



Summer heat waves could counterbalance the increasing incidence of pine processionary due to warmer winters in Mediterranean pine forests

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ABSTRACT

Global warming modulates the spatial and temporal occurrence of insect outbreaks, leading to as-yet-unknown effects on forests ecosystems. Warmer trends may favour the upward and northward expansion of pests, albeit increased exposure to heat events and droughts may also hamper insect growth and development. Thus far, further research is needed about the balance of climate warming on pine processionary moth (PPM) (*Thaumetopoea pityocampa*) development stages, especially at broader scales, despite being the main conifer-defoliating insect in the Mediterranean area. This research analyses the relationships of PPM with the climatic conditions during its most vulnerable development phases in Spain to provide base-information for forest managers. We hypothesize that warmer winter temperatures will increase PPM growth at their larval feeding stage, whereas summer-heat events will reduce PPM rates from egg and early larval stages, leading to counterbalanced effects of climate warming. Furthermore, we expect dry springs will allow an earlier development of PPM and higher incidence of outbreaks. To analyse climate effects on PPM populations in Andalusia, Castilla-La Mancha, and Navarre (37 to 42°N), we compiled information from the Regional Forest Services comprising up to 26 years of monitoring data from 2465 forest stands dominated by *Pinus nigra* and *Pinus sylvestris*. We fitted Cumulative Link Mixed Models (CLMM) to test the climate effects on four PPM defoliation severity levels. Our results support higher PPM larvae survival and incidence due to warmer winter conditions, but also the reduction of PPM population size under summer heat conditions. Particularly, the increasing incidence associated to warmer winters during the larval defoliating stage is counterbalanced by the decreasing population at earlier life stages during summer heat events. Spring drought also plays an important role on PPM incidence rates, but its effect is idiosyncratic to each region, suggesting an adaptation of PPM populations to regional conditions, claiming to tailor-made forest management endeavours. This study reveals that a better comprehension of abiotic effects along the whole PPM life cycle is paramount to understand the impact of climate warming on insect outbreaks which shorten wood production and carbon sequestration of Mediterranean forests.

1. Introduction

The frequency and virulence of insect outbreaks has increased due to climate warming (Azcárate et al., 2023; Hamann et al., 2021). The current warming trend has a direct effect on the development, survival, range of distribution and abundance of defoliators negatively influencing forest growth and vigour (Bale et al., 2002; Bale and Hayward, 2010; Ma et al., 2021). Warmer winters could promote a northward and

upward expansion of species limited by low-temperatures, such as winter-defoliators, expanding currently affected areas (Netherer and Schopf, 2010). However, the rise of temperature as well as the increase in frequency and intensity of climatic anomalies such as heat waves or droughts might interact with this trend in complex ways, promoting unknown responses in forest ecosystems, which may challenge forest management actions. Higher and more intense heat waves increase mortality and reduce growth rates or fecundity in multitude of pest

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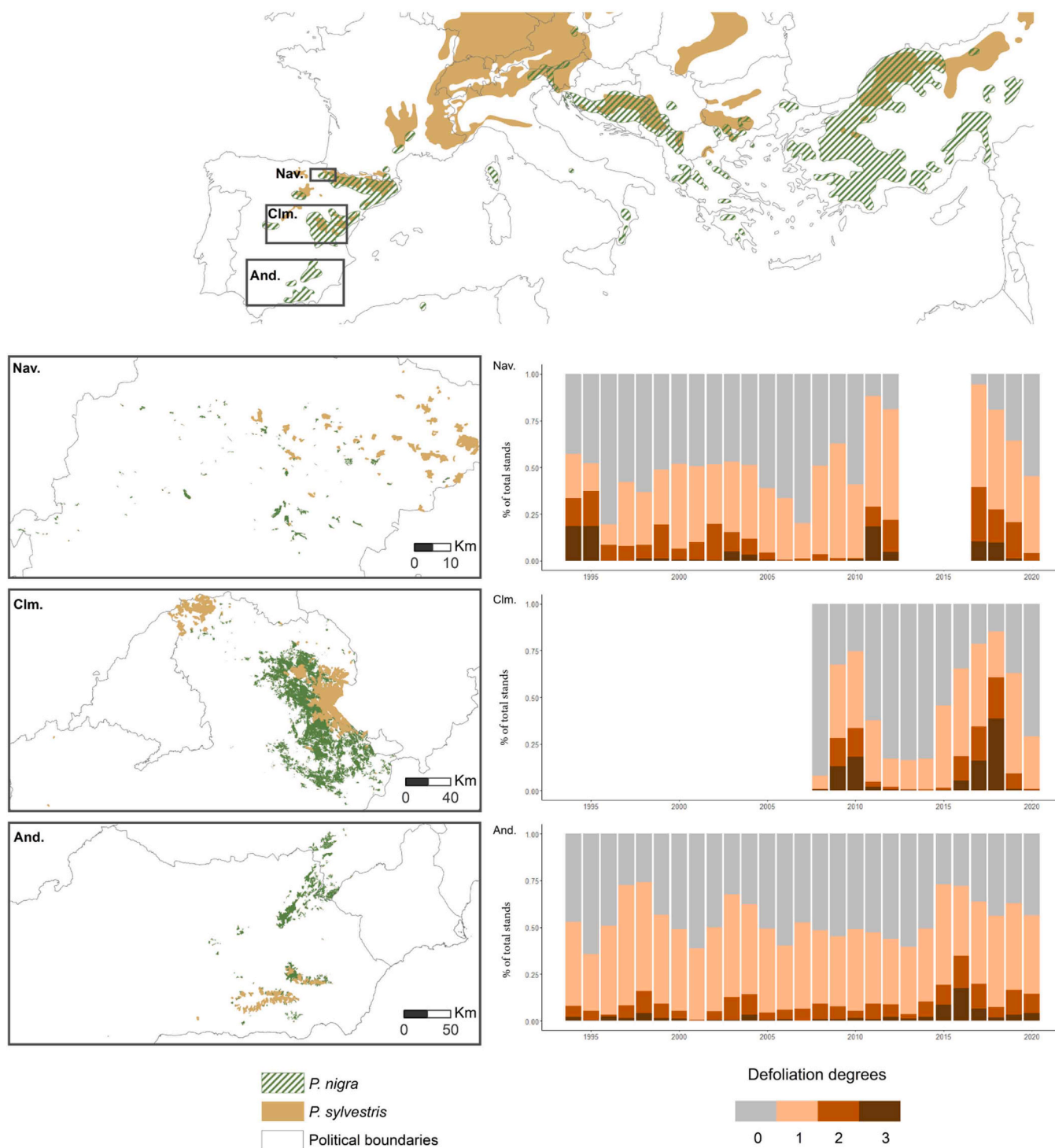


