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Interactive effects of abiotic factors and biotic agents on Scots pine dieback: A multivariate modeling approach in southeast France.

2 Interactive effects of abiotic factors and biotic agents on Scots pine

3 dieback : A multivariate modeling approach in southeast France.

4

Jean Lemaire¹, Michel Vennetier², Bernard Prévosto², Maxime Cailleret²,

5 Abstract

Forest dieback is a high risk factor for the sustainability of these ecosystems in the climate change context. Productivity losses and increased defoliation and mortality rates have already been recorded for many tree species worldwide. However, dieback is a process that depends on complex interactions between many biotic and environmental factors acting at different scales, and is thus difficult to address and predict.

Our aim was to build tree- and stand-level foliar deficit models integrating biotic and abiotic 11 factors for Scots pine (Pinus sylvestris), a species particularly threatened in Europe, and 12 13 especially in the southeastern part of France. To this end, we quantified foliar deficit in 1740 14 trees from 87 plots distributed along an environmental gradient. We also measured tree annual radial growth and the abundance of two parasites: the pine processionary moth 15 16 (Thaumetopoea pityocampa Den. & Schiff.) and mistletoe (Viscum album L.). Topographic, 17 soil, climate and water balance indices were assessed for each plot, together with the stand dendrometric characteristics. Given the large number of environmental factors and the 18 strong correlations between many of them, models were developed using a partial least 19 squares (PLS) regression approach. 20

All the models pointed to a preponderance of the biotic factors (processionary moth and mistletoe) in explaining the intensity of foliar deficit at both tree- and stand- levels. We also show that strong interactions between climate, soil, water balance and biotic factors help to explain the intensity of dieback. Dieback was thus greater in the driest topoedaphic and climatic conditions where the mistletoe and processionary moth were present.

20	This study highlights the need to account for a wide range of biotic and abiotic factors to
27	explain the complex process of forest dieback, and especially the environmental variables
28	that contribute to the water balance on the local scale. The phenomenological modeling
29	approach presented here can be used in other regions and for other species, after a re-
30	calibration and some adaptations to local constraints considering the limited distribution area
31	of some biotic agents.
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38 1. Introduction

Ever since the beginning of the industrial era in the 19th century, human activities have 39 40 been associated with a significant rise in global temperatures, forecast to continue in the range of +1°C to +5.7 °C by 2100 according to climate scenarios (relative to the period 41 1850-1900 ; Masson-Delmotte et al., 2021). This gradual temperature rise has been 42 43 accompanied by an increased frequency and intensity of extreme weather events and 44 summer droughts in some regions, such as the Mediterranean (Cramer et al., 2018). These 45 climate changes intensify the physiological stress undergone by forest ecosystems, leading to short- and long-term modifications in their carbon and water economies (McDowell et al., 46 47 2008), and in their structure and composition (Anderegg et al., 2013).

48

One sign of these dysfunctions at both tree and stand levels is dieback, defined as 49 weakened vitality of a tree relative to a healthy reference tree, or weakened vitality of a 50 large number of trees in a stand (Schütt and Cowling, 1985). Visible clues of dieback 51 52 include reduced radial growth (Helama et al. 2014; Camarero et al. 2018), changes in 53 crown architecture, branch and root death, fewer or smaller seeds (Girard et al., 2012; Vennetier et al., 2013), and most often a leaf area deficit (Becker et al., 1990; Carnicer et 54 al., 2011; Dobbertin and Brang, 2001). Dieback may degenerate in tree death in the 55 56 absence of recovery (Bréda et al., 2006). Besides these visible clues, various physiological and anatomic signs can be reported, including changes in carbon reserves (Adams et al., 57 2013), lower efficiency in the use of resources (Gessler et al., 2018), xylem embolism 58 (Choat et al., 2012), or nutrient imbalance (Gessler et al., 2017). Mechanistically, dieback is 59 described as a complex system in which various biotic and abiotic factors interact in chains 60 (Franklin et al., 1987; Waring, 1987). Commonly cited biotic factors include fungi, insects, 61 bacteria, plant parasites, and inter-tree competition. Abiotic factors are related to climate, 62 topography, soil, and sometimes air pollution. Dieback processes are often triggered by 63 64 weather events, in particular severe droughts (Bigler et al., 2006; Suarez et al., 2004; Das

et al., 2007; Pedersen, 1998; Gaylord *et al.*, 2015), which are increasingly associated with heatwaves (Teskey *et al.*, 2015; Vogel *et al.*, 2021). These factors can be compounded with spells of deep frost, either early or late, but also with biotic agent outbreaks (e.g., Morcillo *et al.*, 2019).

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Forest dieback affects many biomes and species worldwide (e.g., van Mantgem et al. 2009; 70 71 Allen et al., 2010; Hartmann et al., 2018; Hartmann et al. 2022), including Scots pine (Pinus 72 sylvestris), a main European tree species that covers more than 20 million hectares from 73 Scandinavia to southern Spain (Gonthier et al. 2011; Houston Durrant et al. 2016). It is particularly impacted in the southern part of its distribution range, in the Pyrenees and the 74 Alps, but also in central Europe. These dieback events are often attributed to drought 75 (e.g., Bigler et al. 2006; Bose et al. 2020; Buras et al. 2018; Camarero et al. 2015; Etzold et 76 77 al. 2019; Martínez-Vilalta et al. 2009), but it also involves biotic factors such as the pine processionary moth (Thaumetopoea pityocampa Den. & Schiff.) (Hódar et al., 2003), and 78 79 mistletoe (Viscum album L.) a hemiparasitic plant that causes gradual weakening of 80 infested trees (Dobbertin et al. 2005; Galiano et al. 2010; Rigling et al. 2010; Kollas et al. 2018). 81

82

83 Determining the potential interactions between stand attributes, climate, processionary 84 moth and mistletoe in the dieback process is key with regard to climate change. When water and nutrients availability are not limited, pine mistletoes can co-exist with their host 85 tree for years (Solomon et al., 2015; Zuber, 2004). However, during drought, mistletoes 86 maintain high transpiration rates (Zweifel et al., 2012), which may exacerbate the stress 87 88 experienced by the host pine, with negative consequences on the growth performance and on foliar deficit (Dobbertin and Rigling, 2006; Rigling et al., 2010; Wang et al., 2022). 89 Considering that epidemic phases of the processionary moth can also cause strong pine 90 defoliation, and that both biotic factors are favoured by sunny and warm positions, and thus 91

potentially by transparent canopies, synergies between these factors, drought, and the
microenvironment are likely (e.g., Gea-Izquierdo *et al.*, 2019).

Both biotic factors are favored by higher temperature, and upward or northward shifts have been reported in several areas (e.g., Dobbertin *et al.* 2005; Robinet *et al.* 2007 and 2014). However, quantification of this process requires long-term data series, which are rarely available and may show a different trend (e.g., Camarero *et al.*, 2022 in the case of processionary moth).

99

100 In the last 20 years, many numeric models have been developed to predict the endpoint of 101 dieback, namely tree death. On the one side, physiological models explicitly simulate the carbon and hydraulic mechanisms involved in tree death (e.g., McDowell et al., 2013; 102 103 Cochard, 2020; Davi and Cailleret, 2017). On the other side, phenomenological models 104 predict mortality risk using statistical approaches based on local abiotic environmental data (soil, climate, topography) and dendrometric data (type of stand, density, tree size, etc.) 105 without considering the physical and physiological mechanisms behind tree dieback (e.g., 106 Taccoen et al., 2019). Along this continuum are models that couple empirical and 107 mechanistic approaches (e.g., Venturas et al. 2021), and others that use integrative 108 109 indicators of tree vitality, such as radial growth (e.g., Bigler and Bugmann, 2004; Holzwarth et al., 2013; Hülsmann et al., 2018). Physiological models are considered as more accurate 110 in the context of a changing environment, but they require a large amount and diversity of 111 112 high-resolution data, and are not yet fully functional for many species and over large areas. Phenomenological models are more parsimonious and robust within their calibration range, 113 but less reliable outside it. Despite the increasing number, diversity and complexity of 114 models that predict whether a tree will live or die, prediction of mortality at a regional scale 115 116 is still challenging (Trugman et al., 2021), and few models simulate a tree's level of dieback, 117 owing to lack of data and because dieback displays a wide range of signs. These dieback models, for example those that predict foliar deficit (e.g., Galiano et al., 2010; Gonthier et 118

al., 2011), cannot be used directly for forestry diagnostics as they consider only a few factors influencing tree health, either directly or indirectly (through their interactions), and often neglect site factors (e.g., soil and topography). However, in view of the current increase in forest dieback at both local and global scales, operational tools able to predict this risk are urgently needed.

