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1 Title: Temporal trends in tree defoliation and response to
2 multiple biotic and abiotic stresses

3

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24 ABSTRACT

25 The vitality of forests depends on multiple biotic and abiotic stresses that can act in an interactive
26 way. Tree defoliation levels are therefore subject to long-term changes and shorter-term hazards
27 that need to be monitored in the context of ongoing climate change. In this study, we analysed the
28 combined effects of drought, insect attack and tree nutritional status on the level of defoliation in
29 three major hardwood species in Europe: European beech (*Fagus sylvatica*), sessile oak (*Quercus*
30 *petraea*) and pedunculate oak (*Quercus robur*). The forest condition data set was collected in the
31 long-term intensive monitoring network in France (RENECOFOR). The average level of defoliation
32 observed was 20% but varied considerably between plots and trees. From 1997 to 2015, beech
33 defoliation worsened by 10% while oak defoliation stabilized over time. For the three tree species,
34 crown defoliation was generally higher in the event of insect attack (increased by 2.6% to 7.5%
35 depending on the tree species) and under drought (increased by 5.9%), while the effect of the tree
36 nutritional status was less consistent (from – 5.6% to +10%) these factors acting synergistically. This
37 study highlights the fact that the different stresses a tree species undergoes act in a complex and
38 interactive way, with species-specific responses. In a context of increasing abiotic and biotic stresses,
39 their combined analysis appears to be a necessity at a time when forest owners need to adapt their
40 management to cope with climate change, particularly through the choice of tree species to be
41 favoured in the future.

42

43 KEYWORDS

44 drought; pest insect; foliar nutrients; die-off; interactions; temperate forest; crown defoliation; ICP

45 Forests; *Fagus sylvatica*; *Quercus robur*; *Quercus petraea*

46 1.INTRODUCTION

47 Coping with climate change is a major challenge for forest managers because the longevity of trees
48 limits the capacity for rapid renewal of the species or varieties best adapted to the new abiotic
49 constraints. To adapt existing forests or plan future plantations, they need an integrative vision of the
50 effects of the multiple risks to which forest stands are exposed. Climate change has multiple
51 important and interacting impacts on forests globally (McDowell et al., 2020). Forests are the
52 terrestrial ecosystem that contributes the most to carbon sequestration worldwide (Bonan, 2008;
53 Janssens, 2003; Pacala, 2001; Piao et al., 2009) but global warming could alter drastically functioning,
54 reducing primary productivity and thus carbon sequestration (Lindner et al., 2010). Forest growth is
55 favoured by an increase in CO² concentration (Norby et al., 2005; Walker et al., 2019), moderate
56 increase in temperature, and in nitrogen deposition (Myneni, Keeling, Tucker, Asrar, & Nemani,
57 1997) as far as the other needs in water and nutrients are satisfied. Conversely, above a critical value,
58 an increase in temperature and atmospheric compounds such as ozone, nitrogen and sulfur is
59 expected to be detrimental to forest primary productivity through altered photosynthesis, reduced
60 leaf area and leaf longevity (Ainsworth, Yendrek, Sitch, Collins, & Emberson, 2012; Juknys et al.,
61 2014; Magill et al., 2004; Wittig, Ainsworth, Naidu, Karnosky, & Long, 2009).

62 However, these long-term trends can be affected by catastrophic events occurring at shorter
63 time scale. Climate change is indeed characterized by an intensification of abiotic (fire, windstorms,
64 drought) and biotic (insects and pathogens) hazards, leading to severe alteration of tree vitality (Seidl
65 et al., 2017). In particular, drought episodes have intensified in severity and frequency (Diffenbaugh
66 et al., 2017) and are predicted to increase further in the future (Lehner et al., 2017; Ruosteenoja,
67 Markkanen, Venäläinen, Räisänen, & Peltola, 2018). This highlights the need to analyse past long-
68 term changes in forest conditions along with short-term variations due to biotic and abiotic
69 perturbations in order to better predict the complex effects of climate change on forest ecosystem
70 productivity and vitality (Matyssek et al., 2012).

71 Tree growth and defoliation are important indicators of tree vitality (Dobbertin, 2005) since
72 long interruption of tree growth or intense defoliation represent relevant indices of severe decline or
73 imminent death of trees. Numerous studies have documented long-term changes in forest growth as
74 well as biotic and abiotic determinants of tree growth through dendrochronological approaches
75 (Charney et al., 2016; Graumlich, 1991; Piovesan, Biondi, Filippo, Alessandrini, & Maugeri, 2008), but
76 similar studies on tree defoliation are less common as they require long-term monitoring of
77 permanent plots. In Europe, no clear pattern emerged from observation of long-term trend in tree
78 defoliation, the overall mean defoliation remains around 20% and changes in defoliation over time
79 are not significant or show idiosyncratic responses of tree species (Michel, Seidling, Prescher, &
80 editors, 2018) suggesting that local scale might be more relevant to detect anomalies (de la Cruz et
81 al., 2014; Johannes Eichhorn et al., 2005; Ferretti et al., 2014; Popa et al., 2017; Sousa-Silva et al.,
82 2018). Moreover tree defoliation has long been considered a relevant marker of environmental
83 changes due to its sensitivity to abiotic factors such as temperature, precipitation, wind, ozone
84 concentration, soil pH and fertility (Bussotti & Ferretti, 2009; Bussotti, Prancrazi, Matteucci, &
85 Gerosa, 2005; Drobyshev, Anderson, & Sonesson, 2007; Ferretti et al., 2014). Biotic factors such as
86 forest pests (e.g. defoliators), pathogens (e.g. leaf rusts), wild game but also tree competition (e.g.
87 stand density and composition) are also known to cause tree defoliation (Ferretti et al., 2014;
88 Pollastrini et al., 2016). Tree defoliation can thus be used as an integrative marker of multiple
89 interactive stresses (Wim De Vries et al., 2000). It is thus surprising that only few studies investigated
90 the combined and interactive effects of biotic and abiotic stresses on tree defoliation.

