea*-conifer mixed plots with 7 different companion species (Table 1, Figure S1).

Table 1: Mean of environmental and cover variables with the 2.5% and 97.5% quantiles in parenthesis. The number of mixed stands with the companion species is specified, the acronyms of the species reads as follow: Fagus sylvatica (Fa.s), Carpinus betulus (Car.b), Quercus robur (Qu.ro), Castanea sativa (Cas.s), Betula sp (Be.sp), Quercus pubescens (Qu.pu), Fraxinus sp (Fr.sp), Populus tremula (Po.t), Prunus sp (Pr.sp), Tilia sp (Ti.sp),

Robinia pseudoacacia (Ro.p), Pinus sylvestris (Pin.sy), Pseudotsuga menziesii (Ps.m), Abies alba (Ab.a), Pinus pinaster (Pin.p), Picea abies (Pic.a), Pinus nigra (Pin.n), Pinus nigra var corsicana (Pin.cor).

Mixture type	Number of plots by companion species	Annual temperature (°C)	Annual precipitation (mm)	Total canopy cover (%)	*Q. petraea* relative cover (%)
Q. petraea pure stands		11 (9.3-12.8)	824 (629-1278)	85 (27-100)	1
Q. petraea - broadleaved species stands	(Fa.s):1889, (Car.b):1128, (Qu.ro):766, (Cas.s):470, (Be.sp):246, (Qu.pu):142, (Fr.sp):112, (Po.t):50, (Pr.sp):37, (Ti.sp):31, (Ro.p):28	10.6 (9-12.5)	913 (649-1404)	85 (40-100)	0.57 (0.1-0.9)
Q. petraea - coniferous species stands	(Pin.sy):347, (Ps.m):77, (Ab.a):72, (Pin.p):54, (Pic.a):40, (Pin.n):33, (Pin.cor):20	10.5 (8.4-12)	893 (654-1494)	83 (40-100)	0.47 (0.1-0.9)

d. Covariables

Environmental variables are needed to determine *Q. petraea* regeneration in pure stands and mixed stands. It is critical to have an extensive environmental function as it will permit to compare the mixture effect of different companion species on regeneration by ensuring the site-dependent environment variables influencing regeneration are included.

Light is a primary factor when studying the regeneration à. As we did not have a direct measurement of light we computed the total canopy cover by summing all the free cover from a plot in order to have a proxy of stand density and light availability.

Topographic variables such as the steepest slope of the plot and angle of exposition to sunlight were provided by the NFI, as well as the type, depth and percentage of rocks of the soil. The NFI also provide a visual categorical estimation of the vertical structure of the stand and a mention when cut occured in the last 5 years. We estimated soil water holding capacity (SWHC, in mm) for all plots from soil texture, percentage of rock and soil depth (Piedallu et al., 2018). We used the 30-year climatic values of the period 1981-2010 from the AURHELY Météo France spatial layer to obtain monthly mean, minimum and maximum temperature (T in degree celsius) and precipitation (PPT in millimeters). We derived monthly potential evapotranspiration from these variables (Piedallu and Gégout, 2007; Piedallu et al., 2013). We used the floristic survey to infer variables with bio-indication models. These variables were the acidity (pH), the carbon to nitrogen ratio of the organic matter of the soil (C:N) and the base saturation (S:T) of the first layer of the soil (Gégout et al., 2005). The floristic survey was also used to investigate regeneration inhibition by three competitive plants: *Rubus fruticosus*, *Molinia caerulea*, *Pteridium aquilinum* by creating a boolean variable being one when their absolute cover were more than 50%.

In order to have a proxy of the pressure exerted by herbivores on *Q. petraea* saplings, we used the hunting statistics provided by the French Office of Biodiversity (OFB) at the county level. A yearly ungulate pressure index is calculated from the kill statistics of *Sus scrofa*, *Capreolus capreolus* and *Cervus elaphus*, their respective basal metabolic rates estimated from the mean body mass of the species to the power 0.75 (Clarke et al., 2010; Petersson et al., 2019; White and Seymour, 2005), and the surface of the department. The resulting index is then smoothed with a 3 year moving averaging to reduce inter-annual variability and because we were not able to know during which year the saplings were browsed. Plots occurring in 3 counties were discarded for their lack of hunting data. Other various plots were also discarded for their lack of some covariables. Values of shade tolerance of the tree species were provided by Niinemets and Valladares (2006), it is a value ranging from 1 (shade intolerant) to 5 (shade tolerant).

e. Modelling framework

i. Regeneration model

The variable describing *Q. petraea* regeneration provided by the NFI is a categorical classification of the saplings cover ranging between 0 and 5, but, in order to have a quantitative approach, we transformed this variable with the mean of each cover classes, resulting in six values of cover possible: 0, 0.025, 0.125, 0.375, 0.625 and 0.875. Cover values are constrained between 0 and 1, thus the chosen modelling technique must respect this condition.

Saplings cover was modelled as a function of environmental variables, via a logistic model (Wright, 1995) because it uses the inverse of the logit function ($logit^{-1}(x) = \frac{1}{1+e^{-x}}$) in order to constrain the values between 0 and 1. This function provides the regeneration predicted only by environmental factors in a pure stand.

