

21 **Abstract**

22

23 1 *Thaumetopoea pityocampa* is the most important pine defoliator in the Mediterranean
24 basin. Despite being attacked by a number of natural enemies, populations occur
25 frequently at high density in several areas.

26 2 Egg parasitism was studied in 27 pine and cedar forests in Algeria, in relation to the host
27 density (tents per tree) and the proportion of forest cover in the landscape.

28 3 Egg parasitism varied from 2 to 25%, accounted by two parasitoid species the specialist
29 *Baryscapus servadeii* and the generalist *Ooencyrtus pityocampae*.

30 4 Tent density was negatively correlated with parasitism by *B. servadeii* but not with that of
31 *O. pityocampae*. Conversely, parasitism by *O. pityocampae* increased with the proportion
32 of forest and agricultural cover, but not that of *B. servadeii*.

33 5 Maximum summer temperature showed no correlation with parasitism rates. Still,
34 temperature frequently exceeded 40°C during the period of adult parasitoid activity.

35 6 The low performance of the egg parasitoids at the southern edge of the host range could
36 be explained by the reduced fecundity of the host, climate effects, and phenological
37 mismatching between the parasitoids and the egg development. These and other factors
38 potentially involved need to be further explored with a long-term study of population
39 dynamics.

40

41 **Key words:** Egg parasitism, *Thaumetopoea pityocampa*, density-dependent response, land-use,
42 specialist parasitoid, generalist parasitoid, climate

43 1. Introduction

44
45 Top-down regulation by natural enemies is a major driver of population dynamics of forest pests
46 (Berryman, 1996) and it may contribute to explain population cycles of many forest defoliators of
47 the order Lepidoptera, as for example in the larch bud moth *Zeiraphera griseana* (Hübner)
48 (Turchin *et al.*, 2003). A density-dependent response of the predators' to prey abundance is
49 considered highly relevant to control pest species, as it may originate an equilibrium on prey
50 population at low levels, well below its carrying capacity. However, a delay in time in such
51 response may also originate well-known cyclic outbreaks (Berryman, 1996). In order to
52 understand the dynamics of forest defoliators and the factors eliciting the collapse of cyclic
53 outbreaks, it is thus important to study the role of the different natural enemies as top-down
54 regulators.

55 The pine processionary moth, *Thaumetopoea pityocampa* (Denis & Schiffermüller)
56 (Lepidoptera Notodontidae), is a main defoliator of pines and cedars all over the Mediterranean
57 basin (Battisti *et al.*, 2015). Adult flight and mating occur during summer months. Eggs are laid
58 in groups, encircling the pine needles or the cedar twigs. Each female lays a single egg batch.
59 About one month later larvae hatching occur. The larvae develop during fall and winter living
60 gregariously in large silk tents. At the end of winter, larvae descend the trees in procession to find
61 a place in the soil to bury and pupate. Their feeding activity may cause intense defoliation,
62 especially when populations are abundant, which result in tree growth losses (Jacquet *et al.*,
63 2012). The pine processionary moth also causes major public health problems due to urticating
64 setae released by the larvae (Battisti *et al.*, 2017).

65 The pine processionary moth has been observed expanding its distribution to higher latitudes
66 and elevations as a consequence of climate change (Carcanague, 1988, Battisti *et al.*, 2005;
67 Robinet *et al.*, 2007, Imbert *et al.*, 2012). In addition, the lack of natural enemies could be a
68 potential cause of populations attaining high levels in the invaded range (Auger-Rozenberg *et al.*,
69 2015). Still, in the core range of its distribution, the populations of the pine processionary moth
70 are frequently found at high density. Forest management factors, such as the extensive use of pine
71 monocultures could in part justify the abundance of the pine processionary moth (Jactel *et al.*,
72 2015; Damien *et al.*, 2016).

