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Pine processionary moth outbreaks cause longer growth legacies than drought and are linked to the North Atlantic Oscillation

J. Julio Camarero [a,*], Jacques Tardif [b], Antonio Gazol [a], France Conciatori [b]

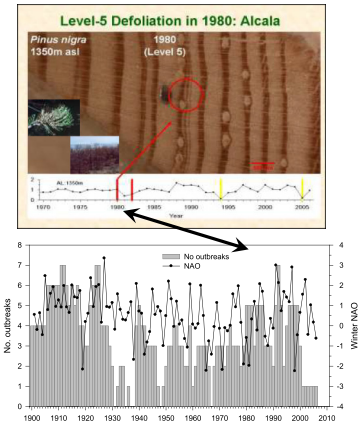
[a] Instituto Pirenaico de Ecología (CSIC), Apdo. 202, 50192 Zaragoza, Spain
[b] Centre for Forest Interdisciplinary Research (C-FIR), University of Winnipeg, 515 Portage Avenue, Winnipeg, MB R3B 2E9, Canada

HIGHLIGHTS

- We tested if warmer winters increased pine processionary moth (PPM) defoliations.
- PPM defoliation negatively impacted longer but weaker growth than drought.
- Neither an upward expansion nor an increase in outbreak frequency was observed.
- PPM defoliations were positively related to the winter North Atlantic Oscillation.

GRAPHICAL ABSTRACT

Is climate warming leading to an upwards shift of severe pine processionary moth (PPM) defoliations in Mediterranean pine forests? Field records of stand defoliation and tree-ring reconstructions of outbreaks did not support an upward shift, but allowed detecting a positive link between PPM defoliations and the winter North Atlantic Oscillation.



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ABSTRACT

Climatic warming is assumed to expand the geographic range of insect pests whose distribution is mainly constrained by low temperatures. This is the case of the pine processionary moth (*Thaumetopoea pityocampa*), which is one of the main conifer defoliators in the Mediterranean Basin. Warmer winters may lead to a northward/upward expansion of this insect, as short-term studies have shown. However, no long-term data, i.e. spanning at least one century, has been used to examine these projections. We test the hypotheses that climatic warming (i) has caused an upward shift of the pine processionary moth, and (ii) has increased the frequency of severe defoliations. We used dendrochronological methods to reconstruct defoliations over the period 1900–2006 in 14 sites spanning a wide altitudinal range (1070–1675 m) in Teruel, eastern Spain. We built local ring-width chronologies for four co-occurring pine species with different degree of susceptibility against the moth defoliations, from highly suitable or palatable species (*Pinus nigra*) to moderately (*Pinus sylvestris*, *Pinus halepensis*) or rarely defoliated species (*Pinus pinaster*). We validated the tree-ring reconstructions of outbreaks using a field record of stand defoliations spanning the period 1971–2006. Outbreaks in the most affected *P. nigra* stands corresponded to abrupt one- to two-year growth reductions (70–90% growth loss). Reconstructed outbreaks occurred on average every 9–14 years. The growth memory of outbreaks was weaker

Abbreviation: NAO, North Atlantic Oscillation.

* Corresponding author at: Instituto Pirenaico de Ecología, IPE-CSIC, Avenida Montañana 1005, Zaragoza E-50192, Spain.
E-mail addresses: jjcamarero@ipe.csic.es (J.J. Camarero), j.tardif@uwinnipeg.ca (J. Tardif).

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but lasted longer (1–6 years) than that due to droughts (1–3 years). Neither an upward expansion nor an increase in outbreak frequency was observed. Severe PPM defoliations did not increase as climate warmed, rather they were positively related to the winter North Atlantic Oscillation.

1. Introduction

The effects of disturbances driven by global change such as insect outbreaks and drought are contributing to reductions in forest productivity and growth decline worldwide (Millar and Stephenson, 2015). For instance, rising temperatures may amplify drought stress (Williams et al., 2013). Increased drought stress can make trees more vulnerable to insect damage by reducing growth, increasing canopy defoliation and enhancing tree mortality risk (Mattson and Haack, 1987; Guarín and Taylor, 2005; Jactel et al., 2012). Climate warming and human-mediated range expansions are also altering the impacts of insect pests on forests (Simler-Williamson et al., 2019). Warmer conditions can lead to earlier emergences, enhance reproduction rates or lengthen the flight or reproductive seasons promoting the dispersal of insect herbivores whose distributions are limited by low temperatures (Harvey et al., 2020). However, it is still unknown how these disturbances translate into different characteristic ecological memory functions reflecting post-disturbance recovery (Anderegg et al., 2015). Ogle et al. (2015) defined ecological memory as the influence of past conditions on current ecosystem function and considered three components: the length of memory (a function similar to legacy effects quantifying the persistence of ecosystem responses to a disturbance; see Anderegg et al., 2015), the relative importance of past conditions over the memory period, and the cumulative effect of past conditions on current function. Quantifying the ecological memory of forests in response to insect defoliation and drought using Bayesian hierarchical models allows for assessing the persistence of growth responses to these disturbances (Itter et al., 2019a).

A widely reported case of range expansion linked to rising temperatures is the pine processionary moth (*Thaumetopoea pityocampa* Den. & Schiff.; hereafter PPM), a major defoliator of Mediterranean, drought-prone conifer forests (Robinet et al., 2007; Netherer and Schopf, 2010; Robinet and Roques, 2010; Roques et al., 2015). The PPM population dynamics follow a positive gradation phase until maximum PPM density is reached, defoliation levels peak and PPM density decreases afterwards starting a negative gradation phase due to reduced food availability (Démolin, 1969; Baraza et al., 2004; Battisti et al., 2005). Since PPM moths feed on conifer needles during winter, recent upward or poleward expansions of PPM have been linked to warmer winter conditions (Hódar et al., 2003; Hódar and Zamora, 2004; Battisti et al., 2005, 2006; Robinet et al., 2007; Roques et al., 2015). Low winter temperatures limit the development of PPM moths (Buffo et al., 2007). The PPM larvae build silky nests in the crowns of defoliated trees, which allow caterpillars feeding on mature needles in the winter (see the PPM cycle in Fig. S1, Supplementary Material).

The studies supporting latitudinal and altitudinal shifts in the PPM distribution and an increase in outbreak were based on short- to mid-term data (e.g., Hódar et al., 2003; Battisti et al., 2005; Robinet et al., 2007), but others did not find any upward shift (Gazol et al., 2019). However, it is still unclear if the PPM upward and poleward shifts and the increase in severity and frequency of PPM defoliations as winter temperatures rise are more negatively impacting tree growth. Long-term reconstructions of PPM defoliation are needed to answer these questions.