The aim of this study was to partly fill this research gap by developing phenomenological 124 125 models to predict foliar deficit of Scots pine. We used a partial least squares (PLS) 126 regression approach to (1) assess the impact of multiple environmental factors (climate, 127 soil, topography) and of the spatial distribution of pine populations at landscape scale on the abundance of biotic agents : pine processionary moth and mistletoe; (2) disentangle the 128 respective and interactive impacts of these abiotic and biotic drivers on foliar deficit on both 129 tree and stand scales; and (3) develop a model that could be used by forest managers to 130 predict the risk of stand dieback. With this multifactorial and multiscale approach, we aimed 131 at improving our understanding of the dieback process on Scots pine and the 132 133 methodologies used to predict dieback risk.

134

135 2. <u>Materials and Methods</u>

136 **2.1 Study area**

The study was conducted in southeast France (Figure 1), where Scots pine is the main 137 138 forest species in terms of area and timber volume. This pioneering species has naturally recolonized a large part of the agricultural land that has been abandoned in the last 150 139 140 years, and has also been planted to protect the soil in mountain areas (Médail, 2001). Scots pine is moderately tolerant of both drought and cold, and not markedly sensitive to pH or 141 142 soil type. It was thus present in our study area in different biomes over a broad range of climatic conditions, from a typical Mediterranean climate, alongside downy oak (Quercus 143 pubescens Willd.), to a mountain climate with common beech (Fagus sylvatica L.) and 144 silver fir (Abies alba Mill.) (Le Houerou, 2005; Joly et al., 2010). Scots pine dieback has 145

been a major concern for the past 30 years in this area (Pauly and Belrose, 2005; Sardin,

147 1997; Thabeet *et al.*, 2009).

148



149

Figure 1. Localization of the 87 plots of Scots pine sampled in southeast France (latitude
43.64–44.58 °N, longitude 5.58–6.93°E).

152 2.2 Sampling design

Our sample set covered a broad range of soil and climate conditions in which Scots pine was present in the study area (elevation from 600 m to 1700 m; Figure 1). The average annual temperature (1981-2010 period) ranged from 4.8 °C to 12 °C (mean 8.9 °C). Average annual rainfall ranged from 680 mm to 1200 mm (mean 980 mm). Soil type, texture, and bedrock also varied widely, with a pH ranging from 4.5 to 9, and soil depth from 20 cm to 80 cm. Soils were mostly calcareous; but 36% of the plots had acidic soils. No evidence of hydromorphy was observed during our soil measurements.

Based on a bioclimatic model defining the water balance in the French Mediterranean region (Vennetier *et al.*, 2008) and earlier studies conducted on the growth and dieback of 162 Scots pine (Thabeet, 2008; Thabeet *et al.*, 2009), three stratification criteria were used to 163 select the plots:

164

Elevation: We used two classes, below and above 1200 m ; this elevation
 corresponding to the boundary between the mountain- and meso-Mediterranean
 climates (Le Houerou, 2005) and to a marked discontinuity in dieback rates recorded
 between 2003 and 2006 (Thabeet, 2008).

169 – Aspect and slope: These were combined in the radiation climate index (IKR) defined by 170 Becker (1984). IKR is computed as the ratio between the solar energy received 171 annually in a given square meter and a reference horizontal square meter at the same 172 place. We used three classes: cold slopes (IKR < 0.95), horizontal areas or neutral 173 slopes (0.95 ≤ IKR < 1.05), and hot slopes (IKR ≥ 1.05).

Topographic position: The topographic position index TPI_100 (see Appendix A) was 174 computed following Weiss (2001) using a radius of 100 m around the center of the plot. 175 176 The data came from a digital elevation model (DEM) developed by the French National Institute of Geographic and Forest Information available at a resolution of 25 m (© 177 178 BDALTI IGN), and was processed using the ©QGis 3.16 software. We chose three 179 classes with contrasting topographical situations: at the bottom of the slope or valley floor (TPI 100 \leq -0.8, indicating favorable conditions in terms of water balance), mid-180 slope $(-0.8 < \text{TPI}_{100} < 0.8)$, and at the top of the slope or on the ridge corresponding 181 182 to unfavorable conditions (TPI_100 \geq 0.8).

183

For each of the 18 combinations obtained (two elevation × three IKR × three TPI_100 classes), five plots were sampled, giving a planned total number of 90 plots. These plots were randomly selected on a systematic 50 x 50 m grid in stands where Scots pine occupied at least 75% of the canopy cover according to the French national forest inventory (© BDFORET v2 IGN). To be finally selected, the plots then had to meet the following criteria: (i) no signs of logging in the last 10 years; (ii) stand height above 3 m or mean

diameter at breast height (DBH) greater than 10 cm to avoid very young stands; (iii) location
in a forested area and easily accessible; and (iv) at least 20 pine trees in the dominant or
co-dominant overstorey available in homogeneous site conditions around the center of the
plot. Sampled plot area ranged from 235 m² to 2375 m² (mean 522 m²). 87 plots met all the
above criteria.

195

196 2.3 Biotic data: health status, dendrometry, and distribution of parasite-prone

197 *pine*

On each plot, the health status of 20 dominant or co-dominant Scots pine trees was recorded during the 2017 growing season, representing an overall of 1740 trees. We followed the health status monitoring protocol used by the French forest health department (protocol DEPERIS; Goudet, Saintonge, and Nageleisen 2018), which is based on the European protocol used in the ICP-Forests network (Eichhorn *et al.* 2020). A single operator carried out all surveys to limit the estimation bias linked to the measurement protocol.

For each tree, DBH was measured and the functional crown (i.e., free of competition from neighboring trees) was delimited. We used binoculars to estimate on the functional crown and in two opposite directions, the:

208 – percentage of foliar deficit (FolDef; in %) relative to a healthy reference tree (Figure 2),

estimated visually in 5% classes, and that integrates microphylly (needle length < 50%

of the regional mean) and the proportion of dead branches;

211 – number of processionary moth nests per tree (NbnestTp);

212 – mistletoe abundance as a percentage of the functional crown occupancy (CrownVa; in
 213 5% classes).



Figure 2. Reference photos used in the French and European protocols for estimating
crown foliar deficit of Scots pine trees with corresponding defoliation rate in percentage of a
fully leafed crown. Source: Müller and Stierlin (1990)

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219 From a subsample of 28 plots representative of all the combinations of stratification classes, two cores per tree were sampled using a Pressler increment borer from the 15 220 trees closest to the center of the plot and whose health status was recorded (402 trees, i.e., 221 804 cores were analyzed). After drying and sanding, ring widths were measured to the 222 nearest 0.01 mm on scanned images using Windendro software (WinDENDRO[™] 2014, © 223 224 Regent Instruments Canada Inc.). Each series was visually cross-dated based on the 225 pointer years characterized by particular ring-width, early/latewood ratio or wood anatomy. From the measured ring widths, we computed the basal area increment, which was 226 227 averaged for five specific periods: during the severe multi-annual drought of 2003-2007 (GSd), before (1997-2002, GSb), and after this event (2008-2016, GSa). The period 2003-228 2007 was identified locally to have caused a strong reduction in growth and high mortality of 229 Scots pine (Thabeet et al., 2009; Vennetier et al., 2013). The average basal area increment 230 231 was then computed considering all years (Gs) and over the last 20 years (1997-2016; Gs20). Finally, considering the non-linearity in the growth trend over this period (see 232 Appendix B), and as tree dieback may be related to a low growth resilience to drought 233 (DeSoto et al., 2020; Trugman et al., 2018), we computed the resistance, recovery and 234 235 resilience indices based on Lloret et al. (2011). Resistance (RS) is quantified by the ratio

GSd/GSb, representing the capacity of the trees to buffer stress and maintain growth during drought. Recovery (RC) is the growth reaction following drought and is defined as the ratio GSa/GSd. Resilience (RE) represents the capacity of trees to recover and regain the growth level of the pre-drought period (ratio GSa/GSb). The absence of subsampling bias was checked to ensure that these 28 plots were representative of all 87 plots (Appendix C).