91 Many studies have already reported tree mortalities caused by severe droughts around the
92 world (Allen et al., 2015; N. McDowell et al., 2018; Meir et al., 2018) and this is worsening as climate
93 becomes hotter and drier (van Mantgem et al., 2009). Water stressed trees are also known to be
94 more prone to many pest insects and disease damages (Bréda, Huc, Granier, & Dreyer, 2006; Jactel et
95 al., 2012). Not only drought but also higher temperatures can enhance insect population dynamics
96 (Jactel, Koricheva, & Castagneyrol, 2019), as shown by the largest bark beetle (*Dendroctonus*

97 *ponderosa*) outbreak ever observed in North America (Carroll, Taylor, Régnière, & Safranyik, 2003)
98 after a series of mild winters. Several hundred million m³ of trees were killed, which transformed the
99 forest ecosystem into a net source of atmospheric carbon (Kurz et al., 2008). Those examples
100 illustrate the fact that multiple biotic and abiotic stresses can cascade or synergize to alter forest
101 vitality.

102 Tree health is also closely linked to soil fertility, disequilibrium in soil nutrients and
103 atmospheric depositions. Deficit or excess in a particular element may affect tree growth or crown
104 condition. For example, high crown transparency of *Picea abies* has been related to deficiency in
105 foliar potassium (K), nitrogen (N), phosphorus (P) and iron (Fe) nutrients (Ewald, 2005). Fertilization
106 trials showed that adding potassium could increase foliar K concentration and decrease defoliation in
107 young balsam fir (Ouimet & Moore, 2015). Moderate nitrogen atmospheric deposition can exert a
108 fertilising effect, enhancing tree growth and decreasing crown defoliation (Thimonier et al., 2010).
109 Conversely, high nitrogen deposition may cause nitrate leaching (Thimonier et al., 2010) and soil
110 acidification (Flückiger & Braun, 1999) affecting tree health. High level of foliar nitrogen
111 concentration has been associated with increased tree sensitivity to frost, drought, pest and diseases
112 (W De Vries et al., 2014; Flückiger & Braun, 1999). Moreover, the fertilising effect of nitrogen supply
113 can be sustained only if other critical nutrients are not limiting. For example, nitrogen addition along
114 with deficit in phosphorus results in unbalanced N:P ratio (Flückiger & Braun, 1999), which can
115 reduce tree growth (Braun, Thomas, Quiring, & Flückiger, 2010) and increase crown defoliation
116 (Veresoglou et al., 2014). In European forests, high nitrogen deposition are currently associated with
117 unbalanced foliar N:P ratio (W De Vries et al., 2014), which is widely used as marker of nutrition
118 limitation in trees (Güsewell, 2004; Tessier & Raynal, 2003). Deficit or excess in foliar nutrients might
119 thus predispose or amplify climate change effects and biotic damages affecting tree vitality.

120 Interactions between those multiple driving stress-factors of tree health were rarely tested
121 (but see Seidl et al., 2017), yet studies are accumulating that show tree declines under more stressful
122 conditions. To make a step forward in the understanding of these interactions, we conducted a

123 thorough analysis of tree defoliation data collected during a time series of 18 years in a network of
124 forest monitoring plots (belonging to ICP Forests Level II) in France. Focusing on three major forest
125 species in Europe, European beech (*Fagus sylvatica*), pedunculate oak (*Quercus robur*) and sessile
126 oak (*Quercus petraea*), our main objectives were:

- 127 1. to characterize the long-term change in tree defoliation;
- 128 2. to investigate the interactive effects of local climate, foliar N:P ratio and insect damage on tree
129 crown defoliation.

130 2. MATERIAL AND METHODS

131 2.1 Study sites

132 Tree health data and forest stand characteristics were retrieved from the database of the
133 RENECOFOR network, which is dedicated to the long-term monitoring of forest vitality in France
134 (Ulrich, 1995). The network was set up in 1992 to cover major European tree species growing in
135 temperate forests of France. In this study, we focused on three broadleaved species: sessile oak
136 (*Quercus petraea*), pedunculate oak (*Quercus robur*) and European beech (*Fagus sylvatica*), because
137 they exhibited more defoliation than coniferous species and they were present in a sufficient number
138 of plots to allow reliable statistical analyses (plots characteristics are summarized in Table 1). The
139 monitoring plots were initially established in healthy and preferably even-aged stands dominated by
140 one main tree species (Ulrich, Vanni re, Duplat, Demolis, & Guyon, 1994). In order to have full time
141 series and plots in comparable ecological conditions, we removed from our dataset the plots
142 damaged by the 1999 storms and the beech plots in the few highland sites.

143 2.2 Defoliation

144 The defoliation assessments started in 1994 on 52 dominant trees of the main tree species in each
145 plot. Then, every summer (from July 1st to August 31st), trained observers recorded defoliation using

146 classes of 5%, in comparison to a healthy referent tree nearby in the same plot, following ICP Forests
147 manual (Eichhorn et al., 2010). In particular, observers focused on defoliation in the upper and lateral
148 parts of the crown, which were not shaded. Preliminary data analysis revealed for some plots a sharp
149 increase in defoliation from 1994 to 1997. This was attributed to a methodological bias due to a
150 progressive improvement of observers' skills in the early years of the monitoring (Ferretti et al.,
151 2014). We thus decided to analyze tree defoliation from 1997 to 2015. Records from 2003 were
152 missing due to budget shortage.

153 In addition to defoliation, observers recorded the plausible causes and amount of leaf damage,
154 according to the French Forest Health Department's reference database, in the spring and summer of
155 the same year. Damage assessment protocols have changed over time. For example, the number of
156 possible causes and levels of damages increased with time. To ensure data comparability across time,
157 we decided to base our analyses on the presence/absence of insect damage instead on damage
158 intensity and to focus on the three main causes of damages (see Table A1 for more details on the
159 types of insects causing damage by tree species studied and by year).

