

Ecological characteristics of pine processionary moth *Thaumetopoea pityocampa* (Lepidoptera: Notodontidae) larval nests in pine and cedar forests of Algeria

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Abstract. Bouzar-Essaidi K, Rahim N, Meftah B, Benfekih L. 2023. Ecological characteristics of pine processionary moth *Thaumetopoea pityocampa* (Lepidoptera: Notodontidae) larval nests in pine and cedar forests of Algeria. *Biodiversitas* 24: 2107-2113. The pine processionary moth *Thaumetopoea pityocampa* (Lepidoptera: Notodontidae) is one of the most serious pests of pine and cedar forests in Southern Europe and North Africa. In northern Algeria, outbreaks occur in the Aleppo pine (*Pinus halepensis*) forest, particularly in the semi-arid area and in the Atlas cedar forest (*Cedrus atlantica*) in the sub-humid elevation area. Under temperate and mountainous climates, the gregarious larvae of this winter-developing insect progressively build a large white, silky nest as a protective shelter during the winter period. We investigated the presence of nests and the environmental parameters (altitude, exposition) and their role in affecting the *T. pityocampa* density. Studies on nests of the pine processionary caterpillar were carried out in 2022 in two forest sites, namely Ghilas and El-Mroudj (NW Algeria). The mean (\pm SD) density of winter nests was higher in the cedar forest of El-Mroudj (1.22 ± 0.26) than the Aleppo pine forest of Ghilas (1.62 ± 0.60). The nest density differed with topographic orientation (F: 96.66, $p < 0.001$). The nests of *T. pityocampa* caterpillars were directed mostly in the south side (the sunny part) of host trees, accounting for 48.5% and 43.5% of the total number of nests in El-Mroudj and Ghilas, respectively. At both sites, larval nest height was positively correlated with tree height ($n = 126$, $P < 0.001$).

Keywords: Aleppo pine forest, Algeria, cedar forest, gregarious larvae, nest density, *Thaumetopoea pityocampa*

INTRODUCTION

The pine processionary moth (PPM) *Thaumetopoea pityocampa* (Lepidoptera: Notodontidae) is the most important forest pest in the Mediterranean and other Southern European areas (Jacquet et al. 2013; Li et al. 2015; Sbay and Zas 2018; Campoa et al. 2021; Camarero et al. 2022; Battisti et al. 2023). *Thaumetopoea pityocampa* is currently showing an expansion northward and higher altitude in Europe due to increased winter temperatures (Hódar and Zamora 2004; Robinet et al. 2013).

The PPM has a univoltine lifecycle. In Algeria, the adults emerge, mate and lay eggs in a single clutch on pine needles or the underside of cedar twigs in July at colder sites and in August at warmer sites (Hezil et al. 2018; Sebti et al. 2022). Each egg batch contains, on average, in the northern regions of Algeria 220 eggs covered with protective scales, which are produced by the female (El-Mokhefi et al. 2021). Embryonic development lasts for 30-45 days. Five-instar larval development occurs in autumn and winter (between September to March), and its duration depends mainly on temperature (Battisti et al. 2015). The threshold temperature for larval development is about 6.5°C, and 564-570 days are required for larval

development from hatching to pupation (Devkota and Schmidt 1990). Larvae are gregarious and build large white silk tents right after they hatch from the eggs, which they leave only for feeding (Uemura et al. 2021). They stay in during the day and get out during the night to feed on needles when conditions are favorable. The shape and thickness of the silk tent depend on the number of individuals, host plant, and climate (Battisti et al. 2015). Due to this host, the pine processionary moth is affected by solar radiation in winter because sunshine can increase the temperature within the tent (Poitou et al. 2021), enabling them to develop during winter. These larval tents are easy to detect and thus, mapping their distribution is relatively straightforward compared to other species. In spring, the mature larvae leave the tree in a single file, head-to-tail processions, searching for soil sites suitable for pupation, where the pupae stay until summer (Uemura et al. 2020). Some pupae have a prolonged diapause lasting 1-6 years which is conditioned by the surrounding environment (Zamoum 1998; Torres-Muros et al. 2016; Salman et al. 2019).

Currently, latitudinal and altitudinal expansions of the PPM range have been attributed to climate warming (Robinet et al. 2013; Roques 2015; Bourougaaoui et al.

2021a). In the last decades, expansion of PPM outbreaks has been reported across all of southern Europe (Netherer et al. 2010; Poitou et al. 2022; Zamora et al. 2022; Azcárate et al. 2023). In Algeria, outbreaks occur in the Aleppo pine (*Pinus halepensis*) forest in the semi-arid area and Atlas cedar forest (*Cedrus atlantica*) in the sub-humid elevation area (El-Mokhefi et al. 2016). The expansion areas of this species in Algeria were favored by the recent large afforestation program of Barrage Vert (plantation of pure stands of Aleppo pines to serve as a barrier to desertification) along the Saharian Atlas (Zamoum 1998), and large areas of forests are periodically affected by severe episodes of defoliation (Ayache et al. 2021; Rahim and Chakali 2022; Sebti et al. 2022). *Thaumetopoea pityocampa* attack can reduce tree leaf cover by up to 20 to 80%, along with a decrease in the tree's ability to photosynthesize and store energy (Jacquet et al. 2012). Canopy damage due to defoliation results in reduced growth, leading to heavy losses of productivity and biomass in forests, changing the carbon flux (Sbabdji and Kadik 2011; Medvigy et al. 2012; Jacquet et al. 2014; Williams et al. 2016). Climate change may also worsen the impacts of defoliation on growth in several ways. For example, increased temperatures can lead to increased rates of herbivory, which can further increase the severity and frequency of defoliation (Lemoine et al. 2014; Zhang et al. 2020; Rauschkolb et al. 2022). Higher temperatures can also increase the metabolic rate of plants, leading to increased water loss and decreased water availability, which can further reduce the plant's ability to photosynthesize and grow (Dusenge et al. 2019; Campoa et al. 2021; Gazol and Camarero 2022; Navarro-Cerrillo et al. 2022). Additionally, this moth can affect humans and animals because of the release of microscopic urticating hairs (setae) present from L3, which are responsible for respiratory problems, skin lesions of varying severity and allergic reactions (Battisti et al. 2017; Galip et al. 2022; Izquierdo-Rodriguez et al. 2022; Olivieri et al. 2023).