Fig. 1. Situation map (top panel). Sampled areas in Navarre (Nav.), Castilla-La Mancha (Clm.), and Andalusia (And.) for *P. nigra* and *P. sylvestris* stands (lower left); time series of the proportion of defoliation severity (DS, according to Sangüesa-Barreda et al., 2014 synthetic scale) in sampled areas (lower right).

species, especially at their southern distribution range (Rouault et al., 2006). Warming also amplifies drought stress in trees potentially altering the nutritional quality of plant tissues (Williams et al., 2012). Water stress reduces tree resistance mechanisms, albeit moderate drought might also improve the tree defence to fungal infections (Gely et al., 2020; Netherer and Schopf, 2010; Rouault et al., 2006). Thus, evaluating the complex effects of novel environmental conditions on pest outbreaks is paramount to forecast their future incidence and design effective forest management.

Higher temperatures generally increase pest metabolic rates and

population growth (Jamieson et al., 2012). For example, warmer winters have triggered the European pine sawfly to expand its range northwards in Fennoscandia (Veteli et al., 2005), and the 2003 summer heatwave led to mass outbreaks of the silver fir bark beetle in north-eastern France and Switzerland (Rouault et al., 2006). However, the relationships between temperature and pest performance are not always linear. Above a certain threshold, temperature may actually reduce pest incidence (Kingsolver, 2009). This reduction may be especially important for pest populations at their southern range (Tüzün and Stoks, 2018). Moreover, the effect of higher temperatures on trees might also

Table 1

Characterization of forest stands affected by the PPM in each region. Abbreviations: And. refers to Andalusia; Clm. stands for Castilla La Mancha; Nav. is Navarre; Pn. refers to *P. nigra*, Ps. refers to *P. sylvestris*.

	And.		Clm.		Nav.	
	Pn.	Ps.	Pn.	Ps.	Pn.	Ps.
N. Stands	578	216	1518	426	121	50
Sampled area (km ²)	1009	297	4075	1182	42	48
Altitude (m a.s.l.)	1541 (204.9)	1877 (205.1)	1187 (167.2)	1453 (131.3)	681 (140.1)	859 (167.2)
Recurrence of severe defoliations	2.3 (9.2)	2.3 (7.9)	8.1 (13.0)	7.1 (13.7)	4.0 (9.2)	4.0 (9.7)
Mean annual precipitation (mm)	775.3 (200.0)	821.7 (246.3)	719.7 (132.2)	802.8 (140.5)	1048.4 (169.8)	1207.1 (190.7)
Mean average temperature (°C)	12.9 (0.6)	11.9 (0.7)	12.3 (0.7)	10.8 (0.7)	11.8 (0.5)	11.2 (0.6)

Values in brackets refer to standard deviation. Recurrence of severe defoliation refer to the average of years with DD3 for the stands, divided by the total number of years within the analysed period.

alter their susceptibility to pests. For example, heatwaves and severe droughts reduce tree primary production and might turn tree foliage less nutritious for defoliators (Netherer and Schopf, 2010). Moderate temperature increases may boost plant productivity, while changes in climate modify pest phenology, leading to mismatches in the tree-defoliator interactions (Ren et al., 2020; Hamann et al., 2021).