160 To avoid any uncertainty about damage identification (e.g. confusion between insect and fungal
161 pathogen damage on leaves) we defined two categories of trees: those with the "presence of insect
162 damage" when at least one insect damage was reported in the absence of any other type of damage
163 and those with "absence of pest damage" when tree did not present any type of damage or
164 presented only traces of damage (Table 1).

165 2.3 Foliar nutrient analyses

166 We characterized the nutritional status of trees by considering two major limiting nutrients for tree
167 growth in French forests: nitrogen (N) and phosphorus (P) and their ratio N:P (Table 1). Reference
168 thresholds for tree foliar nutrients in Europe (Mellert & Göttelein, 2012) were used to define the
169 balanced or unbalanced foliar nutrient status of a tree (Table 1). The lower threshold for foliar N:P
170 ratio was calculated using the lowest threshold of foliar N content and the highest threshold of foliar

171 P content, the upper threshold for foliar N:P ratio was derived from the highest threshold of foliar N
172 content and the lowest threshold of foliar P content. The nutritional status of trees was assessed
173 every second year in all plots. Mature leaves in full sun were sampled in summer on a minimum of 5
174 dominant or sub-dominant trees in the immediate vicinity of the plot (Rautio, Fürst, Stefan, Raitio, &
175 Bartels, 2010). Leaves were then dried at 70°C for 24h and ground for chemical analyses. We used a
176 linear interpolation to approximate nitrogen and phosphorus values in the alternate years (when
177 leaves were not sampled).

178

179 Table 1

180 Overview of stand and tree characteristics and range of ecological conditions in the selected plots for pedunculate oak (*Quercus robur*), sessile oak (*Quercus*
 181 *petraea*) and European beech (*Fagus sylvatica*) from 1997 to 2015: average, minimum and maximum values (in brackets) are specified.

182

		Pedunculate oak	Sessile oak	European beech
Nb. of plots		9	18	12
Plot basal area (m ² /ha)		18 (7.4-26)	21 (5.8-29)	21 (8.4-36)
Stand age in 2015		93 (55-154)	114 (75-159)	92 (61-128)
Species Phenology	budburst	21 april (24 feb.-27 may)	20 april (29 mar.-14 juil.)	29 april (8 apr.-25 may)
	leaf yellowing	23 oct. (23 sep.-11 dec.)	25 oct. (21 sep.-2 dec.)	20 oct. (15 aug.-2 dec.)
Nb. of observed trees		506	1019	671
Tree defoliation (%)		26 (0-100)	23 (0-100)	21 (0-95)
Occurrence of presence/absence of insect damage	absence	2849	7831	5259
	presence	1242	1998	1067
Foliar N: P ratio		21 (14-36)	22 (14-33)	24 (16-33)
Nutritional status (% of obs.)	intermediate	49	34	20
	high	51	66	80
Altitude (m)		188 (20-370)	208 (80-330)	286 (50-700)
Annual temperature (°C)		11.4 (9.4-14.0)	11.2 (9.3-13.4)	10.8 (8.8-13.9)
Annual precipitation (mm)		876 (497-1641)	802 (435-1315)	960 (502-1765)
Standardized Precipitation-Evapotranspiration Index		0.76 (-4-5.5)	0.71 (-4.9-5.9)	0.77 (-3.9-5.4)

183 2.4 Drought index

184 We estimated drought intensity by using the Standardized Precipitation-Evaporation Index (SPEI)
185 (Vicente-Serrano, Beguería, & López-Moreno, 2010). It is extensively used because it can be
186 compared across locations and aggregated at different time scales. Time series of SPEI were
187 calculated on a monthly basis using the difference between the sum of precipitations and the
188 potential evapotranspiration. Precipitations and potential evapotranspiration were obtained from
189 the SAFRAN model of METEO FRANCE at a daily time step for every sampled plot from 1997 to 2015.
190 Potential evapotranspiration was estimated using the Penman-Monteith method according to FAO
191 recommendations (Smith, 1995).

192 We estimated drought intensity for two distinct periods corresponding to the previous year and the
193 year of defoliation assessment, respectively. We calculated SPEI of the previous year on a timescale
194 of 6 months from May to October, to match with the period of broadleaved tree growth. The length
195 of tree growth period was estimated using leaf phenology of the 36 dominants trees, every year on
196 every plot. We used the date at which budburst occurred in at least 90% of dominants trees as the
197 start of the growth period and the date at which 90% of dominants trees were yellowing as the end
198 of the growth period (Table 1). We calculated SPEI of the year of defoliation assessment on a
199 timescale of 3 months (May to July). July is the month at the end of which most of the plots have
200 been visited for defoliation assessment. Finally, to account for the drought experienced by trees
201 during both the previous year and the year of defoliation assessment, we averaged the two values of
202 SPEI. To facilitate the interpretation of analyses outcomes, we used minus SPEI ('- SPEI') instead of
203 'SPEI' as drought index, so that a high and positive value of SPEI indicates an intense drought (Table
204 1).

205 2.5 Plot Basal Area

206 A complete dendrometric inventory of all trees with a diameter at breast height (DBH) above 5 cm
207 within the inner part of the plots (0.5 ha) was made every 5 years as well as before and after logging.

208 Species identity, dominance status and circumference at 1.30 m were recorded for each tree. We
209 then used the basal area (m²/ha) of all dominant trees as an index of stand density (Table 1). Missing
210 values (during the 4 years period in between two inventories) were interpolated assuming a linear
211 increase in basal area with time.

