How much does it take to be old? Modelling the time since the last harvesting to infer the distribution of mature forests in France

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Abstract

Aim

The distribution of mature forests in metropolitan France is poorly known, focuses only on a few sites, and has never been evaluated countrywide. Here, we modelled French forest reserves' time since the last harvesting operation, then inferred the current statistical distribution of mature forests (i.e. forests over 50 years without harvesting) in France.

Location

Metropolitan France

Methods

We used forest inventories from forest reserves and managed forests to calibrate a generalised linear mixed model explaining the time since the last harvesting - a proxy for forest maturity - with selected structural attributes and environmental variables. We then projected this model on the independent National Forest Inventory dataset. We thus obtained an updated estimation of the proportion and a rough distribution of mature forest stands in metropolitan France.

Results

We found that high basal area of very large trees, high volumes of standing and downed deadwood, high diversity of tree-related microhabitats and more marginally diversity of decay stages best characterized the time since the last harvesting. Volumes of stumps and high density of coppices translating legacy of past forest management also distinguished more mature plots. Our projection yielded an estimated 3% of French forests over 50 years without harvesting and a promising proportion for future managed forests if left unharvested.

Main conclusions

Our model showed that the time since the last harvesting is a good proxy for forest maturity in French temperate forest. It highlighted the stand structure attributes that are key in characterising those forests with high conservation values. We found that forests with higher levels of maturity seem to be located in more inaccessible places notably mountainous areas. Our projection gives the first robust statistical estimate of the proportion of mature forests in metropolitan France and may serve to report on the status of mature forests.

Keywords

Forests, maturity, old growth, time since the last harvesting, distribution, proportion, stand structure

1 | INTRODUCTION

Mature forests have a key role in the mitigation of climate change (Achard & Hansen, 2012; Frey et al., 2016), the protection of water resources, the prevention of soil erosion (Brockerhoff et al., 2017; Forest Europe, 2015). They also host a myriad of features with high conservation value promoting biodiversity (Bauhus et al., 2009; Burrascano et al., 2013; Larrieu et al., 2018; Lassauce et al., 2012; Paillet et al., 2015, 2017).

Forest maturity is dependant of tree maturity, which is linked to the tree's biological development and is defined as a combination of tree age and its estimated longevity. Maturity is generally quantified based on the stand's age structure, e.g. a stand is considered mature if its dominant tree species are on average older than half of the species' estimated longevity (Rossi & Vallauri, 2013; Wirth et al., 2009). Although quite straightforward, this definition is problematic in two aspects. First, tree age is best determined by core sampling which is a tedious task. Second, longevity is not a well-known species feature, as it depends on various factors and it might also be altered by the long history of forest management displayed in European forests (Cateau et al., 2015). To work around those issues, international reporting generally uses the time since the last harvesting as a proxy for forest maturity or naturalness (see indicator 4.3 in the State of Europe's forests, Forest Europe 2015). By "harvesting" we mean any human intervention extracting wood biomass from the forest.

Despite the many services they provide, forests undisturbed by man or primary forests remain scarce at the global scale, especially in western Europe and most are, as yet, unprotected (Forest Europe, 2015; Sabatini et al., 2018, 2020). Studies of other high conservation value forests such as mature forests in France are scarce and have targeted, to date, only a few emblematic reserves (Christensen et al., 2005; Mountford, 2002; Pontailler et al., 1997). There is a recognised need for a global map of old-growth forest patches (Chiarucci & Piovesan, 2020), and the "EU Biodiversity Strategy for 2030" explicitly mentions that "it will be crucial to define, map, monitor and strictly protect all the EU's remaining primary and old-growth forests" notably by designating at least 10% of Europe's land to strict protection (European Commission, 2020). The knowledge of the proportion and distribution of mature forests is the first step in facilitating their protection and conservation. Mature forests usually display a long history of harvesting of varied intensity and management regimes. The use of the time since the last harvesting is a way of assessing the degree of naturalness of the forests in question. In France, it is acknowledged that 50 years of abandonment are a minimum for a forest to display sufficient maturity features (MAAPRAT-IFN, 2011). The sole estimation for the proportion of mature forest stands in France dates back to 1993 and was evaluated to about 3% (MAAPRAT-IFN, 2011). This estimation, which has not been updated since, relied more on expertise rather than sound data or rigorous analytical approach. There is therefore a knowledge gap concerning the proportion, distribution and overall characterisation of mature forests that needs to be filled.

The occurrence of mature structural attributes increases in older unmanaged stands, which display more trees with larger diameters at breast height (Burrascano et al., 2013; Heiri et al., 2009; Paillet et al., 2015), an abundance of tree-related microhabitats (Larrieu et al., 2018; Paillet et al., 2017; Winter & Möller, 2008) along with high volumes of deadwood (Harmon, 2009; Siitonen et al., 2000). Those specific structural attributes harboured by mature forests also have high conservation value for biodiversity (Burrascano et al., 2013; Bauhus et al., 2009; Siitonen et al., 2000). More generally, whatever their degree of maturity, these forests also bear the legacy of past – sometimes intensive – forest use in their stand structure, notably silvicultural treatments such as coppice-with-standards (Lassauce et al., 2012).

In this study, we used inventories of forest stand structure issued from forest reserves and managed forests to calibrate a generalised linear mixed model explaining the time since the last harvesting with selected attributes of maturity, herein called structural variables, combined with environmental variables. We hypothesized that time since the last harvesting would be positively influenced by a high volume of large logs and snags and high basal area of very large trees, a high diversity of tree-related microhabitats and decay stages. We expected time since last harvesting to be negatively correlated with the volume of stumps and stem density of medium trees. We also tested other structural variables that would bear witness to past management (e.g. proportion of coppice). We then projected this model on an independent nation-wide dataset issued from the National Forest Inventory. Thus, we obtained an updated estimation of the proportion and a rough distribution of mature forest stands (i.e. abandoned for over 50 years) in metropolitan France.

2 | METHODS

2.1 | Training data

We trained the full model on a dataset issued from a monitoring program that has been implementing forest stand structure description in French forest reserves since 2005, to monitor the evolution of forest attributes. A stratified sample design encompasses the variability within a forest reserve, whose plots can be subject to different management regimes. Indeed, plots comprise strict forests reserves, where harvesting is prohibited, special forest reserves, where management targets specific habitat or species, as well as nature reserves in which harvesting is usually allowed (Table 1). One forest reserve can host up to several hundred plots depending on the size of the represented area and its layout. We kept the plots where the time since the last harvesting was recorded by forest managers, by looking into current or old management plans. Plots from this network show a larger abandonment gradient than French forests in general (see Appendix S1 in Supporting Information).

4 728 plots in 71 reserves were used for modelling (Figure 1). We only kept the plots located by spatial coordinates and classified into one of the six most abundant tree species groups. We did not keep plots over 110 years since the last harvesting as we judged the data too unreliable. We left out reserves with less than 20 remaining plots to ensure sufficient data for the averaging of the random effect (see below). We checked that forests subjected to different management regimes were equivalent in terms of site fertility, therefore not introducing bias in the dataset.