A long-term shift in the PPM distribution and a persistent increase of outbreak defoliation severity would be expected if winter temperature rises and its year-to-year variability decreases since PPM caterpillars do not withstand lethal, very low winter temperatures (Démolin, 1969; Huchon and Démolin, 1971; Hoch et al., 2009). Cold winters can directly limit PPM larvae survival (Buffo et al., 2007) or indirectly by affecting parasitism rates (Pimentel et al., 2011). Warm climate anomalies such as heat waves could also promote PPM spread, but it is unclear if the colonizing populations would persist in their new habitats (Battisti et al., 2006).

Dry and sunny winter conditions in Mediterranean regions are associated to positive winter North Atlantic Oscillation (NAO) indices (Hurrell, 1995; Rodó et al., 1997). This allowed showing a direct relationship between PPM defoliation levels and winters NAO indices (Hódar et al., 2012). This suggests a better performance of PPM larvae during dry and sunny winters, even if nights are cold, than during wet and mild winters (Démolin, 1969; Robinet et al., 2007; Pimentel et al., 2011). Therefore, a higher frequency of PPM outbreaks could be expected if winter NAO indices and temperature rise in southern Europe (López-Moreno et al., 2011). Winter climate conditions could also affect PPM dynamics by altering biotic interactions since the rate of PPM moth parasitism was reduced during winters with positive NAO indices (Hódar et al., 2021).

The combined impacts of PPM defoliation and drought produce negative, often synergistic, effects on tree growth, despite non-structural carbohydrate concentrations are not being necessarily reduced (Hernández et al., 2005; Jacquet et al., 2012, 2014; Palacio et al., 2012; Linares et al., 2014). PPM defoliation reduces tree-ring width and may decrease earlywood density due to the formation of tracheids with thinner secondary walls (Polge and Garros, 1971). Growth reductions due to severe PPM defoliation vary from −30 to −43% on average and pronounced growth losses often last several years after the outbreak (Lemoine, 1977; Laurent-Hervouët, 1986; Kanat et al., 2005; Jacquet et al., 2012, 2013). Thus, tree-ring reconstructions of PPM outbreaks are feasible and robust if they are validated by field assessments of stand defoliation and damage (Hernández et al., 2005; Gazol et al., 2019) or through indirect proxies such as remote-sensing images (Sangüesa-Barreda et al., 2014). Furthermore, this retrospective approach would allow separating drought versus defoliation signals in radial growth series. This is particularly relevant because severe PPM defoliation episodes may last for several years, whereas drought impacts on growth may be stronger and shorter (Gazol et al., 2020).

Therefore, to reconstruct long-term shifts in PPM outbreaks we need: (i) reliable field observations of PPM stand defoliation levels, and (ii) proxies of PPM outbreaks rendering reconstructions of defoliation which can be validated with observational data. Tree-ring attributes can be used to provide century-long reconstructions of insect outbreaks associated with severe defoliation, severe radial growth lost and, sometimes, the production of specific wood anatomical signatures (Swetnam and Lynch, 1993; Speer et al., 2001; Sutton and Tardif, 2005; Waito et al., 2013). Here we use tree ring data to reconstruct conifer defoliation outbreaks with annual resolution (Swetnam et al., 1985; Speer et al., 2001; Paritsis et al., 2009; Paritsis and Veblen, 2011; Lynch, 2012). We analyze the spatio-temporal variability in outbreak frequency and compare defoliation impacts on radial growth series with those due to drought.

In this study, we aim: (i) to reconstruct PPM outbreaks since 1900 based on comparing tree-ring width series from very susceptible or palatable vs. less susceptible or palatable pine species; (ii) to use field observations of PPM defoliation to validate reconstructed outbreaks for the period 1971–2006; (iii) to compare the impacts of drought and defoliations on tree growth through the analyses of ecological memory using Bayesian hierarchical models (Itter et al., 2021); and (iv) to analyze long-term NAO-PPM defoliation relationships. We expect PPM outbreaks to be more frequent in recent years and to steeply increase their frequency upwards if they are positively impacted by climate warming, specifically by warmer winter conditions linked to positive NAO phases.

2. Material and methods

2.1. Study area, tree species and pine processionary moth defoliation data

The monitoring sites are located near Mora de Rubielos (Fig. 1), eastern Spain (Camarero et al., 2015; Gazol et al., 2019). This is an optimum natural setting to evaluate if PPM outbreaks have shifted upwards in response to climate warming for several reasons. First, four drought-sensitive pine