212 2.6 Statistical analyses

213 Statistical analyses were performed with R 3.4.3. We used the log-transformed median of the 5%
214 class of defoliation to normalize the model residuals. The biotic and abiotic determinants of crown
215 defoliation were investigated with a Linear Mixed-Effects Models (function lme package nlme). We
216 considered the nested sampling design and the repeated measurements of trees over time by using a
217 random effect of trees nested in plots. Residual variance was modelled with a power function of
218 fitted values and an autoregressive moving average process estimating the residual temporal
219 autocorrelation (Pineiro & Bates, 2006). We investigated the long-term temporal trend in tree
220 defoliation by introducing a quadratic effect of the calendar year. Moreover, we tested the
221 interactions between stress drivers by including into the models two-way interactions between
222 drought index, foliar N:P ratio and presence/absence of insect damage. We measured model quality
223 by calculating the root mean square error (RMSE), which is based on the difference between
224 predicted and observed values (Janssen & Heuberger, 1995). We thus fitted the following model for
225 each tree species:

$$226 \ln(\text{DEF}_{i,j}) = \beta_0 + b_{0,i} + b_{0,i,j} + \beta_1 \times \text{YEAR} + \beta_2 \times \text{YEAR}^2 + \beta_3 \times G + \beta_4 \times \text{INSECT} + \beta_5 \times \text{DROUGHT} + \beta_6 \times \text{N:P} + \\ 227 \beta_7 \times \text{INSECT} \times \text{DROUGHT} + \beta_8 \times \text{INSECT} \times \text{N:P} + \beta_9 \times \text{DROUGHT} \times \text{N:P} + \varepsilon_{i,j}$$

228

$$229 b_{0,i} \sim \mathcal{N}(0, \sigma_1^2) ; b_{0,i,j} \sim \mathcal{N}(0, \sigma_2^2) ; \varepsilon_{i,j} \sim \mathcal{N}(0, \sigma^2)$$

230

231 Where DEF is the median level of defoliation classes (in %) of tree *i* in plot *j*; $\beta_{0:9}$ are model
232 parameters for the effects of time (YEAR), stand density (G in m²/ha), presence/absence of insect

233 damage (INSECT), drought intensity (DROUGHT) and foliar N:P ratio and their interactions two by
234 two; $b_{0,i}$ is the plot random effect and $b_{0,i,j}$ is the tree random effect.

235 We eventually applied a correction factor when we back-transformed the values fitted by the model
236 in the logarithmic scale to avoid the systematic underestimation of crown defoliation inherent to the
237 log transformation (Chave et al., 2014; Finney, 1941; Shen & Zhu, 2008):

$$238 \quad \widehat{DEF} = \exp(\log(\widehat{DEF}) + CF)$$

239 Where \widehat{DEF} is the average crown defoliation that is predicted by the model; $\log(\widehat{DEF})$ is the average
240 log-transformed value of crown defoliation that is predicted by the model and CF is the correction
241 factor:

$$242 \quad CF = \frac{RSE^2}{2}$$

243 Where RSE is the residual square error.

244 3 RESULTS

245 The mean level of defoliation observed was 20%, but the standard deviations associated with
246 random effects in the models indicated important inter-plot and inter-individual variability (Table 2).

247 3.1 Effect of stand density on tree defoliation

248 Crown defoliation of European beech and pedunculate oak increased significantly (Table 2) with plot
249 basal area (tree density) respectively by 0.4% and 0.3% per m^2/ha , whereas it decreased significantly
250 by 0.4% per m^2/ha in sessile oak.

251 3.2 Long term changes in tree defoliation

252 The three tree species exhibited contrasting temporal trends of tree defoliation over the period
253 1997-2015 (Table 2, Fig. 1). European beech defoliation increased significantly all along the period

254 (Fig. 1) at a rate of 0.5 % per year. Long-term changes in sessile oak defoliation exhibited a humped
255 shape with an increase from 1997 to 2008 followed by a slight decrease in defoliation from 2008 to
256 2015. Defoliation of the pedunculate oak showed an opposite trend with a gradual decrease until
257 2011.

258 3.3 Tree defoliation in presence/absence of insect damage

259 Trees damaged by pest insects were significantly more defoliated than trees not damaged by insects
260 in the three species (Table 2), at an average value of drought index and foliar N:P nutrient content.
261 The increase of crown defoliation due to insect damage was of 7.5 % in European beech, 4.7% in
262 sessile oak and 2.6% in pedunculate oak, as estimated by models.

263 3.4 Interaction between insect damage and drought

264 For European beech, crown defoliation was significantly aggravated by drought, but only in trees
265 damaged by pest insects (Table 2, Fig. 2), i.e. significant drought x insect interaction (estimate=-0.08
266 \pm 0.03; P=0.01). Tree defoliation increased by 5.9% from very wet (drought index =-1.5) to very dry
267 (drought index = 1.5) conditions in trees damaged by insects, as estimated by the model.

268 Regarding sessile and pedunculate oak, the aggravation of crown defoliation was similar in the
269 presence and in the absence of insect damage (P > 0.05, Table 2, Fig.2) and was in average of 2.9%
270 for sessile oak and 3.4% for pedunculate oak between very wet (drought index =-1.5) and very dry
271 (drought index = 1.5) conditions.

272 3.5 Interaction between insect damage and foliar N: P ratio

273 Crown defoliation of European beech increased with higher foliar N:P ratio in trees that were not
274 damaged by insects (Table 2). The variation in tree defoliation estimated by the model was of +10%
275 between low (16) to high (33) level of foliar N:P ratio (Fig. 3). Conversely, the slope of the
276 relationship between defoliation and foliar N:P ratio was not significantly different from zero for

277 European beech trees damaged by insects, i.e. significant interaction N:P x insect (estimate=-
278 0.045 ± 0.006 ; $P < 0.001$).

279 In sessile oak, the effect of foliar N:P ratio was not significant in trees that were not damaged by
280 insects but was negative in trees with an insect damage (-3.5% between low (16) and high (33) level
281 of foliar N:P ratio Table 2), i.e. significant N:P x insect interaction (estimate= -0.007 ± 0.004 ; $P = 0.04$).

282 The trends were more pronounced in pedunculate oak: crown defoliation decreased significantly
283 with higher values of foliar N:P ratio with a steeper slope in trees damaged by insects than in trees
284 not damage by insects (-5.6 % for tree damage by insect and -2.6% between low (16) and high (33)
285 level of foliar N:P ratio), i.e. significant N:P x Insect interaction (estimate= -0.008 ± 0.004 ; $P = 0.03$).