241

242 Stand basal area (m²/ha) was measured using a chain relascope. Finally, because the 243 presence and abundance of mistletoe and processionary moth could be linked to the abundance of tree species sensitive to these pests around the point of measurement 244 (Robinet et al., 2014a), we calculated the area occupied around each plot by the pine 245 species locally hosting mistletoe (Scots pine, Pinus nigra subsp. nigra Arn. and Pinus nigra 246 subsp. laricio (Poiret) Maire) or the pine processionary moth (the same species plus Pinus 247 halepensis Mill.). For these two Pine Presence indices (PPI), we tested different radii: 0.2, 248 0.5, 1, 2, 4, 6, 8, 16, 32 and 64 km, and selected the ones that best explain foliar deficit in 249 250 the statistical models (see section 2.6).

251 2.4 Climate data and indices

Mean monthly climatic conditions were characterized for each plot with the AURELHY 252 model for precipitation (P) and minimum and maximum temperatures (Bénichou and 253 Lebreton, 1987). AURELHY provides the 30-year mean values for 1981-2010 at a 1 km 254 resolution, integrating the effects of elevation and topography as far as possible. This model 255 is based on data from 3400 weather stations for rainfall, and 1500 stations for temperature; 256 257 however, it does not provide extreme values, such as the lowest temperature recorded each year during the 1981-2010 period, an important variable explaining the distribution of 258 the pine processionary moth (see below). This variable has thus been determined with the 259 SAFRAN model, despite its lower spatial resolution (8 km; Quintana-Seguí et al., 2008). 260 Mean monthly solar radiation from 1971 to 2000 was estimated with the DIGITALIS model 261 at a 50 m resolution using data from 88 weather stations, taking into account elevation, 262

latitude and topography (Piedallu and Gégout, 2007). Monthly potential evapotranspiration
(PET) was estimated with Turc's method (Turc, 1955) to determine a monthly climatic water
balance (P-PET). These climatic variables were also calculated for the summer season
(June–August), the growing season (April–October), and the non-growing season
(November–March).

In addition to these climatic variables, we calculated climatic indices of potential colonization by mistletoe and processionary moth. The distribution of mistletoe with elevation and latitude is limited by winter cold and is favored by high summer temperatures (Dobbertin *et al.*, 2005). Iversen (1944) developed a climatic index for the presence of mistletoe based on these two criteria. This index was subsequently improved by Skre (1979) in Scandinavia and tested successfully by Dobbertin *et al.* (2005) in Switzerland and by Odland (2009) in Norway. We calculated the Skre index (SKRE_I) for each plot (Eq. 1).

SKRE_I =
$$0.575 \times T_7 + 0.101 \times T_1 - 2.77$$
 (Eq. 1)

where T_7 is the mean temperature in July and T_1 the mean temperature in January.

Processionary moth dispersion and abundance are also dependent on climatic variables, in particular minimum temperature, radiation, and temperatures in the non-growing season (Hoch *et al.*, 2009). For each plot, we tested the climatic variables of the models developed by Robinet *et al.* (2007, 2014), i.e., the absolute minimum temperature, radiation, minimum, maximum, and mean temperatures for each month between October and March, and Turc's evapotranspiration over this 6 months period.

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284 2.5 Soil and topographic data and indices

285 Local topoedaphic index

For each plot, a detailed survey of bedrock, soil and local topography was carried out in the field to calculate a topoedaphic index (TEI) developed and validated over the studied area by Vennetier *et al.* (2018, for details see Appendix D). This index appraises the local water balance on the plot scale and is correlated with forest productivity. Depending on its value, which ranges from +80 to -80, the water balance is considered as highly favorable (>15), favorable (5 to 15), neutral (-5 to +5), unfavorable (-5 to -15), or highly unfavorable (<-15).

293

294 Soil characteristics were estimated directly from a hand-dug trial pit at the center of each 295 plot and from several core drillings throughout the plot. The useful water reservoir was 296 quantified using the protocol of Baize and Jabiol (2011), and calculated from the 297 pedotransfer functions developed by Jamagne et al. (1977). The nature of the underlying bedrock was surveyed in the field whenever possible, or else using geological maps. The 298 presence of active limestone was estimated in the top 50 cm using 10% hydrochloric acid. 299 The pH was measured at a depth of 20 cm using a ©SoilStik pH meter. The slope and 300 301 aspect were measured using a clinometer and a compass.

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303

Topographic indices at landscape scale

Three landscape topographic indices were calculated using two DEMs from the French 305 National Institute of Geographic and Forest Information available with a respective precision 306 307 of 25 m and 75 m (BD_ALTI © IGN). The topographic position index (TPI) was calculated in 308 a 100 m radius for microtopography (TPI_100, already used for the sampling stratification), 309 and a 1500 m radius (TPI_1500) for macrotopography (Weiss, 2001), with DEMs at 25 m and 75 m resolution respectively, each adapted to a working scale. Plots located at the top 310 of the slope show high TPI values while plots located at the bottom of the valley have low 311 312 TPI. The topographic wetness index (TWI) is an estimate of the water accumulation in a defined area. It was calculated with DEMs at 75 m. TWI is defined as the ratio of the area 313 upslope (i.e., from where water would flow) from a given point on the landscape to the local 314 slope at that point (Galiano et al., 2010; Petroselli et al., 2013). A high TWI corresponds to 315 favorable situations where water inputs are higher than the losses. These three indices 316

illustrate the part of the water balance linked to water flows in the landscape, on a largerscale than the plot (i.e., than the TEI).

319 2.6 Statistical approach

We built two indices quantifying the intensity of colonization by mistletoe and pine processionary moth, and developed three dieback models that related tree and stand health status with all the biotic and abiotic variables mentioned above (Table 1).

323 Target variables

To quantify the intensity of colonization by biotic factors, we focused on the percentage of crown colonized by mistletoe (CrownVa), and the number of nests of processionary moth per tree (NbnestTp).

327 For the first dieback model, the percentage of foliar deficit (FolDef) was analyzed on tree scale, while the second model used the percentage of stems with at least 50% of leaf loss 328 329 (Xstem50) estimated on stand scale. Xstem50 was used instead of the mean foliar deficit as both variables are closely correlated (r = 0.95, p < 0.001), and Xstem50 is often used 330 operationally by forest managers. Indeed, tree dieback is conventionally defined by a foliar 331 deficit greater than or equal to 50% (DGAL 2018; Linares et Camarero 2012; Sergent 332 2011). The third model was developed to predict the probability that a stand experiences a 333 dieback, i.e., that its Xstem50 value is greater than 30%. This risk model was designed for 334 direct use in the field by forest managers. Different threshold values of Xstem50 (20, 25 or 335 30%) are cited in the literature to define dieback in a stand (Brunier et al., 2020; DGAL, 336 337 2018; Linares and Camarero, 2012), but preliminary analyses enabled us to retain the 30% threshold (Appendix E). 338

		Model name	Target variable Y	Type of	Statistical
				variable	approach
Biotic	potential	Viscum album	CrownVa	Continuous	PLS
colonizat	tion		mean of crown percentage		

indices		colonized by mistletoe in the plot		
	Thaumetopoea	NbnestTp	Continuous	PLS
	pityocampa	Mean number of nests per tree in		
		the plot		
Dieback model	Tree dieback	FolDef	Continuous	Kruskall-
		Tree foliar deficit		Wallis+
				PLS
	Stand dieback	Xstem50	Continuous	ANOVA +
		Percentage of stems in the plot with		PLS
		at least 50% leaf deficit		
	Stand dieback	Xstem50 <u>></u> 30%	Binary	LOG PLS
	risk	Presence of at least 30% of stems		
		with at least 50% leaf deficit		

Table 1. Main characteristics of the biotic colonization indices and dieback models

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341

342 Summary statistics and model development

343 A three-way ANOVA was used to determine the pertinence of the stratification variables used for the sampling design: elevation (≥1200 m, <1200 m), IKR (cold, neutral, hot) and 344 345 TEI (favorable, neutral, unfavorable) on the dieback variables FolDef and Xstem50. ANOVA 346 validity assumptions were statistically examined, i.e., the normality of residuals with the 347 Shapiro-Wilk test, and the homogeneity of variance with the Levene test. Two-by-two 348 comparisons of means were carried out with the Tukey test, except when the variables did not meet ANOVA validity criteria, in which case the Kruskall-Wallis and Nemenyi tests were 349 350 used.