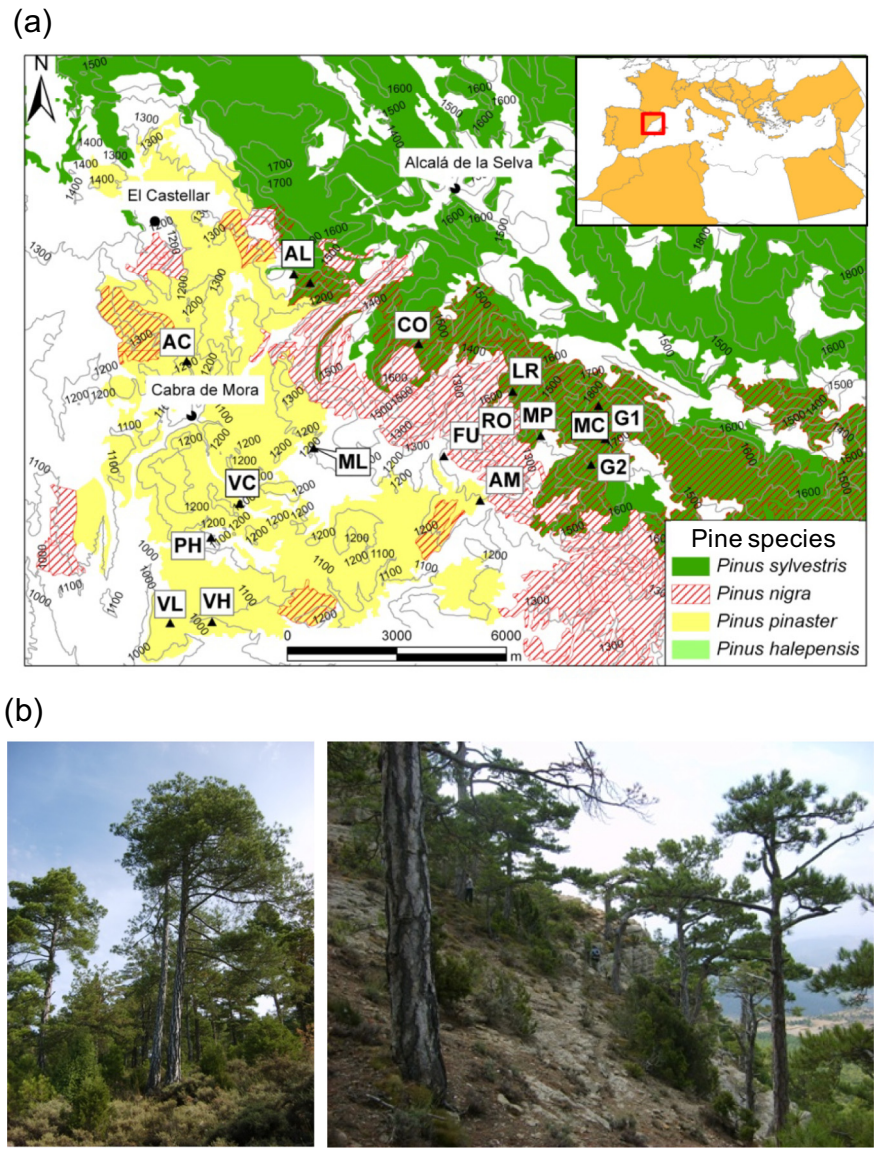


Fig. 1. (a) Situation of the study sites (see sites' codes in Table 1) and (b) views of sampled *Pinus nigra* stands. In the upper plot, the map shows the countries in the Mediterranean Basin affected by PPM outbreaks (in orange) and the location of the study area in eastern Spain (red box).

Table 1
Geographical and topographical characteristics of the sampled mixed and pure *P. nigra* stands. In the case of mixed stands, the two letters of sampled trees correspond to the two sampled species. Abbreviations of pines' names: Ps, *P. sylvestris*; Pp, *P. pinaster*; Pn, *P. nigra*; Ph, *P. halepensis*.

Site	Code	Latitude (N)	Longitude (W)	Elevation (m)	Aspect	Tree species	Basal area (m^2 ha^{-1})
Mora-El Chaparroso	MC	40° 19′ 05″	0° 40′ 28″	1770	SW	Ps	29.2
Gradient-up	G1	40° 18′ 32″	0° 40′ 22″	1675	W	Pn	29.0
Las Roquetas	LR	40° 19′ 19″	0° 42′ 08″	1615	SE	Pn, Ps	38.0
Gradient-middle	G2	40° 18′ 13″	0° 40′ 40″	1605	W	Pn	13.5
Las Roquetas	RO	40° 18′ 36″	0° 42′ 58″	1550	W	Pn	14.8
Camino Olmedilla	CO	40° 20′ 07″	0° 43′ 53″	1505	SW	Pn, Ps	9.5
Masía Peñarroya	MP	40° 18′ 40″	0° 41′ 37″	1435	S	Pn	4.7
Alcalá (Cabra)	AL	40° 21′ 02″	0° 45′ 58″	1350	SE	Pn, Ps	14.2
Alto de Mora	AM	40° 17′ 43″	0° 42′ 51″	1330	SE	Pn	14.1
Fuendenarices	FU	40° 18′ 24″	0° 43′ 30″	1230	W	Pn	19.1
Mora-Los Campillos	ML	40° 18′ 34″	0° 45′ 59″	1200	W	Pn	4.2
Valle de Cabra	VC	40° 17′ 46″	0° 47′ 17″	1165	NE	Pn, Pp	25.3
Valbona-pinos	PH	40° 17′ 17″	0° 48′ 03″	1095	S	Ph	8.0
Alto de Cabra	AC	40° 19′ 55″	0° 48′ 26″	1090	E	Pn, Pp	28.0
Valbona	VL	40° 16′ 00″	0° 48′ 53″	1070	SE	Pp	39.0
Valbona-carrascos	VH	40° 16′ 03″	0° 48′ 02″	1055	SE	Ph	12.2

species are present along a ca. 600-m altitudinal gradient with *Pinus halepensis* Mill. dominating the lowest and driest sites and *Pinus pinaster* Ait. being abundant in mid-elevation warm locations, both under Mediterranean climate conditions, and *Pinus nigra* Arn., and *Pinus sylvestris* L. forming mid- to high-elevation mixed stands subjected to continental Mediterranean climate conditions (Table 1). Second, these climatic and ecological gradients offer the opportunity to compare forests with different susceptibility or palatability to PPM defoliations and outbreaks, from very susceptible or palatable (*P. nigra*, here regarded as "host" species) to less susceptible or palatable tree species (the other pine species, here regarded as "non-host" species; see Avtzis, 1986; Tiberi et al., 1999; Hódar et al., 2002). We selected *P. nigra* as host species because it shows the highest incidence of severe PPM defoliations (Gazol et al., 2019) and it is also very sensitive to drought (Camarero et al., 2015). In some sites, *P. sylvestris* also experienced severe defoliations, but they were usually less severe and this species tends to occupy the highest sites in the study region being less responsive to drought compared with the other three species which dominate in lower, sunnier and warmer locations (Camarero et al., 2015). Third, PPM outbreaks have been monitored *in situ* through evaluations of stand defoliations during the period 1971–2006. Finally, the site has not been intensively managed over the past century allowing reconstructing radial growth patterns of trees older than 100 years for most species (Camarero et al., 2015).

In the study area, 92 stands were monitored annually, in late winter, from 1971 to 2006 (Figs. 2 and S2). Several features of each stand were recorded or calculated including elevation, aspect, and basal area (Table 1). We only considered high and severe PPM stand defoliations, which correspond to levels 4 and 5 of Regional Forest Services in Spain, whereas moderate defoliations correspond to level 3 (Hernández et al., 2005). Levels 4 and 5 indicate many trees present moderate and complete defoliation levels, respectively, whereas the level 3 is characterized by scattered, moderately defoliated trees (see Fig. S1).

Among the 92 stands with available field defoliation data, we selected and sampled 14 stands dominated by different species and encompassing different ecological and climate conditions (Table 1). We discarded two stands (MC and VH sites), which occupied the extreme altitudinal ranges of the selected stands, and showed few years with severe defoliation. Finally, we analyzed data from 12 stands with complete tree-ring and defoliation information (Table 2).

