

Spatial vulnerability assessment of silver fir and Norway spruce dieback driven by climate warming

Christian Piedallu, Donatien Dallery, Célia Bresson, Myriam Legay,

Jean-Claude Gégout, Rodolphe Pierrat

▶ To cite this version:

Christian Piedallu, Donatien Dallery, Célia Bresson, Myriam Legay, Jean-Claude Gégout, et al.. Spatial vulnerability assessment of silver fir and Norway spruce dieback driven by climate warming. Landscape Ecology, 2023, 38 (2), pp.341-361. 10.1007/s10980-022-01570-1. hal-04005898

HAL Id: hal-04005898 https://hal.science/hal-04005898

Submitted on 27 Feb 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

1	Spatial vulnerability assessment of silver fir and Norway spruce dieback
2	driven by climate warming
3	
4	Authors: Christian Piedallu ^{a*} , Donatien Dallery ^a , Célia Bresson ^a , Myriam Legay ^a , Jean-Claude Gégout ^a ,
5	Rodolphe Pierrat ^b
6	^a Université de Lorraine, AgroParisTech, INRAE, Silva, 54000 Nancy, France
7	^b ONF, DT Grand-Est, cité administrative, 14, rue du Maréchal Juin, 37084 STRASBOURG Cedex
8	*Corresponding author, AgroParisTech - Centre de Nancy, 14 rue Girardet - CS 14216, 54042 NANCY Cedex
9	France, email: christian.piedallu@agroparistech.fr, ORCID: 0000-0001-7316-1874
10	
11	Abstract
12	Context: A significant forest decline has been noticed these last years in Europe. Managers need tools to
13	better anticipate these massive events.
14	Objectives: We evaluated the efficiency of easily available data about environmental conditions and
15	stand characteristics to determine different levels of vulnerability.
16	Methods: We combined remote sensing images, photo-interpretation, and digital models describing
17	environmental conditions within a modelling approach to achieve spatial vulnerability assessment of the
18	stands. We focused on silver fir and Norway spruce stands in the Vosges mountains (8,900 km ² ,
19	northeastern France), where severe symptoms of decline are visible.
20	Results: Silver fir were predicted highly vulnerable on 7% of their area versus 33% for Norway spruce.
21	Using an independent dataset, we observed ten-times (silver fir) and two-times (Norway spruce) higher
22	mortality rates in the units with a high level of vulnerability than in the others. About half of the model
23	deviance was directly or indirectly explained by variables related to water stress (soils displaying low
24	water availability, having suffered severe drying events these last years). Furthermore, the stands
25	acclimatised to drought conditions were more resilient. Stand characteristics also influenced dieback
26	spread, suggesting that an evolution of silvicultural practices toward mixed stands with broadleaved
27	species and uneven-aged trees can contribute to better adapt to future climate conditions.

28 **Conclusions**: Vulnerability maps based on easily available geographic information describing climate, 29 soil, and topography can efficiently discriminate canopy mortality patterns over broad areas, and can be 30 useful tools for managers to mitigate the effects of climate change on forests.

31

32 **Keywords:** climate change, forest dieback, decline, drought, tree vulnerability, vulnerability map.

33

34 Introduction

35 With a global mean temperature increase of at least 1.1°C and changes in rainfall patterns, the effects of the 36 ongoing climate change are more and more visible and consequential on ecosystem functioning (Pörtner et al. 37 2022). Increased tree mortality and changes in forest structure and composition have been observed in different 38 biomes (Allen et al. 2015; Michel and Seidling 2018). In the western United States, van Mantgem et al. (2009) 39 demonstrated a doubling of the rate of background tree mortality every 17 to 29 years, while Peng et al. (2011) 40 observed a 4.9% increase in tree mortality per year from 1963 to 2008 in Canadian boreal forests. In Europe, 41 remote sensing data have revealed a 2.4% increase of canopy mortality per year between 1984 and 2016 (Senf et 42 al. 2018), and different hotspots have been identified in the north or the south of the continent (Neumann et al. 43 2017). These trends were most of the time attributed to the recent changes in climate (Han and Singh 2020; Senf 44 et al. 2020). An excess of tree mortality has been associated to the current changes in temperature or rainfall for 45 about half of the most common European tree species (Taccoen et al. 2019). The impact of climate change on forest decline is expected to persist in the future: climate projections predict that warming will continue, involving 46 decreased water availability for plants and more extreme weather events (Pörtner et al. 2022). 47

48

Climate-related forest dieback is a major concern for forest ecosystems because it influences species composition and structure, affects forest carbon sequestration and water cycle regulation, soil protection, refugia for biodiversity, provision of forest products, recreational uses ... (Brockerhoff et al. 2017). Forest dieback also has an effect on local or regional climate conditions by modifying the albedo and heat fluxes (Anderson et al. 2011). Despite the major importance of the issue, the way forests will cope with climate change remains highly uncertain. Vulnerability assessments are done *a posteriori* most of the time, and forest managers cannot anticipate massive mortality events. The choice of the tree species – traditionally based on specific ecological requirements – can no longer correspond to current climate conditions (Torssonen et al. 2015). In a context of increasing impacts of recent droughts on ecosystems in a large part of Europe (Buras et al. 2020), evaluating the mortality risk across broad areas is crucial to adapt management strategies to the new ecological conditions and make the forest more resistant and resilient to ongoing changes (Bastin et al. 2019; Bonan 2008).

60

61 Species mortality is a natural component of the forest dynamics that can be increased by different stresses. 62 Tree decline is often described as a gradual process involving a combination of interchangeable predisposing, 63 inciting, and contributing factors that interact at different time and spatial scales (Sinclair, 1965), sometimes with 64 delayed effects (Lebourgeois 2007). This conceptual framework was popularised by the decline spiral in the 1980s 65 (Manion 1981). Predisposing factors reduce tree ability to withstand a stress on the long term. Tree growth leads 66 to overcrowding and natural mortality through self-thinning, particularly for suppressed trees or in high-density 67 stands (Charru et al. 2012). Predisposing factors are related to tree or stand characteristics (age, competition for 68 light, species interactions), but also poor site conditions (high temperature, low water availability, soil properties), 69 or air pollution (nitrogen, sulphur deposition, ozone) (Brandl et al. 2020; Dietze and Moorcroft 2011; Taccoen et 70 al. 2019). Inciting factors usually result from extreme events like drought, heat waves, frost, snow, forest fires, 71 floods, or storms (Maringer et al. 2021). The deleterious effects of droughts and heat waves on tree fitness are 72 probably the most extensively studied (Choat et al. 2012; Urli et al. 2013; Williams et al. 2013). Allen et al. (2010) 73 identified more than 150 references on forest mortality driven by extreme events since 1970. The impact of inciting factors is expected to increase in the current climate change context (Hartmann et al. 2018; Schelhaas et al. 2003). 74 75 Contributing factors are often insects or pathogens that cause the final decline of the trees that have already suffered 76 from predisposing or inciting factors through hydraulic failure or carbon starvation (Maruini et al. 2017; McDowell 77 et al. 2008). Several recent outbreaks of bark beetles are considered as some of the most severe outbreaks ever 78 seen (Lundquist 2019). At the end of April 2019, the French National Forest Office (ONF) estimated that 60% of 79 spruce were affected by bark beetle attacks, versus 15% in the usual course of events (Office National des Forêts 80 2020^{1}).

¹ https://www.onf.fr/+/4bd::ces-arbres-forestiers-qui-souffrent-de-la-secheresse.html

82 The decline of silver fir or Norway spruce in not new in Europe (Maringer et al. 2021). Northeastern 83 France already experienced severe tree decline events during the last century, during the 1916-1925 or 1943-1951 84 periods for example. During this latter period, an up to 40 % decrease in radial growth of silver fir was attributed 85 to drought (Becker 1987). The 1973-1981 period was also marked by another important crisis. After Germany and 86 many countries of central Europe, severe decline was observed on several thousand hectares in the Vosges 87 mountains (Bouvarel 1984). In 1984, an observatory network recorded that 26% of silver fir, 20 % of Scot pine 88 and 17% of Norway spruce had lost more 20% of their needles. More mortality was observed on old trees in the 89 east of the mountain range, and on acidic substratum whatever the altitude (Bonneau 1985; Thomas et al. 2002). 90 Climatic stress after the 1976 drought and air pollution that increased the nutritional difficulties and led to 91 magnesium deficiencies were identified as the main drivers of this forest decline (Elling et al. 2009; Landmann et 92 al. 1987; Vitali et al. 2017). Following the reduction in SO₂ concentrations in the air and a period with more 93 suitable climatic conditions, strong recovery was observed after 1981 (Lévy 1987). Tree decline was observed 94 again more recently, mainly on Norway spruce and silver fir, after important drought events followed by an 95 increase of bark beetle attacks, as in 2003 (Ciais et al. 2005) or 2018 (Buras et al. 2020). Silver fir and Norway 96 spruce have been gradually declining in Europe since 2016, questioning managers and policy makers about the 97 future of these species (Obladen et al. 2021). In 2019, Norway spruce represented 32 % of damage at the European 98 scale, with an estimated wood loss of approximatively 36 million m³. The countries of central Europe were most 99 affected. Although forest decline has been extensively studied, the causes of mortality and the ecological limits of 100 the species that trigger mortality are not well understood, and this restrains our capacity to consider the risk of 101 dieback in forest management.