Management regime	Number of plots	Mean basal area of living trees ($m^2.ha^{-1}$)	Mean volume of standing dead trees ($m^3.ha^{-1}$)	Mean volume of downed deadwood ($m^3.ha^{-1}$)	Mean time since the last harvesting (years)
Managed forest reserves	228	34.9	10.6	17.4	30.8

Special forest reserves	2628	27.6	14.5	28.8	31.5
Strict forest reserves	1872	28.4	10.7	20.4	33.6

Table 1: Description of the training dataset (4 728 plots and 71 forest reserves) split by the management regime of plots. Special forest reserves include future forest reserves (not yet designated), national and regional forest reserves and Natura 2000 sites

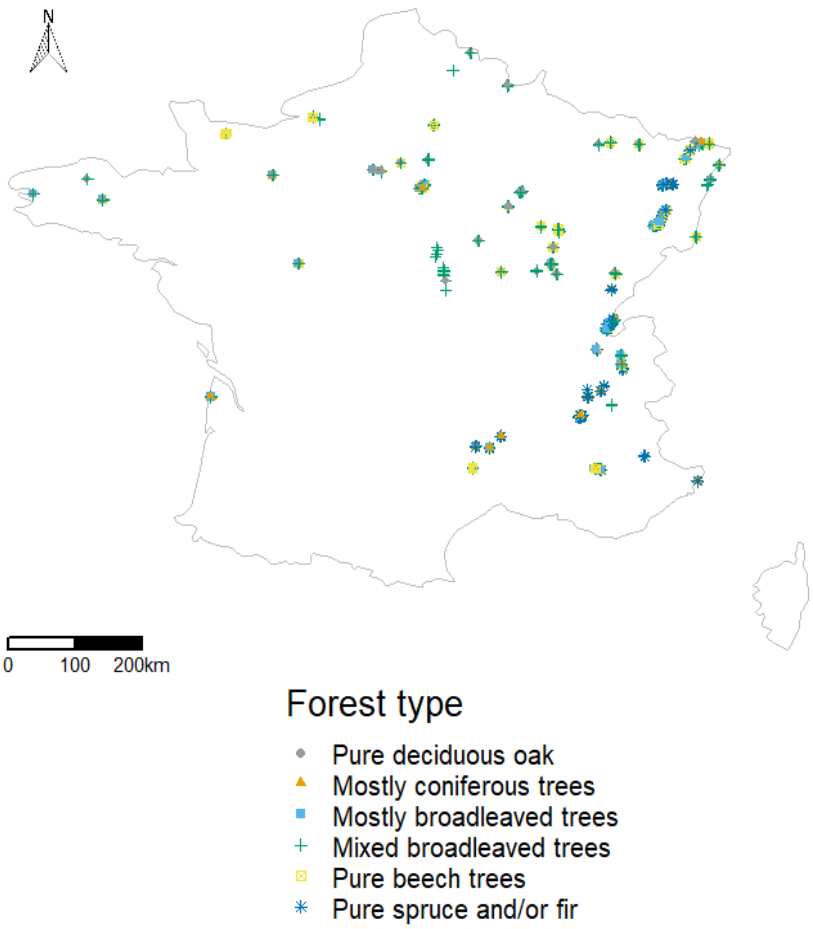

Figure 1: Distribution of the 4728 plots and 71 reserves from the training data kept for modelling. Plots colour and shapes correspond to forest type.

The protocol for the stand structure surveys is detailed in Appendix S2. Living trees with a diameter at breast height (DBH) under 30 cm were all measured within a fixed 10 m radius plot. Larger trees were measured if they were comprised in a 3% angle count sampling (Paillet et al., 2019). Coppice and standard stems were differentiated. Each shoot from the same stump was measured individually. Standing deadwood under 30 cm and standing and downed deadwood over 30 cm in diameter were measured respectively on a 10 m and 20 m radius plot, discriminating between stumps (under 130 cm tall) snags and standing dead trees. Downed deadwood with a diameter under 30 cm was surveyed on three linear 20 m long transects. Decay stage as well as diameter were recorded off all sampled deadwood. Finally, tree-related microhabitat surveys followed the protocol detailed in Paillet et al. (2019) by visually inspecting trees and recording presence of microhabitats. Different microhabitat classifications have been used over the years. Therefore, we created a harmonized classification based on a simplified version of Larrieu et al. (2018)'s microhabitat types to narrow it down to one homogeneous classification.

2.2 | Structural attributes and environmental variables

Among the attributes surveyed, we kept the basal area, volume and stem density of living trees, volume of standing deadwood (stumps, snags and standing dead trees) and volume of downed deadwood (logs). Diversity of decay stages of deadwood and diversity of tree-related microhabitats on living trees and standing deadwood were calculated with the Shannon diversity index (see Table 2). We split observations into diameter classes: small trees [DBH: 17.5, 27.5cm], medium trees [27.5, 47.5], large trees [47.5, 67.5] and very large trees over 67.5 cm.

Table 2: Structural features chosen as candidate variables for modelling the time since the last harvesting of forest plots, and the literature supporting them. "Hypothesis" relates to the expected effect of the structural feature on the time since the last harvesting:
« + » (« - ») means we expect a positive (negative) effect of the feature on the time since the last harvesting
« ++ » means it is a very common feature found in most articles dealing with forest maturity.
This table is based on a literature review, but other attributes were tested considering the specificities of our dataset.

Structural features	Variable	Hypothesis	Source
Living trees	Density and basal area of large and very large trees	++	Paillet et al., (2015) ; Burrascano et al., (2013)
	Density of living trees	+	Portier et al., (2020)
	Total basal area of living trees	+	Heiri et al., (2009)
	Density of medium sized living trees	-	Paillet et al., (2015)
Decay stages	Diversity of decay stages	+	Wirth et al., (2009) ; Winter, Möller, (2008) ; Siitonen et al. (2000)
Tree-related microhabitats	Diversity of tree-related microhabitats	++	Paillet et al., (2017) ; Larrieu et al., (2018) ; Winter, Möller, (2008)
Downed deadwood	Volume of downed deadwood	++	Portier et al., (2020) ; Paillet et al., (2015) ; Heiri et al., (2009) ; Bauhus et al., (2009) ; Vandekerkhove et al., (2009) ; Siitonen et al., (2000)
Standing deadwood	Volume of stumps	-	Paillet et al., (2015) ; Siitonen et al., (2000)
	Volume of standing dead trees and snags	++	Portier et al., (2020) ; Heiri et al., (2009) ; Siitonen et al., (2000)

Diversity of decay stages and tree-related microhabitats were calculated at the plot scale with the Shannon index, one type corresponding to either decay stage associated with tree species and type of deadwood (stump, snag, standing dead tree, downed deadwood) or tree-related microhabitat type associated with species and type of wood (dead or alive).

We extracted environmental variables using plot locations (see Table 3 for the sources):

- edaphic : soil pH, C/N ratio, maximum water holding capacity;
- climatic: mean annual temperature and precipitations;
- topographic: elevation, slope, aspect.

Three other environmental composite variables were also extracted or calculated:

- a site index extracted from Toïgo et al. (2015)'s model predicting tree growth as a function of tree species and environmental variables, to account for site productivity;
- the forested region or "*sylvoécorégions*" accounted for the regional context of the plots. It is a classification of forested areas in metropolitan France within which factors discriminant for forestry and habitat distribution are homogeneous (L'IF n°14, 2011) ;
- the plot's forest type which was created based on an adaptation of an existing French classification, the *BD forêt* version 2 (IGN, 2016a). This classification establishes forest types for plots based on the relative tree cover of each species present on said plot. We approximated tree cover with tree basal area, as tree cover was not accounted for in the reserve inventories. As an example, a plot was considered "pure" when over 75% of the total basal area of the plot was composed of a single species (or a grouping of species with similar characteristics, see Appendix S3 for more details).

Table 3 : Environmental covariates tested for modelling and where they were sourced

Category	Covariate	Units	Source
Topographic	Elevation	meters	BD ALTI v.2.0 : digital terrain model 25 m
	Slope	degrees	Calculated[1] with BD ALTI v.2.0
	cosine(Aspect)	-	Calculated with BD ALTI v.2.0
Climatic	Mean annual temperature (BIO2)	degrees Celsius	WorldClim v.2 (Fick & Hijmans, 2017)
	Total annual precipitations (*BIO12*)	millimetres	WorldClim v.2
Edaphic	Bioindicated soil pH[2]	-	DIGITALIS dataset - Laboratoire SILVA (Université de Lorraine-AgroParisTech-INRA)
	C/N ratio[3]	-	DIGITALIS dataset
	Maximum water holding capacity	Millimetres/cm of soil	DIGITALIS dataset
Forest type		-	Adaptation of the *BD forêt* v.2 (IGN, 2016a)
Forested region	SylvoEcoRegion	-	National Forest Inventory
Site index		-	Toïgo et al. (2015)

[1] « terrain » function from R package *raster* (Hijmans, 2020)
[2] Soil pH is bioindicated using floristic surveys from the National Forest Inventory (NFI) and the EcoPlant database (Gégout et al., 2005) which inventories bioindicator plants and their optimal pH

[3] The C/N (Carbon/Nitrogen) ratio and the maximum water holding capacity are calculated with the measurements from soil surveys from the NFI, and generalised to 500m² resolution maps

2.3 | Statistical methods

We used ascendant variable selection based on AIC (Akaike Information Criterion) scores to select the best model. Considering the large size of our dataset, we chose a conservative five-point AIC threshold instead of the standard two-points threshold. First, we selected stand structure variables, to which we added environmental variables and interactions. We tested first order interactions as well as a few second order interactions that made biological sense. We favoured more specific variables over more generalized ones (e.g. standing and downed deadwood volumes separately vs. total deadwood volume). We checked for correlation and multicollinearity of model covariates, with variance inflation factors (VIF) under five (Zuur et al., 2010).