In Algeria, several control methods have been used against the caterpillars of PPM, from the removal of the larval nests to the spraying of chemical insecticides. Nest removal is still a valuable practice in small areas such as parks and gardens. However, the populations of this pest in large forest areas have been suppressed by the application of preparations of various chemical insecticides (including organophosphates and synthetic pyrethroids).

The nest plays a critical role in the biology and ecology of *T. pityocampa*, and its study is crucial for a deeper understanding of the insect. In the current study, surveys were carried out in 2022 in Ain Defla (NW Algeria). Data about the presence of nests and the environmental parameters (altitude, exposition) were recorded, and their role in affecting the PPM density was investigated. This information can be useful in understanding the behavior and life cycle of the insect, as well as in developing strategies for controlling its population and preventing damage to trees and forests. Studying the nest can provide valuable information about the interplay between the insect and its environment and can contribute to our understanding of the relationships between insects and their hosts.

MATERIALS AND METHODS

Study area

The study area is located in the Aïn-Defla region, Algeria (Figure 1), which is a high montane region in north-western Algeria, where PPMs are currently widespread. Ain-Defla extends from 36°23'N to 35°53'N and from 1°32'E to 2°33'E and is located 80 km southwest of the capital Algiers. It includes lands characterized by subhumid and semi-arid climates across an altitudinal range between 100 and 1700 m asl. Forest stands are composed of Aleppo pine (*Pinus halepensis*), Atlas cedar (*C. atlantica*), and thuja (*Tetraclinis articulata*).

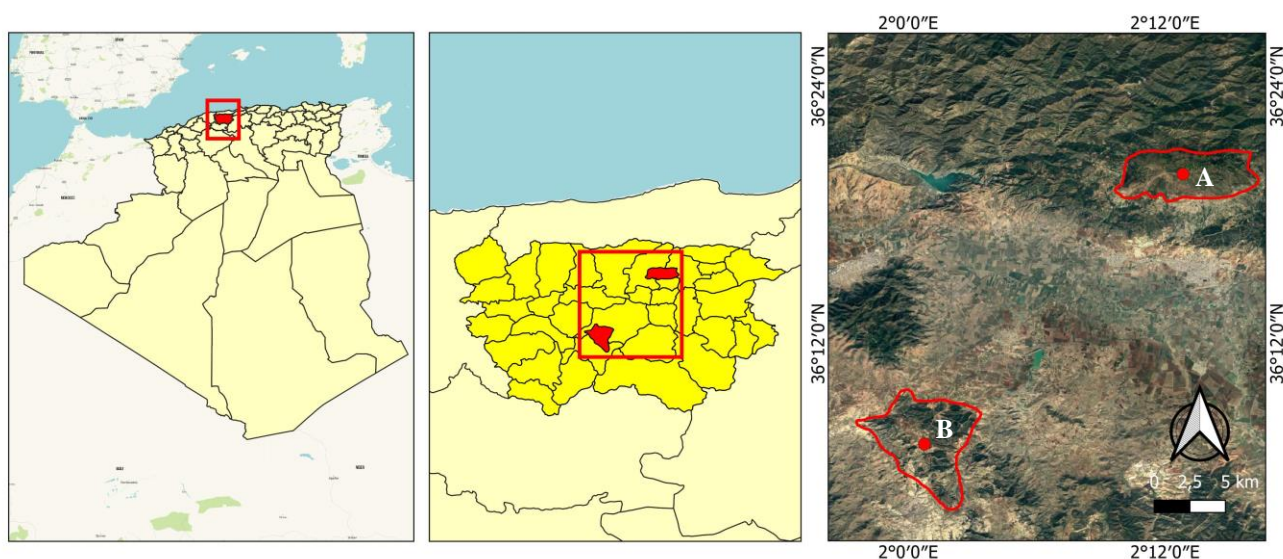


Figure 1. General map of Algeria with the location of the two forest sites: A. El-Mroudj and B. Ghilas of Aïn-Defla region

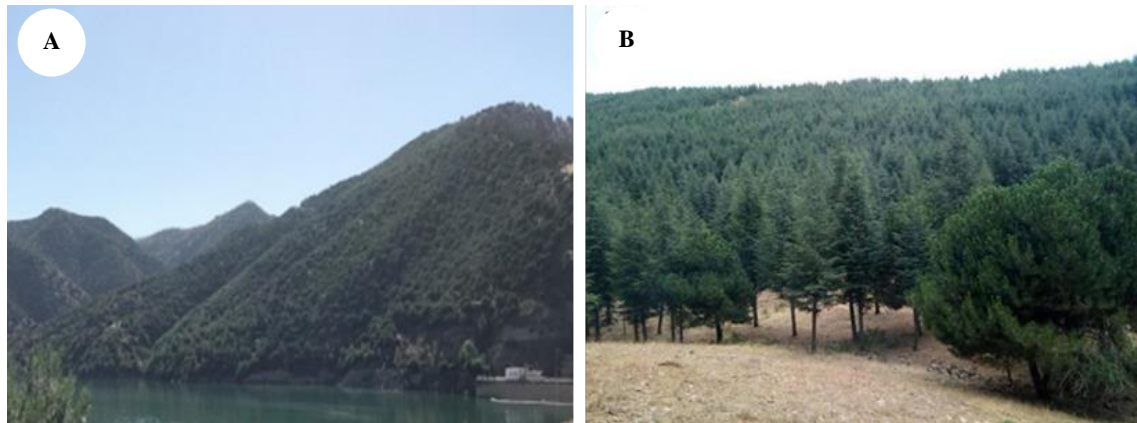


Figure 2. General view showing the two-forest landscape in Algeria. A. Ghilas forest; B. EL-Mroudj forest

Two sites were selected, namely Ghilas (Figure 2A) and El-Mroudj (Figure 2B). The distance between the two forest sites is about 54 km. An overview of the main characteristics of each site is provided in Table 1.