This function is multiplied by a reducer in order to correct regeneration in a mixed stand proportionally to the mixture level. Without the companion species interaction, the reducer acts as a proportional decrease with *Q. petraea* relative cover: a mixed stand with 50% *Q. petraea* relative cover will have 50% less regeneration than a pure stand with the same environmental conditions. For every companion species, an estimated species-specific parameter is added to this reducer, this parameter allows to change the slope of the linear relationship between the environmental function and *Q. petraea* cover. The choice of this linear relationship was based on a scatter plot analysis and for its robustness.

This model can be summarized as in eq (1)

$$Saplings\ cover_{Q.petraea} = F_1(X_n) * F_2(Rel\ cover_{Q.petraea}, SP_i)\quad (1)$$

Where F1 is the environmental function, X_n the environmental variables and F2 is the mixture reducer function. This function uses *Q. petraea* relative cover (Rel cover$_{Q.\ petraea}$) of the trees in the canopy layer and the identity of the companion species SP_i.

The full expression of the model is written as in eq(2)

$$Saplings\ cover_{Q.petraea} =$$

$$logit^{-1}\left(\beta_0 + \sum_n \beta_n * x_n\right) * \left(1 - \left(1 - Rel\ cover_{Q.petraea}\right) * \left(\sum_i sp_i * (1 - a_i)\right)\right) + \varepsilon\quad (2)$$

Where x_n is the n-th environmental variable, Rel cover$_{Q.\ petraea}$ is *Quercus petraea* relative cover in the canopy layer, sp_i is a dummy variable being set to 1 only when the companion species is the i-th species, allowing a_i to be estimated only for the given mixture. Therefore 1-Rel cover$_{Q.\ petraea}$ represent the relative cover of the other species, that is why it multiplies 1-a_i. This allows the effect of the companion species to proportionally increase with its

relative presence in the mixture. We had chosen the form 1-a_i to express the effect of the companion species because it allows to test the significance of this effect, if a_i is not significantly different from 0, the reducer act as a proportional relationship between regeneration and Rel cover$_{Q. petraea}$. β_0 and β_n are the estimated intercept and parameters of the environmental function. This formulation allows to fit the model on all the selected plots at once since it can include both pure and mixed stands.

ε stands for the 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* relative cover. Therefore, a power variance model was used on these two variables in order to take this heteroscedasticity into account. The structure of our cover data is unbalanced, both in distribution in the different categories of cover and the range of cover of these categories, as a consequence ε display a slightly asymmetric normal distribution that is not taken into account.

Three forms of relationship between regeneration and environmental variable were tested, the linear form: $a_n * X_n$, the quadratic form $a_n * X_n + a_{n2} * X_n{}^2$ and the exponential decrease form $a_{n1} * exp(a_{n2} * X_n)$ because it can be more robust and biologically more accurate than the quadratic form for some variables. All the quantitative environmental variables were scaled in order to simplify the fitting procedure and have comparable parameter estimates.

Environmental variables were selected following an ascending step 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 a quadratic or exponential decrease form because they have 2 parameters (Akaike, 1974; Burnham and Anderson, 2002). To avoid collinearity between environmental variables, a variable was excluded from the procedure when its spearman correlation coefficient with an already selected variable exceeded 0.4.

ii.   Shade tolerance model

Once the final model of eq(2) is fitted, tolerances values of the companion species are used in order to test whether they are structuring the estimated species-specific parameters. A linear model is used for that purpose. It is detailed in eq(3):

$a_i = s_0 + s_1 * Tolerance_i + \varepsilon$ (3)

Where a_i are the estimated species-specific parameters fitted in equation 2, *Tolerance$_i$* are the tolerance of the companion species, and s_0 and s_1 the parameters of this model. This model is fitted separately for coniferous and broadleaved companion species, excluding *Pinus nigra var. corsicana* because we don't have the shade tolerance value of this species. ε stands for the normal errors of mean 0 and variance σ^2, since every specie-specific parameters are not evenly accurately estimated in equation 2, this variance is weighted by the inverse of the squared standard error of the estimated parameters in order to give more weight to the more accurate parameters.

iii.   Statistical procedures

We analysed the data with the R software 3.6.2 (R Core Team, 2019). The model in eq(2) is fitted with the generalized least squares method with the *gnls* function of the R package 'nlme' (Pinheiro et al., 2017). The tolerance model presented in eq(3) is fitted with a linear model. Normalized residuals of the regeneration model in eq(2) were plotted against every variables and the X and Y coordinates, and no pattern diverging from the 0 axis were found.