Climate data for the study area (mean seasonal temperature, total precipitation) were obtained by calculating regional climate series for the period 1950–2006 based on local stations (Mora de Rubielos, 40.251° N,

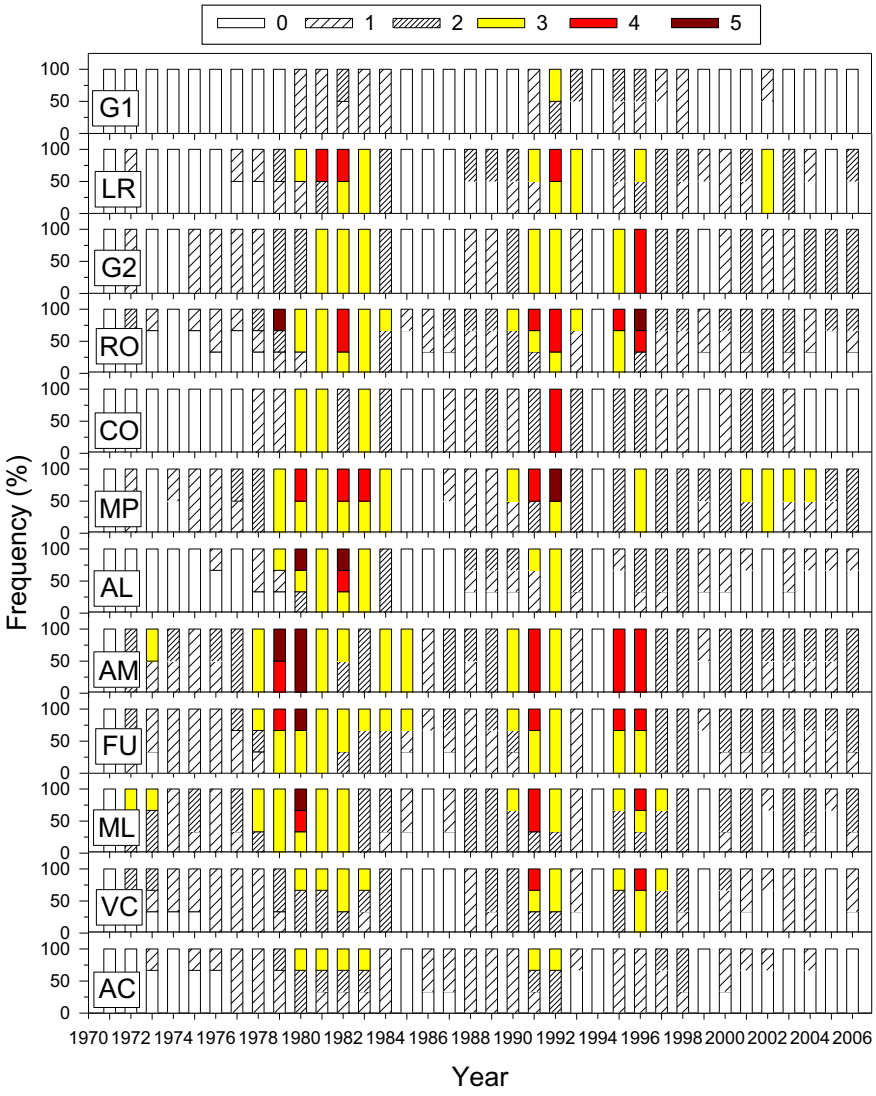


Fig. 2. Observed PPM defoliations in the sampled *P. nigra* stands arranged along the altitudinal gradient from lowest (AC) to highest (G1) site (see Table 1). Different colors show PPM defoliation levels (see levels 3 to 5 in Fig. S1) and the bars show the percentage of sub-areas located near each site (see Fig. S2) showing the different PPM defoliation levels.

0.750° W, 1040 m; Alto de Cabra, 40.332° N, 0.807° W, 1120 m; Valle de Cabra, 40.297° N, 0.791° W, 1160 m; Alto de Mora, 40.315° N, 0.722° W, 1300 m; Alto San Rafael, 40.353° N, 0.710° W, 1500 m; see also Sangüesa-Barreda et al., 2014). In this area the climate is Mediterranean continental with mean temperatures of 9.4 °C and total precipitation of 728 mm at 1492 m a.s.l.

2.2. Drought and PPM defoliation signals in tree rings

Selected sites for tree-ring reconstructions of PPM defoliations often corresponded to mixed forests where host (*P. nigra*) and non-host tree species coexisted. In each stand, from 10 to 26 matures trees were selected and their diameter was measured at breast height (dbh). Then, we took two cores at 1.3 m perpendicular to each other and one of them was perpendicular to the maximum slope. Cores were air dried, glued into wooden supports and carefully sanded until annual tree rings were clearly visible. Tree-ring widths were measured under a binocular scope at a precision of 0.001 mm using Velmex and LINTAB-TSAP measuring systems. Visual cross-dating and tree-ring measurements were validated using the program COFECHA, which calculated shifted correlations between individual and mean site series (Holmes, 1983). The mean correlations of individual tree-ring width series with the mean sites' series were quite high (range 0.64–0.85), confirming the cross-dating robustness (Table 2). Tree age at 1.3 m was estimated by counting rings in cores with pith or in those with curved innermost rings whose arc was visible. In these cores without pith, we followed Duncan (1989) to estimate the number of missing rings by fitting a template of concentric circles to the arc of innermost rings.

We analyzed PPM defoliation signals preserved in the radial growth patterns of *P. nigra* trees by comparing standardized tree-ring width series from host *P. nigra* stands ($n = 12$ sites) and chronologies from non-host pine species (*P. halepensis*, *P. pinaster*, *P. sylvestris*) showing similar responses to drought (Swetnam et al., 1985; Lynch, 2012). Individual tree-ring width measurements for each tree in each site were detrended using a spline with a frequency response of 0.50 at a wavelength of 2/3 of the series length. For the host and non-host species, standardized chronologies for each site were created by averaging the series using a bi-weight robust mean. Detrending and standardization of ring-width series was done with the dplR package (Bunn et al., 2020) in the R statistical environment (R Core Team, 2020).

For each site, individual tree-ring width standardized measures of *P. nigra* were compared to the corresponding standardized chronology of the non-host species (see Tables 1 and 2). The selection of the non-host stands was based on geographical proximity and on a similar response to drought (Fig. S4).