73 A number of natural enemies may cause top-down regulation of the pine processionary moth
74 during its whole development cycle (Auger-Rozenberg *et al.*, 2015). Several insect species prey
75 on eggs, namely bush crickets (Démolin & Delmas, 1967). Insectivorous bird species prey on the
76 larvae and on pupae (Barbaro & Battisti, 2011), while moths are preyed by bats (Charbonnier *et*
77 *al.*, 2014). A number of parasitoid species are found parasitizing eggs, larvae and pupae. Two
78 major egg parasitoid species, *Baryscapus servadeii* (Dom.) (Hymenoptera Eulophidae) and
79 *Ooencyrtus pityocampae* (Mercet) (Hymenoptera Encyrtidae), are widely found parasitizing the
80 eggs all over the Mediterranean Basin (e.g. Tsankov, 1990; Schmidt *et al.*, 1997, Schmidt *et al.*,
81 1999, Arnaldo & Torres, 2006, Tiberi *et al.*, 2015).

82 A large number of studies have analysed the egg parasitoids and egg parasitism rates in
83 several regions of the Mediterranean Basin. Most of these studies aimed at identifying parasitoid
84 species present in each region and comparing parasitism rates (Tsankov *et al.*, 1996) or parasitoid
85 behaviour in relation to position of eggs in the egg batch (Mirchev *et al.*, 2015). Parasitism rates
86 were also related to the presence of the scales covering the eggs (Perez-Contreras & Soler, 2004)
87 and to the height of the egg batches on the tree canopy (Tsankov, 1990). However, at the extent
88 of our knowledge, no previous study has addressed the effects of forest cover in the surrounding
89 landscape on egg parasitism of the pine processionary moth. And yet, recent studies have shown
90 that forest cover at landscape level may play a role on density of herbivores and their natural
91 enemies. In particular, landscape heterogeneity may increase top-down control in fragmented
92 forests by parasitoids (Roland & Taylor, 1997) and insectivorous birds (e.g. De La Vega *et al.*,
93 2012; Valdés-Correcher *et al.*, 2019).

94 As the pine processionary moth lays egg during summer, egg parasitoids need to be active
95 during this warm season. Adults of the two main parasitoid species, *B. servadeii* and *O.*
96 *pityocampae*, can survive up to three weeks as long as nectar sources are available and
97 temperatures are mild (Dulaurent *et al.*, 2011). However, heat waves during summer with
98 extreme high temperatures may compromise their survival. A study made in Italy suggested that
99 temperatures above 30°C would cause a decrease in egg parasitism (Tiberi *et al.*, 2015). No other
100 study however addressed this hypothesis.

101 The present study was carried out in Algeria, i.e. in the southern part of the range of *T.*
102 *pityocampa* known from the literature. The study aimed at analysing the variability of egg
103 parasitism in this region and relate with possible explanatory variables. In particular, the

104 objective was to explain variability of *T. pityocampa* egg parasitism in relation to i) pine
105 processionary moth density; ii) proportion of forest cover in surrounding landscape; and iii)
106 climate variables, in particular high summer temperature.

107

108 **2. Materials and methods**

109

110 *Sampling sites*

111 Three regions were selected in the northern Algeria, namely Tipaza, Ain-Defla, and Theniet El-
112 Had. In each region, 5 sites were sampled in 2017, 2018 and 2019, respectively for a total of 15
113 sites (Figure 1, Table 1, and Supplementary Figure 1). The region of Tipaza is located near the
114 coast and has an average elevation of 150 m. The climate is semi-arid with hot and dry summer
115 and mild winter. In the sampling year, 2017, average temperature was 18.7°C and annual
116 precipitation was 549 mm (source: Agence Nationale des Ressources Hydraulique, ANRH,
117 Algeria, 2017). Landscapes are dominated by natural forests of Aleppo pine (*Pinus halepensis*
118 Miller) mixed with thuja (*Tetraclinis articulata* (Vahl) Mast.) and kermes oak (*Quercus coccifera*
119 L.). Small to large-scale agricultural areas, and human settlements, are also characteristic in the
120 region. The region of Ain-Defla shows a continental, semi-arid with hot summer to cool winter
121 climate. Average annual temperature in 2018 was 18.9°C and precipitation was 530 mm (source:
122 ANRH, 2018). The average elevation is 590 m and sampled sites show a north dominant facing.
123 Landscapes are typically dominated by Aleppo pine forests, alone or mixed with thuja, although
124 agricultural areas and scattered human settlements can also be observed. The region of Theniet
125 El-Had is a national park in a mountain area (average elevation of 1439 m). In this region, in
126 2019, average annual temperature was 12.5°C and precipitation was 652 mm (source: Theniet El-
127 Had National Park Weather Station, 2019). In this region landscapes are dominated by semi-
128 natural forest and scrubland areas. Forest stands are composed by cedar (*Cedrus atlantica* (Endl.)
129 Carrière), zeen oak (*Quercus canariensis* Willd.) and holm oak (*Quercus ilex* L.).