We validated the final model following Zuur and Ieno, (2016) by plotting residuals against fitted values, variables included and variables excluded from the model. We checked for overfitting with 50 iterations of 10-fold cross validation (i.e. random sets of 10% of the plots were consecutively removed from the training dataset). We looked at estimate variations as well as prediction accuracy by measuring the coefficient of determination "r squared" from the linear regression of predicted versus observed time since the last harvesting (Harrel, 2015). Model robustness was also considered by leaving out reserves one by one and running the model to check for influential or problematic reserves.

2.4 | Prediction on systematic nation-wide dataset

We predicted the time since the last harvesting on a systematic nation-wide National Forest Inventory (NFI) dataset. Each year, about 6500 NFI forest plots are surveyed, recording measurements of stand structure, soil related and floristic variables. We inferred time since the last harvesting on an NFI subset from the 2012 to 2018 survey campaigns, assuming that most of the plots included have not been subjected to major disturbance during this six-year period, so that our estimations can be valid currently. We selected 27 075 plots out of the 38 432 NFI plots available, distributed over the whole French territory using the same selection criteria as for training plots (e.g. forest types, see map Fig. S4.1). Since the sampling design of NFI plots is not homogeneous for all regions and forest types, we weighted the time since the last harvesting estimations by the relative proportion of each forest type per forested region (« *sylvoécorégion* ») to account for this heterogeneity.

For the prediction, the final model was simplified as the NFI data was missing some forest attributes included in the initial model fitted on the learning dataset (e.g. tree-related microhabitats, volume of stumps). We ran a new variable selection process with only the variables available in the NFI dataset, which led to the simplified model. Resulting model estimates were then used for prediction, and 95% confidence intervals were calculated using the variance covariance matrix from the fitted model.

3 | RESULTS

2.1 | Selection and description of the training dataset

In the training dataset, pure spruce and fir plots accounted for 11% of the total plots, pure beech plots accounted for 14%, mixed broadleaved 32%, mostly broadleaved [50 – 75% of broadleaved] 8%, mostly conifers [50 – 75% of coniferous] 9% and pure deciduous oaks 7% (Fig. S4.2). As a comparison, overall French production forests is comprised of 65% of broadleaved forests, 21% of coniferous forests and 11% of mixed forests (MAAF & IGN, 2016). Our modelling dataset has therefore slightly less coniferous (-8%) and slightly more broadleaved (+3%) and mixed forest types (+9%) than the average French forest.

Our training dataset plots displayed a mean volume of deadwood of 25 m^3/ha, which is above the national average for similar forest types - about 18 m^3/ha. The volume of standing deadwood was of 13 m^3/ha for our plots, against 8 m^3/ha for the equivalent National Forest Inventory plots. Finally, the mean volume of living trees on our plots was of 303 m^3/ha, against a national average of 208 m^3/ha.

Our dataset showed an overall decreasing trend for the number of plots as the time since the last harvesting got longer, and especially few plots with abandonment times over 75 years since the last harvesting (Appendix S1). The median time since the last harvesting was of 26 years.

3.2 | Selected model

The volume of stumps at an early decay stage was negatively correlated to the time since the last harvesting (standardised β = -0.051, SE = 0.007) (Table 4). The second most important variable, coppice density, had a slightly milder magnitude and was positively correlated to the time since the last harvesting (β = 0.043, SE = 0.009). Other positively correlated variables, but at a lower magnitude than coppices, were the basal area of very large trees (β = 0.026, SE = 0.008), the volume of standing deadwood, i.e. snags and standing dead trees (β = 0.021, SE = 0.007), the volume of downed deadwood (β = 0.018, SE = 0.007) and the diversity of tree-related microhabitats (β = 0.023, SE = 0.008). Furthermore, diversity of decay stages had a negative influence on the time since the last harvesting, but was only marginally significant (β = -0.012, SE= 0.007).

Concerning the environmental covariates, soil pH had a strong positive influence on the time since the last harvesting (β = 0.195, SE = 0.048). The same went for mean annual precipitations (β = 0.211, SE = 0.040). Precipitations and pH were the two effects with the strongest magnitude.

*Table 4: Standardised estimates, standard errors, and p-values for the variables from the generalised linear mixed model with a gamma distribution, log link and "site" random effect explaining the time since the last harvesting of French forest plots. '***' < 0.001, '**' < 0.01, '*' < 0.05, '(*)' <0.1. Volumes and basal areas are all per hectare values.*

		Standardised estimates (β)	***Standard error (SE)***	***p-value (p)***
	Intercept	3.160	0.093	< 2e-16 ***
Structural covariates	Volume of stumps at early decay stages	-0.051	0.007	2.53e-13 ***
	Coppice density	0.043	0.009	3.29e-06 ***
	Volume of standing deadwood	0.021	0.007	0.001 **
	Volume of downed deadwood	0.018	0.007	0.011 *
	Diversity of tree-related microhabitats	0.029	0.008	3.51e-04 ***
	Basal area of very large living trees	0.026	0.008	0.001 **
	Diversity of decay stages	-0.012	0.007	0.094 (*)
Environmental covariates	Mean annual precipitations	0.211	0.040	1.25e-07 ***
	Soil pH	0.195	0.048	5.34e-05 ***
Interactions	Volume of stumps at an early decay stage : Precipitations	0.025	0.007	6.55e-4 ***
	Downed deadwood : Precipitations	-0.016	0.007	0.025 *
	Basal area of very large trees : Precipitations	-0.024	0.007	4.39e-4 ***
	Diversity of decay stages : Precipitations	-0.019	0.007	0.005 **
	Volume of stumps at an early decay stage : pH	0.013	0.005	0.015 *
	Volume of downed deadwood : pH	-0.012	0.006	0.044 *
	Precipitations : pH	-0.286	0.035	< 2e-16 ***

The estimates also showed that when precipitations or pH increased, the negative effect of the volume of stumps on the time since the last harvesting decreased (closer to zero) (β = 0.025, p = 0.007; β = 0.013, SE = 0.005, respectively) and the positive effect of the volume of downed deadwood decreased (β = -0.016, SE = 0.007 ; β = -0.012,

SE = 0.006, respectively) (Figure 2). Positive effect of the basal area of very large trees also decreased with higher precipitations (β = -0.024, SE = 0.007). Furthermore, the negative influence of the diversity of decay stages on the time since the last harvesting decreased with more abundant precipitations (β = -0.019, SE = 0.007). Finally, when the soil pH increased, precipitations had a decreasing positive effect on the time since the last harvesting (β = -0.286, SE = 0.035).