III. <u>Results</u>

a. Q. petraea regeneration

In our complete plot selection, the presence of *Q. petraea* saplings (i.e. regeneration) was observed in 67% of the plots, with this proportion varying between plot types, as 75%, 64% and 72% of respectively pure, mixed *Q. petraea*-Broadleaved companion species and mixed *Q. petraea*-coniferous species stands displayed *Q. petraea* regeneration. The mean cover of *Q. petraea* regeneration was 14.5% in pure stands, 7.3% in mixed *Q. petraea*-Broadleaved stands and 9.1% in mixed *Q. petraea*-coniferous stands. This mean cover displayed a high variability as its coefficient of variation is 1.8. Mean regeneration cover increased linearly with *Q. petraea* relative cover in the canopy. Mean regeneration cover was 3.8%, 8.3% and 12.7% for plots with respectively less than 40% *Q. petraea* relative cover, plots with a *Q. petraea* relative cover between 41% and 69% and plots with more than 70% *Q. petraea* relative cover. The mean cover of *Q. petraea* regeneration per mixed stand type is displayed in Figure 1.
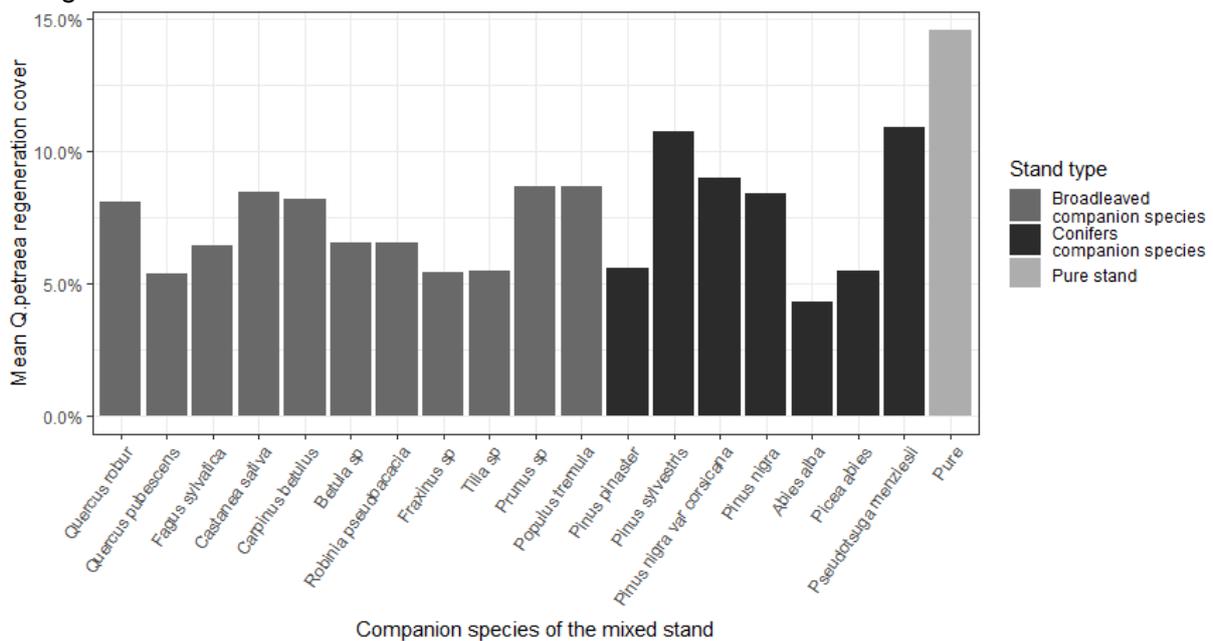

Figure 1: Mean Q. petraea regeneration cover as a function of the companion species of the mixed Q.petraea stands. Pure Q. petraea stands are also included.

However, this result alone cannot demonstrate the effect of the companion species identity on *Q. petraea* regeneration as environmental variables and *Q. petraea* relative cover do have an effect on regeneration too. The regeneration model presented below aims to disentangle species-specific effects and environmental effects.

b. Estimated parameters of the regeneration model

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

The best fitting form for the herbivory index is the exponential decrease, described by two parameters. The negative effect of the herbivory index on regeneration is drastic between 0

and 50 (the mean value of the index), with potential regeneration divided by two over this interval, but stabilizes after that.

The other parameters are associated with the biogeoclimatic variables: PET_7 (Mean evapotranspiration potential in july), $Tmax_{12}$ (mean maximal temperature of december) and the bio-indicated soil pH. All these three variables have a quadratic form, allowing for a parabolic increase until it reach an optimum followed by a decrease. The optimum of the soil PET_7, $Tmax_{12}$ and pH are reached respectively at 134 mm, 5.9 °C and 4.7,. The presence of a carbonated soil, the percentage of rocky outcrop and the exposure North-South and East-West have a minor negative effect in terms of magnitude on *Q. petraea* regeneration 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*) are significantly positive. This result implies that the slope of the relationship between *Q. petraea* regeneration and its relative cover is more beneficial than a proportional relationship in a mixed stands with these companion species (Figure 2). No companion species had a significant negative species-specific parameter thus no companion species have a detrimental effect on *Q. petraea* regeneration.

Table 2: Coefficients (Estimate), standard error (Std.error) and the p-value of the estimated parameters of the selected regeneration model. Variables associated with the parameter of the environmental function are all scaled except for Uneven aged stand, Coppice with regular stand, Molinia caerulea, Soil_{carbonated} , and the companion species variables which are boolean. The degrees of freedom and the parameters of the power variance function are also specified Mean, standard deviation and the range of the continuous variables are available in Table S1.