102

103 The vulnerability assessment evaluates the ability of a tree or a forest stand to tolerate a stress. The level of vulnerability varies according to the species sensitivity (its capacity to resist to changing climate), local 104 105 exposure (related to the intensity of the effects of climate change), and the adaptive capacity of the species (its 106 ability to cope with the new climate conditions) (McCarthy et al. 2001). Different approaches have been 107 implemented for managers to facilitate forest adaptation to the new climatic conditions, e.g., recommendations by 108 expert knowledge according to site type maps, or more sophisticated vulnerability assessment based on large 109 databases from forest inventories or remote sensing data, coupled with mechanistic or statistical models. One of 110 the most popular approaches is based on empirical niche models or process-based models (Coops and Waring

111 2011; Fremout et al. 2020). It simulates the suitable areas of the species according to contemporary or simulated 112 climate. These models can be used to evaluate if the species can maintain itself under warmer climate conditions, 113 or to track their current climate niche (Aubin et al. 2018). They have important limitations because the numerous 114 assumptions often lead to overestimating the risk (Das et al. 2022). Vulnerability can also be estimated by 115 modelling the level of dieback using the different factors that can alter tree fitness (Archambeau et al. 2019; Lu et 116 al. 2019). Using this approach for spatial vulnerability assessment over broad areas remains uncertain. Although 117 many predisposing factors are often easily available, inciting or contributing factors are scarcely available, so that 118 predictive performances may be poor. Here we evaluated if easily available geographic information describing 119 climate variability and evolution, and the main soil and topographic characteristics, can be combined with remote 120 sensing images to efficiently discriminate landscape-level canopy mortality patterns at a regional scale. The 121 challenge consists in identifying and characterising the different factors correlated with the risk of dieback, 122 determining which of them can benefit from adaptive management to mitigate the risk, and determining whether 123 existing maps that describe their geographic distribution can be efficient to calculate a relevant vulnerability map. 124

125

126 Materials and Methods

127

128 Focusing on two emblematic stand types of European mountain ranges – silver fir and Norway spruce 129 - we modelled the tree health status and mapped tree vulnerability across an 8,900 km² area located in the Vosges 130 mountains, in northeastern France. For each species, a dataset was built with randomised plots selected on a 131 systematic grid, and stratified according the stand status (dieback or healthy) collected from sentinel-2 images in 2019 (Fig.1). To identify the conditions that promoted decline, the plots were characterised with variables 132 133 describing the site conditions (climate and soil characteristics, climate evolution) available from Geographic 134 Information System (GIS) layers, and the stand characteristics interpreted from aerial photographs. Based on these 135 datasets, models were calibrated and a vulnerability map was calculated at 50 m resolution for each species. The 136 map performances were evaluated against ground survey data providing the volumes of dead wood harvested from 137 exceptional sanitary cuts.

140



- 151 *Fig. 1*: Workflow illustrating the different steps leading to the construction of the vulnerability map.
- 152

153 Study area

The Vosges mountain range has contrasting soil and climate conditions. Altitude ranges between 200 m in the eastern plains of Alsace to 1,424 m at the "Grand Ballon" (Fig. 2A). Rainfall varies between 500 and 2,000 mm, and mean annual temperatures between 6°C and 11°C for the 1981-2010 period (Aurelhy model, Météo France). Geology mainly consists of acidic sandstones in the north and west of the study area, and magmatic rocks in the centre of the mountain range (Fig. 2B). Forests cover more than 60% of the territory, and provide important economic and social benefits. In the national forest inventory plots², the most common productive tree species in the Vosges mountains are (in order of decreasing frequency): European beech (present in 75% of the plots), silver fir (59%), Norway spruce (53%), sessile oak (40%) and Scot pine (25%). Softwoods represent 70% of the stands, while silver fir or Norway spruce are the dominant species in 40 % of them (IGN BD forêt v2³, Fig 2C). These two species represent approximatively 50% of the annual timber harvested in the massif (500,000 m³).



Fig. 2: Description of the study area: distribution of altitudes (A, IGN BD alti), simplified geology (B, BRGM
geological map) and simplified stand composition (C, IGN BD forêt v2).

167

168 Mapping of dieback using remote sensing data

We used three Sentinel-2 images level N2A downloaded from Theia website⁴. We selected images taken on July 24, 2019, during a period with little cloudiness and maximum vegetation cover to avoid confusion between the soil and dieback, and differentiate dead trees from living trees. These images were corrected for atmospheric, topographic and geometric effects. Dieback was identified through a supervised classification by excluding bare soil, crops, ground vegetation, urban areas, water, and forested areas. The classification was trained using 288 units presenting dieback, and validated with 1,814 others units including 285 units presenting dieback, collected

² https://inventaire-forestier.ign.fr/IMG/pdf/RF-Massif_vosgien.pdf

³ https://inventaire-forestier.ign.fr/spip.php?article646

⁴ <u>https://theia.cnes.fr/atdistrib/rocket/#/search?collection=SENTINEL2</u>

175	by photo-interpretation. The Sentinel-2 images were classified with ArcGIS Pro 2.5.0, using maximum likelihood
176	classification (MLC, Sun et al. (2013)).

178 Sampling strategy

To avoid considering mortality patterns from other species than silver fir and Norway spruce, we used the IGN BD forêt $v2^5$ database to select vegetation units recorded on aerial photographs that showed these two species. A systematic 100-m grid was built, and 1,000 plots were randomly selected in dieback-struck areas and another 1,000 plots in healthy places.

183

184 We used aerial photos at 20 cm resolution to separate plots according to the dominant species (spruce or 185 fir) and to identify the stand characteristics on 15-m-radius plots (seven classes, Table S1). We used photos dating 186 back to 2018, taken prior to the dieback event, to identify the stand characteristics. To avoid the risk of confusion, 187 only the classes where the studied species was dominant or not in mixture with the other studied species were kept 188 for each dataset to avoid confusion (classes 1, 2, 3 and 5 in Table S1; 872 plots were selected for silver fir, and 189 1,043 plots for Norway spruce). For each plot, the stand's status (healthy or dieback) and 112 explanatory variables 190 were collected in a database: 6 variables described the stand characteristics, 50 described the site conditions, and 191 56 described climate evolution.

192

193 Variables describing the stand characteristics

We collected six variables to describe the stand characteristics (Table1). We distinguished four levels of species mixture for stand composition (COMP, modalities 1, 2, 3 and 5, Table S1). For stand density (DENS) we differentiated dense stands from sparsely forested stands, where the ground was visible on more than 10% of the plot area. Age and structure effects (STRUCT) were recorded in three classes: old even-aged forest stand, young even-aged forest stand, and heterogenous structure. We also identified the presence of edges due to interfaces between different land uses (TYP_EDGE: absence of an edge, edge between two forest stands of different heights, and with an open environment), and the presence of edges facing south (variable EDGE S). These variables were

⁵ https://inventaire-forestier.ign.fr/spip.php?article646

- 201 collected using aerial photographs, on 15-m-radius plots (similar to classical forest inventory plots in France), for
- 202 COMP, DENS, and STRUCT, and on 50-m-radius plots for TYP_EDGE and EDGE_S to consider data around
- the plot that could influence the stand health. Finally, we added data about the 1999 windstorm damage that had a
- 204 strong impact on the Vosges mountains forests by rejuvenating some forest stands (STORM). These IGN maps
- differentiated areas with less than 10% damage from those with 10 to 50% damage or more than 50% damage.