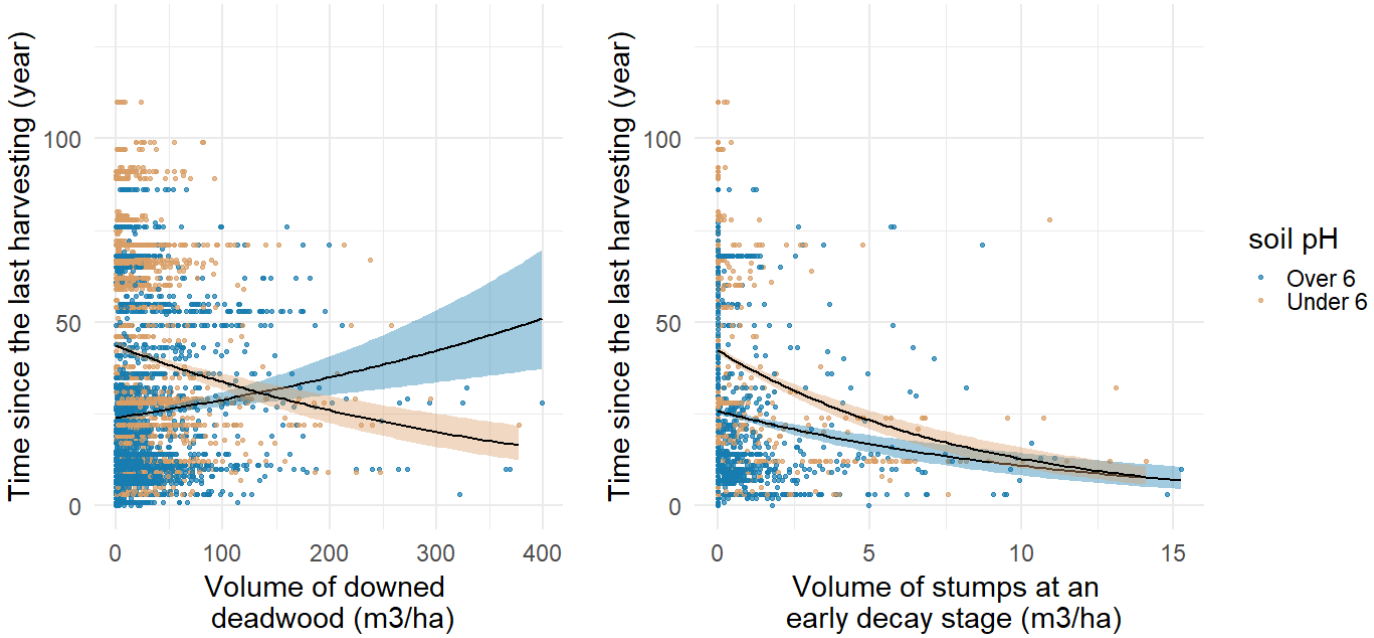

Figure 2: Illustration of the interactions between volume of downed deadwood (β = -0.012, p = 0.044) and volume of stumps at an early decay stage (β = 0.013, p = 0.015) with soil pH. Lines represent a generalised linear model with a log link and 95% confidence interval for pH values over and under 6.

3.3 | Model validation

The distribution of model residuals as a function of the predicted time since the last harvesting showed relative homogeneity, except for a few plots with overestimated time since the last harvesting (Fig. S5. 1). When checked, the residual distribution as a function of the variables both included and excluded from the model showed no noticeable patterns, except for some badly estimated time since the last harvesting on the lower tail of the x axis for the variables “volume of stumps at early decay stages”, “volume of downed deadwood”, “volume of standing deadwood”, and “coppice density”.

Reserves were removed one at a time from the training data to check for any particularly influential sites regarding the estimated values. Cross validation results showed that predictions were relatively constant, with an r^2 linking the predicted values to the observed values varying between 0.756 and 0.900 over 500 simulations (Fig. S5.2). The estimated values were quite stable except for the covariates soil pH and precipitation, as well as for the interaction between those two variables for which estimates slightly varied during simulations, but to a negligible extent (Fig. S5. 3).

3.4 | Model projection on the National Forest Inventory dataset

The simplified model used for projection (see Table S5.1) was comprised of four structural features: the volume of standing and large downed deadwood, coppice density and basal area of very large trees, as well as the two environmental covariates soil pH and precipitations. As for interactions, downed deadwood and basal area of very large trees interacted negatively with precipitations, and coppice density interacted negatively with soil pH. Finally, there was still a negative interaction between soil pH and precipitations.

We predicted an average time since the last harvesting of 26 years for the NFI plots issued from the 2012 to 2018 campaigns (including only the six forest types kept for modelling). According to this projection, about 3.1% of French metropolitan forest has reached or surpassed 50 years of abandonment. 43% of forests were predicted to have a time since the last harvesting of between 26 and 50 years. When varying the maturity threshold from 30 to 300 years of abandonment, we observe the decreasing trend presented in Figure 3a. The confidence interval is very large, around 30 years without harvesting and gets narrower with higher thresholds. There are very few forests predicted above 75 years without harvesting, which is in accordance with the distribution of the time since the last harvesting in the training dataset (French forest reserves). Plots with longer predicted time since the last harvesting are mainly distributed in mountainous regions of eastern France (Vosges, southern Alps and Jura), as well as in the south of France (Pyrenees and Cevennes) and Corsica (Figure 3d).

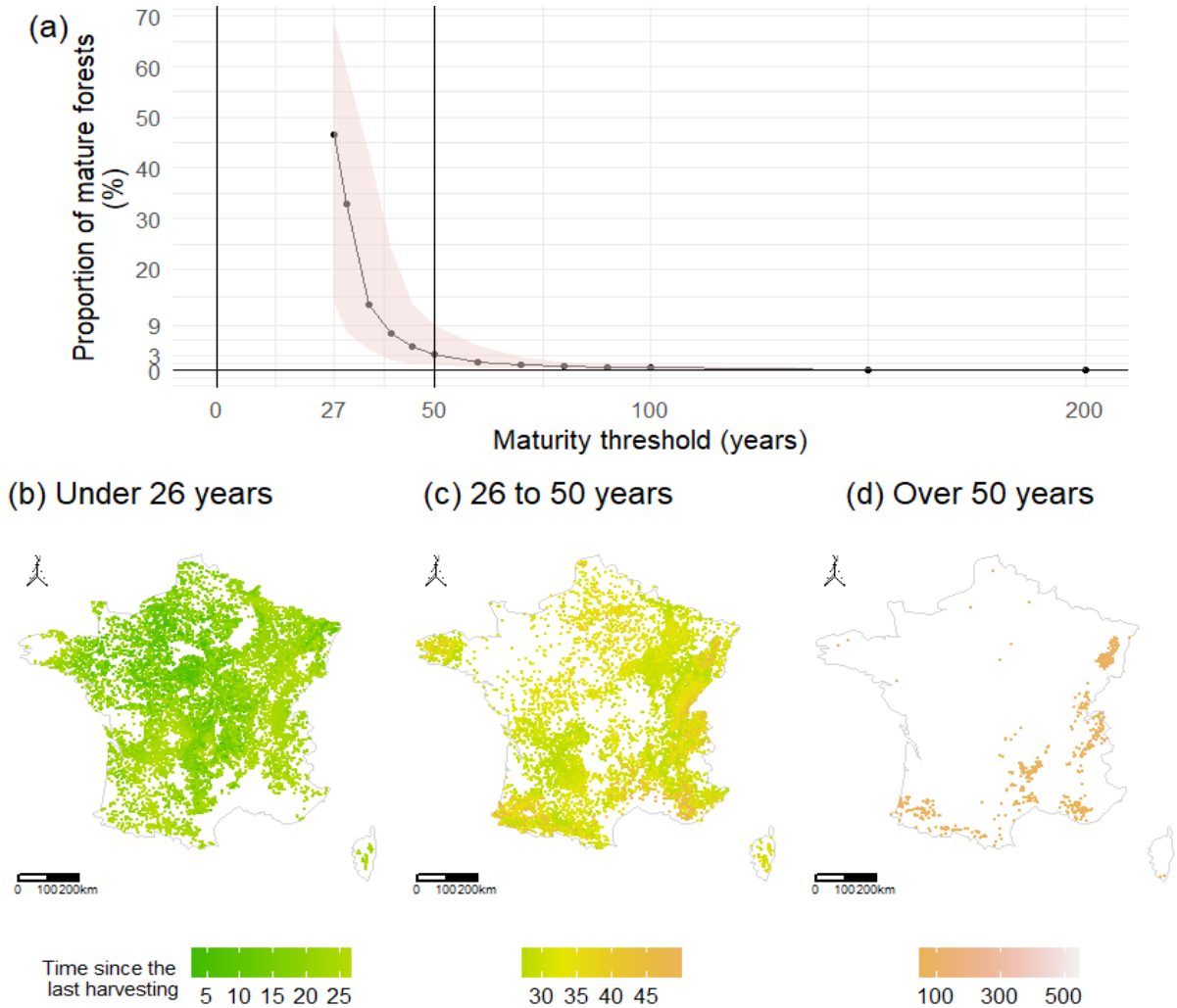

Figure 3: (a) represents how the maturity threshold changes the predicted proportion of mature forests. The ribbon represents the 95% confidence interval. The 50-year threshold (vertical bar) is the one we chose for this study. The confidence interval narrows very fast and at 50 years without harvesting it ranges from 1 to 9%. (b) NFI plots with predicted time since the last harvesting under 26

years, (c) NFI plots with predicted time since the last harvesting between 26 and 50 years, (d) NFI plots with predicted time since the last harvesting over 50 years.