286 3.6 Interaction between drought and foliar N: P ratio

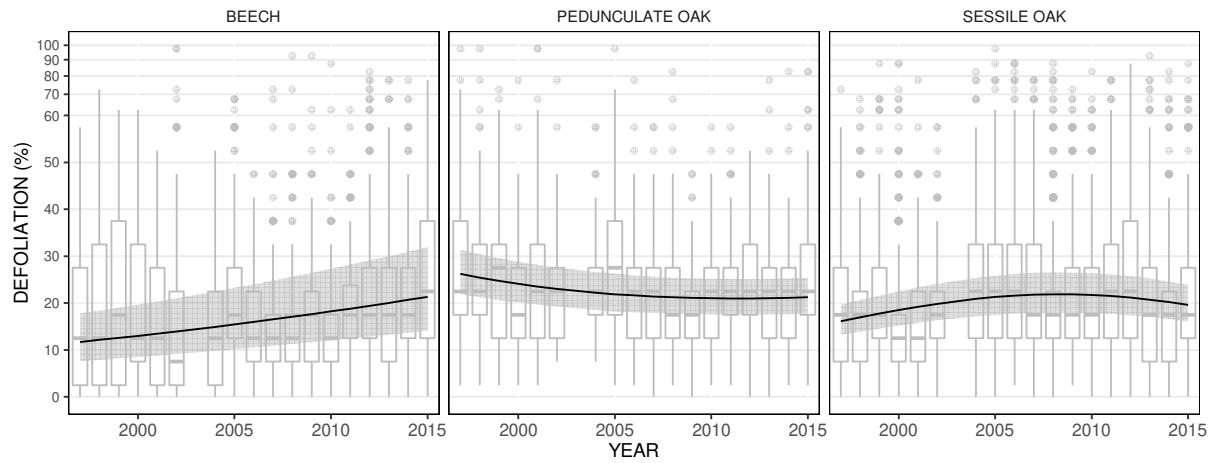
287 In pedunculate oak, there was a significant interaction between drought and foliar N:P ratio
288 (estimate= -0.008 ± 0.002 ; $P < 0.001$, Table 2). Trees were more defoliated under dryer conditions and
289 at lower levels of foliar N:P ratio (Fig. 4). The interaction between drought and foliar N:P ratio was
290 not significant in European beech and sessile oak ($P > 0.05$).

291 Table 2

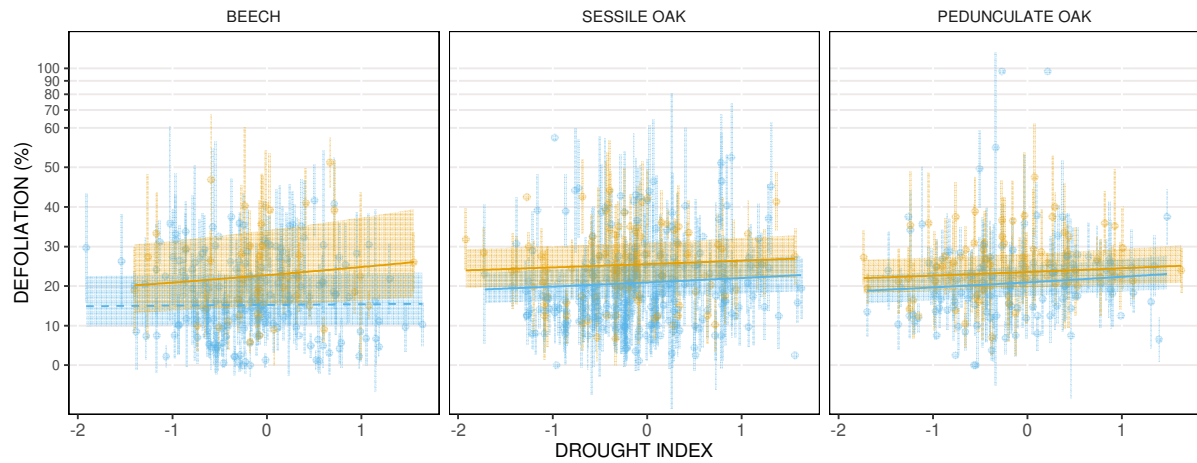
292 Summary of the effects of year, stand density (Basal area), presence/absence of insect damage, drought index and foliar N:P ratio on crown defoliation (log
 293 transformed) at the tree level in European beech (*Fagus sylvatica*), sessile oak (*Quercus petraea*) and pedunculate oak (*Quercus robur*). Model estimates
 294 (*est.*) are given with associated standard deviation (*sd*) and p-values (*pval*). Significant effects (*pval*<0.05) are in bold. Random effects (*sd*) correspond to the
 295 standard deviation of the random effect at the plot level and the random effect of trees nested within plots, RMSE corresponds to the root mean square
 296 error of the linear mixed models.