The pine processionary moth (PPM, *Thaumetopoea pityocampa* Den. & Schiff) is the major defoliator of pines and cedars in the Mediterranean region (Roques, 2015), with pine species being the most affected ones. PPM life cycle starts when adult female moths lay PPM eggs on pine needles in summer, thereafter, emerging as larvae. PPM caterpillars feed in winter, and their performance and survival is strongly limited by temperature (Hoch et al., 2009; Hódar and Zamora, 2004). In early spring they form processions on the ground to pupate, eventually emerging as adult moths in the first summer, or remaining in diapause (Battisti, 1988). PPM outbreaks are expanding northward and upward in elevation due to milder winters (Battisti et al., 2005). However, higher temperatures may also reduce PPM rates at other life cycle stages (Robinet et al., 2013; Tamburini et al., 2013). PPM eggs and larvae suffer lethal temperatures at 36–40 °C (Bourougaaoui et al., 2021a; Rocha et al., 2020; Rocha et al., 2017; Santos et al., 2011). Therefore, the expected higher frequency and severity of heat events in the Mediterranean region (Seneviratne et al., 2021) might reduce PPM density (Bourougaaoui et al., 2021b; Robinet et al., 2013; Bouhot-Delduc, 2005). In addition, climate projections also anticipate an increase of drought severity (Vicente-Serrano et al., 2022) contributing to a reduction of tree growth and an increase in tree mortality in southern Europe (Gazol et al., 2018). Water-stressed pines have tougher needles increasing lignin content in detriment of starch, leading to lower nutritional properties which could affect detrimentally on PPM population size, especially during the hatching of PPM eggs and larval stages (Hódar et al., 2003; Rocha et al., 2020). Though, drier conditions during spring, eventually linked to higher temperatures, have been attributed to an earlier emergence of the moths (Hódar et al., 2016) given their high sensitiveness to rainfall (Tamburini et al., 2013) or indirect effects of larval-pupal parasitoids (Battisti et al., 2000). In this sense, little is known about the combined effect of increasing summer temperatures and reduced water availability on PPM incidence in pine forests. To our knowledge, the balance between the positive and negative effects of global warming on PPM, beyond the relatively well-known positive effect of warmer winters, is not completely known and requires further attention. Understanding the effect of climate warming on PPM populations requires considering its impact along the whole life cycle. Without this essential information, we are unable to accurately predict its future impact in forest ecosystems.

In this study, we leverage multi-decadal records of PPM defoliations, a robust proxy of late winter PPM abundance, from Spanish forest health monitoring programs to analyse how climatic conditions influence PPM performance along a wide latitudinal gradient (ca. from 37° to 42°N). The main objective of this work is to evaluate the effect of climate on PPM considering climate factors occurring along the insect life cycle from egg to larva under the current warming trend. Specifically, we

hypothesize that (i) summer heat events reduce PPM incidence by negatively affecting larvae development, (ii) an earlier development of PPM after a dry spring will provide favourable conditions for PPM population survival and growth in winter, and (iii) summer heat events might counterbalance the favourable effect of warmer winters on PPM populations. To test these hypotheses, we focus on two pine species, *Pinus nigra* and *Pinus sylvestris*, both reaching their southernmost, and therefore warmest distribution limit, in Spain.

2. Material and methods

2.1. Sample description and pine processionary moth defoliation severity

We prepared a data set of 2465 black pine (*Pinus nigra*) and Scots pine (*Pinus sylvestris*) forest stands along a wide latitudinal gradient from 37° up to 42°N in Spain (Fig. 1). Data belong to monitoring programs of three Autonomous Regions of Spain: Navarre, Castilla-La Mancha and Andalusia, covering 6653 km². Black pine and Scots pine reach their southwestern and southernmost distribution limit, respectively, in the study area, with only small isolated *P. nigra* populations further south in Morocco and Algeria (Herrero et al., 2013; Linares et al., 2014). Water stress during summer is the major climate constraint for both species in this area (Sánchez-Salguero et al., 2017, 2015; Sangüesa-Barreda et al., 2019).

The latitudinal gradient comprises a wide climatic variability, from humid and oceanic conditions in the north of Navarre to Mediterranean conditions towards the southern regions of Castilla-La Mancha and Andalusia. Moreover, both pine species occupy a large altitudinal range, black pine from 390 to 2030 m a.s.l. and Scots pine from 610 to 2370 m a.s.l. (Table 1). Both pine species can grow on a range of soil types, albeit black pine shows a strong preference for alkaline soils.

PPM defoliations were annually monitored in 2465 forest stands at the end of wintertime by three Spanish regional administrations, as part of their forest health monitoring programs (Table 1). Data from Navarre Forest Health service were collected from 1994 to 2020, albeit years 2013 to 2016 were not sampled. Castilla-La Mancha Forest Health service collected data from 2008 to 2020, and Junta de Andalusia Health services recorded PPM defoliations from 1994 to 2020 (Ros-Candeira et al., 2019). Forest health services, by means of forest rangers, carried out systematic field surveys over forest stands of variable size. The study is based on stands where black or Scots pine are dominant accounting for more than 50% of coverage. PPM damage at each forest unit was recorded at the stand level based on a six-level visual scale, from 0 to 5, according to Montoya and Hernández (1998). This scale is the standard for recording PPM defoliations, and it has been tested as a robust proxy of PPM population size at the end of the life cycle of that generation and the next generation (Cayuela et al., 2014). The ordinal scale allows analysing summer and winter effects simultaneously capturing PPM population sizes modulation at different stages of the life cycle. We grouped this PPM damage scale into four levels of stand defoliation severity (hereafter abbreviated as DS) following Sangüesa-Barreda et al. (2014) and in line with forest management treatment endeavours. The