4 | DISCUSSION

We evaluated French forest's state of maturity using time since the last harvesting as a proxy for maturity. We showed that most old growth variables highlighted in the literature did indeed explain time since the last harvesting quite well, and other variables translating legacy of past forest management also played a role in the modelling approach. Our projection gives the first robust statistical estimate of the proportion of mature forests in metropolitan France and may serve to report on the status of mature forests here. Our multivariate modelling approach is quite original, as previous studies (e.g. (Larrieu et al., 2019; Paillet et al., 2015; Vandekerkhove, 2005)) used the opposite reasoning, i.e. modelling structural attributes as a function of the time since the last harvesting.

4.1 | Influence of parameters on the models

As expected, the volume of stumps at early decay stages was negatively correlated with the time since the last harvesting (Paillet et al., 2015; Siitonen et al., 2000). When plots are unharvested for a long period of time, stumps that originated from human disturbance decompose, hence the decline in abundance of fresh stumps in more mature forests. Stumps at an early decay stage are characteristic of recent harvesting, and their absence is a token of longer abandonment times.

Higher basal area of very large living trees is also a known characteristic of mature forests (Bauhus et al., 2009; Burrascano et al., 2013; Paillet et al., 2015). Additionally, larger trees often bear higher diversity of tree-related microhabitats and therefore promote biodiversity at the stand level (Larrieu et al., 2018; Paillet et al., 2017): tree-related microhabitats are the result of tree alteration by biotic and abiotic processes (Larrieu et al., 2018), their presence is thus mostly related to the timespan during which trees are subjected to those processes and thus to time since the last harvesting.

We also expected the diversity of decay stages on standing and downed deadwood to be positively correlated to the time since the last harvesting. Although it was, the observed effect was only marginally significant. Wood decomposition dynamics depends on other factors than time only, such as environmental conditions prone to microorganisms (Herrmann & Bauhus, 2013), the chemical composition of wood (i.e. species), its diameter, micro-climatic conditions as well as edaphic parameters (Heiri et al., 2009; Larrieu et al., 2019; Přívětivý et al., 2018; Zell et al., 2009). Those characteristics were not selected in the model interactions, it therefore seems that there is no univocal correlation between the time since the last harvesting and decay stages, hence the marginal effect observed here. Furthermore, Wirth et al. (2009) suggested that deadwood volume and decay stages could potentially be misleading and could not be taken as sole indicators of maturity. Indeed, deadwood dynamics follow a U-shaped pattern as a result of stand succession (Aakala, 2010), but some punctual disturbances such as storms or droughts can result in locally high amounts of deadwood (Aakala, 2010; Harmon, 2009). In our case, some plots have been subjected to major disturbances, e.g. the 1999 storms that caused damage to a large portion of the French forests, which could still bear the legacy of those events. Our results confirm that deadwood is a key component of mature French forest

reserves, but that the relationship between decay stages and the time since the last harvesting might be more complex than anticipated and would require non-linear relationships or more information on individual plot to better characterise it.

Finally, coppice density was strongly and positively correlated to the time since the last harvesting. Coppicing is a legacy of past management for fuel (heating) and is a practice that has decreased over the last century (IGN, 2016b). Many coppice-with-standards plots have now been abandoned (Unrau et al., 2018) resulting in what Lassauce et al. (2012) call "coppice-with-standard stands with an overmature component". In their study, they also found a significant increase in the basal area of large living trees and downed deadwood for more mature plots with a history of coppicing. This trend seems widespread among stands with a history of coppice-with-standard management. Indeed, (Becker et al., 2017) also noticed that after 40 years of abandonment of coppicing, legacies of this practice still remained in species composition. These mature coppices could constitute another form of mature forests (Lassauce et al., 2012), and it would be interesting to consider coppice density as another indicator for forest maturity, especially considering coppice forests currently represent up to 15% of Europe's forest resources (Unrau et al., 2018).

Environmental context (soil pH and annual precipitations) interacted significantly with stand characteristics in the model, notably interactions between deadwood volumes and pH/precipitations. Plots with higher pH and higher precipitations, where high basal areas and higher stem densities have the potential to be reached sooner, are sites with higher productivity. Nonetheless, we observed a negative interaction between soil pH and precipitations, meaning that overall, productive sites show shorter times since the last harvesting. Rainier plots and/or plots with higher pH conditions show lessened effects of the volume of stumps, the diversity of decay stages, and the volume of downed deadwood and basal area of very large trees on the time since the last harvesting. These interactions could be linked to sites with higher amounts of precipitations being more attractive for harvesting. Surprisingly, elevation was not selected in favour of mean annual precipitations (which increased model AIC of 22 points compared to elevation). Precipitation was nonetheless strongly correlated to elevation (correlation coefficient = 0.9). Precipitations seem to have a broader role and a higher explanatory power than elevation, since they condition both biotic (tree growth, decay rates, soil properties) and abiotic (atmospheric humidity) phenomena.

4.2 | The projected proportion and rough distribution of mature forests

Our model predicted that 3.1% of the national forested area has a time since the last harvesting above 50 years (95% confidence interval ranges from 1 to 9 %). This prediction is valid only for the six forest types kept for modelling (pure beech, pure deciduous oak, mixed broadleaved, pure spruce and/or fir, mostly broadleaved and mostly coniferous types). The prediction is in accordance with the early expertise that had been proposed in 1993. Forested areas abandoned more than 50 years ago seem to occur mostly in more remote and mountainous areas in southern and eastern France (Figure 3c). Indeed, it has been shown that accessibility and favourable topographic, climatic, and soil conditions characterise intensively managed areas, whereas de-intensification and abandonment trends occur in more marginal areas (Levers et al., 2014, 2018; Sabatini et al., 2018). Those highlighted areas therefore

show high conservation potential. More interestingly, our prediction also showed evidence of a large proportion of French forest with abandonment times comprised between 26 and 50 years, with "hotspots" such as Corsica, Brittany and middle-eastern France. Those forests could - in a relatively close future - display interesting conservation attributes which would deserve more attention, especially if some larger continuous and connected areas, particularly interesting for biodiversity, could be restored or managed sensibly (Bauhus et al., 2009; Portier et al., 2020; Sabatini et al., 2020). Indeed, French metropolitan forested surface area has grown since the last century and now occupies 31% of the metropolitan France or about 16.9 million hectares (IGN, 2018). Whereas strict forest reserves compose a mere 0.15% of the French forests (Cateau et al., 2017). Private forests represent 75% of the French forested area (MAAF & IGN, 2016) and considering that the harvesting in these - often small and fragmented - properties is usually low or inexistent, they could potentially account for this large portion of "in between" forest in our prediction. Those areas are not accounted for in most studies and conservation decisions. If we consider that each country is equally responsible for contributing to the "EU Biodiversity Strategy for 2030" goal for 10% of strictly protected land (European Commission, 2020), then France, with 3% of estimated mature forest – not all protected and probably quite fragmented - still has a long way to go. But the recognition that areas with high potential for achieving this goal exist and are identified, is a first step forward.

4.3 | Limits and perspectives to our modelling approach

The distribution of mature forests predicted by our model should not be taken as a precise map but as an overview of the state of French forests to this day. Indeed, the plot density is quite scarce with 27 075 plots for the whole French territory. The time since the last harvesting used for training the model could introduce some error, since the older the last known harvesting the more uncertain the estimation of the time since the last harvesting. Also, our model did not consider the intensity of harvesting (e.g. volume of wood harvested, type of management), although this knowledge would probably further refine our predictions. Additionally, removing covariates for the predictive model probably hampers the performance of the prediction, which would be more precise with information about volume of stumps and tree-related microhabitats. Nonetheless, large areas with potential for hosting forests with high conservation value were highlighted, and further validation, e.g. by crossing our findings with maps and data on previously studied mature sites, along with field validation, would enable us to refine our knowledge of the distribution of more mature forests, and evaluate the precision of our predictions.