F1: Environmental Parameter	Estimate	Std.Error	p-value
Intercept	-1.97	0.0693	***$<10^{-4}$
Total cover	-0.0624	0.0322	(*)0.0525
Total 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	*0.0134
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	(*)0.0601
Rocky outcrop	-0.0827	0.0265	***<10^{-4}
North-South exposure	-0.112	0.0432	***<10^{-4}
East-West exposure	-0.0922	0.0401	*0.0216
F2: Companion species parameter	**Value**	**Std.Error**	**p-value**
Pinus nigra var corsicana	**0.635**	**0.0968**	***<10^{-4}
Pinus sylvestris	**0.467**	**0.0471**	***<10^{-4}
Pinus pinaster	**0.331**	**0.115**	***<10^{-4}
Tilia sp	0.3	0.252	0.235
Pseudotsuga menziesii	**0.251**	**0.0661**	***<10^{-4}
Castanea sativa	**0.171**	**0.0403**	***<10^{-4}
Pinus 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
Fitting parameters	**Value**		
Degrees of freedom	7274		
Power of the *Q. petraea* relative cover 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

The values of these species-specific parameters (Table 2) can be used to predict how the mixture affects the potential regeneration for every companion species mixed with *Q. petraea*. For a non-significant species-specific parameter, the relationship between regeneration and *Q. petraea* is close to a proportional one, meaning in a 50% *Q. petraea* relative cover stand, the regeneration will be 50% of a pure stand with the same condition. However, for *Pinus nigra var corsicana, Pinus sylvestris, Pinus pinaster, Pseudotsuga menziesii* and *Castanea sativa,* which have positive significant parameters, a 50 % *Q. petraea* mixed stands with these species display respectively 81%, 73%, 67%, 63% and 59% of the potential regeneration (i.e. the regeneration of a pure stand with the same environmental conditions) (Figure 2).
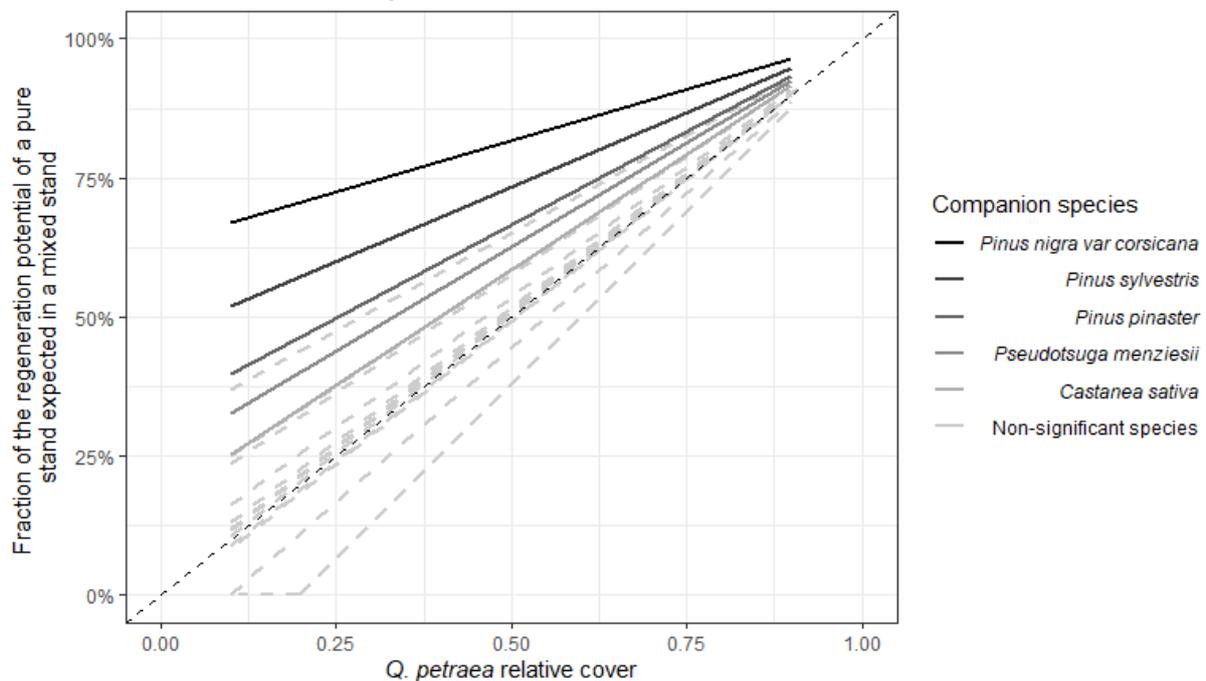

Figure 2: Fraction of the regeneration potential of a pure stand expected to occur in a Q. petraea mixed stand according to the regeneration model (i.e. the value of the reducer function F2), as a function of the companion species identity and Q. petraea relative cover in the canopy. Dashed line represent species with non-significant species-specific parameters. The segments stop at the minimal and maximal Q. petraea relative cover observed in each type of mixtures.