	Category	Variable	Description	Source
7		COMP **	Stand composition: 4 levels of mixture	
ō	STAND	DENS **	Stand density	
θĘ		STRUCT **	Stand structure	
A P		TVP EDGE **	Presence of edges in the plot	photographs
CI SI		EDGE S **	Presence of an edge southward	
ES		STOPM **	Earest demaged by the 1000 storm	ICN
		STORM **	Forest damaged by the 1999 storm	IGN
	GEOLOGY	GEOL**	Simplified geological map	BRGM
		ALT *	Altitude (m)	
	TOPOGRAPHY	COS ASP *	Cosine of aspect	-
		SIN ASP *	Sine of aspect	-
		SI O*	Since of aspect	50 m resolution
		CONT*	Containment in a 1 500 m radius (m)	digital elevation
		CUDV*	Share of the tene even hired surface (1.500 m rediue)	model (DEM)
		CURV*	Snape of the topographical surface (1,500-m radius)	
		TOPO*	Relative distance between ridge and talweg (m.)	_
		REL_ALT*	Relative altitude between ridge and talweg (m.)	_
		CURV*	Shape of the topographical surface (1,500-m radius)	
	SOIL	PH*	Bioindicated soil surface pH	(Gegout et al. 2003)
	NUTRITION	CN*	Bioindicated soil surface C/N	
s S	SOIL WATER-	TW*	Bioindicated temporary waterlogging	
Ž	LOGGING	PW*	Bioindicated permanent waterlogging	
E		RAD	Solar radiation (2009-2019 period, J/cm ²)	(Piedallu and
		(wi, sp, su, an)		Gegout 2007)
Z		TMIN (wi, sp)	Minimum temperature (2009-2019 period, °C)	(Piedallu et al.
0	ENERGY	TMEAN	Mean temperature (2009-2019 period °C)	2016)
E E		(wi sp su au an)		
E		TMAX (su)	Maximum temperature (2009-2019 period °C)	-
\sim	CLIMATIC		Cumulated rainfall (2009-2019 period, mm)	-
	WATER		Cumulated Talman (2009-2019 period, min)	
	CONTENT	CWP	Climatic water balance (2000-2010 period)	-
	CONTENT		Chinade water balance (2009-2019 period)	
			Soil denth	(Diadallu at al
			Soil water holding connective (mm)	2011
	SOIL WATED	SWIC	Soli water holding capacity (iiiii)	(Diadalla at al
	CONTENT	SwC	Soli water content (Thornthwatte formula, 2009-2019 period)	(Pledallu et al. 2012 Tl $(1 - 1)$
	CONTENT	(sp, su, au, an)		2013; Thornthwaite
		SWD	Soil water deficit (PET-AET, 2009-2019 period)	and Mather 1955)
		(sp, su, au, an)		
	SOIL WATER	Kh	Horizontal hydraulic conductivity at saturation (m per day)	
	FLUXES	Kv	Vertical hydraulic conductivity (m per day)	(Ondo et al. 2017)
		FLUX (su, an)	Lateral surface and subsurface fluxes (mm)	
	CLIMATE	evTMIN (wi, sp)	Evolution of minimum temperature (°C)	
	ANOMALIES	evTMEAN	Evolution of mean temperature (°C)	
		(wi, sp, su, au, an)		
		evTMAX (su)	Evolution of maximum temperature (°C)	
		evRAIN	Evolution of rainfall (mm)	
		(wi, sp, su, au, an)		
		evCWB	Evolution of CWB (mm)	
		(wi, sp, su, au, an)		
		evSWC	Evolution of SWC (mm)	
		(wi, sp, su, au, an)		
		evSWD	Evolution of SWD (mm)	
		(wi, sp, su, au, an)		
	CLIMATE	regTMIN (wi, sp)	Minimum temperature trend	
	TRENDS	regTMEAN	Mean temperature trend	
Z		(wi, sp, su, au, an)		
Ξ		regTMAX (su)	Maximum temperature trend	
Б (regRAIN	Rainfall trend	
10		(wi, sp, su, au, an)		
		regCWB	CWB trend	
E		(wi, sp, su, au, an)		
AT.		regSWC	SWC trend	
MA		(wi, sp, su, au, an)		
		regSWD	SWD trend	
		(wi, sp, su, au, an)		

- 207
 Table 1: List of the 113 explanatory variables. All climate data were averaged over the 2009-2019 period,

 208
 dimensional difference data were de 2000 2010 and 1000 and 10000 and 10000 and 10000 and 1000 and 10000 and 1000 and 1000 and 1
- climate anomalies were differences between the 2009-2019 and 1961-1985 periods, and climate trends were the
- 209 coefficients of regression calculated over the 1986-2019 period. wi = winter, sp = spring, su = summer, au =
- 210 *autumn, an = annual values.* * *monotonic and quadratic responses were evaluated,* ** *qualitative variables.*
- 211

212 Variables describing the site conditions

213 Fifty variables described the site conditions. They concerned geology (n=1), topography (n=9), soil 214 nutrition (n=2), waterlogging (n=2), energy for plants (n=12) and water availability (n=24) (Table 1). A simplified geological map (GEOL) was drawn by merging similar substrates on the local maps at 1:50,000 scale elaborated 215 216 by the BRGM. Topographical indices were calculated with the IGN 50-m digital elevation model for altitude 217 (ALT), aspect - cosine of aspect (COS ASP), sine of aspect (SIN ASP), and slope (SLO). Topographical position 218 was represented by four indices: containment (CONT), the difference of altitude between the pixel and the average 219 altitude within a 1,500-m radius, curvature (CURV) that describes the shape of the topographical surface in the 220 direction of the maximum slope within a 1,500-m radius (convex, flat or concave), and the relative distance 221 (TOPO) and altitude (REL ALT) of the cell along the toposequence (the ratio of the distance or altitude between 222 the cell and the nearest ridge to the total length or the difference of altitude found in the toposequence), 223 respectively. We characterised soil nutrition and waterlogging according to 1-km resolution maps built using 224 bioindication techniques (Gegout et al. 1998) for soil surface pH, nitrogen nutrition estimated from the C/N ratio 225 (CN), temporary waterlogging (TW) and permanent waterlogging (PW).

226

GIS layers of monthly climate variables were used to estimate energy and water available for plants over the 2009-2019 period (Table 1). Solar radiation (RAD) was calculated at 50 m resolution using Helios model (Piedallu and Gegout 2007). Monthly minimum, average and maximum temperatures and rainfall (TMIN, TMEAN, TMAX, and RAIN, respectively), were modelled and mapped at 1 km resolution (Piedallu et al. 2016). Climatic water balance (CWB) is the difference between rainfall and potential evapotranspiration according to Turc's formula (Turc 1961). One-km resolution maps of soil depth (DEPTH) and soil water holding capacity (SWHC) (Piedallu et al. 2011) were used to evaluate the soil water content (SWC, available water in the soil) and the soil water deficit (SWD, the difference between potential evapotranspiration and actual evapotranspiration) according to Thornthwaite formula (Thornthwaite and Mather 1955). In addition, three indices characterising lateral fluxes in the soil were extracted from GIS layers. Kh and Kv represented the horizontal and vertical hydraulic conductivity at soil saturation, respectively, and FLUX estimated the balance between the input and output surface and subsurface fluxes (Ondo et al. 2017).

239

All the variables including climate were averaged over the ten years before data collection (2009-1019), *per* season (winter -wi, December to February-; spring -sp, March to May-; summer -su, June to August; and autumn -au, September to November), and over the whole year (an).

243

244 Variables describing climate evolution

Two sets of calculations – climate anomalies and climate trends – were used for temperatures (TMIN, TMEAN, TMAX), and water availability (RAIN, CWB, SWC and SWD, Table 1). Climate anomalies represented the evolution between a reference period and a contemporary period. A period of ten years before data collection (2009-2019) was selected to represent the contemporary period because tree death can be triggered by the cumulative effects of many disturbances (Das et al. 2013). We selected 1961-1985 as the reference period because significant warming occurred in France after 1986 (Taccoen et al. 2019).

251

Climate trends were calculated for the same variables over the 1986-2019 period. For each variable and each pixel of 1-km resolution, the trends were regressed against time for the 32 studied years, and the linear regression coefficients were mapped. A positive slope indicated an increase of the climatic constraint for TMIN, TMEAN, TMAX and SWD, and a decrease for RAIN, CWB and SWC.

256

257 Modelling approach and vulnerability map calculation

258 We modelled silver fir and Norway spruce mortality with logistic regression (McCullagh and Nelder 259 1997). For each species, we evaluated the 113 explanatory variables through a forward stepwise procedure. At each step, the variable explaining the maximum deviance was selected if it was statistically significant (P < 0.01), and little correlated with the previously selected variables (Pearson's r < 0.7). Because monotonic responses were expected, quadratic responses were not considered for the climate variables. However, monotonic and quadratic response curves were both evaluated for the other variables. The process ended when the selection of a new variable led to a d² increase lower than 0.01 or a p-value > 0.01.

265

The receiver operating characteristic (ROC) curve was calculated to evaluate the performances (Fielding and Bell 1997), and different metrics were used: the area under the ROC curve (AUC), the kappa index, success (the rate of good prediction), sensitivity (the rate of good prediction of presence), and specificity (the rate of good prediction of absence) (Manel et al. 2001). The relative importance was calculated for each variable using the drop contribution (Lehmann et al. 2002), *i.e.*, the difference in explained deviance between the full model and a partial model when the variable was dropped. The ratio of the drop contribution of the variable over the sum of the drop contributions for all the variables gave the relative importance of each predictor.

273

The ROC curve also provided the optimal threshold for predicting the presence / absence of dieback. It was used to calculate the vulnerability map: upper values delineated the "high level of vulnerability" class where the stands were predicted dead by the model, while lower values were divided in three classes with equal intervals of increasing vulnerability. The map was calculated using the GIS layers describing the environmental predictors selected in the model. The best resolution among the selected variables was kept (i.e. 50 m). The vector layers were rasterised, and the 1km resolution maps were resampled using the bilinear interpolation algorithm. The map included four levels of vulnerability, calculated from a type stand used across the whole area.

281

282 Validation dataset

A map of the volumes of harvested dead wood from exceptional sanitary cuts was provided by the ONF for public forests, which cover 2/3 of the forested area of the Vosges mountains. We selected areas where one of the studied species was dominant or not in mixture with the other studied species. For 7,355 management units identified for silver fir (11,218 for Norway spruce), the average volume of dead wood was compared for the different vulnerability levels. Our vulnerability maps were drawn using 2019 satellite imagery, but dieback may have occurred before or after this date in the most vulnerable areas. As a consequence, we considered both the volumes of dead trees recorded in 2019 and the sum of the volumes over the 2018-2020 period.