The overall results of our study are encouraging, in the sense that a large portion of the French forest has potential to attain interesting states of maturity in a close future and therefore to contribute to the race against climate change, by acting as carbon and biodiversity pools (Portier et al., 2020; Sabatini et al., 2020; Carey et al., 2001). We expect our results to be used in ensuring that the existing 3% of mature forest are properly managed and protected, and that our work will constitute a stepping-stone to further refining our knowledge of the state of maturity of French forests.

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6 | DATA ACCESSIBILITY

The two datasets we worked with for this study were the Nature Forest Reserve data (PSDRF), ONF-RNF and the French national forest inventory data (raw data, annual surveys from 2005 to 2018, https://inventaire-forestier.ign.fr/spip.php?rubrique159).

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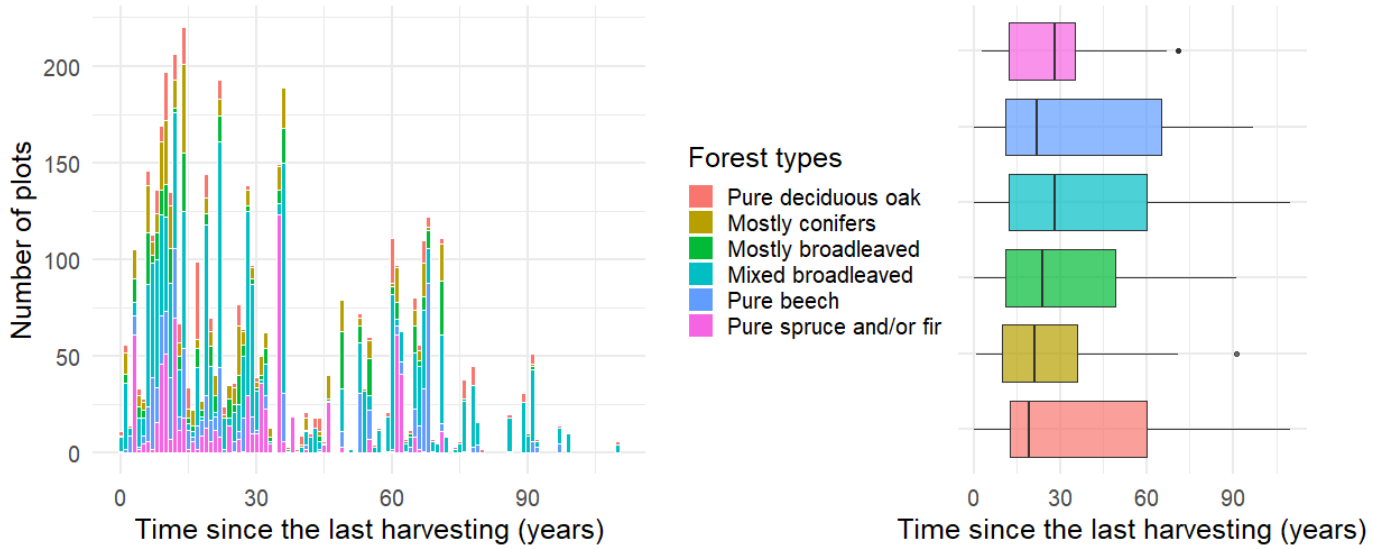
8 | SUPPLEMENTARY MATERIALS

Appendix S1: Distribution of time since the last harvesting of the PSDRF plots coloured by forest type.



Appendix S2: Protocol for the French nature forest reserves stand structure description

On each circular plot, forest stand structure was characterized using the following protocol (Paillet et al., 2015, 2019):

- All living trees larger than 7.5 cm were measured considering, by checking if they issued from the same base or not, the difference between coppice and standard trees.
- For living trees with a diameter at breast height (DBH) above 30 cm, a fixed angle plot method was used to select the individuals within a relascopic angle of 3%. Practically, this meant that sampling distance was proportional to the apparent DBH of a tree. For example, a tree with a DBH of 60 cm was included in the sample if it was within 20 m of the center of the plot. This technique allowed us to better account for larger trees at a small scale.
- All other variables were measured on fixed-area plots. Within a fixed 10-m (314 m2) radius plot, the diameter of all living trees and standing deadwood (stumps, snags (height > 130 cm), standing dead trees) was measured from 7.5 to 30 cm DBH.
- Within a 20-m radius (1256 m2), all standing deadwood and downed deadwood (logs) with a diameter > 30 cm were recorded.
- Downed deadwood (logs) with a diameter under 30 cm was recorded along three separate 20 m long radial transects (every 127°).
- All standing trees (alive and dead) were visually inspected for the recording of tree-related microhabitats. Observers attended a training session and were given a field guide with pictures to help them better determine microhabitat types and detailed criteria to include in the inventories.

On every piece of deadwood decay stage of the bark and of the wood were recorded, respectively on a scale of one to four and one to five. Whenever possible, all trees, both alive and dead, were identified to species level.

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Appendix S3: Table presenting the classification used to derive plot forest types from plot species composition. This classification is inspired from the "BD forêt version 2" classification, which is based on the species' relative tree cover. We chose to use tree basal area instead, as tree cover was not unknown in our dataset. Each plot forest type is defined as the proportion of a specific species' basal area on the said plot. Therefore, plots are called "pure" if over 75% of the total plot basal area is occupied by one (or two in a few cases) species. We then called mixed any plots where a mixture of two or more species occupied over 75% of the total basal area. Finally, the last two broader forest types correspond to plots where a true mixture of tree species occur and the only definition we can give is if either broadleaved or coniferous trees are preponderant. In the end, only the six highlighted types out of the 22 included enough plots to be kept for modelling.

Code *BD forêt version 2*	**Class**	**Label**	**Definition**	**Species**
FF1G01-01	Broadleaved	Pure deciduous oak	Basal area of deciduous oaks ≥ 75%	*Quercus cerris, Quercus rosacea, Quercus robur, Quercus pubescens, Quercus rubra, Quercus petraea, Quercus tauza*
FF1G06-06	Broadleaved	Pure evergreen oak	Basal area of evergreen oaks ≥ 75%	*Quercus suber, Quercus ilex*
FF1-09-09	Broadleaved	Pure beech	Basal area of beech trees ≥ 75%	*Fagus sylvatica*
FF1-10-10	Broadleaved	Pure chestnut	Basal area of chestnut trees ≥ 75%	*Castanea sativa*
FF1-14-14	Broadleaved	Pure black locust	Basal area of black locust trees ≥ 75%	*Robinia pseudoacacia*
FF1-49-49	Broadleaved	Other pure broadleaved trees	Basal area of a single other broadleaved species ≥ 75%	Ash tree (*Fraxinus sp*), Maple trees (*Acer sp*), Birch (*Betula sp*), Charm (*Carpinus betulus*), Alder (*Alnus sp*), Hazel tree (*Corylus sp*)
FF1-00-00	Broadleaved	Mixed broadleaved trees	Combined basal area of at least two broadleaved species that are not either deciduous oak or evergreen oak ≥ 75% (without any single species occupying a basal area ≥ 75%)	*Fagus sylvatica, Castanea sativa, Robinia pseudoacacia*, Ash trees (*Fraxinus sp*), Maple trees (*Acer sp*), Birch (*Betula sp*), Charm (*Carpinus betulus*), Alder (*Alnus sp*), Hazel tree (*Corylus sp*)
FF2-51-51	Coniferous	Pure maritime pine	Basal area of maritime pine ≥ 75%	*Pinus pinaster*
FF2-52-52	Coniferous	Pure scots pine	Basal area of scots pine ≥ 75%	*Pinus sylvestris*
FF2G53-53	Coniferous	Pure laricio pine and/or black pine	Basal area of laricio pine and/or black pine ≥ 75% (can be either a mixture of both species or each species individually)	*Pinus nigra*