297

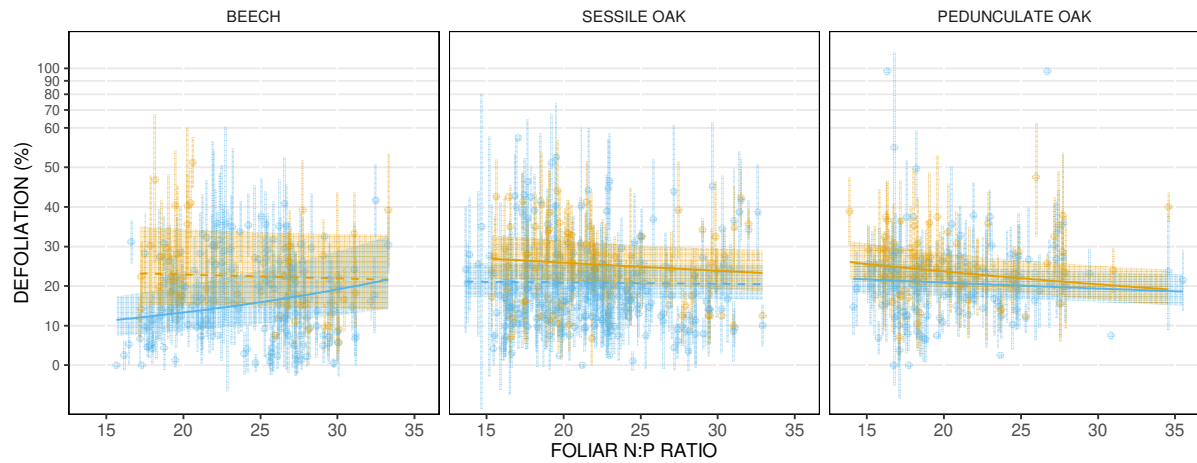
Species	Fixed effects											Random effects (<i>sd</i>)			
	Year	Year ²	Basal area	Insect damage	Drought		Drought		Foliar N: P ratio		Foliar N: P ratio		Plot	Tree	RMSE
					and		x		and		x				
					Insect damage		Insect damage		Insect damage		Insect damage				
Absence	Presence	Δ Abs .-	Pre.	Absence	Presence	Δ Abs. - Pre.	Δ Abs. - Pre.	Foliar N:P ratio							
European beech												0.68	0.000090	0.8	
<i>est.</i>	0.042	-0.00024	0.025	0.43	0.012	0.093	0.080	0.041	-0.0046	-0.045	0.0045				
<i>sd</i>	0.009	0.00040	0.005	0.03	0.013	0.029	0.032	0.0039	0.0064	0.006	0.0028				
<i>pval</i>	<0.001	0.56	<0.001	<0.001	0.35	0.002	0.012	<0.001	0.47	<0.001	0.11				
Sessile oak												0.42	0.28	0.63	
<i>est.</i>	0.069	-0.0028	-0.019	0.22	0.059	0.037	-0.023	-0.0019	-0.009	-0.0070	-0.0020				
<i>sd</i>	0.0057	0.0003	0.003	0.016	0.0083	0.014	0.016	0.0034	0.005	0.0035	0.0019				
<i>pval</i>	<0.001	<0.001	<0.001	<0.001	<0.001	0.007	0.16	0.56	0.048	0.044	0.29				
Pedunculate oak												0.28	0.27	0.51	
<i>est.</i>	-0.038	0.0012	0.014	0.14	0.077	0.045	-0.032	-0.0092	-0.018	-0.0083	-0.0076				
<i>sd</i>	0.006	0.0003	0.005	0.02	0.011	0.018	0.021	0.0035	0.005	0.0039	0.0022				
<i>pval</i>	<0.001	<0.001	0.0012	<0.001	<0.001	0.011	0.13	0.0087	<0.001	0.032	<0.001				



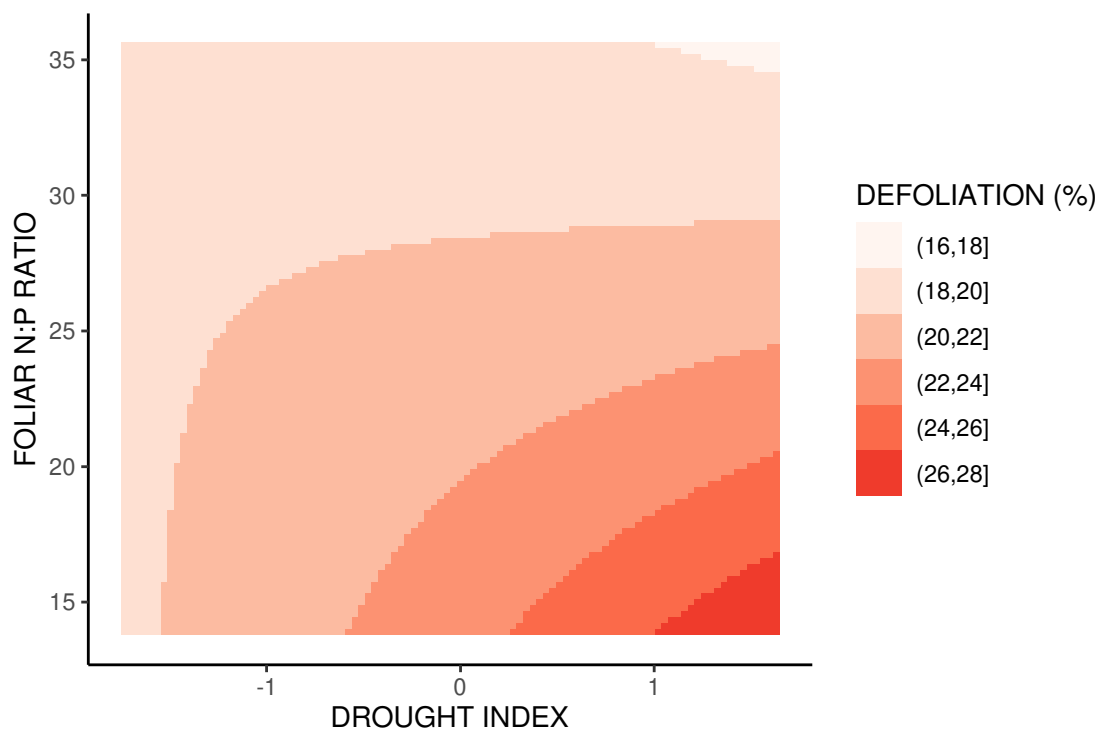
298
 299 Fig. 1. Temporal change in percentage of defoliation from 1997 to 2015 in European beech, sessile
 300 oak and pedunculate oak. Boxplots represent the distribution of raw data. Solid lines represent the
 301 crown defoliation of a tree predicted by models after a back-transformation of the logarithmic values
 302 at an average level of stand density, N:P ratio and drought index. Shaded areas represent the
 303 confidence intervals at 95%