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

A significant linear relationship between the value of the species-specific parameter described in Table 2 and the shade tolerance of the associated companion species is detected by the linear model for the coniferous companion species with a significant R^2 of 0.987 but not for the broadleaf species (R^2 : -0.00341, p-value : 0.884) (Table 2, Figure 3).

Table 2: Estimate, standard error and P-value of the estimated parameters and the R^2 of the linear regression (species-specific parameter ~ shade tolerance of the species) presented in eq(3). The model is fitted separately for the coniferous and the broadleaved companion species.

Conifer	Estimate	Std. Error	p-value	R^2
Intercept	0.686	0.0531	***<10^{-4}	0.941
Shade tolerance	-0.147	0.0185	***<10^{-4}	

Broadleaf	Estimate	Std. Error	p-value	R^2
Intercept	0.0603	0.0839	0.491	0.00251
Shade tolerance	-0.00341	0.0228	0.884	
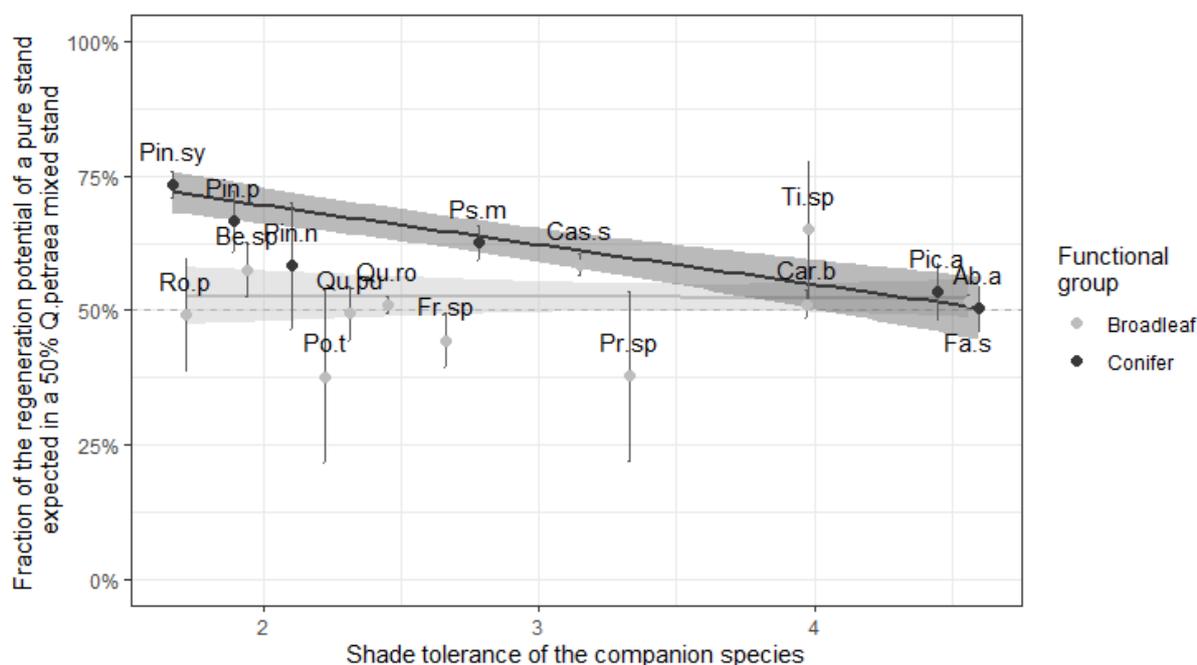
Figure 3: Fraction of the regeneration potential of a pure stand expected to occur in a 50% Q. petraea mixed stand according to the regeneration model (i.e. the value of the reducer function F2 at 50% Q. petraea relative cover), as a function of the companion species shade tolerance and functional group. The vertical segment depicts the prediction ± the prediction with the standard error of the associated parameter from Table 2. The linear model of the relationship between the fraction of regeneration and the shade tolerance of the companion species is represented with straight lines, and the confidence interval of this model with ribbons, for the two functional groups. Abbreviations for companion species : Abies alba

(Ab.a), Betula sp (Be.sp), Carpinus betulus (Car.b), Castanea sativa (Cas.s), Fagus sylvatica (Fa.s), Fraxinus sp (Fr.sp), Picea abies (Pic.a), Pinus nigra (Pin.n), Pinus pinaster (Pin.p), Pinus sylvestris (Pin.sy), Populus tremula (Po.t), Prunus sp (Pr.sp), Pseudotsuga menziesii (Ps.m), Quercus pubescens (Qu.pu), Quercus robur (Qu.ro), Robinia pseudoacacia (Ro.p), Tilia sp (Ti.sp). Pinus nigra var corsicana is not shown because of the lack of shade tolerance value.