Table 2

Best fitted cumulative linked mixed models selected to explain the effect of temperatures and spring drought in pine processionary moth defoliation at three study regions: Navarre, Castilla-La Mancha and Andalusia. The fixed effects intercept values indicate the strength effect on defoliation severity. Abbreviations: And. refers to Andalusia; Clm. stands for Castilla-La Mancha; Nav. is Navarre; Pn. refers to *P. nigra*; Ps. refers to *P. sylvestris*; Tmax. is summer maximum weekly temperature; Tmin. refers to winter mean minimum temperature; SPEI⁻¹ and SPEI⁻² are spring Standardised Precipitation-Evapotranspiration Index with one or two-year lag, respectively; DS⁻¹ and (DS⁻¹)² are previous year DS and previous year squared DS, respectively.

Model	Fixed effects						Random effects	Pseudo R ²
	Tmax.	Tmin.	SPEI ⁻¹	SPEI ⁻²	DS ⁻¹	(DS ⁻¹) ²		
Nav.	-0.37	0.23	0.31	0.15	1.48	-0.18	Forest stand	0.22
Nav. Pn.	-0.35	0.16	0.30	0.11	1.37	-0.16		0.22
Nav. Ps.	-0.45	0.29	0.36	0.26	1.65	-0.19		0.23
Clm.	-0.16	0.15	-0.55	-0.19	1.41	-0.19		0.23
Clm. Pn.	-0.22	0.11	-0.57	-0.23	1.33	-0.19		0.25
Clm. Ps.	-0.09	0.11	-0.44	-0.07	1.67	-0.24		0.17
And.	-0.12	0.14	-0.09	-0.18	1.28	-0.21		0.12
And. Pn.	-0.10	0.10	-0.10	-0.22	1.25	-0.18		0.11
And. Ps.	-0.17	0.23	-0.07	-0.10	1.38	-0.27		0.11

stands without PPM for a given year were classified as DS0. Montoya and Hernández classes 1 and 2, which represent stands with some PPM nests but scant defoliation, were defined as DS1. Areas with partial to moderate defoliation (Montoya and Hernández class 3), which mostly affects stand edges and isolated trees, were defined as DS2. Finally, severe defoliation affecting the whole stand (Montoya and Hernández classes 4 and 5) were defined as DS3.

2.2. Climate data

We gathered local climatic series for each forest stand from a weekly 1.1 km spatial resolution gridded dataset (Vicente-Serrano et al., 2017). The gridded dataset was created using 2269 series of precipitation and 1304 of temperature from the National Spanish Meteorological Services (AEMET) archives for the 1961–2014 period. We retrieved mean, maximum and minimum weekly temperature for the period 1993–2020. We computed the mean of the maximum temperatures and the week with the highest maximum temperatures to characterize summer season (June to September). Likewise, we computed the mean of the minimum temperatures, and the week with the lowest minimum temperatures to characterize the coldest months of winter season (January to February). Additionally, we computed frost frequency, defined as the percentage of weeks with minimum temperatures below 0 °C in winter season (January to February) to account for chill injury due to cumulative negative temperatures (Hoch et al., 2009). We also estimated drought severity using the greatest temporal resolution (weekly values) of Standardised Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010). Negative and positive SPEI values correspond to dry and wet periods, respectively. The SPEI was computed at a temporal scale of 3 months to roughly characterize spring season (March to May) aiming to assess drought effects in forest stands based on our hypothesis that drier springs benefit earlier development of larvae, providing better conditions for PPM survival in the following winter.

2.3. Analysis of drought and temperature impacts on PPM defoliation levels

We tested the relationship between climate covariates and PPM population size based on ordered categorical data. We modelled DS classes using cumulative link models (Agresti, 2002) that are specifically developed to deal with categorical ordinal data. Cumulative linked mixed models (CLMM) constitute a variant of cumulative link models that enable the analysis of categorical ordinal response variables and integrate random effects (Christensen, 2023). CLMMs were applied to test whether the PPM DS, a proxy of PPM population size at the end of the life cycle, was influenced by climate conditions. The proposed models included climate metrics that characterize winter and summer temperature conditions (see “Climate data”) and spring drought

severity, by means of SPEI index, of previous and current year that were treated as fixed effects to account for the PPM stages along the life cycle. Climatic variables were normalized to enable comparison of intercept values within a model. The intercept values of the variables included in the models indicate the strength effect on defoliation severity. The previous year DS and the squared DS from previous year were included as fixed effects to account for the temporal autocorrelation in the models, considering that DS tends to increase over time until reaching a maximum after which the population collapses and the DS decrease (Li et al., 2015). Forest stands were treated as random factors affecting the intercept parameter in the model to account for the temporal autocorrelation.