304 Fig. 2. Effect of drought index on crown defoliation in European beech, sessile oak and pedunculated
 305 oak in absence (blue) and presence (yellow) of insect damage. The raw data are represented by an
 306 average value of crown defoliation by plot (dots) and its standard deviation (vertical lines). Solid lines
 307 represent the crown defoliation of a tree predicted by the models after a back-transformation of the
 308 logarithmic values at an average value of stand density, N: P ratio and for a median year (2006). The
 309 line patterns indicate whether the slope of the relationship was significant (solid line) or not (dashed
 310 line). Shaded areas represent the confidence intervals to the regression lines at 95%



311 Fig. 3. Effect of foliar N: P ratio on crown defoliation in European beech, sessile oak and
 312 pedunculated oak in absence (blue) and presence (yellow) of insect damage. The raw data are
 313 represented by an average value of crown defoliation by plot (dots) and its standard deviation
 314 (vertical lines). Solid lines represent the crown defoliation of a tree predicted by the models after a
 315 back-transformation of the logarithmic values at an average value of stand density, drought index
 316 and for a median year (2006). The line patterns indicate whether the slope of the relationship was
 317 significant (solid line) or not (dashed line); Shaded areas represent the confidence intervals to the
 318 regression lines at 95%



320

321 Fig. 4. Interacting effect of foliar N:P ratio and drought intensity on defoliation in pedunculate oak
322 (values back transformed). Defoliation levels have been divided into 2% interval categories including
323 the lowest value of the interval but not the highest value.

324 4 DISCUSSION

325 Long-term changes in defoliation that have been observed at the European scale are low or non-
326 existent for European beech and temperate hardwood oaks (Michel et al., 2018). However, in France,
327 until the end of the 2000s, oaks and beeches seemed to show an increase in defoliation (Ferretti et
328 al., 2014). Despite a high variability between plots and between trees, our study updated the trends
329 at the French level and confirmed the increase in beech defoliation. We also showed a stabilization
330 of defoliation for both oaks more in line with what was observed at the European level. Furthermore,
331 we found that tree defoliation was in general exacerbated by the presence of insect damage and
332 drought events. The effect of the tree nutritional status was more species specific. Interestingly, we
333 also detected interactive effects between these factors, which lead to additive or synergistic effects
334 of stresses for most tree species.

335 4.1 Long term change in tree defoliation

336 We found a long-term trend of declining crown condition in European beech forests, as tree
337 defoliation was consistently increasing with time. This is consistent with a previous study conducted
338 in the same forest monitoring network in France (Ferretti et al., 2014), which reported a similar
339 increase during the period 1997-2009. Recently, Sousa-Silva et al. (2018) observed a similar pattern
340 in Belgian forests from 1997 to 2015 and suggested that the decline in European beech condition was
341 related to a progressive increase in drought intensity over time. European beech is a species well
342 known for its high susceptibility to dry conditions (Rubio-Cuadrado et al., 2018) with strong negative
343 correlations between drought intensity and growth loss (Farahat & Linderholm, 2018; Lebourgeois,
344 Bréda, Ulrich, & Granier, 2005; Seynave, Gégout, Hervé, & Dhôte, 2008) and most species
345 distribution models have predicted European beech decline in the future under dryer conditions (e.g.
346 Saltré, Duputié, Gaucherel, & Chuine, 2015).

347 The temporal pattern was quite different in oak species. Sessile oak exhibited a deterioration trend
348 approximatively until 2007, which was followed by a period of slight recovery, while pedunculate oak
349 showed a general trend for a slow crown condition improvement. Oak species are more drought
350 tolerant than European beech (Rubio-Cuadrado et al., 2018). It is thus possible that in the recent
351 years, from 2007 onward, precipitations were below the tolerance threshold of European beech but
352 above the tolerance thresholds of oaks. Higher CO₂ concentration causes an increase in
353 carbohydrates and a reduction in N, thus increasing C:N ratio which is unfavorable to leaf feeders. It
354 can also enhance C-based tree defenses against defoliating herbivores (Robinson, Ryan, & Newman,
355 2012) and particularly against gypsy moth, a common oak defoliator (Foss, Mattson, & Trier, 2013).
356 The lack of degradation, or even the slight improvement, in oak crown conditions might thus be due
357 to positive effects of CO₂ enrichment on tree growth and defense against leaf feeders
358 counterbalancing negative effects of droughts on tree health.

359 4.2 Effects of Intraspecific competition, insect damage, drought and foliar N:P

360 High tree density emerged as a cause of defoliation in all three species, probably due to increased
361 competition for canopy space (Getzin et al., 2008; Hajek et al., 2015). Competing trees may also be
362 more prone to pest attacks, due to trade-offs between growth and defenses (Huang et al., 2019).
363 This calls for new studies targeting the effect of forest thinning on resistance to multiple stresses
364 (Jactel et al., 2009).

365 Tree defoliation usually increases with summer drought of the current year (Seidling, 2007) because
366 leaf abscission allows avoiding disruption of sap flow flux and xylem cavitation (Bréda et al., 2006).
367 Defoliation can also arise from lagged effect of previous summer drought (Seidling, 2007), which can
368 affect carbohydrates reserves and bud viability (Bréda et al., 2006).

369 The negative effect of foliar N:P ratio on tree defoliation did not exhibit a consistent pattern among
370 the studied tree species contrary to what was observed at the European scale. Veresoglou et al.
371 (2014) found a segmented response of tree defoliation to foliar N:P, with a positive relationship

372 between nutrient content and defoliation beyond the breaking point of 14.8 in broadleaved species
373 (corresponding to the minimum level of the foliar N:P ratio observed in our study). We found such a
374 positive correlation (higher defoliation at higher level of N:P ratio, *i.e.* high level of N and low level of
375 P) only for European beech not damaged by insect. European beech covered a larger range of N:P
376 ratio than oak species for which approximately 80% of the observations belong to the intermediate
377 group. The increase in defoliation observed in European beech may thus arise from the fact that
378 European beech occurs in sites with a stronger nutritional imbalance of N and P than oaks.