To calculate the growth response to drought, Pearson correlations were calculated by relating the standard site chronologies with a regional drought index considering the common period 1950–2006. This index corresponded to the Standardized Precipitation and Evapotranspiration Index (SPEI). High and low SPEI values correspond to wet and dry conditions, respectively (Vicente-Serrano et al., 2010). We obtained 0.5°-gridded SPEI values for the study area (grid coordinates 0.5°–1.0° W, 40.0°–40.5° N) from the global SPEI database (available at https://spei.csic.es/database.html) at temporal resolutions from 1 to 48 months. Winter maximum and minimum temperatures have risen in the study area since 1950 (Fig. S3a). Based on previous studies assessing drought-growth relationships in Mediterranean pines (Pasho et al., 2011) we selected the June SPEI at a 9-month resolution, which highlighted two major droughts occurring in 1994–1995 and 2005 (Fig. S3b).

A growth suppression index (GSI) was calculated for each host tree in each year as the difference in growth between *P. nigra* and the non-host species (Guiterman et al., 2020). Then, a normalized GSI (NGSI) was calculated by converting the GSI to a z-score, thus reflecting negative values below a threshold (-1.28) when a defoliation event was assumed to occur. Based on this, we calculated the percentage of trees showing defoliation events every year in the study period. The minimum number of years in which the tree is defoliated was set to three. The identification of defoliation events was done with the dfoliatR package (Guiterman et al., 2020). A limitation of this method is that it assumes similar growth responses to drought among the compared species, which may show some seasonal differences modulated by site conditions such as elevation (Camarero et al., 2015). After reconstructing PPM outbreaks, we compared their total number and

Table 2
Structural and dendrochronological characteristics of the sampled stands, and annual outbreaks reconstructed during the period 1900–2006 (last column). Sites' codes are as in Table 1. In bold, the *P. nigra* stands for which defoliation signals in tree ring-width series were analyzed. The non-host column indicates the site and pine species (abbreviated) to which each *P. nigra* stand was compared and the memory effect column indicates *P. nigra* sites (*) used in the ecological memory analyses. Non-host pine species are abbreviated as in Table 1.

Site	Dbh (cm)	Species	No trees	No cores	Age at 1.3 m (years)	Tree-ring width (mm)	AC[a]	*r*	Site (non-host species)	Memory effect	No. outbreak years
G1	37.9 ± 1.8	*P. nigra*	17	34	187 ± 8	0.74 ± 0.09	0.72	0.78	LR (Ps)		35
LR	46.6 ± 2.7	*P. nigra*	10	20	137 ± 5	1.15 ± 0.16	0.73	0.71	LR (Ps)	*	19
LR	41.0 ± 2.0	*P. sylvestris*	11	22	134 ± 13	1.13 ± 0.14	0.76	0.64			
G2	46.9 ± 2.9	*P. nigra*	17	34	153 ± 3	1.09 ± 0.11	0.70	0.74	LR (Ps)	*	42
RO	36.6 ± 1.4	*P. nigra*	26	52	238 ± 13	0.46 ± 0.04	0.71	0.71	LR (Ps)	*	31
CO	49.6 ± 1.5	*P. nigra*	20	40	155 ± 4	1.11 ± 0.16	0.70	0.78	CO (Ps)	*	34
CO	40.3 ± 1.6	*P. sylvestris*	15	29	103 ± 6	1.37 ± 0.16	0.72	0.68			
MP	42.0 ± 0.9	*P. nigra*	17	32	115 ± 2	1.30 ± 0.16	0.73	0.75	CO (Ps)	*	34
AL	35.9 ± 1.4	*P. nigra*	17	34	121 ± 4	1.07 ± 0.14	0.75	0.78	AL (Ps)	*	
AL	33.9 ± 1.2	*P. sylvestris*	22	44	108 ± 5	1.10 ± 0.12	0.77	0.71			33
AM	33.3 ± 1.4	*P. nigra*	15	30	125 ± 4	0.85 ± 0.12	0.67	0.76	VL (Pp)	*	15
FU	40.0 ± 1.6	*P. nigra*	21	42	169 ± 7	0.84 ± 0.10	0.75	0.67	AL (Ps)	*	34
ML	33.8 ± 2.9	*P. nigra*	21	42	75 ± 5	1.57 ± 0.17	0.65	0.72	PH (Ph)	*	33
VC	32.3 ± 0.9	*P. nigra*	15	30	105 ± 4	1.03 ± 0.15	0.66	0.84	VC (Pp)		25
VC	32.2 ± 1.2	*P. pinaster*	15	30	78 ± 3	1.28 ± 0.12	0.58	0.83			
PH	40.0 ± 2.7	*P. halepensis*	16	32	73 ± 4	1.75 ± 0.18	0.55	0.77			
AC	38.8 ± 2.7	*P. pinaster*	16	32	91 ± 3	1.28 ± 0.15	0.74	0.81			
AC	35.6 ± 1.4	*P. nigra*	17	34	105 ± 8	1.11 ± 0.13	0.68	0.75	AC (Pp)		21
VL	39.1 ± 0.9	*P. pinaster*	25	50	105 ± 5	1.13 ± 0.10	0.64	0.85			

[a] AC, first-order autocorrelation of raw tree-ring width series; *r*, mean correlation of individual tree-ring width series with the mean sites series.

the mean NGSI of all sites with winter (December to February) temperatures and NAO indices. The NAO indices were retrieved from the website https://crudata.uea.ac.uk/cru/data/nao/.

2.3. Drought and PPM defoliation impacts on growth memory

We applied a recently developed Bayesian hierarchical model to quantify the ecological memory of *P. nigra* growth to past droughts and PPM defoliation events (Itter et al., 2019b). The ecological memory was quantified by estimating latent weights reflecting the relative importance of past conditions on current forest ecosystem function (Ogle et al., 2015). The weights' values show the relative importance of covariate values at specific temporal lags. Within a linear model framework, the model estimated ecological memory functions for the effect of drought (continuous distribution) and defoliation events (binary distribution) on tree growth based on Markov chain Monte Carlo (MCMC) simulations (Itter et al., 2021). As a response variable, we used standardized ring-width chronologies of *P. nigra* in 9 out of the 12 studied stands (Table 1). Two of the stands (G1 and AC) were not included in the analyses because no severe defoliations were observed in them in the period 1971–2006. Another stand (VC) was also removed because it was far from the study site. The analyses were restricted to the period 1971–2006 for which we have field-based observations of defoliation outbreaks in the studied stands. As covariates, we used the occurrence of severe defoliation events (Fig. 2) and the 9-month June SPEI (Fig. S3).

We proposed a model in which growth rate (standard ring-width indices) was modelled as a function of the interaction between defoliation (dummy variable indicating whether a severe defoliation occurs "1" or not "0") and drought (SPEI). The maximum lag for memory variables was fixed to six years, as we did not expect significant longer impacts of drought or defoliation on growth beyond six years. The model was fitted using the EcoMem R package (Itter et al., 2021).