351

The two indices of potential colonization by biotic agents and the three dieback models were developed using partial least squares (PLS) regression (Ter-Braak and Juggins, 1993).

The PLS approach is known to well define complex interacting systems (Fernandes, 2012). 355 This regression method predicts the values taken by the target variables from a series of 356 357 predictor variables using a multivariate approach. This approach sidesteps two difficulties often met in ecology, namely the collinearity of explanatory variables, and the high number 358 of these variables relative to the number of observations (Cramer III et al., 1988; 359 Tenenhaus, 1998). The method has proved to be effective in forestry : i.e., to study forest 360 productivity (Bikindou et al., 2012; Paulo et al., 2015; Rathgeber et al., 2005), stand health 361 362 (Tenenhaus, 1998), and flora composition based on a bioclimatic model (Vennetier et al. 2008). We chose the PLS approach because the number of variables used to build the 363 models was large (99 in total, see Appendix A) and exceeded the number of plots. Also, 364 some climatic and topographic variables based on digital elevation models are highly 365 correlated. For instance, The AURELHY and DIGITALIS models use topography 366 information to derive high-resolution climatic maps (Bénichou and Lebreton, 1987; Piedallu 367 and Gégout, 2007). A stepwise method based on the Q² coefficient of Stone-Geisser was 368 369 used to select the number of components in the PLS regression (Bertrand, F., Maumy-Bertrand, M., 2018; Bastien, P., Vinzi, V.E., Tenenhaus, M., 2005). Only the variables 370 whose partial correlation coefficient was significantly different from zero (p < 0.05) after 371 372 bootstrapping were then retained. To model the probability of the presence or absence of 373 dieback in a plot, we used a PLS binary logistic regression approach (LOG PLS); the 374 logistic regression being regularly used to predict tree mortality risk (e.g., Cailleret et al., 2016; Hülsmann et al., 2018; Monserud, 1976). The LOG PLS combines a PLS regression 375 model with the binary prediction model of logistic regression. The PLS regressions were run 376 377 with the plsRglm package (Partial Least Squares Regression for Generalized Linear 378 Models; Bastien et al., 2005; Bertrand and Maumy-Bertrand, 2018) from the R 4.0.5 opensource software (RStudio Team, 2021). 379

380

Finally, we partitioned the variance of the stand dieback models to assess the relative weights of the biotic, climatic, and topoedaphic factors. Venn diagrams were drawn with the eulerr R package (Larsson, 2021) to evaluate the specific and combined weights of these three groups of variables in the explained variance of Xstem50 and of biotic potential colonization indices. In such diagrams, the area of the ellipse plotted for each group is proportional to the sum of its individual coefficient of determination and its joint contribution with one or several other groups. The joint contributions are represented by the area of the intersections of the individual ellipses.

389

390 **3.** <u>Results</u>

391 The stands studied were relatively young, 88 years on average, with a quite broad range of 392 tree age and diameter between and within plots (Table 2 and Appendix F). This variability is 393 related to the gradual recolonization of abandoned farmlands by Scots pine over the last century (Médail, 2001). Their health status is poor; the foliar deficit (FolDef) and percentage 394 of stems with more than 50 % of foliar deficit (Xstem50) respectively averaged 48% and 395 396 31% (Table 2). No plot showed less than 25% of foliar deficit, and 51% of the plots were 397 considered as declining as XStem50 was higher than 30%. A broad variability in the 398 presence and abundance of biotic agents was observed between plots: mean crown infestation by mistletoe in the crown ranged from 0 to 29%, and the mean number of 399 400 caterpillar nests per tree ranged from 0 to 6 (for details see Appendix G).

401

Variable	Mean	Standard	Min	Max
		deviation		
Age (years)	88	30	48	181
Diameter at breast height	26	4.6	17	40
(cm)				
Stand basal area (m ² /ha)	23.1	8.8	8	48
FolDef (%)	48.3	11.7	25.8	84.5
Xstem50 (%)	31	24.9	0	90
NbnestTp	0.66	1.25	0	6
CrownVa (%)	8.1	7.6	0	29

402 **Table 2.** Main stand characteristics. The target variables are defined in Table 1.

404 <u>3.1 Influence of elevation, IKR, and topoedaphic index</u>

405 Below 1200m of elevation, the mean tree foliar deficit (FolDef) and the percentage of stems in the plot with at least 50% of leaf deficit (Xstem50) were significantly higher than above this 406 407 threshold (p < 0.05; Figure 3A and 3D; Appendix H). The effect of IKR was less obvious as 408 there were no significant differences in Xstem50 (Figure 3E), and only the trees growing in 409 the hot situations had higher FolDef (p<0.01; Figure 3B). FolDef and Xstem50 were higher in 410 the unfavorable topoedaphic situations than in the neutral and favorable classes, while the difference between these two classes were only significant for FolDef (Figure 3C and 3F). 411 There were no interactive effects of the elevation, IKR and TEI classes on both dieback 412 variables. 413



Figure 3. Differences in tree foliar deficit (FolDef, %; *Top*) and in stand XStem50 (%; *Bottom*) between classes of elevation (A and D), IKR (B and E) and topoedaphic index (TEI; C and F). Rectangles delimit two central quartiles separated by the median. Points indicate the value of each tree (A, B, C) or each stand (D, E, F). Groups sharing the same letter did not differ significantly (p < 0.05).

414 <u>3.2 Potential colonization indices for mistletoe and processionary moth</u>

The proportion of the crown colonized by mistletoe (CrownVa) was highly correlated with 415 biotic, climatic, and topoedaphic factors ($R^2 = 0.38$, p < 0.001; Table 3 and Figure 4). 416 417 Concerning the biotic factors, it was positively impacted by the cumulative area of pine 418 species sensitive to mistletoe (pine presence index; PPI) in an 8 km radius around the 419 studied plot. Mistletoe was more abundant when water deficit was marked (i.e., low P-PET), 420 and when mean January and July temperatures (Skre index) were high. Likewise, mistletoe 421 was more abundant in situations with unfavorable topography, where temperatures are higher and the water balance lower, such as on convex terrain or at the top of the slope 422 423 (low TEI and high TPI_100). In the PLS regression, climatic variables had standardized 424 coefficients that are ~2 times higher than those of the other variables with significant effects, highlighting the strong importance of climate on the colonization by mistletoe. 425

426 Like mistletoe, the number of processionary moth nests per tree (NbnestTp) was closely 427 correlated with biotic, climatic, and topoedaphic variables ($R^2 = 0.32$, $p \le 0.001$; Table 3 and 428 Figure 4). The PPI and climatic variables had the highest standardized coefficients in 429 absolute values; PPI being positively associated with the number of nests, but this time in a radius of 6 km. The PET from October to March and the absolute minimum temperature 430 also influenced significantly and positively the number of nests. The warmer the winter 431 months, the more nests were found. Finally, the two topographic factors TEI and TPI (here 432 TPI_1500) were significant, as they were for mistletoe. Caterpillars were more abundant in 433 situations with unfavorable topography and water balance (low TEI) such as on convex 434 435 terrain or at the top of the slope (high TPI_1500).