The first site, Ghilas (36°29'N, 4°01'E, 1403-1825 m), is a natural stand of *P. halepensis*, covering an area of almost 50 ha. This area is situated in a semi-arid bioclimate, characterized by average annual temperatures of 11°C and 28.5°C in winter and summer, respectively, and an average annual rainfall of 440 mm (Bouzar-Essaidi et al. 2021). Tree age ranged from 5 to 34 years, and tree density varied in the range 300-700 pine ha⁻¹.

The second site, El-Mroudj is a pure planted stand of *C. atlantica*, covering an area of 100 ha. The locality is under a subhumid bioclimate, with average temperatures of 5.6°C in winter and 20.8°C in summer and an average annual rainfall of 600 mm (Boudrissa et al. 2017; Figure 3). The stand age varied in the range of 05-40 years. The tree density varied in the range of 700-1000 cedar ha⁻¹.

Population density, exposition of nests and larval nest height of *Thaumetopoea pityocampa*

During winter, PPM larvae spin characteristic silk nests where they gather during the daytime while they feed on pine and cedar needles at night (Battisti et al. 2005). Due to their large size (approximately 0.10-0.25 m in diameter) and white color, these nests are easy to detect in the tree crowns. Nests of the current year were easily distinguishable from older nests, as they were white and full of larvae, unlike old nests, which were greyish-brown and empty of larvae. In each stand, the number of silk nests per tree was counted, and the heights of nests from ground level were measured using height poles.

Trees were observed by conducting two transects, about 100 m long, one at the edge of the forest stand and another about 50 m in the interior of the stand. The censuses were

conducted at Ca. bi-weekly intervals from January 15, 2022, to April 10, 2022, when the formed nests on the trees were more easily visible. Overall, 390 trees were sampled at each sampling location. Trees were carefully inspected for the presence of tents by looking at tree canopy in all directions. We used the average density of the winter nests per tree as a proxy for local pine processionary moth density (Hóðar et al. 2004; Régolini et al. 2014).

Data analysis

A one-way ANOVA test was carried out to compare the density of *T. pityocampa* (nests/per tree), exposition of nests and height of nest above the ground between sites after assessing for normality and homoscedasticity of the data. The correlation analysis was used to determine the correlation between larval nest height and tree height. All analyses were performed using SPSS v25.

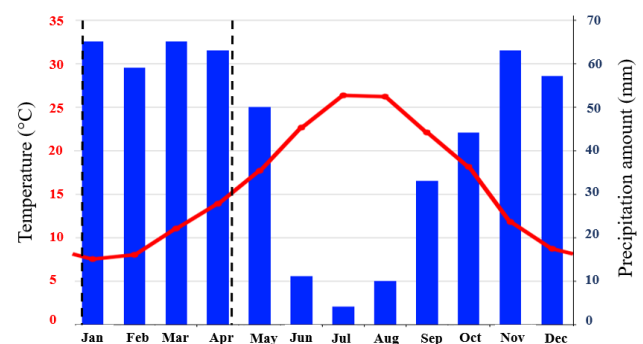


Figure 3. Monthly precipitation amount (mm) and monthly mean temperature (°C) recorded in Ain-Defla during the year 2022. Vertical discontinuous lines represent the start and end of study period

Table 1. Main environmental characteristics of the studied sites

Site	Latitude (N)	Longitude (E)	Elevation (m)	Topog. orientation	Slope (%)	Tree height (m)
Ghilas	35°19'10"	2°02'47"	580	North-East	20-50	3-20
El-Mroudj	36°20'52"	2°12'39"	780	North-East	10-15	5-20

RESULTS AND DISCUSSION

Population density

During this study, the population density of *T. pityocampa* varied significantly between the two sites ($F_{1,68} = 17.65$, $P < 0.01$) (Table 2). The mean (\pm SD) density of winter nests was slightly higher in the cedar forest of El-Mroudj (1.22 ± 0.26) than in the Aleppo pine forest of Ghilas (1.62 ± 0.60). The highest number of winter nests per tree in the El-Mroudj and Ghilas sites was 6 and 5, respectively.

Exposition of larval nests

The results on the orientation of caterpillar nests in El-Mroudj (Figure 5A) and Ghilas forests (Figure 5B) are shown in Figure 5.

At both sites, the nest density differed with topographic orientation ($F: 96.66$, $P < 0.001$). The nests of *T. pityocampa* caterpillars (Figure 4) were directed mostly in the south side (the sunny part) of host trees, accounting for 48.5% and 43.5% of the total number of nests in El-Mroudj and Ghilas, respectively.

Distribution of *Thaumetopoea pityocampa* nests according to the height of the tree

At both sites, nest height was positively correlated with tree height ($n = 126$, $P < 0.001$). In the El-Mroudj cedar forest, most nests (43.3%) were placed in cedar trees ranging in height from 9 to 12 m, 38.4% of nests were located between 5-9 m in height, and 18.3% of nests were on the top of tree (between 12-15 m) (Figure 6A). In the Ghilas pine forest, most nests (56.4%) were concentrated in pine trees ranging in height from 1 to 5 m, 31.9% of nests were located between 5-10 m in height, and 11.7% of nests were on the top of the tree (between 10-15 m) (Figure 6B).