3. Results

3.1. Drought and PPM outbreaks lead to different growth legacies

The PPM defoliations peaked in several periods (1979–1983, 1991–1992, and 1995–1996), particularly in *P. nigra* stands located at low to mid elevations (1200 to 1550 m) such as the RO, MP, AL, AM, FU and ML sites (Table 1, Fig. 2). Interestingly, few PPM defoliations were observed during very dry years such as 1994–1995 and 2005 (Fig. S3). The number of severe defoliations (sum of stands showing severe defoliations) observed during the period 1971–2006 was positively related to mean winter temperature ($r = 0.35$, $p = 0.03$). However, no significant association ($r = 0.07$, $p = 0.59$) was found between the elevation of *P. nigra* stands and the number of PPM defoliations (Fig. 2).

Drought-growth relationships showed that growth was constrained by mid-term droughts lasting from 6 to 12 months, with correlations peaking from May to September (Fig. S4). Correlations between growth rates and the SPEI peaked in the low-elevation *P. pinaster* and *P. halepensis* stands, but decreased in high-elevation *P. sylvestris* stands.

During the monitoring period (1971–2006), the synchrony among *P. nigra* stands regarding the frequency of missing rings caused by droughts in 1994–1995 and 2005 (reaching 35–40% of trees in years such as 1994) was higher than in the case of missing rings due to severe PPM defoliations (reaching 20–25% of trees in years such as 1996; Fig. S5).

The ecological memory analyses showed different lagged responses of *P. nigra* growth to drought and PPM defoliations (Fig. 3). Posterior mean weight values above 0.01 for lags 1 to 6 years reflect persistent impacts of PPM defoliation on growth. We found a short but intense response to SPEI lasting for lags 1 to 3 years, in agreement with the high first-order correlation of growth series (Table 2). Conversely, the impacts of PPM defoliations on growth were weaker than in the case for drought but lasted longer. The same results were obtained using the PPM outbreak reconstructed prior to the observational data (Figs. S6 and S7).

3.2. PPM reconstructions and links with the NAO winter index

We reconstructed PPM outbreaks by comparing growth series of host and non-host tree species (Figs. S6, S7 and S8). Tree-ring signatures of PPM outbreaks often corresponded to two narrow rings (Fig. S5), whereas signatures associated to droughts were restricted to one narrow ring and, often, missing ring (Fig. S9). Outbreaks in the most affected *P. nigra* stands corresponded to abrupt one- to two-year growth reductions (70–90% growth loss).

There was a high spatial variability among *P. nigra* stands with a lower frequency of reconstructed PPM outbreaks observed in high-elevation sites (e.g., G1 site), and a higher frequency in low-elevation sites (e.g., sites ML, VC and AC) (Fig. S10). The reconstructed PPM outbreaks were in agreement with field records of severe defoliations with high-elevation *P. nigra* sites such as G1 showing few moderate defoliation events, whilst mid-elevation sites such as FU and RO presented recent PPM defoliations in the 1990s, which were captured by our reconstructions (Fig. 2 and Table S1).

On a site basis, PPM outbreaks were not more frequent during recent decades in the high-elevation sites (Fig. S11). The NGSI significantly increased in two sites, the frequency of outbreaks decreased in three sites and increased in one site (Table S3). Reconstructed outbreaks were common in the 1910s, 1920s, 1940s, 1980s and 1990s (Figs. 4 and S10, Table S1). On average, they occurred every 9–14 years. There was no significant association ($r = 0.35$, $p = 0.26$) between the site elevation and the number of reconstructed oubreaks during the period 1900–2006 (Tables 1 and 2).

The reconstructed number of outbreaks was positively correlated with the winter NAO index (Spearman $r_s = 0.34$, $p = 0.0003$, period 1900–2006, Fig. 4a). Consequently, the mean NGSI was negatively related to the winter NAO index ($r = -0.29$, $p = 0.002$, Fig. 4b).

4. Discussion

Reconstructed PPM outbreaks showed no increase in frequency. Overall, they were less frequent in high- than in low-elevation sites for the period 1900–2006. These results were corroborated by field records of PPM outbreaks for the period 1971–2006. Thus, our findings do not support the hypothesis of an upward expansion of PPM defoliations during the period 1900–2006. Outbreaks were not more frequent in the early 21st century than in other previous periods such as the 1920s, 1940s or 1990s. The number of PPM defoliations during the period 1971–2006 was positively related to mean winter temperature, which has steadily increased in the

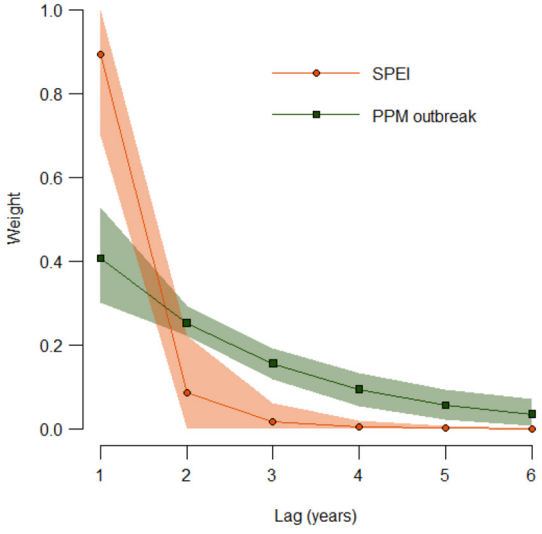


Fig. 3. Ecological memory recovered in *P. nigra* tree-ring width series due to drought (June SPEI at a 9-month resolution) or PPM outbreaks causing severe defoliation. Values are mean weights (with 95% credible intervals) calculated for 1- to 6-year long lags (see also Table S2).

study area during that period (Gazol et al., 2019), but this did not lead to a higher frequency of severe PPM defoliations. In contrast, the pseudo-cyclic behaviour of PPM defoliation outbreaks suggests their dynamics are tightly coupled to oscillatory climatic conditions (Robinet et al., 2007; Hódar et al., 2021).