CLMMs models were fitted separately for the three study regions (Navarre, Castilla-La Mancha, and Andalusia). For each region, we built individual models for each pine species, and an aggregated model for both species, summing up a total of 3 models per region with six fixed effects. The existence of multicollinearity among fixed effects (temperatures, drought indices and DSs from previous years) was tested using the Variance Inflation Factor (VIF). The selection of statistically significant fixed effects was carried out by comparing the possible candidate models for each of the nine combinations of region and species (see Appendix Table 1) to a null model that included only an intercept random parameter. Best model was selected using Akaike’s Information Criterion corrected for small samples (AICc), which assumes that two models are different when $\Delta AICc$ is greater than 2 units. For cases with $\Delta AICc$ lower than 2 units, the model with a minimum number of fixed effects was selected. The number of quadrature points (nAGQ) was set to 10 to provide better maximum likelihood estimations. We computed the theoretical pseudo-R² as a measure of goodness of fit to quantify the explained pseudo variance. Statistical analyses were conducted with *ordinal* (Haubo et al., 2022), *MuMin* (CRAN - Package MuMin, 2022) and *performance* (Lüdtke, 2022) packages in R environment.

CLMMs are effective to analyse ordinal data, though are limited to create predictions with the original DS datasets when including several covariates or random factors. In this sense, we used the original dataset to analyse the influence of minimum winter and maximum summer temperatures on PPM DS to evaluate the effect of lethal thresholds reported in the literature (Huchon and Demolin, 1970; Robinet et al., 2014; Santos et al., 2011). As the percentages of stands in different DS categories were not normally distributed, a pairwise Wilcoxon test was used to determine whether statistically significant differences exist between the percentage of stands above or below a specific temperature for each DS (i.e. % stands with DS3 > 34 °C versus % stands with DS3 < 34 °C, and % stands with DS3 > -4 °C versus % stands with DS3 < -4 °C). The Wilcoxon test was computed using the stats package in R environment with a confidence level of significance of 95% (p < 0.05). We carried out the test using data from 26 years of monitoring for two temperature values (34 °C and -4 °C), four DS levels (DS0, DS1, DS2, DS3)

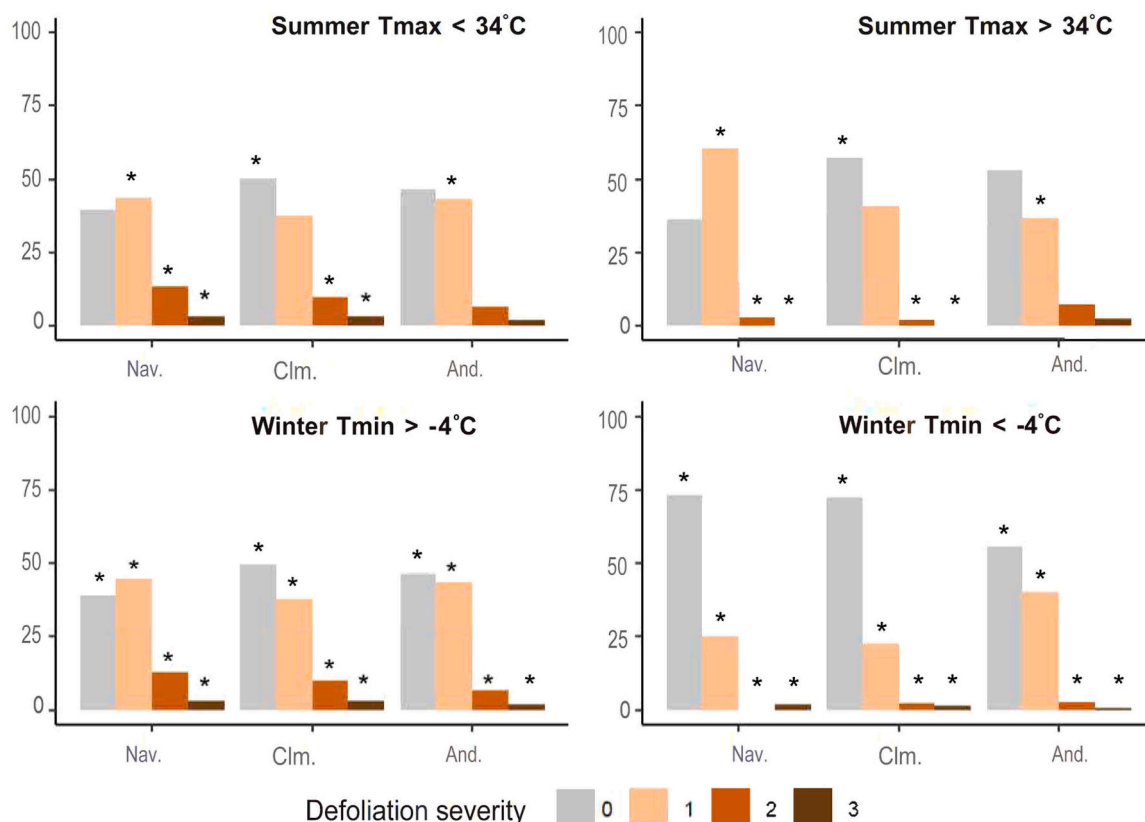


Fig. 2. Average percentage of forest stands for each defoliation severity under selected maximum (34°C) and minimum (−4°C) weekly temperatures. These example values were selected based on the distribution of temperatures within the analyzed stands and previous literature. Asterisks indicate that statistically significant differences exist ($P < 0.05$), based on Willcoxon tests, between summer Tmax < 34 °C vs summer Tmax > 34 °C, or between winter Tmin > −4 °C vs winter Tmin < −4 °C.

and three regions (Navarre, Castilla-La Mancha and Andalusia).