	Number of components of the PLS	Q ²	RSS	∑ <i>R</i> ² <i>Y</i>
Biotic index for mistletoe	1	0.34	3067	0.38
Potential colonization index of V. album CIVA	•	0.01	0001	0.00
Biotic index for processionary moth	1	0.25	91	0.32
Potential colonization index of <i>T. pityocampa</i> CITP	-	0.20		0.02

Tree dieback model	1	0.32	97613	0.33				
FolDef (%)	2	0.34	90580	0.38				
Stand dieback model	1	0.62	20228	0.65				
Xstem50 (%)	-	0.02	20220	0.00				
			Misclassi					
		CHI ²	fied*	AUC				
Stand dieback risk model	1	67	21.6%*	0.88				
<i>Xstem50</i> ≥ 30%	-	01	211070	0100				
436 Table 3 . Summary statistics for the different Partial Least Square (PLS) regression models.								
437 Q^2 the coefficient of Stone-Geisser, RSS the Residual Sum of Squares, $\Sigma R^2 Y$ the								
438 coefficient of determination, and AUC the Area Under the receiver operating characteristics								

439 Curve.* The misclassification rate was calculated by cross-validation

Biotic indexes



Legend

Figure 4. Standardized partial correlation coefficients of the significant variables selected in the Partial 442 Least Squares regression models developed to predict the potential colonization of the biotic factors, and 443 to predict tree and stand dieback. CrownVa% is the percentage of pine crowns colonized by mistletoe (% 444 per tree or per plot according to the model); *NbnestTp* is the number of processionary moth nests (per 445 tree or per plot according to the model); PPI is the Pine Presence Index expressed in area occupied by 446 447 pine species sensitive to mistletoe or to pine processionary moth (ha; calculated in a radius of 8 km and 6 km, respectively); DBHm is the mean stand DBH (cm); DBHt/DBHm is the ratio between tree DBH and 448 the mean stand DBH; Gs20 is the mean BAI over the last 20 years (1997-2016; mm²/year); Gsd is the 449 450 mean BAI during the major climatic stress (2003-2007; mm²/year); RE is the resilience, defined as the 451 ratio between mean BAI after drought (2008-2016; Gsa) and before drought (1997-2002; Gsb); RC is the recovery, defined as the ratio between mean BAI after drought (2008-2016; Gsa) and during drought 452 (2003-2007; Gsd); P-PET_1103 and P-PET_0410 are the difference between precipitation and potential 453 evapotranspiration calculated from November to March, and from April to October, respectively; SKRE 1 454 is the Skre index (see eq. 1). PET_1003 is the potential evapotranspiration October to March; TNABS is 455 the absolute minimum temperature (°C); TEI is the field-based topoedaphic index; TWI is the 456 topographic wetness index; TPI 100 and TPI 1500 are the topographic position indices calculated using 457 100m and 1500m radii, respectively. Finally, CIVA and CITP are the potential colonization indices 458 calculated for V. album and T. pityocampa, respectively. All climatic variables are calculated for the 459 1981-2010 period. 460

461

462 <u>3.3 Dieback models</u>

463 Tree model

The model explaining the foliar deficit of the 402 cored trees had a coefficient of determination of 0.38 with 12 significant variables (Table 3 and Figure 4). The two most influential variables were the percentage of the crown colonized by mistletoe (CrownVa) and the number of caterpillar nests (NbnestTp) per tree, which were positively correlated with foliar deficit. Then, in decreasing order of importance, came the topographic wetness index (TWI) and the topoedaphic index (TEI), for which the foliar deficit was negatively correlated, followed by the summer and winter climatic water balance (P-ETP), which positively influence tree health status (negative correlation with foliar deficit). Trees that grow the best, i.e., with higher mean BAI over the last 20 years (Gs20), and that best experienced the 2003-2007 drought (high Gsd, resilience RE and recovery RC values) showed the lowest foliar deficit. Finally, stand mean DBH was positively correlated with the foliar deficit; but in these stands, the suppressed trees (with a low DBHt/DBHm ratio) tend to be more defoliated.

475 Stand model

At stand scale, the model predicting Xstem50 had the highest coefficient of correlation ($R^2 = 0.65$; 476 Table 3). It involved three variables, CrownVa, TEI and NbnestTp, in order of decreasing 477 478 importance. A high mean abundance of mistletoe and caterpillar nests increased the percentage of 479 stems with at least 50% of foliar deficit; and both biotic factors contributed to 42.3% of the explained variance in Xstem50 (Figure 5A). The stand dieback level was lower in favorable 480 topoedaphic conditions (high TEI), whose contribution on the variance in Xstem50 is limited when 481 analyzed alone (5.6%), but much higher when considering its joint contribution with the biotic 482 variables (16.6%; Figure 5 A). This model does not emphasize the direct effect of climatic 483 484 variables on Xstem50, but the climate is involved indirectly via its contribution in the PLS regressions quantifying the potential colonization of mistletoe (it explained 31.5% of the variance; 485 Figure 5B) and of the processionary moth (19.6% of the variance; Figure 5C). 486



Figure 5. Venn diagrams for the stand dieback model and the two biotic colonization indices: mistletoe and processionary moth. The independent and joint contribution of each type of variable (defined in Figure 4) is expressed as respectively the area of circles and of their intersections, which are proportional to their contribution to the explained variance of the model.

The interaction between the climatic factors and biotic factors explains part of the variability in 489 490 dieback observed among stands (Figure 6). In the situations where mistletoe was present in the 491 field, Xstem50 increased with the mistletoe potential colonization index (CIVA index), and indicator of favorable environmental conditions. In contrast, when mistletoe was absent, the percentage of 492 493 stems with dieback did not increase with these favorable conditions (Figure 6). Stand health status was thus degraded when the presence of mistletoe in the field is combined with warm and dry 494 495 climate and topoedaphic conditions. In contrast to mistletoe, the number of processionary moth 496 nests did not act as interactive factor with climate, but as additive effect (Figure 6). The presence of nests increased defoliation in the plots significantly (p < 0.05), on average by 10 %, irrespective 497 498 of whether mistletoe was present in the field.



Figure 6: Xstem50 as a function of the potential colonization index for mistletoe (CIVA index) and according to the actual presence or absence of mistletoe and processionary moth on the plot.

502

503 Risk model

The dieback risk model developed here performed well: its cross-validation misclassification rate was 21.6%, and its AUC was 0.88 indicating an excellent predictive quality (Hosmer *et al.*, 2013). It tends to lightly overestimate dieback proportion in medium risk classes, i.e., when the dieback risk predicted by the model is between 20 and 80%, the proportion of stand with observed dieback is lower than expected (Figure 7).

509 Four variables were significant in this model; of these two were linked to mistletoe (Figure 4). The first was its potential colonization (CIVA) index, which integrates 510 biotic (PPI), climatic, and soil factors (Figure 6B). The second was its actual presence in the field 511 (CrownVa). Introduction of these two variables in the risk model takes account of the interaction 512 between the presence of mistletoe and the environmental conditions prone to its development 513 (underlying factors in the CIVA index). The other two variables were also included in the stand 514 515 model, namely the topoedaphic index and the average number of processionary caterpillar nests per tree. Although only marginally significant (p = 0.06) and consequently not considered in the 516

517 best model (Figure 4), the processionary moth potential colonization index (CITP) confirmed the

518 indirect influence of climatic variables on dieback risk.

519



Figure 7. Distribution of healthy stands (Xstem50<30%) or stands with dieback (Xstem50 \geq 30%) by the dieback probability class as predicted by the risk model. These 20% classes were set to include at least five plots each. Significant differences in the proportion of plots with observed dieback were observed between risk classes predicted by the model (chi-square = 40.17, df = 4, p < 0.001).

526

527 4. Discussion

Tree dieback is a complex process that requires a multifactorial and multiscale approach (Franklin *et al.* 1987; Manion 1991; Allen *et al.* 2015). This study, based on multivariate statistical models and conducted on Scots pine, confirms the importance of incorporating a range of biotic factors (tree and stand characteristics, and abundance of mistletoe and processionary moth), topographic and soil factors representing the local- and landscape-scale water balance, and climatic factors, which are important both directly and through their interactions with the other factors.

534 4.1 Biotic factors

535 Mistletoe and the pine processionary moth play essential roles in the Scots pine dieback process. 536 When considering their interaction with the topoedaphic variables, these biotic factors explain 537 64.5% of the variance in the percentage of stems with 50% of leaf deficit (stand model predicting 538 Xstem50 ; Figure 5).