Code *BD forêt version 2*	Class	Label	Definition	Species
FF2-57-57	Coniferous	Pure Aleppo pine	Basal area of Aleppo pine ≥ 75%	*Pinus halepensis*
FF2G58-58	Coniferous	Pure mountain pine and/or swiss pine	Basal area of laricio pine and/or black pine ≥ 75% (can be either a mixture of both species or each species individually)	*Pinus mugo, Pinus cembra*
FF2-81-81	Coniferous	Other pure pine	Basal area of another pine species ≥ 75%	*Pinus mugo, Pinus pinea*
FF2-80-80	Coniferous	Mixed pine	Combined basal area of at least two pine species ≥ 75% (without being a mixture of black pine and laricio pine or of mountain pine and swiss pine and without any single species occupying a basal area ≥ 75%)	*Pinus pinaster, Pinus sylvestris, Pinus nigra, Pinus halepensis, Pinus mugo, Pinus cembra, Pinus mugo, Pinus pinea*
FF2G61-61	Coniferous	Pure spruce and/or fir	Basal area of spruce and/or fir ≥ 75% (can be either a mixture of both species or each species individually)	*Abies cephalonica, Abies nordmanniana, Abies grandis, Abies alba,* *Picea abies, Picea sitchensis*
FF2-63-63	Coniferous	Pure larch trees	Basal area of larch trees ≥ 75%	*Larix decidua*
FF2-64-64	Coniferous	Pure douglas fir	Basal area of Douglas firs ≥ 75%	*Pseudotsuga menziesii*
FF2-91-91	Coniferous	Other pure coniferous trees	Basal area of a single other coniferous species ≥ 75%	Cedar trees *(Cedrus atlantica, Cedrus libani, Thuja sp)* Cypress *(Cupressus sp)* Yew *(Taxus baccata)*
FF2-90-90	Coniferous	Other mixed coniferous trees	Basal area of a mixture of at least two coniferous species which are not either a mixture of pine trees or spruce and fir ≥ 75% (without any single species occupying a basal area ≥ 75%)	Spruce, fir, cedar, cypress, yew (see above)
FF2-00-00	Coniferous	Mixed pine and other coniferous trees	Basal area of a mixture of at least a pine tree and another coniferous species ≥ 75% (without any	*All coniferous species above*

Code *BD forêt version 2*	Class	Label	Definition	Species
			single species occupying a basal area ≥ 75%)	
FF31	Broadleaved /Coniferous	Mostly broadleaved trees (mixture of broadleaved and coniferous trees)	50% ≤ Basal area of broadleaved trees ≤ 75%	All broadleaved and coniferous species above
FF32	Broadleaved /Coniferous	Mostly coniferous trees (mixture of broadleaved and coniferous trees)	50% ≤ Basal area of coniferous trees ≤ 75%	All broadleaved and coniferous species above

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Appendix S4 : maps and graphs of the two datasets

Fig. S4.1: Map of the 27 075 National Forest Inventory plots from the 2012 to 2018 campaigns in metropolitan France which served as the spatial prediction dataset. Plots are coloured by forest type.

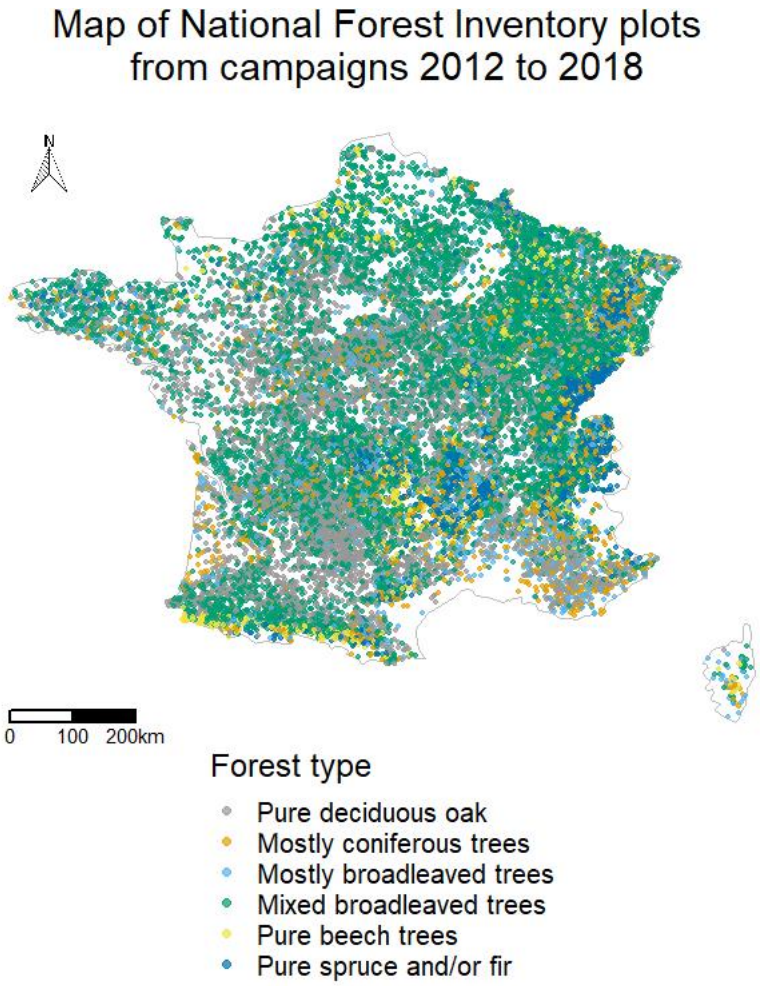
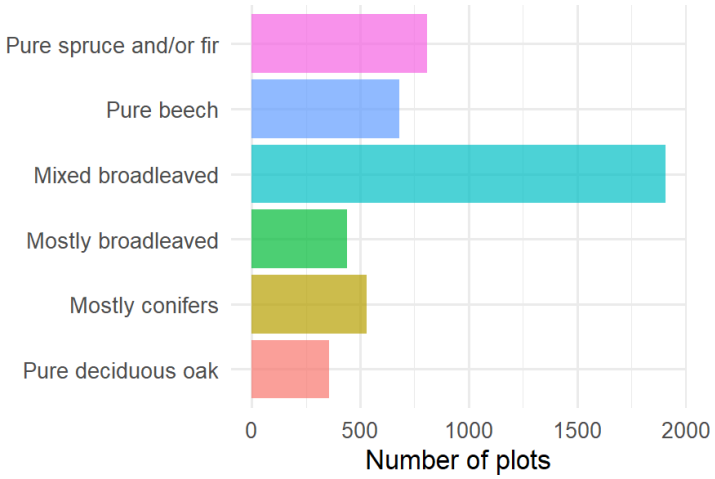


Fig. S4.2: Six most abundant forest types among the 4728 ploys kept from the PSDRF data
" Pure » types: species group represents over 75% of total basal area,
« Mostly » types: > 50% of total basal area,
« mixed » types: > 75% of total basal area



Appendix S 5 : model validation

Fig. S5. 1: Distribution of the Pearson residuals from the generalised linear mixed model explaining the time since the last harvesting using structural features and environmental variables. The trend is satisfyingly neutral, although a few plots have overestimated time since the last harvesting.