The average height of the nest above the ground was 140 ± 60 cm ($n = 72$) and 180 ± 60 cm ($n = 59$), respectively, in El-Mroudj and Ghilas, with significant differences between the two forests sites ($F_{1,79} = 13.36$, $P < 0.01$).



Figure 4. Larval nest of *Thaumetopoea pityocampa*

Table 2. Population density of *Thaumetopoea pityocampa* in the two study sites

Site	Number of sampled trees	Number of nests	Mean \pm SD (min-max)
El-Mroudj	390	634	1.62 ± 0.60 (6-0)
Ghilas	390	477	1.22 ± 0.26 (5-0)
One-way ANOVA		$F: 17.65$: $P < .001$	

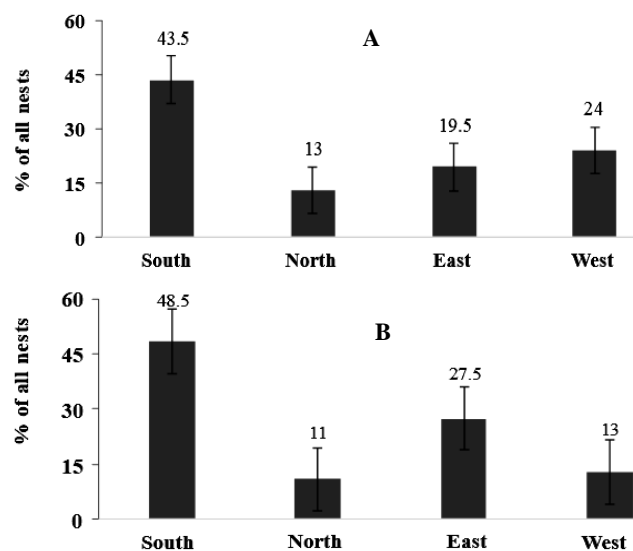


Figure 5. Topographic orientation of larval nests in: A. El-Mroudj and B. Ghilas sites

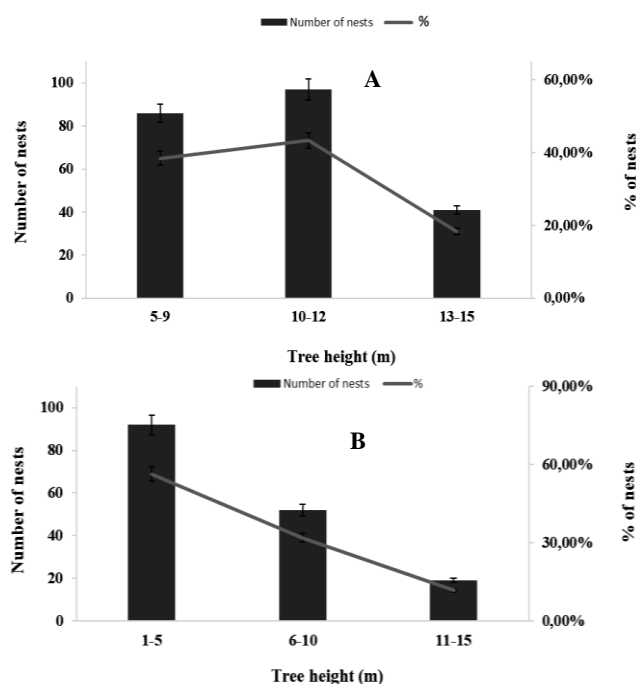


Figure 6. Distribution of *Thaumetopoea pityocampa* nests according to the height of the tree (A. Site of El-Mroudj; B. site of Ghilas)

Discussion

Our study found that the population density *T. pityocampa* varied significantly between sites. The population density of the pine processionary moth *T. pityocampa* was higher in the in El-Mroudj site, which had a higher tree density (700-1000 tree/ha), while the density level of host trees in Ghilas site was relatively lower (300-700 tree/ha). Similar results (1.5 ± 0.23 tents/tree) were found in Bordj-Bou-Arreridj region (Northeastern Algeria) (Ziouche et al. 2017). A higher level of population density of *T. pityocampa* was observed in the National Park of Chrea (Northern Algeria) (5.3-15.2 tents/tree for the years 1991-2014) (Sebti and Chakali 2014; Sbabdji et al. 2015). In several European countries, repeated outbreaks of *T. pityocampa* have been recorded (Arnaldo et al. 2010; Sbabdji and Kadik 2011; Salman et al. 2016; Bourougaaoui et al. 2021b). The periodicity of these outbreaks varies considerably. However, Zamoum et al. (2015) found a cyclic abundance in the *T. pityocampa* populations of Algeria, and outbreaks of various sizes have been observed every 5-6 years. According to these authors, the mortality of the trees is low, and the growth losses can rise up to 60% of the annual growth.

Forest parameters such as stand height, age, and tree density were the most important factors determining the population density of *T. pityocampa*. Alsanousi and Hamad-Sheip (2022) and Régolini et al. (2014) found that *T. pityocampa* tent density decreased significantly with stand density. However, Lombardero et al. (2012) found no significant impact of thinning on *T. pityocampa* density in *Pinus pinaster* Aiton stands. Geri et al. (1985) showed that the low density of *T. pityocampa* is associated with old natural forest sites that are characterized by a greater tree height. In addition, several studies have shown that the natural enemies (e.g., parasitoids, predators, fungi, etc.) can play a significant role in the natural regulation of *T. pityocampa* and contribute to maintain their populations at low abundance levels within its distribution range (Tarasco et al. 2016; Zamoum et al. 2017; Rahim and Chakali 2022; Sebti et al. 2022; Hein et al. 2023; Lagogiannis et al. 2023). Pimentel et al. (2017) showed that the population density of *T. pityocampa* decreases dramatically after a year of severe defoliation as a consequence of both activity of the natural enemies and change in food quality (Pimentel et al. 2017; Rahim et al. 2021; Sebti et al. 2022).