3. Results

The best CLMMs models in all nine combinations of region and species had the same structure of fixed factors, which were in all cases statistically significant (Table 2, see also Table 1-3 in Appendix for further information), suggesting the existence of similar environmental constraints on PPM behavior across regions and pine species. The variance explained by the models accounted for 22% in Navarre, 23% in Castilla-La Mancha, and 12% in Andalusia.

Best models included a positive effect of the previous year DS and a negative effect of the previous year quadratic DS, in agreement with the hypothesized PPM cyclic dynamics. Best models also supported the existence of a negative effect of extreme heat conditions during previous summer on DS, as well as a positive effect of minimum winter temperatures. However, the effect of spring drought severity differed across regions. In the northern and wetter region (Navarre) spring drought had a positive effect, indicating that drier springs increase PPM density with a one- or two-year lag, whereas at the southern localities the effect is reversed, drier springs reduce PPM infestation rates.

The normalized metrics enabled within model comparisons among environmental variables, revealing that the effect of winter minimum temperature and summer maximum temperature had similar magnitude in Andalusia and in Scots pine of Castilla-La Mancha, but not in Navarre nor in black pine stands of Castilla-La Mancha, where the negative effect of summer maximal temperature was much larger (Table 2). Interestingly, the magnitude of spring SPEI on PPM population size was of similar magnitude as summer maximum temperature in Navarre and Andalusia, but much larger in Castilla-La Mancha, especially in Scots pine stands.

The increase of cumulative exposure to weekly maximum summer temperatures reduced the proportion of defoliated forest stands with DS2 or DS3 levels. Summer maximum temperatures above 34 °C significantly lowered the incidence of PPM for DS2 or DS3 levels in Navarre and Castilla-La Mancha, albeit in Andalusia only DS1 showed significant differences (Fig. 2). The cumulative exposure to weekly negative temperatures during winter limited PPM development, reducing the percentage of forest stands with presence of PPM. As shown in Fig. 2, minimum winter temperatures with values below −4 °C significantly lowered the incidence of PPM for the three regions and DS levels.

4. Discussion

PPM incidence in pine forests show alignment with a common set of biotic and climatic constraints along a latitudinal gradient (37 to 42). Higher minimum winter temperatures increase PPM growth and survival during the feeding period. However, this positive effect is counterbalanced by the effect of summer maximum temperatures, which reduce PPM population size during egg hatching and early larval stages. Across all combinations of models for three regions and two pine host species, we observed a consistent PPM behavior along the latitudinal gradient. Notably, the effect of spring precipitation varied depending on regional conditions. Spring precipitation increased PPM population rates in the northern and wetter region, but reduced them in the southern regions. Furthermore, we found that the PPM population size in the previous year influenced the severity of defoliation in the following year, exhibiting a quadratic relationship indicative of density-dependent effects. These findings provide essential insights to inform the development of regional forest management guidelines for controlling PPM pest in the context of climate change trends. Particularly, our

results support the forecasting of PPM future incidence, which constitutes a base indicator to design effective forest management actions. Current PPM management actions in Spain, which mainly focus on creation of open spaces in parkland areas, may benefit from the occurrence of particular climate conditions to support the timing to perform a management action. PPM reduction strategies such as promoting diversity in forest structure and species (i.e.: non-host tree species) (Azcárate et al., 2023) may be promoted, specially in those more climatically vulnerable areas.

The response of PPM to environmental conditions is intrinsically linked to the size of the PPM population itself. The positive effect of the previous year DS and the negative impact of its quadratic term, suggest a positive influence at lower infestation levels and a demographic collapse when high DS levels are attained (Li et al., 2015). Thus, forest management actions should be promoted under intermediate DS levels, while endeavours at high severity levels may be less effective due to intrinsic PPM dynamics (Cayuela et al., 2011). The periodicity observed in PPM dynamics indicates a cyclic behaviour at stand level, which in the absence of forest treatments, relies not only on climatic factors but also on biological variables such as predators-parasitoids and host plant availability (Battisti, 1988; Hódar and Zamora, 2009). Our findings regarding the PPM periodicity behaviour are primarily based on the direction of model intercepts, without accounting for potential non-linear relationships. Consequently, these findings should be regarded as preliminary and not definitive. The existence of PPM cycles has received broad support in previous research (Hódar et al., 2012; Li et al., 2015). Disagreements in the literature tend to focus on the specific dynamics and forces that explain PPM development patterns (Gazol et al., 2019), rather than questioning the existence of a cyclic behaviour itself. Therefore, it is clear that the combined effects of both biotic and abiotic factors on PPM populations can lead to complex interactions that might obscure PPM cycles at certain spatial or temporal resolutions.