290

291 **Results**

292 Distribution of silver fir and Norway spruce dieback in the Vosges mountains

293 The classification of sentinel-2 data predicted 92% of the stand status of the validation dataset correctly. 294 It identified 2,072 ha of dieback in the Vosges mountains, representing 1.4% of the studied stands. We observed 295 dieback on 362 plots out of the 872 plots selected for silver fir, and on 627 plots out of the 1,043 plots selected for 296 Norway spruce, mainly in the south and the north of the studied area (Fig. 3). Eighty-five plots were deleted due 297 to the risk of confusion because the two species were in mixture and neither was dominant, or the stands were too young and the species were impossible to identify. The selected plots were distributed across the whole studied 298 299 area: the average distances to the nearest plot were 1,015 and 932 m for silver fir and Norway spruce, respectively. 300 These distances increased up to 1,105 and 1,356 m in the dieback stands, even though they were oversampled.



Fig. 3: Localisation of the stands with dieback symptoms for silver fir (n = 872) and Norway spruce (n = 1,043) in the Vosges mountains.

305

306 Silver fir and Norway spruce dieback modelling

307 With respective AUCs of 0.80 and 0.78 and nine variables selected, the silver fir and Norway spruce 308 dieback models showed similar performances and near predictors (Figures 4 and 5). They combined variables 309 describing stand composition and structure, local conditions and climate evolution to various extents according to 310 the species (Figure S1). Environmental conditions explained 59% of the deviance for silver fir versus 62% for 311 Norway spruce. Geology and stand composition were among the most important variables correlated with dieback 312 for both species, in addition to the presence of an edge southward for silver fir and temporary waterlogging for 313 Norway spruce. The trend in summer soil water deficit was directly linked to climate change (relative importance 314 ranging between 6 and 7%).

315 Less dieback occurred for both species when they were in mixture in stands dominated by broadleaved species. Mortality was significantly higher in pure stands for Norway spruce (Fig. 4 and 5). More dieback was also 316 317 identified in even-aged stands compared to uneven-aged or young stands when a forest edge was present (with a 318 clear effect of a south forest edge for silver fir), and in stands that underwent little damage during the 1999 storm. 319 Silver fir and Norway spruce mortality also responded to five environmental variables (Fig. 4 and 5). Silver fir 320 showed a higher risk of dieback when it grew on volcanic pyroclastic rocks, neutral to basic rocks, principal 321 conglomerate or acidic granite. Norway spruce showed lower substratum-dependent differences than silver fir did, 322 and was more prone to dieback on sedimentary basic rocks, Voltzia or shell sandstone. Both species were also sensitive to topographical position, with a higher risk of dieback in areas near the ridges, on the south slopes, and 323 when waterlogging was present. Finally, increased dieback was observed with soil drying. High values 324 325 corresponded to a strong increase of the soil water deficit during the 1986-2019 period (Fig. 4 and 5, equations for 326 the two species can be found in Table S2 and S3).

The risk of dieback linked to environmental conditions and stand characteristics varied according to the location for both species (Fig. 6, 7, B, C). The vulnerability maps⁶ calculated at 50 m resolution (Fig. 6-D and 7-

⁶ The vulnerability maps for silver fir and Norway spruce dieback can be downloaded from the SILVAE website (https://silvae.agroparistech.fr/home/)

- 329 D) identified 7% of the stands with a high level of vulnerability for silver fir versus 33 % for Norway spruce, while
- 330 83% of the stands were classified as presenting a low or very low level of vulnerability for silver fir *versus* 26 %
- for Norway spruce (Fig. 8). In the validation dataset (Fig. 9), we observed a significantly higher volume of dead
- trees for the class showing a high level of vulnerability than for the other classes. This difference was higher for
- 333 silver fir (about ten-fold) than for Norway spruce (about two-fold).



- 337 *Fig. 4*: Performances of the silver fir model and differences in the probability of dieback according to the variables (A: qualitative variables, B: quantitative variables). The
- 338 response curves were calculated using mean values for the other quantitative variables, and the following modalities for the qualitative variables: GEOLOGY, "Neutral
- 339 magmatic and metamorphic rocks", COMPOSITION: "Pure silver fir stand", STRUCTURE, "Even-aged stand", STORM: "Less than 50% damage during the 1999 storm".
- 340 and EDGE S (Presence of an edge southward), "Absence of a south forest edge". Black dots in fig. 4A: numbers of plots for each modality.



1.0

- 343 Fig. 5: Performances of the Norway spruce model and differences in the probability of dieback according to the
- 344 variables (A: qualitative variables, B: quantitative variables). The response curves were calculated using mean
- 345 values for the other quantitative variables, and the following modalities for the qualitative variables:
- 346 GEOLOGY, "Vosges or intermediate sandstone, granites, gneiss", COMPOSITION: "pure Norway spruce
- 347 stand", STRUCTURE, "even-aged stand", STORM, "Less than 10% damage during the 1999 storm", and TYPE
- 348 EDGE "Absence of a forest edge". Black dots in fig. 5A: numbers of plots for each modality.



- Fig. 6: Silver fir dieback observed (A) or predicted in the sampled plots (B, C, n = 872), and vulnerability map
 (D). B: Dieback explained by environmental conditions only (variables GEOL, REL_ALT, regSWD_su, TW and
- 352 COS ASP). C: modulation of vulnerability predicted on map B due to the stand characteristics (variables
- 353 COMP, STRUCT, EDGE S and STORM). D: The vulnerability map was calculated with the modalities
- 354 "Absence of a south forest edge", "Even-aged stand", "Pure silver fir stand" for the variables EDGE S,
- 355 STRUCT and COMP, respectively). The "high level of vulnerability" class corresponds to the values greater

- than the optimal threshold obtained from the ROC curve; lower values were divided in three classes of equal
- 357 *interval (the break values are used for the legend on map B).*



359



- 362 vulnerability map (D). B: Dieback explained by environmental conditions (variables GEOL, REL ALT,
- 363 regSWD su, TW and COS ASP). C: modulation of vulnerability predicted on map B due to the stand
- 364 *characteristics (variables COMP, STRUCT, STORM and TYP_EDGE). D: The vulnerability map was calculated*
- 365 with the modalities "pure Norway spruce stand", "even-aged stand", and "absence of a forest edge" for the
- 366 variables COMP, STRUCT and TYP EDGE, respectively. The "high level of vulnerability" class corresponds to
- 367 the values greater than the optimal threshold from the ROC curve; lower values are divided in three classes of
- 368 equal interval (the break values are used for the legend on map B).



Fig. 8: Distribution of the surfaces (%) with the different levels of vulnerability for the silver fir and Norway

spruce stands. 371



Fig. 9: Volume of dead trees (m³/ha) recorded in the silver fir and Norway spruce stands (ONF), according to
the four levels of vulnerability (trees inventoried in 2019 or between 2018 and 2020).

377

378

379 **Discussion**

380

381 A relevant method for large-scale spatial vulnerability assessment

382

383 Tree species vulnerability is an issue of growing concern round the world, but it is not new in managed 384 forests. After the 1911 drought in the centre and west of France, Roulleau already reported, "I see everywhere 385 [...], in the cooler parts like the drier ones, a lot of trees are dying [...] I have long recommended caution in the 386 use of Norway spruce" (Roulleau 1912). These observations concerned lowland areas, where the species was introduced outside of its natural range. Conditions are different in the Vosges mountains, that benefit from colder and wetter conditions typical of middle mountains of European climate. In this area, silver fir is a native, emblematic species, while Norway spruce is considered as natural near the top of the mountain range (Guinier 1959). Yet, we found large surfaces threatened by forest decline (ranging between 7% for silver fir and 33% for Norway spruce). In agreement with observations in Germany (Maringer et al. 2021), we observed a higher vulnerability of Norway spruce than of silver fir.

393

394 The levels of vulnerability estimated on the map successfully discriminated the volumes of dead trees 395 recorded in public forests, highlighting the benefit of using easily available geographic information for the spatial 396 vulnerability assessment of silver fir and Norway spruce dieback. Despite less precision compared to traditional 397 ground surveys, the use of satellite imagery, photointerpretation and digital maps of environmental factors allowed 398 us to sample a large number of plots distributed along large environmental gradients. As far as the mapping results 399 are concerned, the better performance of silver fir compared to Norway spruce can be explained by the large extent 400 of Norway spruce dieback across a wide variety of ecological conditions, and its higher susceptibility to bark beetle 401 attacks (de Groot and Ogris 2019). Existing vulnerability assessment was mostly based on mortality observed the 402 previous years (Preisler et al. 2017), changes in tree fitness visible by satellite imagery (Verbesselt et al. 2009), or 403 the identification of weakened trees with declining growth (Suarez et al. 2004). We propose a method based on easily available geographic information, that can be implemented over broad areas, to monitor dieback of different 404 405 species and over different periods of time. When data is available, it can be coupled with forest inventory information for a better description of the stand characteristics. 406

407

The selected variables were linked to stand characteristics, geology, and water availability, with a clear effect of climate change. Large differences were highlighted relatively to the latest important tree decline event experienced in Europe during the 1973-1981 period. At that time, more mortality was observed for old trees located at low or high altitudes, on acidic substratum, and in the east of the mountain range (Bonneau 1985; Thomas et al. 2002). We are now observing lower mortality at high altitude, no more mortality on acidic substratum compared to the other areas, and a greater decline in the south and the north of the mountain range. These differences suggest that dieback is currently triggered by different factors than those identified during the 1980s.