Our results indicate that the choice of winter nest placement by *T. pityocampa* larvae appears to be dependent on tree height. In the EL-Mroudj cedar forest, most larval nests (43.3%) are placed in cedar trees ranging in height from 9 to 12 m. In the Ghilas pine forest, most larval nests (56.4%) are placed in pine trees ranging in height from 1 to 5 m. Higher solar radiation and warmer temperatures might be responsible for such observed spatial distributions. Pérez-Contreras et al. (2014) found that the frequency and intensity of attack by *T. pityocampa* are closely related to the height of Aleppo pine trees. Female moths use the shape of a tree silhouette against a clear background to select the host tree prior to egg-laying (Demolin 1969). This behavior is consistent with the common observation of

higher infestation levels of PPM at forest stand edges than in forest interiors (Dulaurent et al. 2012).

We found that the density of *T. pityocampa* nests differed significantly according to topographical orientation and that the nests were mainly located on the south side with direct exposure to solar radiation. Due to this tent, the PPM is affected by solar radiation in winter because the sunshine can make the temperature increase within the tent (Hódar et al. 2012; Parlak et al. 2019) and generates a microclimate warmer than surrounding conditions (Poitou et al. 2021). Previous studies showed that the temperature in the PPM nest could be higher than the environmental temperature during the day (Breuer and Devkota 1990). According to Poitou et al. (2021), the temperature within the nest can be much higher than the ambient air temperature, by 16°C on average, when exposed to intense solar radiation on a cloudless day.

Finally, it is the density of *T. pityocampa* larval nests on the pine and cedar trees that are significant in terms of whether any management intervention is required, and the significance of a particular pheromone trap catch and the associated number of nests can only be determined using local knowledge of the numbers of host trees, the likely distribution of nests between trees, and information on how many *T. pityocampa* nests per tree might represent a risk to human or animal health, or might result in defoliation.

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REFERENCES

- Alsanousi A, Sheip YH. 2022. Prevalence and distribution of pine processionary moth (*Thaumetopoea pityocampa*) in Shahat's Aleppo Pine (*Pinus halepensis*) plantations, Al-JabalAl-Akhdar, Libya. *Al-Mukhtar J Sci* 37 (4): 394-404. DOI: 10.54172/mjsc.v37i4.990.
- Arnaldo PS, Chacim S, Lopes D. 2010. Effects of defoliation by the pine processionary moth *Thaumetopoea pityocampa* on biomass growth of young stands of *Pinus pinaster* in northern Portugal. *iForest* 3 (6): 159. DOI: 10.3832/for0553-003.
- Ayache S, El Mokhefi M, Bonifácio L, Chakali G. 2021. Egg batches parasitism of processionary moth *Thaumetopoea pityocampa* (Lepidoptera, Thaumetopoeidae) from two Atlas cedar ecotypes in Algeria. *Zoodiversity* 55 (3): 239-250. DOI: 10.15407/zoo2021.03.239.
- Azcárate FM, Seoane J, Silvestre M. 2023. Factors affecting pine processionary moth (*Thaumetopoea pityocampa*) incidence in Mediterranean pine stands: A multiscale approach. *For Ecol Manag* 529: 120728. DOI: 10.1016/j.foreco.2022.120728.
- Battisti A, Stastny M, Netherer S, Robinet C, Schopf A, Roques A, Larsson S. 2005. Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecol Appl* 15 (6): 2084-2096. DOI: 10.1890/04-1903.
- Battisti A, Avci M, Avtzi DN, Jamaa MLB, Berardi L, Berretima W, Branco M, Chakali G, Fels MAEAE, Frérot B, Hódar JA, Ionescu-Mălăncuș I, İpekdağ K, Larsson S, Manole T, Mendel Z, Meurisse N, Mirchev P, Nemer N, Paiva M, Pino J, Prosatov A, Rahim N, Rousselet J, Santos H, Sauvard D, Schopf A, Simonato M, Yart A, Zamoum M. 2015. Natural history of the processionary moths