Warm winters may pose a threat to pine forests as they foster an increase in PPM population rates, potentially leading to extensive outbreaks. During cold winter spells, PPM populations can experience dramatic reduction due to lethal temperature thresholds ranging from -12 to -16 °C (Huchon and Demolin, 1970) causing a crash in their numbers (Battisti et al., 2005; Buffo et al., 2007; Camarero et al., 2022; Gazol et al., 2019). However, the impact on PPM incidence is not only attributable to lethal temperatures; extended exposure to suboptimal temperatures also diminishes larval survival (Hoch et al., 2009; Roques, 2015). Interestingly, larval feeding activity is influenced by minimum temperatures, with warm winters leading to higher PPM population growth rates (Buffo et al., 2007). In line with this, our findings corroborate that the exposure to negative temperatures during winter reduces the percentage of forest stands with DS2 or DS3 levels (Fig. 2). It is worth noting that while some positive impacts of low winter temperatures on PPM, such as parasitoid reduction, have been reported (Hódar et al., 2016), these positive effects are outweighed by the negative ones. Our results confirm the assessment that winter temperatures are the primary limiting factor for the upward expansion of PPM (Battisti et al., 2005).

Pine forests exhibit reduced vulnerability to PPM infestation during years with warmer summers. Previous studies have documented a decline in PPM populations following the 2003 heatwave in France (Robinet et al., 2013; Bouhot-Delduc, 2005). Additionally, Bourougaaoui et al. (2021b) demonstrated PPM retreat from southern Tunisia, driven by local warming trends contributing to elevated PPM mortality rates. Notably, this study represents the first investigation into the contrasting effects of summer temperatures, reducing PPM population size, in contrast to the positive incidence of PPM due to warm winters. Albeit the precise biological mechanisms underlying this phenomenon remain not entirely elucidated (Netherer and Schopf, 2010), the primary hypothesis suggests a decrease of egg hatching rates and/or heightened larval mortality due to thermal stress as previously found in Portugal (Santos et al., 2011; Rocha et al., 2020) and Tunisia (Bourougaaoui et al., 2021a). Furthermore, Rocha et al., 2017 analyzed three

populations with different phenologies: a Portuguese population with a classical life cycle (egg laid in summer), an allochronic Portuguese population reproducing in spring, and a Tunisian population (egg laid in fall) showing, in all cases, that heat waves had a severe negative effect on egg survival. This reduction in PPM population size prior to winter diminishes the capacity of PPM groups to construct larger nests, thereby reducing thermal insulation and increasing vulnerability to natural predators. Experimental research has estimated the lethal temperature for PPM eggs to be within the range of 36 – 42 °C air temperature (Robinet et al., 2014; H. Santos et al., 2011; Rocha et al., 2017), although some authors have proposed slightly lower temperature thresholds (32 °C) (Huchon and Demolin, 1970). Particularly noteworthy is the observation that the most northern region, Navarre, experienced the most significant impact from high summer temperatures, resulting in a reduction in PPM rates. This may suggest that, despite PPMs ability to adapt to local climatic conditions (Huchon and Demolin, 1970), it might not be well-suited to warmer conditions in this region. According to climate change models, the current distribution range of PPM encompasses a vast territory where these maximum summer temperature thresholds could be easily surpassed (IPCC, 2022). In this sense, the expected increase of summer temperature in Mediterranean environments would trigger a stronger climate control for PPM populations.

Spring moisture conditions had a strong influence on PPM populations, and this effect extends to the two years preceding the current observation. In contrast to the temperature effects observed earlier, the impact of spring hydric conditions displays regional variation. In the arid central region (Castilla-La Mancha) and southern region (Andalusia) forests, dry springs promote an increase in PPM population growth. A similar effect was previously documented in Southern Spain (Hódar et al., 2016), based on egg hatching with pheromone traps by surveillance of 30 egg masses, attributed to an earlier larval emergence that allows for more advanced development before winter, ultimately enhancing survival rates. This hypothesis aligns with the sensitivity of PPM egg masses and instar larvae to rainfall levels (Tamburini et al., 2013). Conversely, in the northern Spanish forests (Navarre), rainy springs foster PPM development. This effect may be indirect, as increased precipitation has been shown to benefit PPM by reducing predation by natural enemies, including birds like the hoopoe, a phenomenon observed in *Pinus nigra* stands of Northern Italy (Battisti et al., 2000). Notably, climatic conditions in Navarre resemble those in Northern Italy, in contrast to the drier climates of Castilla-La Mancha and Andalusia. Interestingly, all models for the three regions incorporate the climatic signal from previous one-year and two-year spring droughts. This aligns with the concept of a two-year delay effect of climate on PPM population size proposed by Hódar et al. (2012). PPM development is influenced not only by climatic conditions in the previous year but also by conditions two to three years prior, enabling the possibility of advanced prediction of PPM outbreaks. The regional variations in response to hydric conditions may also apply to other pest defoliators, emphasizing the importance of considering regional conditions when predicting the dynamics of pests and managing forests ecosystems to minimize insect infestations.