416 Importance of water availability in silver fir and Norway spruce dieback

417 Dieback of both silver fir and Norway spruce responded markedly to water balance variables in our 418 models. The soil water deficit trends performed better than climate anomalies or variables describing average 419 climate. This result stresses the importance of the dynamic of soil water availability in dieback evaluation. The 420 effects of drought on tree decline have been largely studied, but most of the large-scale studies tried to relate forest 421 dieback to average climate conditions over long periods (Lu et al. 2019). For a given current soil water deficit, we 422 observed that impacts on trees were greater when the deficit had sharply increased in the last years compared to 423 areas under recurring deficit (Figure S2). These outcomes suggest that a tree of a given species can be more 424 resilient to drought when it has grown in drier conditions, as observed by Gazol (2017) both in the north of America 425 and Europe. They also highlight that the dynamic of water stress over time should be considered rather than average 426 climate to forecast mortality patterns. Our understanding of the time span that should be investigated to efficiently 427 evaluate stand vulnerability should also be improved.

428

429 Several other selected variables were related to water availability. The higher risk of dieback observed 430 near the ridges was related to the lateral redistribution of the soil moisture along a topographical hillslope gradient (Ondo et al. 2017). Some authors reported 15 to 90% lower soil moisture near the crests compared to the valleys 431 432 (Western et al. 2004). The more severe dieback symptoms on south slopes can be attributed to their higher 433 evaporation and transpiration, and differences in thawing. Rouse et al. (Rouse and Wilson 1969) observed 50% 434 more water stored in the north slope soils than in the south slope soils in early spring. The increasing mortality 435 with temporary waterlogging intensity can be interpreted in different manners. Both silver fir and Norway spruce 436 avoid compact or waterlogged soils. Waterlogging also influences the plant water uptake by affecting the spatial 437 distribution of fine root growth and limiting their depth (Fujita et al. 2021). Finally, the presence of edges 438 (particularly south edges for silver fir), stresses the importance of microclimatic conditions. Increased temperature, 439 light, and wind speed that increased evapotranspiration and decreased the soil water content have been recorded 440 from 40-50 m from the edge (Chen et al. 1995), leading to higher tree mortality rates (Mesquita et al. 1999). These predictors related to the water balance represented 51% and 48% of the explained model deviance for silver fir 441 442 and Norway spruce, respectively. They all showed an increase of dieback when the water balance components 443 shifted toward less available water for trees.

445 Stand characteristics complement environmental predictors to explain dieback

446 Although stand data were collected by photo-interpretation – a less accurate method than field inventories 447 - we demonstrated that stand characteristics could also explain dieback, with similar responses of the two studied 448 species. We observed less mortality for uneven-aged stands and mixtures. These results are in agreement with previous studies showing lower resistance to disease and damage in even-aged stands than in uneven-aged stands 449 (Pukkala et al. 2013). The negative effect of pure stands supports the results of previous studies demonstrating the 450 451 benefits of functional diversity on tree resilience (Gazol and Camarero 2016), which can be explained by 452 facilitation and resource partitioning. Facilitation is an interaction between species that benefits to at least one of 453 them, while resource partitioning refers to the way different species can share resources over time or across space 454 (Mc Cook 1994). Lower Norway spruce dieback was shown in stands dominated by beech (Pretzsch et al. 2020), 455 attributed to complementarity in water uptake. A temporal shift between the two species provided Norway spruce 456 better resistance to drought events (Rotzer et al. 2017). These effects are greater in low-productivity sites, as 457 already observed in the Vosges mountains (Lebourgeois et al. 2013).

458

459 We also found less dieback in young stands or stands that had suffered important damage during the 1999 storm. The lower mortality of small trees compared to large ones could be attributed to differences in fine root 460 461 distribution, in vulnerability to biotic factors, and to the greater water uptake difficulties of tall, large trees (Pfeifer 462 et al. 2011). Because silver fir and Norway spruce dieback increase with basal area (Taccoen et al. 2019), this lower mortality could also be linked to limited competition for light or water in young stands. Lowering the basal 463 464 area is often considered as a silvicultural tool to decrease tree vulnerability to drought and improve productivity 465 (Pretzsch 2005). In agreement with studies demonstrating the strongest negative growth trends in pure and even-466 aged productive forests of conifers (Ols and Bontemps 2021), we suggest to promote an evolution of silvicultural 467 practices toward mixed stands of uneven-aged trees to limit the stand basal area and avoid brutal cuts to limit edge effects (that can also reduce wind damage). The cumulated effect of these measures would lead to a significant 468 469 decrease of the dieback vulnerability for the two studied species.

470

471 Using the map to mitigate the effects of climate change on silver fir and Norway spruce 472 forests

473 The map makes it possible to prioritise the level of vulnerability for each studied species in view of 474 helping forest managers to mitigate the effects of climate change. It can help to adapt the stands by forward 475 planning, by guiding forest policies and silvicultural practices and helping to select suitable species or 476 provenances. The map can be used directly because it instantly provides an evaluation of the vulnerability based 477 on environmental conditions according to the geographic location. When basic information about stand structure 478 and composition can be surveyed (using ground surveys or aerial photographs), the prediction can be improved: 479 the effects of the stand characteristics can be evaluated, and the map gives information about the potential 480 decreasing vulnerability if the stand characteristics allow for better tree resilience.

481

482 The future of Norway spruce and silver fir is probably strongly compromised in the most vulnerable areas 483 identified by a high level of vulnerability on the map. These two species should be monitored in these areas on a 484 priority basis, e.g., by raising the rate of transparency of the crown in some representative plots, or by using NDVI 485 indices based on remote sensing data (Rogers Brendan et al. 2018). They should be preferentially cut when the 486 first signs of degradation appear, and should not be replanted afterwards. Reforestation should rely on adequate 487 forest regeneration promoting drought-tolerant species if available. Species more resistant to drought could also 488 be introduced by selecting species that are visually close to those they replace in areas of high landscape interest. 489 When the level of vulnerability is low or moderate, the strategy can be to promote a rapid evolution of silvicultural 490 practices to adapt stand structure and composition in priority. The aim is to mitigate the effects of climate change 491 in areas that can become highly vulnerable in the next decades. The areas with the lowest level of vulnerability 492 would not be a priority in the first place but should also be monitored. The vulnerability map should be updated at 493 regular time intervals to take the evolution of the soil water deficit and observed mortality changes into account, 494 and adjust recommendations accordingly.

495

496 Limitation and uncertainties

497

The risk of decline was predicted efficiently although inciting and contributing factors were not explicitly considered. We expected them to be indirectly and partly taken into account by the climate variables selected in the models. The trend of the soil water deficit variable was probably influenced by the extreme drought events and 501 linked to the distribution of pathogens, which is also influenced by climate - particularly temperature (Baier et al. 502 2007). This result was probably observed because bark beetle attacks - which are severe in the area - occur 503 preferentially on weakened trees (Kolb et al. 2019). Data describing the dynamics of pathogen populations could 504 probably successfully complement the variables selected in the model, but spatial data depicting their spatial 505 distribution and evolution remains scarce (Jaime et al. 2019). The model performance could also probably be 506 improved by including variables of extreme events and disturbances when available, e.g., wind conditions and 507 storm frequency, drought intensity, forest fires (Carnicer et al. 2011), or air pollution (Pedersen 1998). In addition, 508 different modelling techniques could be compared to evaluate if the map performance could be improved.

509

510 We chose a spatial approach aimed at linking spatial heterogeneity related to the site conditions and stand 511 characteristics on the one hand with the regional patterns of dieback on the other hand. We probably under-512 estimated the surfaces concerned by dieback because isolated dead trees or low symptoms were probably not 513 identified by remote sensing approaches, and the dead trees in some of the dead stands were probably felled by 514 forest managers before the satellite images were taken. This probably decreased the model performances, but with 515 a limited influence on the estimation of vulnerable areas, as cuts probably concern a wide variety of ecological 516 and stand conditions. This approach should be complemented by a temporal follow-up of the dieback dynamic 517 using time series images and requiring inventories at different periods, to better identify recent cuts of dead trees, take the effect of extreme events into account, and simulate probabilities of dieback according to future climate 518 519 conditions (Knight et al. 2013; Staupendahl and Zucchini 2011).

520

521 According to the classification of sentinel-2 images, dieback observed at a specific date is a relatively 522 rare statistical event. To overcome this limitation, the proportion of areas with dieback was oversampled by 523 selecting 50% of plots in dieback areas to calibrate the models. This method yielded correct regression coefficients, 524 but it increased the intercept value, so that the probability of dieback in the model outputs was overestimated (King 525 and Zeng 2001). Therefore, the probability of dieback provided by our model should not be interpreted as real probabilities, but it makes it possible to compare the effects of the qualitative variables and to interpret the shape 526 of the response curve for the quantitative ones. This oversampling effect was corrected for the vulnerability map 527 528 by using the ROC curve, which determines the classes of increasing levels of vulnerability according to the optimal statistical threshold for each species. Despite a great average distance between each plot and its nearest neighbour,
further analysis could also test for an effect of autocorrelation.