- (*Thaumetopoea* spp.). In: Roques A (eds). New Insights in Relation to Climate Change. Springer, Dordrecht, Netherlands.
- Battisti A, Larsson S, Roques A. 2017. Processionary moths and associated urtication risk: Global change-driven effects. *Ann Rev Entomol* 62: 323-342. DOI: 10.1146/annurev-ento-031616-034918.
- Battisti A, Hódar JA, Hernández R, Larsson S. 2023. Aggregative oviposition varies with density in processionary moths-Implications for insect outbreak propensity. *Ecol Entomol* 48 (1): 102-111. DOI: 10.1111/een.13205.
- Boudrissa N, Cheraitia H, Halimi L. 2017. Modelling maximum daily yearly rainfall in northern Algeria using generalized extreme value distributions from 1936 to 2009. *Meteorol Appl* 24 (1): 114-119. DOI: 10.1002/met.1610.
- Bourougaaoui A, Jamâa MLB, Robinet C. 2021a. Has north africa turned too warm for a mediterranean forest pest because of climate change?. *Clim Change* 165: 1-20. DOI: 10.1007/s10584-021-03077-1.
- Bourougaaoui A, Robinet C, Jamâa MLB, Laparie M. 2021b. Effects of climate warming on the pine processionary moth at the southern edge of its range: A retrospective analysis on egg survival in Tunisia. *BioRxiv*. DOI: 10.1101/2021.08.17.456665v2.
- Bouzar-Essaidi K, Branco M, Battisti A, Garcia A, Fernandes MR, Chabane Y, Benfekih L. 2021. Response of the egg parasitoids of the pine processionary moth to host density and forest cover at the southern edge of the range. *Agric For Entomol* 23 (2): 212-221. DOI: 10.1111/afe.12423.
- Breuer M, Devkota B. 1990. Studies on the importance of nest temperature of *Thaumetopoea pityocampa* (Den. & Schiff.) (Lep. Thaumetopoeidae) 1. *J Appl Entomol* 109 (1-5): 331-335. DOI: 10.1111/j.1439-0418.1990.tb00060.x.
- Camarero JJ, Tardif J, Gazol A, Conciatori F. 2022. Pine processionary moth outbreaks cause longer growth legacies than drought and are linked to the North Atlantic Oscillation. *Sci Total Environ* 819: 153041. DOI: 10.1016/j.scitotenv.2022.153041.
- Campo J, Calvão T, Firmino PN, Pimentel CS. 2021. Disentangling the effects of climate and defoliation on forest growth: The case of an outbreak of a *Thaumetopoea pityocampa* population with a shifted phenology in a *Pinus pinaster* monoculture. *For Ecol Manag* 498: 119548. DOI: 10.1016/j.foreco.2021.119548.
- Demolin G. 1969. Bioecologia de *Thaumetopoea pityocampa* Schiff., incidencia de los factores climáticos. *Boletín del Servicio de Plagas Forestales* 12 (3): 9-22.
- Devkota B, Schmidt GH. 1990. Larval development of *Thaumetopoea pityocampa* (Den. & Schiff.) (Lep., Thaumetopoeidae) from Greece as influenced by different host plants under laboratory conditions. *J Appl Entomol* 109: 321-330. DOI: 10.1111/j.1439-0418.1990.tb00059.x.
- Dulaurent AM, Porté AJ, Van Halder I, Vitillard F, Menassieu P, Jactel H. 2012. Hide and seek in forests: colonization by the pine processionary moth is impeded by the presence of nonhost trees. *Agric For Entomol* 14 (1): 19-27. DOI: 10.1111/j.1461-9563.2011.00549.x.
- Dusenge ME, Duarte AG, Way DA. 2019. Plant carbon metabolism and climate change: Elevated CO₂ and temperature impacts on photosynthesis, photorespiration and respiration. *New Phytol* 221 (1): 32-49. DOI: 10.1111/nph.15283.
- El Mokhefi MH, Kerdellhue C, Burban C, Battisti A, Chakali G, Simonato M. 2016. Genetic differentiation of the pine processionary moth at the southern edge of its range: Contrasting patterns between mitochondrial and nuclear markers. *Ecol Evol* 6: 4274-4288. DOI: 10.1002/ece3.2194.
- El Mokhefi M, Chakali G, Rahim N, Bouchou L, Battisti A. 2021. Is body size a good indicator of fecundity in the genus *Thaumetopoea*? A story told by two intrageneric Mediterranean forest defoliators. *Agric For Entomol* 23: 23-31. DOI: 10.1111/afe.12399.
- Galip N, Şanlıdağ B, Babayiğit A, Bahçeciler NN. 2022. Cutaneous Allergic reactions to pine processionary caterpillar (*Thaumetopoea Pityocampa*): A complicated cutaneous reaction in an infant and review of the literature. *Turk J Pediatr Dis* 64 (2): 389-393. DOI: 10.24953/turkjped.2021.385.
- Gazol A, Camarero JJ. 2022. Compound climate events increase tree drought mortality across European forests. *Sci Total Environ* 816: 151604. DOI: 10.1016/j.scitotenv.2021.151604.
- Geri C, Miller C, Xeuxet D. 1985. Mesure des populations de processionnaire du pin (*Thaumetopoea pityocampa* Schiff-Lepidoptere Thaumetopoeidae) au Mont-Ventoux. *Ann Sci For* 42 (2): 143-184. DOI: 10.1051/forest:19850202.