Since the early 20th century, reconstructed defoliations were related to the winter NAO index, suggesting that dry and sunny winters linked to positive NAO phases enhanced PPM defoliation as was previously found (Hódar et al., 2012). There was a strong coincidence between the two main periods of high outbreaks (1900–1930 and 1970–2000) and two periods of high winter NAO shown by multidecadal trends: the early (1910s, 1920s) and late (1980s, 1990s) 20th century (see Hurrell, 1995; Eade et al., 2021). The lack of association between winter temperatures and long-term PPM defoliations could be explained by the negative effects of sharp drops in night air temperatures (cold spells) on PPM larvae performance (Démolin, 1969; Battisti et al., 2005). As stated before, PPM larvae can perform better in sunny dry winters, even if nights are cold, than during wet and mild winters (Démolin, 1969; Robinet et al., 2007; Pimentel et al., 2011). However, if several extremely cold nights occur this may reduce the feeding activity and survival of PPM caterpillars (Démolin, 1969; Huchon and Démolin, 1971; Hoch et al., 2009). Regional or continental atmospheric patterns as winter NAO indices are more associated to PPM defoliations than site winter temperatures because of the local variability in climate extremes (López-Moreno et al., 2011). Further research could also consider decadal climate changes associated to the NAO index and their impacts on PPM defoliations such as changes in winter cloudiness and soil moisture or the contrasting climate conditions between wet-cool (e.g., 1970s) and dry-warm decades (e.g., early 1980s, late 1990s) (Eade et al., 2021).

In sight of climate change, extreme climate events such as drought or cold spells may become more common and be of local extent (Thornton et al., 2014), even if mean winter temperatures keep rising in response to large-scale atmospheric patterns such as the NAO. Further research should disentangle the effects of warmer or drier climate conditions on defoliators and tree growth depending on the insect and host phenology, which may differ from winter- to spring-feeding species. Warming could increase the phenological synchrony between defoliators and its host species or lengthen the growing season exposing leaves to herbivores for longer periods leading to more severe outbreaks as temperatures rise (Paritsis and Veblen, 2011; Pureswaran et al., 2019; Meineke et al., 2021).

In addition to biotic disturbances such as PPM outbreaks we considered the impacts of abiotic disturbances such as droughts. The negative impacts of drought on tree growth were stronger but shorter than those due to PPM defoliations. The negative impacts of drought on tree growth were more synchronous along the study altitudinal gradient (e.g., 1995 drought) than those of PPM defoliations since most sites showed growth reductions due to water deficit, albeit each species showed characteristic time-scales of response as previously described (Pasho et al., 2011). Growth sensitivity to drought increased downwards, particularly in the case of *P. pinaster*, but *P. nigra* stands showed a similar response to dry conditions which agrees with other studies on tree-ring growth and water-use efficiency in the study area (Camarero et al., 2015; Shestakova et al., 2017). Therefore, host and non-host stands showed similar climatic constraints driven by

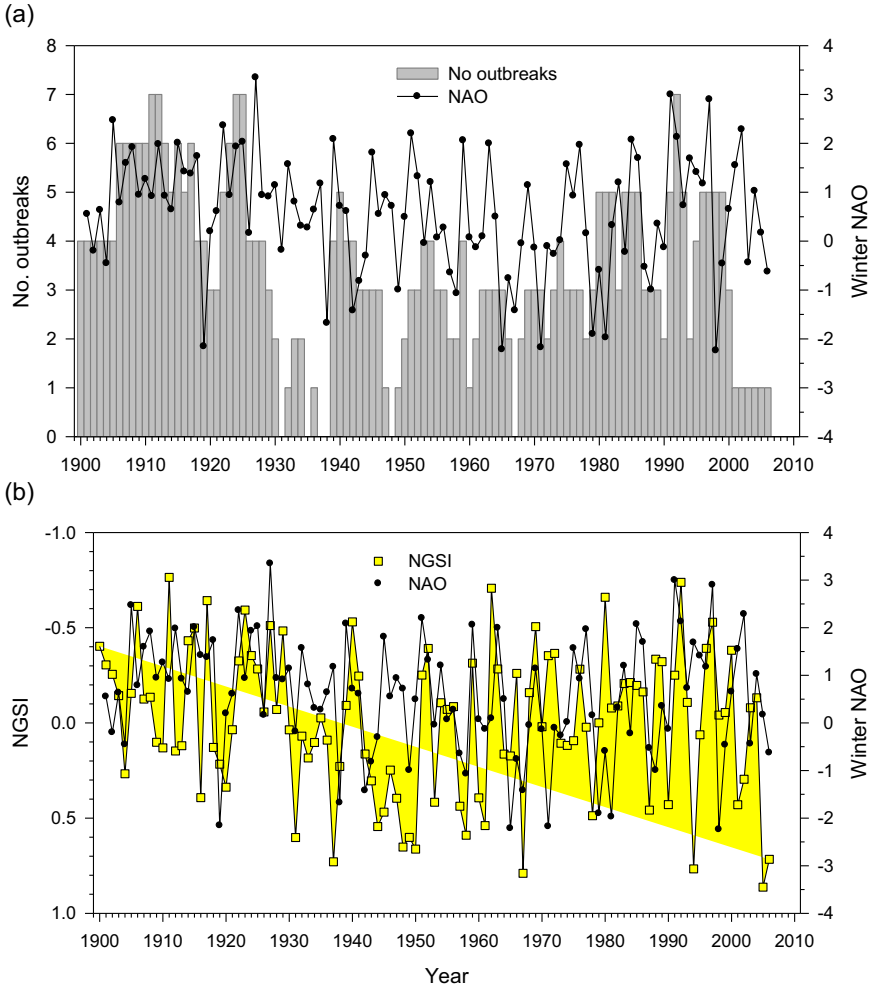


Fig. 4. Relationships between the winter NAO index and reconstructed PPM outbreaks in *P. nigra* stands. The plots show (a) the number of stands recording outbreaks and (b) the mean normalized growth suppression index (NGSI). Note the inverse scale of the NGSI.

spring to autumn soil moisture deficit. This pattern also reflects the disparate nature of the two considered stressors because droughts have a more regional context whereas PPM outbreaks have a local behaviour as its effect is density dependent. Extreme droughts such as those which occurred in 1994–1995 or 2005 created marked growth reductions over large areas and affecting different tree species in the region (Gazol et al., 2020). In contrast, as shown by Gazol et al. (2019), there is a clear spatio-temporal signature in the PPM defoliations because moths move from one stand to neighbouring stands and so defoliation years can vary accordingly.