531

532 The resolution of the GIS layers describing the spatial variations of the environmental predictors also probably influenced the performance of the vulnerability map (Cavazzi et al. 2013). The variables selected in the 533 534 models were at different spatial resolution: 50 m for relative altitude and the cosine of aspect, 1:50,000 map scale 535 for geology, and 1 km resolution for temporary waterlogging and the trend in soil water deficit. We calculated the map at the finest spatial resolution (i.e., 50 m) to keep the contribution of local information available in the models. 536 537 The other raster variables were resampled at 50 m resolution using the bilinear method, and geology was rasterised 538 at 50 m resolution. It would also have been possible to aggregate the 50m resolution variables at 1km resolution. 539 These different approaches could be compared to evaluate the effect of spatial resolution on the map performance. 540 Dieback can vary at a very local scale, so we can reasonably believe that finer resolution predictors could improve 541 the vulnerability map. Further work could also evaluate if the spatial resolution of the different predictors can be 542 decreased with efficiency.

543

544 We demonstrated a good correlation between the different vulnerability levels and the ground survey 545 quantifying the volumes of dead wood. However, the data or methods used in this study have their own limitations. 546 Validating dieback data is a tricky task because it is difficult to collect independent and relevant datasets about 547 dead trees, which are usually rapidly harvested and do not appear in forest inventory plots. In the studied area, this 548 level of information is available about public forests through recordings of volumes of harvested dead wood from 549 exceptional sanitary cuts. It was first collected for each management unit by different managers, and then 550 aggregated at the massif scale. As a consequence, uncertainties can exist due to differences or changes in the 551 methods, or locally lacking data (mainly for private forests which cover 1/3 of the forested area of the Vosges mountains), leading to uneven data quality according to the location. However, our validation is based on a high 552 553 number of observations (7,300-11,200 management units per species), hence a high number of replicates for each 554 of the vulnerability classes, scattered across large ecological gradients. The smallest number of observations was 172 for silver fir for the moderate level of vulnerability, and 286 for Norway spruce for the very low level of 555 556 vulnerability. This large dataset limits the effect of local uncertainties on the global estimation of map performance.

559 Conclusion

560 Our results demonstrate an important impact of recent climate change that increased forest dieback by limiting water availability in Norway spruce stands, and also in silver fir stands to a lesser extent. Vulnerability 561 maps can help to adapt forests to current new climate conditions. Harvesting trees following dieback events causes 562 563 a financial loss, is a logistical challenge, contributes to pathogen infestation, and creates an important opening up of the environment that modifies microclimates and impairs future reforestation. The massive disappearance of 564 565 trees could also have significant impacts on biodiversity and human activities by increasing the risk of natural 566 hazards, preventing the preservation of water resources, and altering landscape quality on the long term. We calculated a vulnerability map for the current period; its extrapolation to future conditions remains questionable. 567 568 The risk of decline will probably be influenced by the evolution of water availability in the next years, and the 569 maps should be updated at regular intervals. In the short term, a potential succession of wet summers might limit 570 dieback. In the long term, increasing temperatures and drought leave little hope for the future of Norway spruce in 571 a large part of the Vosges mountains, where its decline is already widespread. The situation is more contrasted for 572 silver fir, and the evolution of water availability in the coming years will influence its evolution. We can reasonably 573 expect stands with a low level of vulnerability to be spared in the next decades.

574

575 Statements & declarations

576

577 Fundings

The Unité Mixte de Recherche (UMR) SILVA is supported by a grant overseen by the French National Research
Agency (ANR) as part of the 'Investissements d'Avenir' program (ANR-11-LABX-0002-01, Lab of Excellence
ARBRE).

581

582 Competing Interests

583 The authors declare no conflict of interest or competing interests.

585 Author's contribution

586 D.D. performed the remote sensing analysis, C.B. contributed to the GIS analysis, I.S. and J.C.G. provided 587 bioindicated indices, R.P. provided data from exceptional sanitary cuts, M.L. and C.P. developed the study 588 conception and design, C.P. performed the data collection, realized the analysis and wrote the paper. All of the 589 authors read and corrected the paper, and gave their final approval for publication.

590

591 Data availability of data

592 The datasets analysed during the current study are available from the corresponding author on reasonable request.

594 **REFERENCES**

- Allen CD, Breshears DD, McDowell NG (2015) On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6(8)
- Allen CD, Macalady AK, Chenchouni H et al (2010) A global overview of drought and heat-induced tree
 mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259(4):660-684
- 598 mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259(4):660-684
- Anderson RG, Canadell JG, Randerson JT et al (2011) Biophysical considerations in forestry for climate
 protection. Frontiers in Ecology and the Environment 9(3):174-182
- Archambeau J, Ruiz-Benito P, Ratcliffe S et al (2019) Similar patterns of background mortality across Europe
- are mostly driven by drought in European beech and a combination of drought and competition in Scots pine.
 bioRxiv:551820
- Aubin I, Boisvert-Marsh L, Kebli H et al (2018) Tree vulnerability to climate change: improving exposure-based assessments using traits as indicators of sensitivity. Ecosphere 9(2)
- Baier P, Pennerstorfer J, Schopf A (2007) PHENIPS A comprehensive phenology model of Ips typographus
 (L.) (Col., Scolytinae) as a tool for hazard rating of bark beetle infestation. Forest Ecology and Management
 249(3):171-186
- Bastin JF, Finegold Y, Garcia C et al (2019) The global tree restoration potential. Science 365(6448):76
- 610 Becker M (1987) Bilan de santé actuel et rétrospectif du sapin (Abies alba Mill) dans les Vosges. Etude
- 611 écologique et dendrochronologique. Annales des Sciences Forestières 44(4):379-402
- Bonan GB (2008) Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. Science
 320(5882):1444-1449
- Bonneau M (1985) Le «nouveau dépérissement» des forêts. Symptômes, causes possibles, importance éventuelle
 de la nature des sols. Revue Forestière Française XXXVI(4): 239-251
- Bouvarel P (1984) Le déperissement des forêts attribué aux dépôts atmosphériques acides. Revue Forestière
 Française XXXVI(3):173-180
- Brandl S, Paul C, Knoke T, Falk W (2020) The influence of climate and management on survival probability for
 Germany's most important tree species. Forest Ecology and Management 458
- Brockerhoff EG, Barbaro L, Castagneyrol B et al (2017) Forest biodiversity, ecosystem functioning and the provision of ecosystem services. Biodiversity and Conservation 26(13):3005-3035
- Buras A, Rammig A, Zang CS (2020) Quantifying impacts of the 2018 drought on European ecosystems in
 comparison to 2003. Biogeosciences 17(6):1655-1672
- 624 Carnicer J, Coll M, Ninyerola M, Pons X, Sanchez G, Penuelas J (2011) Widespread crown condition decline,
- food web disruption, and amplified tree mortality with increased climate change-type drought. Proceedings of
 the National Academy of Sciences of the United States of America 108(4):1474-1478
- 627 Cavazzi S, Corstanje R, Mayr T, Hannam J, Fealy R (2013) Are fine resolution digital elevation models always 628 the best choice in digital soil mapping? Geoderma 195:111-121
- Charru M, Seynave I, Morneau F, Rivoire M, Bontemps J-D (2012) Significant differences and curvilinearity in
 the self-thinning relationships of 11 temperate tree species assessed from forest inventory data. Annals of Forest
 Science 69(2):195-205
- Chen J, Franklin JF, Spies TA (1995) Growing-Season Microclimatic Gradients from Clearcut Edges into Old Growth Douglas-Fir Forests. Ecological Applications 5(1):74-86
- Choat B, Jansen S, Brodribb TJ et al (2012) Global convergence in the vulnerability of forests to drought. Nature
 491(7426):752-756
- Ciais P, Reichstein M, Viovy N et al (2005) Europe-wide reduction in primary productivity caused by the heat
 and drought in 2003. Nature 437(7058):529-533
- Coops NC, Waring RH (2011) Estimating the vulnerability of fifteen tree species under changing climate in
 Northwest North America. Ecological Modelling 222(13):2119-2129
- 640 Das AJ, Slaton MR, Mallory J, Asner GP, Martin RE, Hardwick P (2022) Empirically validated drought
- vulnerability mapping in the mixed conifer forests of the Sierra Nevada. Ecological Applications 32(2)