539 The impact of mistletoe on the health and growth of Scots pine is well documented. Mistletoe does not regulate its transpiration even under drought, and consequently reduces the water available to 540 the host tree, worsening its physiological stress. It also uses a significant proportion of the 541 542 nutrients from the tree sap, which it stores in its own structure (Mutlu et al., 2016). Consequently, 543 infested trees close their stomata earlier and longer (Zweifel et al., 2012) and produce smaller 544 leaves (Rigling et al., 2010) thereby limiting their carbon absorption capacity and growth potential 545 (Meinzer et al., 2004). Stand-scale productivity losses have been estimated at between 29% in Germany (Kollas et al. 2018) and 64% in Spain for high levels of infestation (Camarero et al., 546 547 2018), with lower resistance and resilience to severe drought. Infestation by mistletoe is on average more marked in the upper part of the crown due to the parasite's heliophilous nature 548 (Briggs, 2021; Mellado and Zamora, 2014) and the behavior of the birds that spread it. This 549 explains why it was mostly present in our study area in sunny locations such as on convex terrain 550 (high TPI; Figures 4 and 5), and in open stands. 551

552 The presence of mistletoe is also linked to climate (Jeffree and Jeffree, 1996), especially to temperatures in the coldest and hottest months, as shown by its significant correlation with the 553 554 Skre index (Figure 4). Although temperature is the variable that best explains the presence of 555 mistletoe, the population density of fruit-eating birds, and more specifically of its main dispersion agent the thrush genus Turdus, also explains the spatial distribution of mistletoe at landscape 556 scale (Ramsauer et al., 2021). The most significant radius (8 km) used to calculate the area of 557 pines sensitive to mistletoe around our plots is in line with the literature, e.g., with the minimum 558 559 radius of 3.5 km estimated in Catalonia by Ramsauer et al. (2021). The propagation of mistletoe from a point source is fast, accelerates over time with the progressive increase in population 560 density in neighboring areas, but is still modulated by vegetation distribution in the landscape and 561

especially by the availability of host species (from 0.04 km/year to 0.35 km/year ; Hawksworth and
Scharpf 1986, Shaw and Lee 2020).

The processionary moth is a forest pest that can cause severe damage to leaves, especially in 564 newly infested areas (Battisti et al., 2005; Stastny et al., 2006). Its distribution in our study area 565 566 was closely linked to climate, to the area covered by pine stands on the landscape, and to soil and topography factors. The potential evapotranspiration from October to March and minimum 567 absolute temperature were the two dominant climatic variables in the colonization model, in line 568 569 with the model of Robinet et al. (2007) calibrated in central France. Low minimum temperature 570 limits the expansion of the processionary moth toward higher elevations and latitudes (Hoch et al., 571 2009; Hódar et al., 2003) as it needs heat in winter and large amounts of sunlight to feed and 572 survive (Battisti et al., 2005). It is accordingly found on sunny exposition (e.g., at the top of the slopes, south-facing aspect; Figures 4 and 5) and in open forests where tree canopies are well 573 exposed. The optimal radius to compute its pine hosts density (6 km), is consistent with the study 574 by Robinet et al. (2014b), stating that females can fly 6 km on average, and up to 10 km. 575

576 The density of both mistletoe and processionary moth populations seem thus reduced when the 577 stands sensitive to these parasites are young, have low stand density, and are scattered over the landscape (low PPI; see also Shaw and Lee 2020). Because Scots pine naturally and gradually 578 579 colonized abandoned farmland over the last century (Médail, 2001), its age and spatial distribution is irregular within the landscape. This explains why some plots were not or only slightly affected by 580 these parasites, and thus relatively healthy, despite climatic and site conditions favorable to these 581 pests (Figure 6). Such plots, though few in number, reduced the predictive capacity of the dieback 582 583 models by partly masking the effects of climatic variables.

584

585 For these two heliophilous parasites, the significant weight of topography and soil is explained by 586 their relationship with the water balance and landscape structure. Stands located at the top of the 587 slopes, on ridges, on convex terrain well-exposed to sunlight, and on shallow or stony soils (often 588 found in such locations due to erosion), (i) usually have a low stem density and canopy cover 589 favoring the infestation of dominant trees with sunny crowns, and (ii) have limited water retention

590 capacities, weakening trees and increasing their vulnerability to these parasites and so 591 accelerating dieback (Mutlu *et al.*, 2016). These stands have especially experienced high 592 defoliation and mortality rates during and following the 2003–2007 drought (Vennetier *et al.*, 593 2007), opening them, and favoring both mistletoe and processionary moth populations.

594

595 Independently of the factors cited above, stands with large mean tree DBH had higher foliar deficit (see also Galiano et al. 2010). These large trees generally have larger crowns, which would be 596 597 preferred by both mistletoe and processionary moth that demand light. They also provide more sites 598 for birds involved in the spread of mistletoe (Kolodziejek J and Kolodziejek A, 2013). Nevertheless, 599 in these stands, shaded trees smaller than the stand average had higher foliar deficits, probably due 600 to the relative intolerance of Scots pine to high levels of shade (Gaudio et al., 2011). This result is supported by the studies from Taccoen et al. (2021) who reported an excess of mortality in shaded 601 602 Scots pine in South-East France linked to the climate and its change, and from Galiano et al. (2010) 603 in the Spanish Pyrenees.

604

Finally, trees with the lowest foliar deficit were also those with the higher mean growth over the last 605 20 years, and with the higher recovery and resilience after the 2003-2007 drought. The causal link 606 between growth and crown health (i.e., defoliated trees show low growth rates and recovery after 607 608 drought, or trees with low growth and recovery rates are more sensitive to further drought and prone 609 to dieback) is unclear because the information on the temporal change in foliar deficit is missing. 610 However, the negative relationships between foliar deficit and mean growth rates and resilience to 611 drought were consistent with previous physiological and dendroecological studies (e.g., DeSoto et al., 2020; Dobbertin, 2005; Guada et al., 2016; Poyatos et al., 2013). Interestingly, growth 612 613 resistance to drought does not seem related to Scots pine dieback, just as it does not seem related 614 to the mortality of gymnosperms (DeSoto et al., 2020).

615

616 <u>4.2 Climatic factors</u>

617 Climatic variables alone only partly explained tree dieback in the PLS regression models. The more 618 unfavorable the climatic water balance (P-PET) during the growing and non-growing seasons, the

higher the foliar deficit, reflecting the well-known sensitivity to drought of Scots pine (e.g., Camarero
et al., 2015; Galiano et al., 2010; Matías et al., 2017; Rigling et al., 2013). These climatic variables
were calculated for the period 1981–2010. This period was warmer than the previous decades
(Cramer et al., 2018), thus favorable towards the dissemination of mistletoe with more effects on the
health of stands.

This period also corresponded to the first reports of massive dieback in southeast France, partly linked to the presence of biotic agents and drought (Lieutier et al., 1988; Sardin, 1997). As previously shown, the strong interactions of climate with biotic and topoedaphic factors (Figure 6), added to the irregular spatial distribution of these biotic agents on the regional scale, probably limited the ability of the models to isolate the impact of some climatic variables.

629 4.3 Soil and topography factors

Our analysis highlights a strong effect of topographic and edaphic conditions on foliar deficit, which are important in offsetting or worsening climatic water balance. Scots pine presents high foliar deficits on shallow soils (i.e., low TEI) with low water holding capacity (Galiano *et al.* 2010) but also low growth rate (Bigler *et al.* 2006).

The topoedaphic index (TEI) had a significant effect in all the dieback models developed, 634 confirming its relevance to assess at least roughly the water balance at local scale, independently 635 of the vegetation and climate. A more accurate quantification of this water balance could be 636 obtained from fine soil measurements and from the evaluation of the water demand at stand scale 637 (e.g., with the leaf area index; see Granier et al., 2000), but would require additional work beyond 638 our possibilities. Operationally, the TEI offers the advantage of being of use in varied topographic 639 640 conditions, notably in conditions where slope or hillside effects are very marked, such as in our study area. 641

However, this index still needs calibration at regional scale and to be evaluated in other contexts, and is not sufficient to estimate water fluxes and pools at landscape level. Topographic indices calculated from DEMs on a scale of 100 m (microtopography) or 1500 m (macrotopography) must also be integrated, as revealed by our tree dieback model and several previous studies (Petroselli et al., 2013; Raduła et al., 2018; Kopecký et al., 2021).