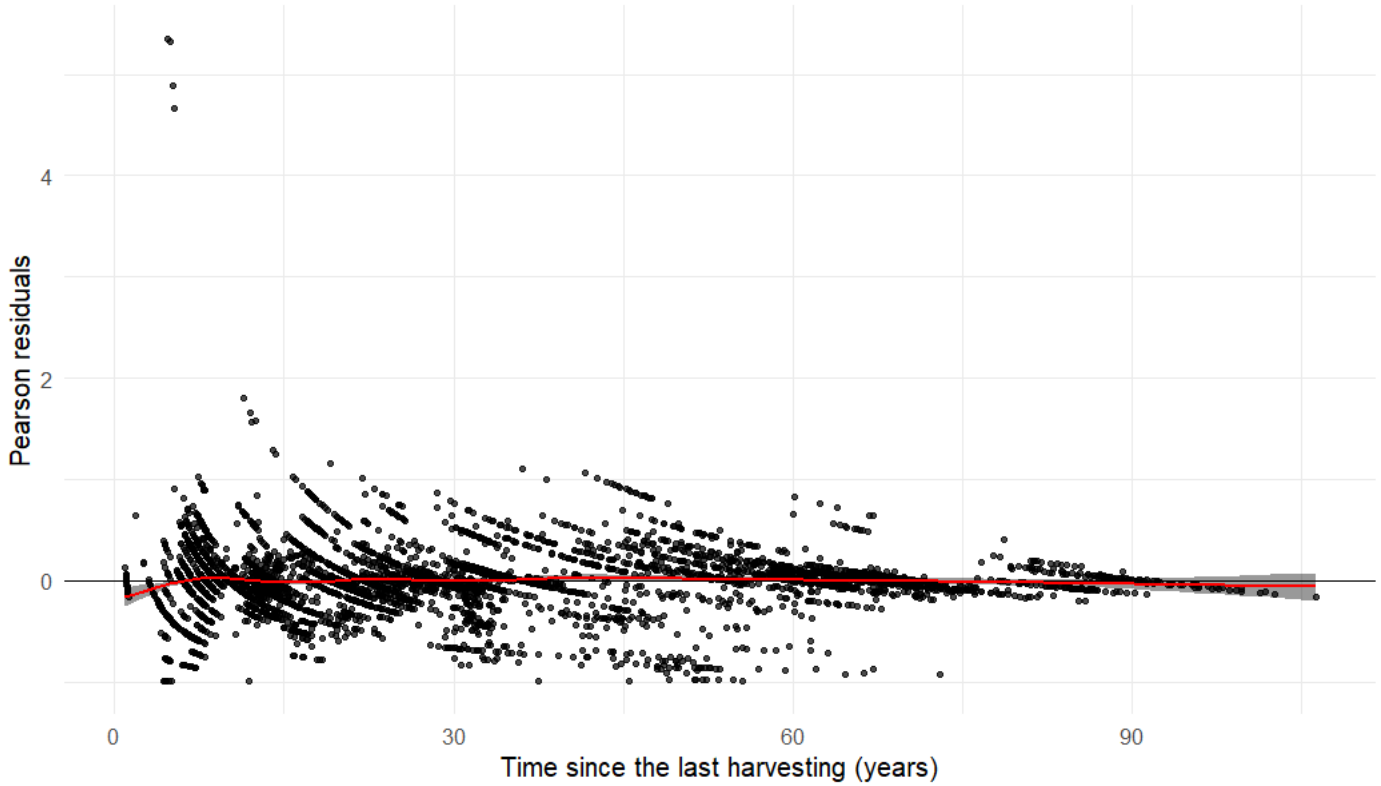


Fig. S5.2: Distribution of the values of the correlation coefficient r squared over the 500 simulations of cross validation. The r squared varied between 0.756 and 0.900.

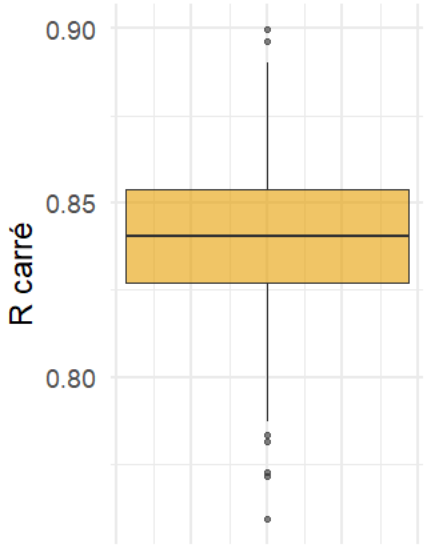


Fig. S5. 3: Estimate variation (mean and standard deviation) after 500 cross validation simulations.

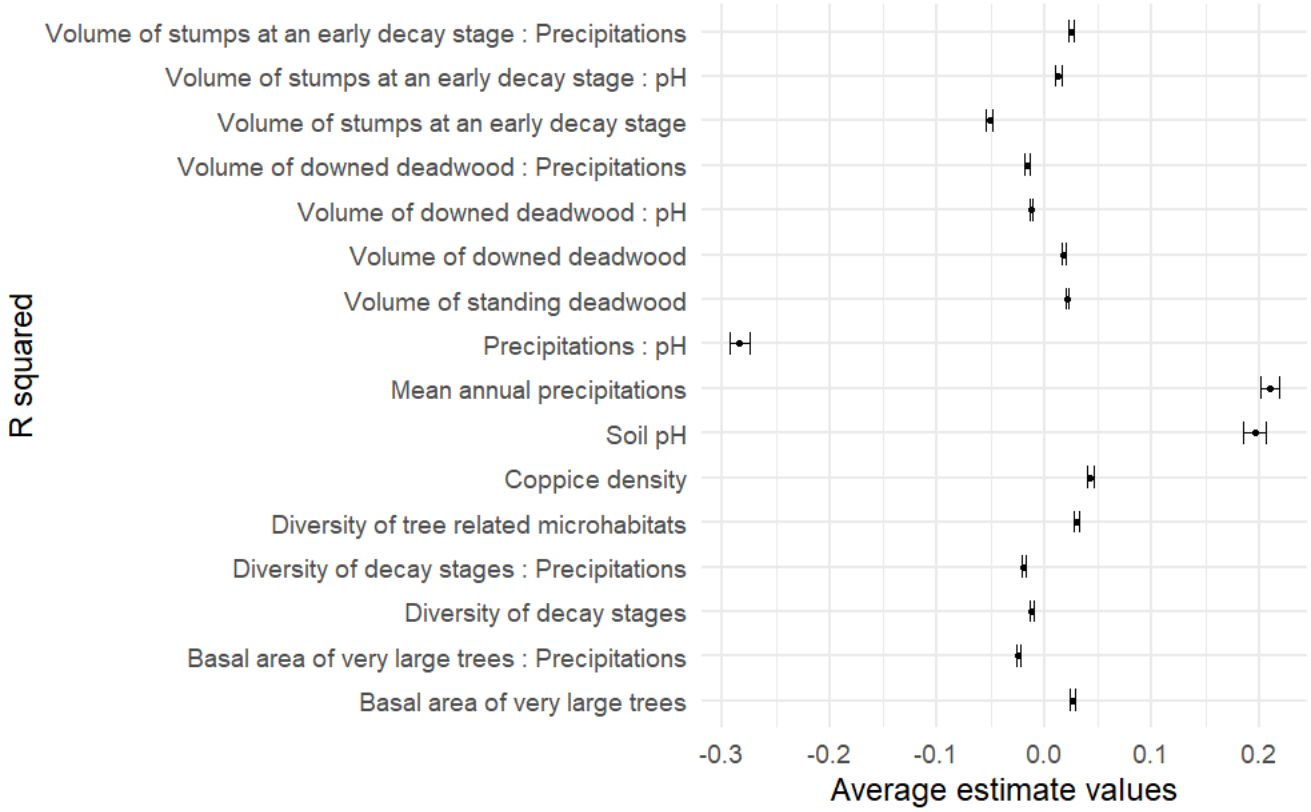


*Table S5.1: Standardised estimates, standard errors and p-values rounded to three decimal places for the variables from the simplified generalised linear mixed model with a gamma distribution, log link and "site" random effect explaining the time since the last harvesting of French forest plots. '***' < 0.001, '**' < 0.01, '*' < 0.05, '(*)' <0.1. Volumes and basal areas are all per hectare values.*

		Standardized estimates (β)	***Standard error***	***p-value (p)***
	Intercept	3.172	0.095	< 2e-16 ***
Structural features	Coppice density	0.052	0.006	8.71e-8 ***
	Volume of standing deadwood	0.024	0.006	1.36e-4 ***
	Volume of large downed deadwood	0.020	0.006	1.48e-3 ***
	Basal area of very large trees	0.029	0.008	2.89e-04 ***
Envrionmental covariates	Mean annual precipitations	0.244	0.040	1.17e-09 ***
	Soil pH	0.191	0.049	9.08e-05 ***
Interactions	Large downed deadwood : Precipitations	-0.010	0.006	7.98e-2(*)
	Basal area of very large trees : Precipitations	-0.025	0.007	2.65e-04 ***

Coppice density : pH	-0.018	0.011	9.59e-2 (*)
Precipitations : pH	-0.324	0.034	< 2e-16 ***