- Hein N, Hainz AA, Wehren T, Fischer K. 2023. Effects of an entomopathogenic nematode applied against *Thaumetopoea processionea* on non-target arthropods under field conditions. *Biol Control* 179: 105177. DOI: 10.1016/j.biocontrol.2023.105177.
- Hezil S, Chakali G, Battisti A. 2018. Plant phenotype affects oviposition behaviour of pine processionary moth and egg survival at the southern edge of its range. *iForest* 11 (5): 572. DOI: 10.3832/for2675-011.
- Hódar JA, Zamora R, Castro J, Baraza E. 2004. Feast and famine: Previous defoliation limiting survival of pine processionary caterpillar *Thaumetopoea pityocampa* in Scots pine *Pinus sylvestris*. *Acta Oecol* 26 (3): 203-210. DOI: 10.1016/j.actao.2004.05.004.
- Hódar JA, Zamora R. 2004. Herbivory and climatic warming: A Mediterranean outbreaking caterpillar attacks a relict, boreal pine species. *Biodivers Conserv* 13 (3): 493-500. DOI: 10.1023/B:BIOC.0000009495.95589.a7.
- Hódar JA, Zamora R, Cayuela L. 2012. Climate change and the incidence of a forest pest in Mediterranean ecosystems: Can the North Atlantic Oscillation be used as a predictor?. *Clim Change* 113 (3): 699-711. DOI: 10.1007/s10584-011-0371-7.
- Izquierdo-Rodriguez C, Dorronzoro-Ramirez E, Gonzalez-Martin-Moro J, Moreno-Martín P, Gómez-Sanz F, Cobo-Soriano R. 2022. *Ophthalmia nodosa* due to the pine processionary caterpillar: Report of three cases and review of the literature. *J Fr Ophtalmol* 45 (2): e81-e83. DOI: 10.1016/j.jfo.2021.03.026.
- Jacquet JS, Orazio C, Jactel H. 2012. Defoliation by processionary moth significantly reduces tree growth: A quantitative review. *Ann For Sci* 69: 857-866. DOI: 10.1007/s13595-012-0209-0.
- Jacquet JS, Bosc A, O'Grady AP, Jactel H. 2013. Pine growth response to processionary moth defoliation across a 40-year chronosequence. *For Ecol Manag* 293: 29-38. DOI: 10.1016/j.foreco.2012.12.003.
- Jacquet JS, Bosc A, O'Grady A, Jactel H. 2014. Combined effects of defoliation and water stress on pine growth and non-structural carbohydrates. *Tree Physiol* 34 (4): 367-376. DOI: 10.1093/treephys/tpu018.
- Lagogiannis I, Mantzoukas S, Eliopoulos PA, Poulas K. 2023. First record of *Beauveria varroae*, *Cordyceps blackwelliae*, and *Purpureocillium lavendulum* from greece and their pathogenicity against *Thaumetopoea pityocampa*. *Diversity* 15 (3): 312. DOI: 10.3390/d15030312.
- Lemoine NP, Burkepile DE, Parker JD. 2014. Variable effects of temperature on insect herbivory. *Peer J* 2: e376. DOI: 10.7717/peerj.376.
- Li S, Daudin JJ, Piou D, Robinet C, Jactel H. 2015. Periodicity and synchrony of pine processionary moth outbreaks in France. *For Ecol Manag* 354: 309-317. DOI: 10.1016/j.foreco.2015.05.023.
- Lombardero MJ, Alonso-Rodríguez M, Roca-Posada EP. 2012. Tree insects and pathogens display opposite tendencies to attack native vs. non-native pines. *For Ecol Manag* 281: 121-129. DOI: 10.1016/j.foreco.2012.06.036.
- Medvigy D, Clark KL, Skowronski NS, Schäfer KVR. 2012. Simulated impacts of insect defoliation on forest carbon dynamics. *Environ Res Lett* 7 (4): 045703. DOI: 10.1088/1748-9326/7/4/045703.
- Navarro-Cerrillo RM, González-Moreno P, Ruiz-Gómez FJ, Sánchez-Cuesta R, Gazol A, Camarero JJ. 2022. Drought stress and pests increase defoliation and mortality rates in vulnerable *Abies pinsapo* forests. *For Ecol Manag* 504: 119824. DOI: 10.1016/j.foreco.2021.119824.
- Netherer S, Schopf A. 2010. Potential effects of climate change on insect herbivores in European forests-general aspects and the pine processionary moth as specific example. *For Ecol Manag* 259 (4): 831-838. DOI: 10.1016/j.foreco.2009.07.034.
- Olivieri M, Ludovico E, Battisti A. 2023. Occupational exposure of forest workers to the urticating setae of the pine processionary moth *Thaumetopoea pityocampa*. *Intl J Environ Res Public Health* 20 (6): 4735. DOI: 10.3390/ijerph20064735.
- Parlak S, Özçankaya İM, Batur M, Akkaş ME, Boza Z, Toprak Ö. 2019. Determining the edge effect of pine processionary moth (*Thaumetopoea pityocampa*) in its horizontal distribution in the stand. *J For Res* 30 (1): 347-352. DOI: 10.1007/s11676-018-0634-5.
- Pérez-Contreras T, Soler JJ, Soler M. 2014. Host selection by the pine processionary moth enhances larval performance: An experiment. *Acta Oecol* 55: 15-22. DOI: 10.1016/j.actao.2013.10.006.
- Pimentel CS, Ferreira C, Santos M, Calvão T. 2017. Spatial patterns at host and forest stand scale and population regulation of the pine processionary moth *Thaumetopoea pityocampa*. *Agric For Entomol* 19 (2): 200-209. DOI: 10.1111/afe.12201.