- Das AJ, Stephenson NL, Flint A, Das T, van Mantgem PJ (2013) Climatic Correlates of Tree Mortality in Water and Energy-Limited Forests. Plos One 8(7)
- de Groot M, Ogris N (2019) Short-term forecasting of bark beetle outbreaks on two economically important
 conifer tree species. Forest Ecology and Management 450
- Dietze MC, Moorcroft PR (2011) Tree mortality in the eastern and central United States: patterns and drivers.
 Global Change Biology 17(11):3312-3326
- Elling W, Dittmar C, Pfaffelmoser K, Rotzer T (2009) Dendroecological assessment of the complex causes of
- decline and recovery of the growth of silver fir (Abies alba Mill.) in Southern Germany. Forest Ecology and
 Management 257(4):1175-1187
- Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation
 presence/absence models. Environmental Conservation 24(1):38-49
- Fremout T, Thomas E, Gaisberger H et al (2020) Mapping tree species vulnerability to multiple threats as a guide to restoration and conservation of tropical dry forests. Global Change Biology 26(6):3552-3568
- Fujita S, Noguchi K, Tange T (2021) Different Waterlogging Depths Affect Spatial Distribution of Fine Root
 Growth for Pinus thunbergii Seedlings. Frontiers in Plant Science 12
- Gazol A, Camarero J, Anderegg W, Vicente-Serrano S (2017) Impacts of droughts on the growth resilience of
 Northern Hemisphere forests. Global Ecology and Biogeography 26(2):166-176
- Gazol A, Camarero JJ (2016) Functional diversity enhances silver fir growth resilience to an extreme drought.
 Journal of Ecology 104(4):1063-1075
- Gegout JC, Hervé JC, Houllier F, Pierrat JC (1998) Using vegetation to predict PH in the Vosges mountains
 Forests. pp. 17
- Gegout JC, Hervé JC, Houllier F, Pierrat JC (2003) Prediction of forest soil nutrient status using vegetation.
 Journal of Vegetation Science 14(1):55-62
- 665 Guinier P (1959) Trois conifères de la flore vosgienne. Bulletin de la société botanique de France 106(85):168666 183
- Han J, Singh VP (2020) Forecasting of droughts and tree mortality under global warming: a review of causative
 mechanisms and modeling methods. Journal of Water and Climate Change 11(3):600-632
- Hartmann H, Moura CF, Anderegg WRL et al (2018) Research frontiers for improving our understanding of
 drought-induced tree and forest mortality. New Phytologist 218(1):15-28
- Jaime L, Batllori E, Margalef-Marrase J, Pérez Navarro MÁ, Lloret F (2019) Scots pine (Pinus sylvestris L.)
 mortality is explained by the climatic suitability of both host tree and bark beetle populations. Forest Ecology
 and Management 448:119-129
- 674 King G, Zeng L (2001) Logistic Regression in Rare Events Data. Political Analysis 9:137 163
- Knight KS, Brown JP, Long RP (2013) Factors affecting the survival of ash (Fraxinus spp.) trees infested by
 emerald ash borer (Agrilus planipennis). Biological Invasions 15(2):371-383
- Kolb T, Keefover-Ring K, Burr SJ, Hofstetter R, Gaylord M, Raffa KF (2019) Drought-Mediated Changes in
 Tree Physiological Processes Weaken Tree Defenses to Bark Beetle Attack. Journal of Chemical Ecology
- 679 45(10):888-900
- Landmann G, Bonneau M, Adrian M (1987) Le dépérissement du Sapin pectiné et de l'Epicéa commun dans le
 massif vosgien est-il en relation avec l'état nutritionnel des peuplements ? Revue forestière Française XXXIX
 (1):5-11
- 683 Lebourgeois F (2007) Climatic signal in annual growth variation of Silver Fir (Abies alba Mill.) and Spruce
- 684 (Picea abies Karst) from the French Permanent Plot Network (RENECOFOR). Annals of Forest Science, 64 685 (3):333-343
- Lebourgeois F, Gomez N, Pinto P, Mérian P (2013) Mixed stands reduce Abies alba tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. Forest Ecology and Management 303:61-71
- Lehmann A, Overton JM, Leathwick JR (2002) GRASP: generalized regression analysis and spatial prediction.
 Ecological Modelling 157(2-3):189-207

- Lévy GB, M. (1987) Le dépérissement du sapin dans les Vosges Rôle primordial du déficit d'alimentation en
 eau. Annales des Sciences Forestières 44(4):403-416
- Lu LL, Wang HC, Chhin S, Duan AG, Zhang JG, Zhang XQ (2019) A Bayesian Model Averaging approach for
- modelling tree mortality in relation to site, competition and climatic factors for Chinese fir plantations. Forest
 Ecology and Management 440:169-177
- Lundquist JE (2019) Impacts of Bark Beetles on Ecosystem Values in Western Forests-Introduction. Journal of
 Forestry 117(2):136-137
- Manel S, Williams HC, Ormerod SJ (2001) Evaluating presence-absence models in ecology: the need to account
 for prevalence. Journal of Applied Ecology 38(5):921-931
- 699 Manion PD (1981) Tree disease concepts. Prentice-Hall
- 700 Maringer J, Stelzer AS, Paul C, Albrecht AT (2021) Ninety-five years of observed disturbance-based tree
- mortality modeled with climate-sensitive accelerated failure time models. European Journal of Forest Research
 140(1):255-272
- Marini L, Økland B, Jönsson AM et al (2017) Climate drivers of bark beetle outbreak dynamics in Norway
 spruce forests. Ecography 40(12):1426-1435
- Mc Cook LJ (1994) Understanding ecological community succession: Causal models and theories, a review.
 Vegetatio 110:115-147
- McCarthy JJ, Canziani OF, Leary NA, Dokken DJ, White KS (2001) Climate Change 2001: Impacts,
 Adaptation, and Vulnerability
- 709 McCullagh P, Nelder JA (1997) Generalized linear models. Chapman & Hall, London, UK
- McDowell N, Pockman WT, Allen CD et al (2008) Mechanisms of plant survival and mortality during drought:
 why do some plants survive while others succumb to drought? New Phytologist 178(4):719-739
- 712 Mesquita RCG, Delamonica P, Laurance WF (1999) Effect of surrounding vegetation on edge-related tree
- 713 mortality in Amazonian forest fragments. Biological Conservation 91(2-3):129-134
- 714 Michel A, Seidling W (2018) Forest Condition in Europe: 2018 Technical Report of ICP Forests. Report under
- the UNECE Convention on Long-Range Transboundary Air Pollution (CLRTAP). BFW Austrian Research
 Centre for Forests, Vienna, pp. 128
- Neumann M, Mues V, Moreno A, Hasenauer H, Seidl R (2017) Climate variability drives recent tree mortality in
 Europe. Global Change Biology 23(11):4788-4797
- Obladen N, Dechering P, Skiadaresis G et al (2021) Tree mortality of European beech and Norway spruce
 induced by 2018-2019 hot droughts in central Germany. Agricultural and Forest Meteorology 307
- Ols C, Bontemps JD (2021) Pure and even-aged forestry of fast-growing conifers under climate change: on the
 need for a silvicultural paradigm shift. Environmental Research Letters 16(2):5
- Ondo I, Burns J, Piedallu C (2017) Including the lateral redistribution of soil moisture in a supra regional water
 balance model to better identify suitable areas for tree species. Catena 153:207-218
- Pedersen BS (1998) Modeling tree mortality in response to short- and long-term environmental stresses.
 Ecological Modelling 105(2-3):347-351
- Peng CH, Ma ZH, Lei XD et al (2011) A drought-induced pervasive increase in tree mortality across Canada's
 boreal forests. Nature Climate Change 1(9):467-471
- Pfeifer EM, Hicke JA, Meddens AJ (2011) Observations and modeling of aboveground tree carbon stocks and fluxes following a bark beetle outbreak in the western United States. Global Change Biology 17(1):339-350
- 731 Piedallu C, Gégout J-C, Perez V, Lebourgeois F (2013) Soil water balance performs better than climatic water
- variables in tree species distribution modelling: Soil water balance improves tree species distribution models.
 Global Ecology and Biogeography 22(4):470-482
- Piedallu C, Gegout JC (2007) Multiscale computation of solar radiation for predictive vegetation modelling.
 Annals of Forest Science 64(8):899-909
- Piedallu C, Gegout JC, Bruand A, Seynave I (2011) Mapping soil water holding capacity over large areas to
 predict potential production of forest stands. Geoderma 160(3-4):355-366