IV. Discussion

We identified various structuring variables of *Q. petraea* regeneration that are in accordance with current knowledge of *Q. petraea* ecology. These variables entered the regeneration potential part of the model, the function F1. This allows to take them into account when the species-specific parameters of the companion species are estimated. When a species-specific parameter is positive, the relationship between *Q. petraea* regeneration and *Q. petraea* cover, described by the reducer function F2, are higher than a proportional relationship (Figure 2), implying that this companion species has a positive effect on *Q. petraea* regeneration. Four out of the five significant species-specific parameters belong to a conifer companion species, the value of these parameters were strongly correlated with the shade tolerance of the conifer companion species, but no correlation was found for the broadleaf companion species.

a. Environmental drivers of Q. petraea regeneration

The environmental variables we included in the model are used to predict the regeneration potential in pure stand and to limit confounding effects when estimating the species-parameter in mixed stands, but they still are relevant ecological variables that can be linked to *Q. petraea* regeneration ecology. As for many intermediate shade-tolerant species, light condition plays a major role in *Q. petraea* regeneration. Our results confirm other findings as our proxy for light availability, total canopy cover, was negatively correlated with *Q. petraea* saplings cover (Ádám et al., 2013; Annighöfer et al., 2015; Jarvis, 1964). However the relationship between total canopy cover and regeneration is not linear, it starts with a drastic decrease between 0 and 50% canopy cover and then stabilizes. This can be a consequence of the ability of *Q. petraea* to adapt its light acquisition strategy to a certain extent when growing under a heavy shading, by allocating more carbon and resources to the leave and shoot development (Jarvis, 1964; Rodríguez-Calcerrada et al., 2008). We can interpret the positive effect of the vertical structure variable 'coppice with standard stand' as an extension of this interpretation, as vertical heterogeneity can increase light disponibility and heterogeneity, but this relation is still unclear and dependant of many factors (Ligot et al., 2016).

The only understorey variable identified was the presence of an important *Molinia caerulea* absolute cover, but with a low magnitude and significance. This is surprising as several understorey species can have a significant influence on regeneration via competition for light and soil water and nutrients resources. The effect of competitive vegetation on regeneration interacts with a lot of 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., 2011a; Ward et al., 2018). These effects are hard to disentangle with a large plot selection like ours and identifying vegetation interference variables will benefit from a finer plot selection and a comprehension of which environmental factors affects both regeneration and competitive vegetation.

Q. petraea saplings are subject to browsing by ungulates, sometimes to the point where it can affect negatively and drastically its regeneration. Our result goes in the same way as these findings as *Q. petraea* regeneration is negatively linked to our herbivory index via an exponential decrease (Kelly, 2002; Kuiters and Slim, 2002; Petersson et al., 2019). The regeneration cover we modelled is mostly composed of *Q. petraea* saplings, and herbivory by deer has a larger impact on already established saplings by browsing their leaves, especially the newly grown palatable ones, thus limiting their overall growth and competitiveness (Götmark et al., 2005; Mårell et al., 2018; Ramirez et al., 2018).

However, our herbivory index is calculated at the department scale. Therefore it does not accurately represent the spatial heterogeneity the browsing pressure actually displayed. The browsing effect on regeneration would be assessed more accurately with finer scale data and by including interactions with the presence or absence of other palatable species (Jensen et al., 2012), deadwood presence that can act as a physical barrier (Hagge et al., 2019), the interactions with humans (Miller et al., 2009) such as the distance to the closer forest edges and as our study focuses on mixed stands, the interactions with the trees species of the mixture (Bernard et al., 2017; Boulanger et al., 2009).

Biogeoclimatic variables can be challenging to interpret as they encompass many processes and are highly correlated with other variables not included in the model. The two selected variables, July mean PET and December mean maximum temperature are only variable in space because they come from meteorological models, thus they give spatial informations on *Q. petraea* regeneration distribution and preferences. The increase of *Q. petraea* regeneration with July PET until the optimum can be attributed to more light availability (as solar radiation is included in PET calculation) and more warm and productive forests, and the decrease after the optimum can be linked to an insufficient water balance and a higher probability of drought (Piedallu and Gégout, 2007). Soil pH is also a determinant variable, with a concave shaped response curve that has an optimum located at 4.8. This result corroborates findings of other authors, who located the optimum pH for even-aged *Q. petraea* stand to acidic to neutral soils (Bergès et al., 2005). Following this reasoning, the negative parameter of carbonated soil can be explained by a less acidic soil.

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

We showed that the extent of the stand mixing i.e. *Q. petraea* relative cover had a proportional relationship with *Q. petraea* saplings cover for most of the species, and that this relationship can be modified in a mixed stand with certain companion species. Having this simple proportional relationship as a null hypothesis i.e. no effect of the companion species can be justified by anterior regeneration compositions studies which positively linked oak regeneration to the proportion of adult oaks in the overstorey or the distance dependencies between oaks and its regeneration (Ádám et al., 2013; Annighöfer et al., 2015; Battaglia et al., 2008; Fei and Steiner, 2008; Tinya et al., 2019). We used this relationship to test the companion species effect on *Q. petraea* regeneration since a significant positive species-specific parameter can modify this relationship to be more beneficial to *Q. petraea* regeneration. We interpret this modification as an evidence of a positive effect of the companion species on regeneration. This is the case for the five mixtures with the following species as companion species: *Pinus nigra var corsicana, Pinus sylvestris, Pinus pinaster, Pseudotsuga menziesii* and *Castanea sativa*. We also demonstrated that the extent of this positive effect on *Q. petraea* regeneration expressed by the species-specific parameter value is well structured by the shade tolerance value of the conifer companion species but not for the broadleaf ones. The positive effect on regeneration is greater when the

companion species is a conifer intolerant to shade, but if the companion species is a shade tolerant conifer, it does not have a detrimental effect on regeneration because these mixtures do not differ from the null proportional relation.