- Poitou L, Robinet C, Suppo C, Rousselet J, Laparie M, Pincebourde S. 2021. When insect pests build their own thermal niche: The hot nest of the pine processionary moth. *J Therm Biol* 98: 102947. DOI: 10.1016/j.jtherbio.2021.102947.
- Poitou L, Laparie M, Pincebourde S, Rousselet J, Suppo C, Robinet C. 2022. Warming causes atypical phenology in a univoltine moth with differentially sensitive larval stages. *Front Ecol Evol* 10 (26): 1-16. DOI: 10.3389/fevo.2022.825875.
- Rahim N, Chakali G, Battisti A. 2021. Impact of natural enemies on larvae of *Thaumetopoea bonjeani* (Lepidoptera: Notodontidae) in association with *Thaumetopoea pityocampa* in northern Algeria. *Redia J Zool* 104: 199-207. DOI: 10.19263/REDIA-104.21.23.
- Rahim N, Chakali G. 2022. Pupa mortality of *Thaumetopoea pityocampa* Denis & Schiffmüller 1775 (Lepidoptera: Notodontidae) in Algeria. *Proceedings of the XIII International Scientific Agricultural Symposium. Bosnia and Herzegovina, 6-9 October 2022*.
- Rauschkolb R, Li Z, Godefroid S, Dixon L, Durka W, Májeková M, Bossdorf O, Ensslin A, Scheepens JF. 2022. Evolution of plant drought strategies and herbivore tolerance after two decades of climate change. *New Phytol* 235 (2): 773-785. DOI: 10.1111/nph.18125.
- Réglolini M, Castagneyrol B, Dulaurent-Mercadal AM, Piou D, Samalens JC, Jactel H. 2014. Effect of host tree density and apparency on the probability of attack by the pine processionary moth. *For Ecol Manag* 334: 185-192. DOI: 10.1016/j.foreco.2014.08.038.
- Robinet C, Rousselet J, Pineau P, Miard F, Roques A. 2013. Are heat waves susceptible to mitigate the expansion of a species progressing with global warming?. *Ecol Evol* 3 (9): 2947-2957. DOI: 10.1002/ece3.690.
- Roques A. 2015. Processionary Moths and Climate Change: An update. Springer-Quae, Dordrecht-Versailles.
- Salman MHR, Hellrigl K, Minerbi S, Battisti A. 2016. Prolonged pupal diapause drives population dynamics of the pine processionary moth (*Thaumetopoea pityocampa*) in an outbreak expansion area. *For Ecol Manag* 361: 375-381. DOI: 10.1016/j.foreco.2015.11.035.
- Salman MH, Bonsignore CP, El-Fels AEA, Giomi F, Hodar JA, Laparie M, Marini L, Merel C, Zalucki MP, Zamoum M, Battisti A. 2019. Winter temperature predicts prolonged diapause in pine processionary moth species across their geographic range. *PeerJ* 7: e6530. DOI: 10.7717/peerj.6530.
- Sbabdji M, Lambs L, Haddad A, Kadik B. 2015. Effect of periodic defoliations by *Thaumetopoea pityocampa* Schiff. on radial growth in cedar woodland in Chréa, Algeria. *Revue d'Ecologie* 70 (4): 371-386. DOI: 10.3406/rev.2015.1798.
- Sbabdji M, Kadik B. 2011. Effects of Atlas cedar (*Cedrus atlantica*) defoliation on performance of the pine processionary moth (*Thaumetopoea pityocampa*). *J Pest Sci* 84: 213-217. DOI: 10.1007/s10340-010-0346-x.
- Sbay H, Zas R. 2018. Geographic variation in growth, survival, and susceptibility to the processionary moth (*Thaumetopoea pityocampa* Dennis & Schiff.) of *Pinus halepensis* Mill. and *P. brutia* Ten.: Results from common gardens in Morocco. *Ann For Sci* 75 (3): 69. DOI: 10.1007/s13595-018-0746-2.
- Sebti S, Chakali G. 2014. Distribution and importance of the pine processionary moth winter nests *Thaumetopoea pityocampa* (Denis and Schiffmüller) (Lepidoptera: Notodontidae) in the forests cedar of the national park of Chréa (Algeria). *Intl J Agric Sci Res* 4 (5): 77-84.
- Sebti S, Bonifácio L, Chakali G. 2022. Role of egg parasitoids in controlling the pine processionary moth in the cedar forests of Chréa National Park (Algeria). *Forests* 13 (2): 211. DOI: 10.3390/f13020211.
- Tarasco E, Triggiani O, Zamoum M, Oreste M. 2016. Natural enemies emerged from *Thaumetopoea pityocampa* (Denis & Schiffmüller) (Lepidoptera Notodontidae) pupae in Southern Italy. *Redia* 98 (1): 103-108.
- Torres-Muros L, Hódar JA, Zamora R. 2016. Effect of habitat type and soil moisture on pupal stage of a Mediterranean forest pest (*Thaumetopoea pityocampa*). *Agric For Entomol* 19 (2): 130-138. DOI: 10.1111/afe.12188.
- Uemura M, Perkins LE, Zalucki MP, Battisti A. 2020. Movement behaviour of two social urticating caterpillars in opposite hemispheres. *Mov Ecol* 8: 1-10. DOI: 10.1186/s40462-020-0189-x.
- Uemura M, Zalucki MP, Battisti A. 2021. Behavioural plasticity and tree architecture shapes tent and foraging locations of pine processionary larval colonies. *Entomol Gen* 41: 121-136. DOI: 10.1127/entomologia/2020/1091.
- Williams CA, Gu H, MacLean R, Masek JG, Collatz GJ. 2016. Disturbance and the carbon balance of US forests: A quantitative review of impacts from harvests, fires, insects, and droughts. *Glob Plan Change* 143: 66-80. DOI: 10.1007/s10533-016-0186-8.
- Zamora R, Hódar JA, Pérez-Luque AJ, Barea-Azcón JM. 2022. Responses of animal populations and communities to climate change and land-use shifts. In: Zamora R, Oliva M (eds). *The Landscape of the Sierra Nevada: A Unique Laboratory of Global Processes in Spain*. Springer International Publishing, New York.
- Zamoum M. 1998. Données sur la Bioécologie, les Facteurs de Mortalité et la Dynamique des Populations de *Thaumetopoea pityocampa* Denis et Schiffmüller. (Lepidoptera, Thaumetopoeidae) Dans les Pinares Subsahariennes de la Région de Djelfa (Algérie). [Dissertation]. University of Sciences of Rennes, France. [France]
- Zamoum M, Martin JC, Bensidi A. 2015. Fecundity of the pine processionary moth *Thaumetopoea pityocampa* (Lepidoptera: Notodontidae) at the southern edge of its distribution range. *Biologia* 70: 386-392. DOI: 10.1515/biolog-2015-0036.
- Zamoum M, Bouragba-Brague N, Rahim N, Khemici M, Gachi M, Battisti A, Claude J. 2017. Structure of the natural enemies' community composition to *Thaumetopoea pityocampa* and *Thaumetopoea bonjeani* (Lepidoptera Thaumetopoeidae) in the Algerian cedar forests. *J Entomol Zool Stud* 5 (4): 1536-1542.
- Zhang P, van Leeuwen CH, Bogers D, Poelman M, Xu J, Bakker ES. 2020. Ectothermic omnivores increase herbivory in response to rising temperature. *Oikos* 129 (7): 1028-1039. DOI: 10.1111/oik.07082.
- Ziouche S, Baali F, Moutassem D, Djazouli ZE. 2017. Strategies for choosing location of winter nests of *Thaumetopoea pityocampa* (Denis & Schiffmüller, 1775) in three pine forests of Bordj Bou Arreridj region (Algeria). *AgroBiologia* 7 (2): 412-426.