- 738 Piedallu C, Gegout JC, Lebourgeois F, Seynave I (2016) Soil aeration, water deficit, nitrogen availability, acidity
- and temperature all contribute to shaping tree species distribution in temperate forests. Journal of Vegetation
 Science 27(2):387-399
- 741 Pörtner H-O, Roberts DC, Tignor M et al (2022) IPCC, 2022: Climate Change 2022: Impacts, Adaptation, and
- Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel
 on Climate Change. (eds.). Cambridge University Press. In Press.,
- Preisler HK, Grulke NE, Heath Z, Smith SL (2017) Analysis and out-year forecast of beetle, borer, and drought induced tree mortality in California. Forest Ecology and Management 399:166-178
- 746 Pretzsch H (2005) Stand density and growth of Norway spruce (Picea abies (L.) Karst.) and European beech
- (Fagus sylvatica L.): evidence from long-term experimental plots. European Journal of Forest Research
 124(3):193-205
- 749 Pretzsch H, Grams T, Haberle KH, Pritsch K, Bauerle T, Rotzer T (2020) Growth and mortality of Norway
- spruce and European beech in monospecific and mixed-species stands under natural episodic and experimentally
 extended drought. Results of the KROOF throughfall exclusion experiment. Trees-Structure and Function
- 752 34(4):957-970
- Pukkala T, Lähde E, Laiho O (2013) Species Interactions in the Dynamics of Even- and Uneven-Aged Boreal
 Forests. Journal of Sustainable Forestry 32(4):371-403
- Rogers Brendan M, Solvik K, Hogg EH et al (2018) Detecting early warning signals of tree mortality in boreal
 North America using multiscale satellite data. Global Change Biology 24(6):2284-2304
- 757 Rotzer T, Haberle KH, Kallenbach C, Matyssek R, Schutze G, Pretzsch H (2017) Tree species and size drive
- water consumption of beech/spruce forests a simulation study highlighting growth under water limitation. Plant
 and Soil 418(1-2):337-356
- Roulleau (1912) Bulletin trimestriel de l'office forestier du centre et de l'Ouest tome 3(1ere série)
- 761 Rouse WR, Wilson RG (1969) Time and Space Variations in the Radiant Energy Fluxes Over Sloping Forested
- Terrain and Their Influence on Seasonal Heat and Water Balances at a Middle Latitude Site. Geografiska
 Annaler: Series A, Physical Geography 51(3):160-175
- Schelhaas MJ, Nabuurs GJ, Schuck A (2003) Natural disturbances in the European forests in the 19th and 20th
 centuries. Global Change Biology 9(11):1620-1633
- Senf C, Buras A, Zang CS, Rammig A, Seidl R (2020) Excess forest mortality is consistently linked to drought
 across Europe. Nature Communications 11(1)
- Senf C, Pflugmacher D, Zhiqiang Y et al (2018) Canopy mortality has doubled in Europe's temperate forests
 over the last three decades. Nat Commun 9(1):4978
- Sinclair WA (1965) Comparisons of recent declines of white ash, oaks, and sugar maple in northeastern
 woodlands. Cornell Plant 20:62-67
- 772 Staupendahl K, Zucchini W (2011) Estimating survival functions for the main tree species based on time series
- data from the forest condition survey in Rheinland-Pfalz, Germany. Allgemeine Forst Und Jagdzeitung 182(78):129-145
- Suarez ML, Ghermandi L, Kitzberger T (2004) Factors predisposing episodic drought-induced tree mortality in
 Nothofagus site, climatic sensitivity and growth trends. Journal of Ecology 92(6):954-966
- 577 Sun JB, Yang JY, Zhang C, Yun WJ, Qu JQ (2013) Automatic remotely sensed image classification in a grid
- environment based on the maximum likelihood method. Mathematical and Computer Modelling 58(3-4):573581
- Taccoen A, Piedallu C, Seynave I et al (2019) Background mortality drivers of European tree species: climate
 change matters. Proceedings of the Royal Society B-Biological Sciences 286(1900)
- Thomas AL, Gegout JC, Landmann G, Dambrine E, King D (2002) Relation between ecological conditions and
 fir decline in a sandstone region of the vosges mountains (northeastern France). Annals of Forest Science
 29:265-273
- Thornthwaite CW, Mather JR (1955) The water balance. Laboratory of Climatology, Publication in Climatology.
 n°8

- Torssonen P, Strandman H, Kellomaki S et al (2015) Do we need to adapt the choice of main boreal tree species
 in forest regeneration under the projected climate change? Forestry 88(5):564-572
- Turc L (1961) Estimation of irrigation water requirements, potential evapotranspiration: a simple climatic
 formula evolved up to date. Ann Agron 12(1):13-49
- Urli M, Porté AJ, Cochard H, Guengant Y, Burlett R, Delzon S (2013) Xylem embolism threshold for
 catastrophic hydraulic failure in angiosperm trees. Tree Physiology 33(7):672-683
- van Mantgem PJ, Stephenson NL, Byrne JC et al (2009) Widespread Increase of Tree Mortality Rates in the
 Western United States. Science 323(5913):521-524
- Verbesselt J, Robinson A, Stone C, Culvenor D (2009) Forecasting tree mortality using change metrics derived
 from MODIS satellite data. Forest Ecology and Management 258(7):1166-1173
- Vitali V, Buntgen U, Bauhus J (2017) Silver fir and Douglas fir are more tolerant to extreme droughts than
 Norway spruce in south-western Germany. Global Change Biology 23(12):5108-5119
- Ward NL, Masters GJ (2007) Linking climate change and species invasion: an illustration using insect
 herbivores. Global Change Biology 13(8):1605-1615
- 801 Western AW, Zhou S-L, Grayson RB, McMahon TA, Blöschl G, Wilson DJ (2004) Spatial correlation of soil
- moisture in small catchments and its relationship to dominant spatial hydrological processes. Journal of
 Hydrology 286(1):113-134
- Williams AP, Allen CD, Macalady AK et al (2013) Temperature as a potent driver of regional forest drought
 stress and tree mortality. Nature Climate Change 3(3):292-297
- 806

807 Supporting information

808

Id	Silver fir	Norway spruce
1	+95% Silver fir	+95% Norway spruce
2	\geq 50% silver fir, + Norway spruce and others	≥50% Norway spruce, + silver fir and others
3	≥50% silver fir, + others; no Norway spruce	≥50% Norway spruce, + others; no silver fir
4	<50% silver fir, + Norway spruce and others	<50% Norway spruce, + silver fir and others
5	<50% silver fir, + others; no Norway spruce	<50% Norway spruce, + others; no silver fir
6	<5% silver fir	<5% Norway spruce
7	Young stands	Young stands

809

810 *Table S1:* Evaluation of mixture classes for the silver fir and Norway spruce stands.







Variable	Modalities for qualitative variables	Coefficient	Coefficient ^2
Intercept		-2.3462	
REL ALT		2.9993	- 1.6372
COS_ASP		-0.4539	-0.4225
RegSWD su		0.7869	
TW		27.2816	
GEOL	Principal conglomerate and acidic granite	0	
	Quaternary deposits, granites, sandstones little acidic	-0,8239	
	Voltzia sandstone, metamorphic rocks, acidic deposits	-1,8119	
	Acidic Vosges sandstone	-0,6203	
	Neutral magmatic and metamorphic rocks	-0,2841	
	Neutral to basic rocks and migmatite	1,0868	
	Volcanic pyroclastic rock	0,1552	
СОМР	Pure silver fir stand	0	
	More than 50% silver fir with Norway spruce	0,1046	
	More than 50% silver fir with broadleave sp.	0,6036	
	Less than 50% silver fir with broadleave sp.	-1,4861	
STRUCT	Even-aged stand	0	
	Young stand	-0,686	
	Uneven-aged stand	-0,7077	
STORM	Less than 50% damage	0	
	More than 50% damage	-0,6936	
EDGE S	Absence of south forest edge	0	
_	Presence of south forest edge	1,1293	

el.
e

820		
821		
822		
823		
824		
825		
826		

Variable	Modalities for qualitative variables	Coefficient	Coefficient ^2
Intercept		1.3578	
REL_ALT		1.1820	
COS ASP		-0.4005	
RegSWD su		0.7660	
TW		33.8845	
GEOL	Granites, quaternary deposits, primary	0	
	Granodiorites, migmatic rocks, sedimentary neutral to acidic	-1,1875	
	Voltzia or shells sandstone, magmatic, volcanic	0,6745	
	Vosges or intermediate sandstone, granits, gneiss	-0,2069	
	Magmatic basic rock	-0,4483	
	Sedimentary basic rock	2,4633	
	Pure Norway spruce stand	0	
COMP	More than 50% Norway spruce with Silver fir	-0,9841	
	More than 50% Norwauy spruce with broadleave sp.	-1,1953	
	Less than 50% Norway spruce with broadleave sp.	-2,0768	
	Even-aged stand	0	
STRUCT	Young stand	-1,0156	
	Uneven-aged stand	-0,5555	
	Less than 50% damage	0	
STORM	More than 50% damage	-0,825	
	Absence of forest edge	0	
EDGE	Presence of edge between two stands	0,5407	
	Presence of edge with an open environment	0,2568	

Table S3: Coefficients for the Norway spruce model.



830

831 Figure S2: Comparison of the summer SWD trend (variable regSWD_su) for three contrasted locations over the 832 1986-2019 period: A) map of summer SWD trends and localisation of the three time series, B) summer SWD time series for the 1986-2019 period. Vulnerability was most important in site $n^{\circ}1$ (regSWDsu > 2), where the 833 time series showed a substantial increase of water stress from 2012, with a high probability of dieback (0.70 and 834 0.78 for silver fir and Norway spruce respectively, see figures 5 and 6). Site n°3 showed similar water stress 835 levels from 2012, but a higher one than site n°1 between 1986 and 2012. The probability of dieback was much 836 837 lower (0.15 and 0.30 for silver fir and Norway spruce, respectively), suggesting that trees were more adapted to 838 drought than in site n°1. Site n°2 was at a higher altitude, with little moisture stress and a low level of risk 839 despite a slight increase of the water deficit from 2015 (probability of dieback: 0.15 and 0.30 for silver fir and 840 Norway spruce, respectively).