Our results show a consistent PPM behavior independently of the pine host species. Though, our data also show that colder winters have, in Navarre and Andalusia, slightly higher incidence on *P. sylvestris* than in *P. nigra* according to model intercept values. One reasonable explanation is that *P. sylvestris* generally occupies higher altitudes (Azcárate et al., 2023) with the subsequent increase of exposure to lethal temperatures or prolonged negative temperatures. The negative effect of warmer summers is consistent for both species. *P. nigra* is particularly sensitive to PPM infestation (Hódar et al., 2012), which may determine the slight differences when comparing the effects of summer temperatures with respect to *P. sylvestris*. In this sense, altitude and continentality are factors that may interact to provide specific regional outcomes.

In this research, we used PPM defoliation data at the end of winter,

which serves as a robust proxy of the population size resulted of that generation and the next generation (Cayuela et al., 2014). We acknowledge the absence of population data at various stages of PPM life cycle (e.g. egg hatching rates, larval survival or caterpillars in autumn and late winter). Obtaining such data over extensive time periods and across vast territories (hundreds or thousands of kilometres) is exceedingly challenging and probably unfeasible. The insect population at various phases is interconnected; when there is a reduced number of insects at the outset of the PPM cycle, we can anticipate lower levels of defoliation. However, sometimes there are mismatches between the beginning and the end of the cycle by the climate impact (Cayuela et al., 2014). Our approach, which utilizes long time series data and accounts for the influence of the previous year's population size, enables us to discern these climate impacts that undoubtedly affect the ultimate population size. Finally, and most importantly, our findings and hypothesis are mechanistically supported by previous studies.

Climate projections indicate an increase in temperatures and the likelihood of climatic anomalies over the coming decades (Seneviratne et al., 2021). It is important to note that while warmer winter temperatures may favour PPM growth at the mature larval stage, the potential negative impacts of summer heatwaves on egg and larvae development cannot be overlooked. These contrasting effects are crucial findings with direct implications for forest management. Moreover, the influence of increasing spring droughts may vary across the distribution range of PPM. Future research should also delve into the repercussions of heat events and summer droughts on tree productivity. These factors can indirectly affect PPM populations by altering food quality and availability. We are still far from fully comprehending the future impact of PPM, and pest monitoring programs will play a relevant role in the coming decades, particularly in sensitive areas at the northern and southern PPM distribution limits. Therefore, gaining a more comprehensive understanding of the abiotic effects throughout the entire PPM life cycle is imperative. Such knowledge is essential for accurately predicting the vulnerability of pine forests to PPM development under emerging climate change scenarios.

5. Conclusions

To gain a comprehensive understanding of the impact of climate on PPM populations in pine forests, it is crucial to consider climate effects at multiple stages of the PPM life cycle. Our findings underscore the significance of this holistic approach in predicting PPM incidence and offer valuable insights for informed forest management decisions. The results support the primary hypotheses that PPM populations are influenced by both winter and summer temperatures, resulting in counterbalanced effects. These insights are instrumental for guiding forest management strategies. Warmer winter temperatures are expected to favour the expansion of PPM populations in their northern range (Battisti et al., 2005 and 2006). However, in a future scenario characterized by more frequent and intense heat events, the survival of PPM larvae may be jeopardized more frequently, particularly in the southern range. Moreover, spring moisture conditions also contribute to our understanding of PPM development, albeit with unique regional responses, highlighting the need for tailored forest management approaches. In drier regions, PPM populations benefit from dry springs, potentially due to a direct effect that accelerates hatching and adult emergence. Conversely, in regions with wetter climates, the effect of spring precipitation reverses, possibly owing to an indirect impact by the limitation of PPM natural enemies. Overall, our results suggest a potential shift in PPM distribution toward colder areas, although the regional differences indicate the PPMs remarkable adaptability to specific climatic conditions, emphasizing its ability to respond to changing environmental conditions.

CRedit authorship contribution statement

Sangüesa-Barreda Gabriel: Conceptualization, Investigation,

Methodology, Resources, Writing – review & editing. **Domingo Dario:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Vicente-Serrano Sergio M.:** Data curation, Methodology, Resources, Writing – review & editing. **Gómez Cristina:** Data curation, Methodology, Resources, Writing – review & editing. **Ollano José Miguel:** Methodology, Resources, Writing – review & editing.

Declaration of Competing Interest

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Data availability

The climatic datasets analysed during the current study are available at <https://doi.org/10.3390/data2030022>. The pine processionary moth database from Castilla-La Mancha is publically available at <https://www.castillalamancha.es/gobierno/desarrollosostenible/estructura/dgapfyen/actuaciones/plan-de-lucha-integrada-contra-la-procesionaria-del-pino-en-castilla-la-mancha>.

The pine processionary moth databases from Navarre and Andalucía are available from Navarre and Junta de Andalucía forest health services but restrictions apply to the availability of these data, which were used under licence for the current study, and so are not publicly available. Data are however available from the authors upon reasonable request and with permission of Navarre and Junta de Andalucía forest health services.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2024.121695](https://doi.org/10.1016/j.foreco.2024.121695).

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