This beneficial effect on regeneration with a companion shade intolerant conifer species suggests a better light transmission through the crown of the companion species. This is especially relevant in situations where the canopy is fully or nearly closed. Shade intolerant species have a less optimized crown architecture in terms of light interception (Aiba and Nakashizuka, 2009) as these species have a better growth and tree height at the expense of a narrower and a less dense crown. Trees exhibiting this architecture have higher light transmittance, leading to brighter environment in the regeneration layer (Ligot et al., 2013; Messier et al., 1998; Perot et al., 2017). These properties are found in mixed stands too, where species mixing, especially mixing with intolerant species, can enhance understorey light and light heterogeneity (Ligot et al., 2016; Messier et al., 1998).

A positive relationship between *Q. petraea* productivity and the shade tolerance of the companion species regardless of the functional group had been documented by Toïgo et al. (2018), the effect was more marked with coniferous companion species. The shade tolerance effect on productivity can be explained by a release of the intraspecific competition thanks to complementary of differents crown architecture and a better light acquisition by these crowns (Jucker et al., 2015; Ligot et al., 2016; Williams et al., 2017). These effects do not seem to apply to regeneration as this layer does not fully access light yet, this could explain why the effect of the better transmittance of light by the companion species alone may be not enough for mixtures of *Q. petraea* and a shade intolerant broadleaf species to have significant positive effect on regeneration.

This corroborates the fact that conifers and broadleaves species with the same shade tolerance still greatly differ in their crown shape and other traits that could explain the observed significant difference between conifers and broadleaves companion species effect on regeneration (Pretzsch and Schütze, 2009). For example, broadleaf species are known to have more plastic crown than conifers, and will more efficiently fill canopy gaps between adult trees, leading to a darker understorey environments (Jucker et al., 2015; Purves et al., 2007). Other significant relations that could explain the positive effect of certain mixture can be due to belowground interactions, for example an enhanced complimentary of the root system that decreases the intra and interspecific competition for water when this resource is limiting (Forrester, 2014).

The positive effect on regeneration identified in mixtures with coniferous shade intolerant species may also be explained by competition in the regeneration layer. Shade tolerant species can still grow in a context of heavy shading, meaning they will continue to outcompete *Q. petraea* by capturing the available light. Conversely, a stand with a shade intolerant companion species will cast a lesser shade, *Q. petraea* could be able to win the competition for light in this condition when opposed to the saplings of the companion species, which growth will be inhibited by *Q. petraea* saplings and the lack of light (De Lombaerde et al., 2019; Klopčič et al., 2015; Leuschner et al., 2001; Ligot et al., 2013). However, this effect is harder to investigate with French NFI data, because the floristic survey is unique (plots are not permanent), implying we have no temporal data to study the relative growth and competitions between saplings. Additionally, the regeneration cover data from this survey does not include a vertical classification but only an absolute cover. Using these data to study understorey competition could lead to biased results as these absolute covers could be measured for different vertical strata of the regeneration layer.

Mixed stands present numerous advantages, as for example a significant increase in productivity in naturally less productive site and an enhanced resilience to global changes (DeClerck et al., 2006; Toïgo et al., 2015a, 2015b), but ensuring the regeneration of the species present in the overstory can be challenging as they differ in tolerance and ecological preferences. Our results imply that the companion species can have a significant and positive effect on regeneration. Future studies on regeneration in mixed stands will benefit from including the regeneration of both species of the mixture to include competitive interactions between the regenerating species, as pine for example can be the most difficult species to regenerate due to its shade intolerance. Previous studies have shown the capacity of *Pinus sylvestris* to regenerate in *Q. petraea - P.sylvestris* mixtures but the regeneration success of this species was highly light dependant and more difficult to ensure than *Q. petraea* regeneration (Gaudio et al., 2011).