647 <u>4.4 Comparison of dieback models</u>

The model developed at tree level had quite low performance ($R^2 = 0.38$), which may partly due to 648 the difficulties when estimating tree leaf deficit despite a careful application of the protocols. The 649 650 presence of understorey may limit the view of the functional crown in several directions and the 651 microphylly, which is very frequent in our study area, is not easy to estimate with binoculars. However, this was mainly caused by the high variability in foliar deficit within stands (see Table 3), 652 which was only partly captured by the variables measured at tree scale (age, diameter, and annual 653 radial growth). The integration of an individual-based competition index (e.g. Heygi index 1974) 654 could have improved the predictive ability of the tree model (e.g. Galiano et al., 2010). 655

656 In the geologically complex environments we studied, the vertical and horizontal heterogeneity in 657 soil properties (e.g., texture, percentage of coarse elements) and in bedrock fracture levels was very high, sometimes only a few meters away, and could not be evaluated with a single soil pit. 658 659 This intra-plot variability in foliar deficit can also be linked to different microclimatic conditions 660 between trees depending on their neighborhood and on the micro-topography. Some trees have also undergone other climatic damages, such as snow breaks, often observed in these 661 environments (Vennetier et al. 2007). They may have different genetic potential, for example 662 causing differences in water use efficiency, even though this effect of genetic differentiation may 663 be negligible (Santini et al., 2018). 664

At stand scale, the models predicting the percentage of declining tree (i.e., with a foliar deficit higher than 50%), and the probability of having more than 30% of declining trees model offered a higher prediction quality ($R^2 = 0.65$ and AUC = 0.88, respectively). The risk model reliably predicted dieback in successive 20% classes (Figure 7), making it operational for a direct use in the field; although a slight tendency to overestimate dieback between 20 and 80% was noted. This model seems to offer a valuable support for decision-making in forest management in a context of increasing drought recurrence and intensity.

This modeling approach was designed to be continuously improved, generalized to all tree species and other pedoclimatic contexts, and enhanced by the improved quality and availability of foliar deficit data, for example at European scale (Ferretti, 2021). Another option was to make the risk

model available as an application to allow simple diagnostics in the field and make use of data collected by users, so increasing the size and diversity of the database used for calibration and validation. This would make the model more general, i.e., of use in regions where other abiotic or biotic factors are involved in the dieback process (e.g., presence of other pathogens, high competition intensity, hydromorphy; see Oliva *et al.*, 2016 or Taccoen *et al.*, 2021).

680

681 **5.** <u>Conclusion</u>

682 This work emphasizes the importance of taking into account the respective and interactive effects of multiple abiotic and biotic environmental factors to model tree foliar deficit and dieback. The 683 684 abiotic factors cannot be reduced to the climatic conditions alone and must also include soil variables observed in the field and the local and landscape topography, which contribute to the 685 local water balance. Finally, the abundance of biotic factors, here processionary moth and 686 mistletoe, is of key importance to accurately predict foliar deficit and dieback of Scots pine. 687 Considering that their potential colonization on the host pine tree is also dependent of biotic, 688 climatic, soil and topographic factors, this study highlights the interdependencies between biotic 689 agents and abiotic factors. 690

691

692 6. <u>Acknowledgments</u>

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699 **7.** <u>References</u>

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8. <u>Appendices</u>

1074 Appendix A. List of variables used in the different dieback models

Tune of uniable	Verieble	11	Coole	Deviad		Description	Course
Type of variable	variable	Unit	scale	Period	variables	Description	Source
Targatuariahlas Y	FolDet	%	tree	2017	1	Foliar deticit of the tree microphylls included	Field management
larget variables Y	XStem50	%	piot	2017	1	Percentage of stems per plot with at least 50% leat loss and/or branching	Field measurement
	DECL_XSTEM_th	0 or 1	plot	2017	3	Number of plots with Xstem50 above a given threshold (th = 20%, 25%, 30%)	
	%CrownVa	%	tree	2017	1	Percentage of crown colonized by mistletoe	Field measurement
	NbNestTp	nb	tree	2017	1	Number of nests per tree on the plot	Field measurement
	G_Tot	m²/ha	plot	2017	1	Basal area	Field measurement
	DBHm	cm	tree	2017	1	Mean diameter of Pinus sylvestris at breast height	Field measurement
	Hmean	m	tree	2017	1	Mean height of Pinus sylvestris	Field measurement
	Age	years	tree	2017	1	Age of the tree	laboratory measurement
	DBHt	cm	tree	2017	1	Diameter of the tree t at breast height (130 cm)	Field measurement
	DBHt/DBHp	/	tree	2017	1	Ratio of DBHt to the mean diameter of the trees growing in the same plot p	Field measurement
	Gs	mm²/y	tree		1	Mean annual basal area increment	laboratory measurement
	Gs20	mm²/y	tree	1997-2016	1	Mean annual basal area increment for the last 20 years	laboratory measurement
Piotic factors	Gsb	mm²/y	tree	1997-2002	1	Mean annual basal area increment before the major climatic stress	laboratory measurement
BIOLIC IACLOIS	Gsd	mm²/y	tree	2003-2007	1	Mean annual basal area increment during the major climatic stress	laboratory measurement
	Gsa	mm²/y	tree	2008-2016	1	Mean annual basal area increment after the major climatic stress	laboratory measurement
	RS	/	tree		1	Resistance, ratio GSd/GSb	laboratory measurement
	RC	/	tree		1	Recovery, ratio Gsa/Gsd	laboratory measurement
	RE	/	tree		1	Resilience, ratio Gsa/Gsb	laboratory measurement
						Area covered by pine species (P. sylvestris, P. halepensis, P. nigra ssp nigra, P. nigra ssp laricio) susceptible to the	
						caterpillar (Thaumetopoea pityocampa) within different radius (r) around the center of the study plot ($r = 500 \text{ m}, 1$	
	PPI caterpillar r	ha	plot	2014	9	km. 2 km. 4 km. 6 km. 8 km. 16 km. 32 km. 64 km)	
			p			Area covered by pine species (P. sulvestris, P. nigra ssp nigra, P. nigra ssp laricia) susceptible to mistletoe (Viscum	Database of French national land su
						album so gustrigrum) within different radius (r) around the center of the study plot (r = 500 m, 1 km, 2 km, 4 km, 6	
	PPI mistletoe r	ha	plot	2014	9	km 8 km 16 km 32 km 64 km)	
	Tmean m	°C	plot	1981-2010	12	Mean monthly temperature for the months January (m=1) to December (m=12)	
	Tmean year	- ۰۲	nlot	1981-2010	1	Mean annual temperature	
	Tmean 1202	°C	plot	1981-2010	1	Maan winter temperature (December to Eebruan)	
	Tmean_1202	°C	plot	1981-2010	1	Mean white temperature (reamber of rebuilty) Mean summer temperature (reamber of rebuilty)	
		°C	plot	1081 2010	1	Mapa of the myself sector 1091 2010 from lune to August	
	TN m	°C	plot	1081-2010	6	Mean of the minimum temperature 1561-2010 from the collegest $(m=2)$	
-	TN 1002	°C	plot	1081-2010	1	Mean of the maximum temperature for the months occuber (h=10) to March (h=5)	
-	TN_1005		plot	1081-2010	1		
_	P_year		pior	1981-2010	1		
	P_0608	mm	piot	1981-2010	1	Precipitation 1981-2010 from June to August	
	P_0509	mm	plot	1981-2010	1	Precipitation 1981-2010 from May to September	
	P_0410	mm	plot	1981-2010	1	Precipitation 1981-2010 from April to October	
	P_1103	mm	plot	1981-2010	1	Precipitation 1981-2010 from November to March	Climatic model AURELHY © METEC
_	PET_m	mm	plot	1981-2010	12	Potential evapotranspiration (Turc Formula) for the months January (m=1) to December (m=12)	(precipitation and temperatu
_	PET_1003	mm	plot	1981-2010	1	Potential evapotranspiration (Turc Formula) 1981-2010 October to March	
Climatic factors	PET_1004	mm	plot	1981-2010	1	Potential evapotranspiration (Turc Formula) 1981-2010 October to April	
-	PET_0410	mm	plot	1981-2010	1	Potential evapotranspiration (Turc Formula) 1981-2010 October to April	
	PET_0509	mm	plot	1981-2010	1	Potential evapotranspiration (Turc Formula) 1981-2010 May to September	
	PET_0608	mm	plot	1981-2010	1	Potential evapotranspiration (Turc Formula) 1981-2010 June to August	
	PET_year	mm	plot	1981-2010	1	Annual potential evapotranspiration (Turc formula) 1981-2010	
	PET_1103	mm	plot	1981-2010	1	Potential evapotranspiration (Turc formula) 1981-2010 November to March	
	P-PET_0608	mm	plot	1981-2010	1	Climatic water balance (P-PET) 1981-2010 June to August	
	P-PET_0509	mm	plot	1981-2010	1	Climatic water balance (P-PET) 1981-2010 May to September	
	P-PET_0410	mm	plot	1981-2010	1	Climatic water balance (P-PET) 1981-2010 April to October	
	P-PET_1103	mm	plot	1981-2010	1	Climatic water balance (P-PET) 1981-2010 November to March	
	P-ETP_year	mm	plot	1981-2010	1	Annual climatic water balance (P-PET) 1981-2010	
	ray_year	J/cm ²	plot	1971-2000	1	Sum of annual radiation 1971-2000	DIGITALIS © AGROPARISTECH r
							Climatic model SAFRAN © METEOFRANC
	TNABS	°C	plot	1981-2010	1	lowest temperature recorded each year during the 1981-2010 period	Lemaire and Pigeon 2015
	SKRE I	1	plot	1981-2010	1	Skre index	See Equation 1 section 2.4 (Skre 1979. D
	TEI	. /	plot			Topoedaphic index Appendix A *	Field measurement
	Elevation	m	plot		1	Elevation	DEM IGN 25 m resolution
	TPI 100	1	plot	-	- 1	Topographic position index in a radius of 100 m around the center of the plot	DEM IGN 25 m resolution
Soil and topographic	TPI 1500	1	plot		1	Topographic position index in a radius of 1500 m around the center of the plot	DEM IGN 75 m resolution
factors	IKR	1	plot		1	Radiation index of Becker 1982	Field measurement
lactors	pH Hz Ah	1	plot		1	pH groundwater at 20 cm depth	Field measurement
	TW/		plot	-	1	Tonographic wetness index	DEM IGN 75 m resolution
	1 991					LODGEI GDUILE WELLESS HIVEA	LIE VERSING A STREET AND A STRE