379 In all three species, insect damaged trees exhibited significantly higher defoliation than non-attacked
380 trees, which confirms the significant impact of insect feeding on crown condition (Kozlov, Lanta,
381 Zverev, & Zvereva, 2015). We found a higher sensitivity of sessile oak than pedunculate oak to insect
382 attack, which is consistent with recent findings on the sensitivity of sessile oak to the oak
383 processionary moth (Damestoy et al., 2020). From a management point of view, the sessile oak
384 appears be more resistant to drought events than the pedunculate oak, suggesting that sessile oak
385 should be favored to adapt oak forests to climate change. However, this choice could be made at the
386 cost of making oak stands more vulnerable to attack by defoliators. This trade-off calls for caution
387 when choosing to favor one tree species over another in a substitution logic and suggests that mixing
388 tree species would be a more effective long-term strategy for dealing with multiple risks (Jactel et al.,
389 2017; Sousa-Silva et al., 2018). Both beech and oak species can be infested by many insect
390 defoliators, with for example 41 species of Lepidoptera associated with European beech and 189
391 with pedunculate oak and sessile oak in Britain (Kennedy & Southwood, 1984). In addition, it has
392 been demonstrated that insect damage can accelerate leaf abscission, thus explaining higher
393 defoliation recorded in early summer on insect damaged trees (Zvereva & Kozlov, 2014).

394 4.3 Interactions between pest damages, drought and foliar N: P ratio

395 In all tree species, we could observe significantly higher damage (defoliation) in trees that were both
396 attacked by insects and under drought conditions. Interestingly, in our study, we found that the

397 combined effects of drought and insect attack were additive for oaks but synergistic for European
398 beech (Fig. 2). This suggests that, in oak trees, insect damages and drought cumulated their effect on
399 tree defoliation whereas, in beech trees, insect damages increased with water stress intensity. This is
400 consistent with the general pattern of higher forest insect damage following droughts (Ferretti et al.,
401 2014; Logan, Regniere, & Powell, 2003; Rouault et al., 2006; Toïgo, Barraquand, Barnagaud, Piou, &
402 Jactel, 2017) and more particularly the higher susceptibility of water stressed trees to defoliating
403 insects (Jactel et al., 2012). The direct effect of drought on forest insect herbivores, e.g. on survival
404 and fecundity, lacks experimental evidence (Jactel et al., 2019). By contrast, it is well known that
405 drought can indirectly benefit forest defoliators through improved host plant quality (e.g. higher
406 nitrogen content (Jactel et al., 2012)) or reduced plant resistance (Castagneyrol, Jactel, et al., 2018;
407 Holopainen et al., 2018). It would now be necessary to better identify the species of defoliating
408 insects attacking oaks on the one hand and beeches on the other hand to understand why the
409 synergy between drought and insect attacks was only observed in the case of European beech.

410 We also showed cumulative, negative effects of pest damage and low N:P ratio on all tree
411 species. This confirms that nutrient imbalance has to be considered when searching the causes of
412 tree crown decline. One possible explanation for the combined effect of pest feeding and low N:P is
413 that insect herbivory is higher on leaf with low N content as more leaf tissue have to be consumed to
414 meet the nutritional requirement of insect herbivores (i.e. compensatory feeding, (Castagneyrol,
415 Moreira, et al., 2018)). In one species, beech, we detected a synergistic effect of insect damage and
416 low N:P leaf ratio, with no effect of nutrient imbalance in undamaged trees and large defoliation
417 increase with increasing N:P in damage trees. This might be due to specific nutrient requirements of
418 *Orchestes fagi*, the main insect defoliator of European beech in our sample.

419 4.4 PERSPECTIVES AND LIMITATIONS

420 Our study has several limitations. Tree crown conditions, and in particular level of defoliation, are
421 difficult to estimate accurately. However, observers involved in ICP forests network were trained

422 each year with inter-calibration workshops. In addition, a selection of plots (16 out of 102) between
423 2001-2005 and 2008-2009 was controlled to assess the quality of the observations of crown
424 defoliation (Ferretti et al., 2014). The observation bias (the difference in score between the field
425 team and the control team) was between $\pm 5\%$ for 76% of the defoliation scores and $\pm 10\%$ for 92%
426 of them. This confirms the reliability of crown defoliation score attributed on the field. In addition,
427 we focused on the three tree species with largest sample size and only retained trees for which all
428 necessary data were available. We therefore believe that our results on long-term trend and
429 explanatory factors are conservative. More problematic is the lack of precise information on the
430 insect species that made the observed leaf damage. This would have required collecting branches
431 and assessing a sample of leaves, which is technically and economically difficult. Nevertheless, a
432 more focused long-term study on a few well-known and easily monitored insect defoliators would
433 provide more insights into physiological processes involved in drought, nutrient imbalance and pest
434 damage. Likewise, other potential interactive drivers of crown conditions like storm, air pollution or
435 presence of mycorrhizae would be worth considering.

436 5 CONCLUSIONS

437 Our findings confirm the gradual worsening of crown condition in European beech and the
438 stabilization in oaks, which has been observed at the European scale, suggesting species-specific
439 response to ongoing climate changes. They also demonstrate that events of crown defoliation result
440 from the complex interplay between biotic and abiotic stresses, which are more or less relevant to
441 particular tree species. In particular, insect attacks deteriorated crown condition, especially after dry
442 periods for the three broadleaved species while the effect of imbalanced nutritional status was less
443 consistent among tree species. More importantly, we showed that these stress factors generally act
444 synergistically. It therefore seems important for the adaptive management of forests to address
445 issues related to forest conditions in an integrative way, especially in a context where biotic and
446 abiotic hazards are likely to intensify. Long-term monitoring of forest condition remains more useful

447 than ever, but it should be accompanied by a more accurate analysis of the causes of decline, in
448 order to better predict future trends and better adapt forests to future threats.

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453

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