A limitation of our field defoliation data is that they were taken at stand level; however, data on growth and defoliation at individual level should be more suitable to investigate drought–PPM defoliation interactions. The use of standardized and detrended series or ring-width indices is common in dendroentomological studies which allows maximizing defoliation and climatic signals (e.g., Speer et al., 2001; Paritsis et al., 2009; Lynch, 2012). Alternatively, mixed models could be applied to basal area increment data which provide more realistic measures of growth change (e.g., Linares et al., 2014). However, using basal area increment also requires other assumptions which may not be met such trees with circular stems, cores reaching the pith, and mature trees showing a stable growth phase. Therefore, we are confident on the robustness of ring-width indices to detect growth losses due to PPM defoliations. We also assumed that stand structure did not greatly vary since the 1970s, when field defoliation records starts, and data from the Spanish National Forest Inventory confirm this, although basal area and tree density have increased since the 1980s in most Spanish forests (Gazol et al., 2021). Therefore, it seems not probable that a change in stand structure could explain the lack of increased frequency of PPM defoliations.

The tree-ring signatures associated to drought differed from those related to PPM defoliations, characterized by the production of two very narrow rings. This concurs with the ecological memory analyses showing a longer memory of defoliation than drought. This is in agreement with previous results showing that legacies of drought in the growth of Mediterranean conifers from dry regions were intense but short (Gazol et al., 2020, 2021). That is, the studied species are able to recover to their previous growth as long as the drought conditions ameliorated rapidly. However, they might need more time to recover after severe PPM outbreaks probably because the insect caused a stronger reduction of leaf area than water deficit. Since PPM moths feed on old needles during winter, severe defoliation forces the formation of new needles from stored carbon reserves, and this may allow defoliated trees to rapidly recover their non-structural carbohydrate pools to levels similar to those measured before PPM defoliation (Palacio et al., 2012). Indeed, experiments based on induced PPM defoliation only reduced non-structural carbohydrate concentrations in roots (Hernández et al., 2005; Jacquet et al., 2014). A reduction in root carbon reserves could negatively impact ectomycorrhizal fungi and nutrient uptake, thus slowing down post-defoliation growth recovery (Castaño et al., 2020). Lastly, the stronger impact of drought on wood formation is also supported by tree-ring studies near the *P. sylvestris* xeric, southernmost limit, where growth was less impacted by PPM defoliation than by drought (Linares et al., 2014).

Despite PPM outbreaks having weaker impacts on radial growth of Iberian pine species than drought, defoliation legacies lasted longer than drought legacies in the affected Mediterranean pine forests. The longest growth legacies of PPM defoliations could affect *P. nigra* vulnerability to drought if both stressors occur consecutively and produce cumulative effects since post-drought growth recovery usually takes 1–2 years (Anderegg et al., 2015). Severe defoliations followed by severe drought could jeopardize some *P. nigra* stands, particularly in the case of plantations with low productivity and a limited growth resilience capacity (Castaño et al., 2020). If climate keeps warming and severe droughts become more frequent, further opportunities would arise to study interactions between PPM defoliations and drought at the individual level. In boreal forests, a strong ecological memory in tree growth related to past insect defoliation was found suggesting the accumulation of defoliation stress on growth over time, but drought and defoliation did not interact (Itter et al., 2019a). In contrast, drought and insect outbreaks contributed to forest decline in trembling aspen (*Populus tremuloides* Michx.) forests from western Canada, but their impacts differed and showed contrasting spatiotemporal variability (Chen et al., 2018; Navarro et al., 2018). We did not explicitly account for interactions between PPM defoliation and drought, but few outbreaks occurred during the severe 1994–1995 and 2005 droughts. Nevertheless, this does not discard that drought and defoliation could act synergistically on tree growth, particularly in the most palatable species, leading to different signatures in ecological memory functions. For instance, a synergistic impact of both stressors could lead to more persistent and longer growth reductions, and even contribute to growth decline. The impacts of drought–defoliation interactions on growth should be tested using long-term records of defoliation and drought, preferably taken at the individual level and considering tree species with different susceptibility to PPM defoliations (e.g., pines vs. junipers), under controlled conditions such as those provided by plantations and induced PPM defoliations (e.g., Castaño et al., 2020). Severe soil moisture deficit reduces forest productivity or alters leaf nutrient composition, thus reducing the quantity and quality of available food. In contrast, insect defoliators succeed better during warm-wet periods in boreal and temperate forests, which may be linked to a reduction in the concentration of defensive chemicals such as tannins in needles (Pureswaran et al., 2018). Recent warmer and drier conditions have enhanced the expansion of bark beetle outbreaks to higher latitudes and elevations than in the past, but similar trends are not clear for Lepidoptera (e.g., Weed et al., 2013) as we show in this study.

Severe PPM defoliations can also reduce leaf biomass and trigger the post-outbreak collapse of PPM populations, explaining the pseudo-cyclic behaviour of outbreaks (Battisti, 1988). In addition, PPM population dynamics are also controlled by predators and larval parasitoids which could also depend on climate variability and influence the temporal patterns of PPM outbreaks (Battisti et al., 2015; Hódar et al., 2021). Lastly, the local climatic drivers of PPM population dynamics may change as a function of density-dependent factors (Toïgo et al., 2017), which can explain why large-scale climatic and atmospheric patterns, such as those reflected by the NAO index, are associated to long-term PPM dynamics.

5. Conclusions

Reconstructed PPM outbreaks in eastern Spain and along an elevational gradient (1070–1675 m) did not reveal an increase in frequency nor in severity since the early 20th century. Consequently, our results do not support the hypothesis that PPM outbreaks are shifting upwards as climate warms. Our reconstructions could be further improved given drought signals may still be confounded with PPM signatures. However, our results showed that drought impacts were more synchronized along the altitudinal gradient and among tree species than PPM outbreaks were; the latter tended to be less synchronized, to occur locally and mainly affected *P. nigra* stands. Furthermore, the impact of PPM outbreaks on growth was weaker, but presented a longer memory than that of drought. The comparison between host and non-host tree-ring series remains suitable to reconstruct PPM outbreaks, and especially, when observational defoliation data can be used for validation. Additional tree-ring signatures of PPM outbreaks should be investigated including wood anatomy, wood stable isotope ratios, and chemical analyses. Further combining long-term field monitoring and tree-ring reconstructions will improve our ability to track changes in PPM outbreaks in particular and defoliating insect dynamics in general.

CRediT authorship contribution statement

J. Julio Camarero and Antonio Gazol: Conceptualization, Methodology, Software. J. Julio Camarero, Jacques Tardif and France Conciatori: Data curation, Writing - Original draft preparation. J. Julio Camarero and Antonio Gazol: Visualization, Investigation. J. Julio Camarero and Jacques Tardif: Supervision. Antonio Gazol and France Conciatori: Software,

Validation. J. Julio Camarero, Jacques Tardif and Antonio Gazol: Writing - Reviewing and Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.153041.

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