V. Conclusion

To study the influence of environmental factors and species mixing on *Q. petraea* regeneration at the country scale, we built a regeneration model which explicitly takes into account both of these effects thanks to the French NFI regeneration and cover data. The main environmental drivers identified were total canopy cover, the herbivory index, which had a negative impact on regeneration, and the mean PET of July, the mean maximum temperature of December and soil pH, which had a structuring effect on regeneration via a concave shaped curve. For mixed stands, regeneration increased linearly with the relative cover of *Q. petraea* in the canopy, and this increase was more marked and beneficial with mainly conifer companion species. The companion species that have a positive effect on *Q. petraea* regeneration were Corsican pine, Scots pine, maritime pine, Douglas fir and chestnut. The effect of the companion species on *Q. petraea* regeneration was highly correlated with its shade tolerance for coniferous companion species, but not for broadleaved ones. This suggests that mixed stands with intolerant conifers present a brighter light environment when the canopy is closed that is beneficial to *Q. petraea* regeneration, but this effect is masked by other trait differences when the companion species is broadleaved. These results shows that the mixture effect on *Q. petraea* regeneration depends on the companions species, thus the mixed stand composition can have an impact on the resilience of the stand and its capacity to carry on the positive productivity-diversity mixed stands exhibit for the next generations as mixed stand are in need of a diverse regeneration layer.

VI. References

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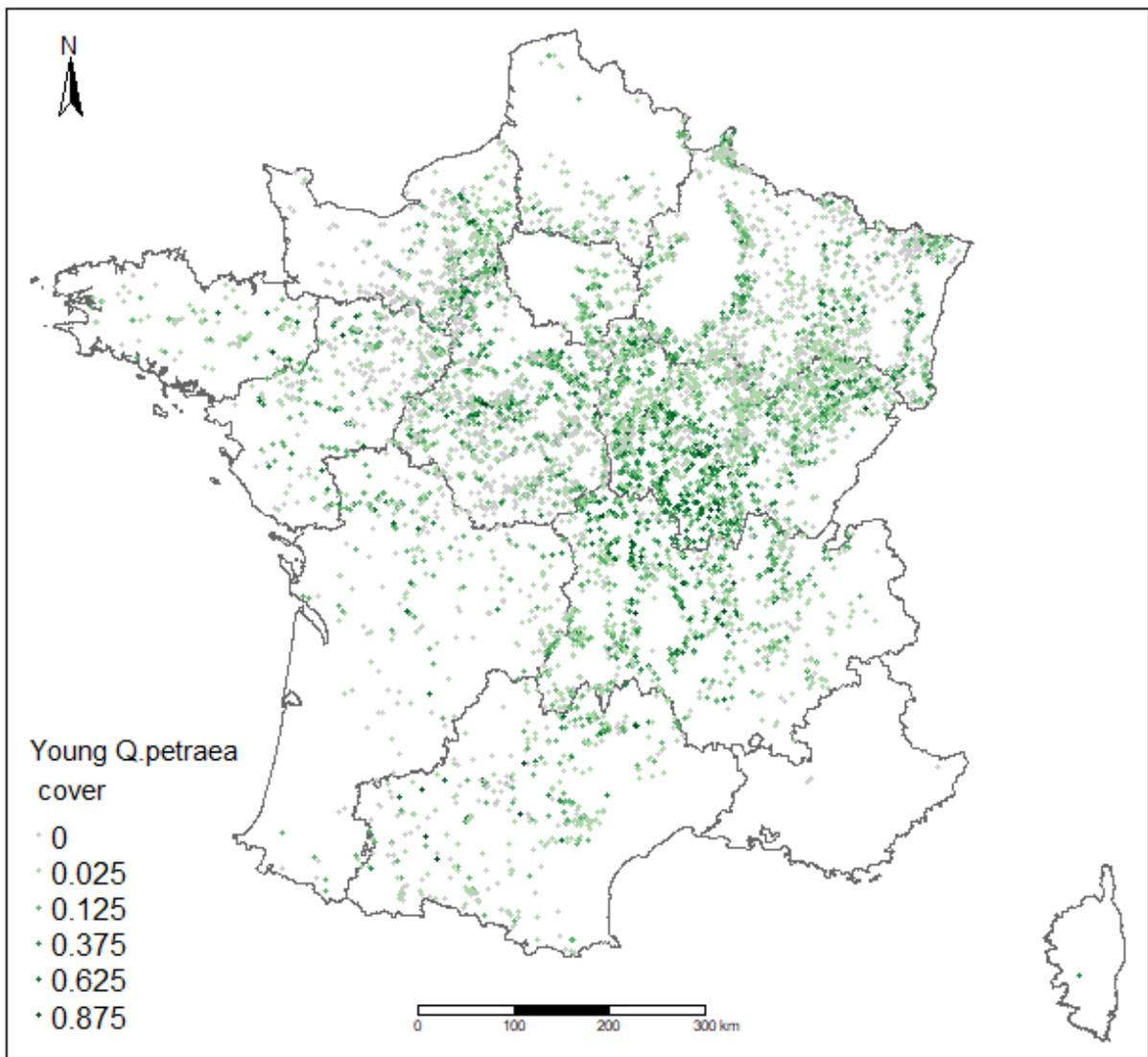
VII.Supplementary materials

Figure S1: Map of the final plot selection and the cover of regenerating Q. petraea in each plots, the outlines are the borders of France and the administrative regions

Table S1: Mean, standard deviation and range of the continuous variables of the regeneration model prior to the centering-scaling procedure. We remind that we can rescale the variable using the equation $X_{unscaled} = X_{scaled} *$ Standard deviation + Mean

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