Figure B1. Temporal change in mean basal area increment of healthy (HEALTHY) and declining (DECL) trees

1083 Appendix C. Effect of the sub-sampling on the development of the stand dieback model

To develop the foliar deficit model at tree scale, which includes annual radial growth data from cores, a subsample of 28 plots was selected among the 87 plots of the study, covering all the stratification classes (see 2.2 in main text).

The absence of bias arising from subsampling was checked to ensure that this subsample of 28 plots (FolDef: mean = 51.8%, SD = 13.1%) was representative of the whole set of 87 plots (FolDef: mean = 48.3%, SD = 11.7%).

1090 In this way, we compared the stand dieback models constructed over the whole set of 87 plots 1091 (see Table 1 in the main text) with this same dieback model calibrated on those 28 plots. The 1092 significant variables retained in the two models were the same, and their non-standardized 1093 coefficients were not significantly different (Figure B1).



1094

Figure C1. 95% confidence interval of centered values (standardized coefficients) of 1095 significant variables for the stand dieback model constructed over the whole set of 87 plots 1096 (DECL_STAND) and for the subsample of 28 plots (SUB-SAMPLE).CrownVa is the 1097 1098 percentage of pine crowns colonized by mistletoe per plot (%); NbnestTp is the number of 1099 processionary moth nests per plot; TEI is the field-based topoedaphic index.

1100 Appendix D. Estimation of the Topoedaphic index TEI

		UNFAVORABLE FACTORS NEUTRAL FACTORS								FAVOR	FAVORABLE FACTORS			
ldform	General topography	Convex ridges, peaks and higher slopes	-14	Regular top of slope	-6	Regular slope	-3	plateau	0	Concave lower slope	10	Valley, thalweg bottom	18	
Lar	Plot scale			convex	-8			Flat	0	concave	8			
	topography													
	Former farmland Terraces						_	absence	0	presence	13			
	Slope angle	000/		140.000/1		<u>></u> 50%	-1	<50%	0					
	Rock outcrop (%)	<u>></u> 30%	-8]10-30%]	-3	[1-10%]	-1	0%	0					
к	(%)			<u>></u> 30	-3	[10-30%[-2	[1-10%[0	0	2			
Ro	Dip angle vs slope					unfavorable	-1	neutral	0	favorable	1			
	Joints and cracks through					_		_ / _	-		-			
	rock layers (per m)					<5	-2	5-15	0	> 15	3			
	Reference material	Mother rock	-4	alterite	-2	lapiaz	-1			colluvium	5			
	Earth reaction to HCI					strong	-2	weak	0	none	3			
terial	Hard rocks coarse fragments in soil	<u>></u> 90%	-7	[60-90%[-3			[30-60%[0	<30%	4			
Ň	Horizontal imbricated alterite plates			presence	-6			absence	0					
	Fine earth Water Holding Capacity (mm/cm)*	<u><</u> 0.7	-10]0.7-1.3]	-3]1.3-1.6]	0]1.6-1.95]	2	>1.95	10	
Ч	Colluvium thickness (cm)			absence	-2	[5-20]	-1	[25-50]	0	>50	3			
ept	total depth (cm)	[0-22.5[-12	[22.5-47.5[-5			[47.5-75[0	[75-100]	5	>100	10	
Ō	Mean depth 5 auger tests (cm)					[0-20]	-2]20-40]	0]40-75]	2	>75	3	
Т	poedaphic Index (TEI)	=		+		+		+		+		+		

1101

1102 Table D1. Description of the determination of the topoedaphic index (TEI) according to 1103 field-based topography, bedrock, soil material, and soil depth variables. The plot TEI is 1104 obtained by adding the coefficients (grey columns) corresponding to each variable. More 1105 details are available in Vennetier et al. (2018), especially concerning the relationship between Water Holding Capacity and fine earth texture. 1106

1108 Appendix E. Choice of Xstem50 threshold

- 1109 Three thresholds in Xstem50 were tested during the development of the risk model
- 1110 corresponding to values published in the literature: 20% (DGAL, 2018), 25 % (Linares and
- 1111 Camarero, 2012), and 30% (Brunier *et al.*, 2020).
- 1112 Based on comparisons of the confusion matrix and the AUC, the threshold that best
- discriminated stands with and without dieback was 30% (Table D1).
- 1114

XSTEM50%	AIC	Misclassed on 87 plots	Chi2_Pearson	RSS	R ² Y	AUC	Error rate
20%							
Nb_Comp_1	88.79	24	70.86	14.24	0.30	0.830	27.6%
25%							
Nb_Comp_1	77.6	21	71.23	12.28	0.43	0.877	24.1%
30%							
Nb_Comp_1	77.48	19	73.53	12.11	0.44	0.882	21.8%

Table E1. Comparison of the performance of the risk models with different Xstem50 thresholds. AIC is the Akaike Information Criterion, RS the residual sum of squares, R²Y the coefficient of determination, AUC the Area Under the receiver operating characteristics Curve.

1119





Figure F1. Distribution in age of the trees cored (n = 402; *Left*) and in diameter at breast height (DBH) of all trees measured (n = 1440; *Right*).









1131

1132 **Figure H1**. Differences in tree foliar deficit (FolDef, %) between each combination of class

of elevation (<1200m; >=1200m), IKR (HOT, NEUTRAL, COLD) and topoedaphic index

1134 (TEI; FAVORABLE, NEUTRAL, UNFAVORABLE). Rectangles delimit two central quartiles

separated by the median. Groups sharing the same letter did not differ significantly (Nemeyi

- 1136 test; p < 0.05).
- 1137