130 For the landscape study, twelve additional sites studied by Bouchou (2015) (data from 2012)
131 (Fig 1) were included in order to cover a broad range of Algeria territory and increase diversity of
132 landscapes. Both studies used the same protocol for egg batches collection and parasitoids
133 sampling. Similar land-use dominated by Aleppo pine forests was also observed at these sites

134 (Bouchou & Chakali, 2014). Field surveys were carried out before inclusion of these sites in the
135 larger dataset, in order to make sure they would be comparable.

136

137 *Egg batch sampling*

138 In each site, 30 egg batches were collected by sampling along two transects, one along an edge of
139 the forest stand and another about 6-10 m inside the stand. Tree height in Tipaza, Ain-Defla, and
140 Theniet El-Had sampled forests varied from 2 to 20 m (Table 1, Figure 1). Egg batches were
141 always collected from the lower branches after visual observation of its presence on tree crown.
142 On pines, most of the egg batches were collected from the ground but for the highest cedar trees
143 in Theniet El-Had, egg batches were collected after climbing the trees or pulling the branches
144 with a rope. A total number of 450 egg batches were gathered. Egg batches were collected before
145 larval hatching, in Tipaza region from 31 August till 16 September 2017, in Ain-Defla from 30
146 August till 15 September 2018, and in Theniet El-Had from 30 July to 5 August 2019. During the
147 period of egg laying, that is August in Tipaza and Ain-Defla and July in Theniet El-Had, the
148 average of the mean and maximal temperatures were, respectively, 28°C and 40°C in Tipaza
149 (source: ANRH, 2017), 37°C and 42.8°C in Ain-Defla (source: ANRH, 2018), and 24.8°C and
150 39°C in Theniet El-Had (source: Theniet El-Had National Park Weather Station, 2019)

151 Egg batches were placed individually in glass tubes with cotton stoppers and stored under
152 laboratory conditions (20 - 24°C) until emergence. The emergence of egg parasitoids was
153 monitored daily for a total of 45 days starting from the first emergence, which was observed
154 between August and October of each year. These data represent part of the emergences of the
155 summer generation of parasitoids, as some of them could have already emerged in the field
156 before collection.

157 Egg batches were then maintained in vials in laboratory conditions until parasitoid emergence
158 in the spring of the next year, after winter diapause. Then each egg batch was examined, the
159 scales were removed, and the total number of eggs hatched, parasitized, and unhatched were
160 counted under a binocular microscope. The parasitoid species were identified by adult traits,
161 meconium and remains left inside the egg shell (Tzankov *et al.*, 1996; Schmidt *et al.*, 1999).

162

163

164

165 *Tent density*

166 The number of silk tents per tree was evaluated on each site on 30 trees in the winter following
167 egg batches collection on the following periods: Tipaza, February 2018; Ain-Defla, January
168 2019; Theniet El-Had, November 2019. Like for the egg batch sampling, trees were observed by
169 conducting two transects, about 100 m long, one at the edge of the forest stand and another about
170 5 m in the interior of the stand. Trees were carefully inspected for the presence of tents by
171 looking at tree canopy on all directions. Average tent density per tree was used as a proxy for
172 local pine processionary moth density.

173

174 *Climate data*

175 Mean temperatures of the three hottest months (June, July, August) for the 27 sites were retrieved
176 using WorldClim Version2 (Fick & Hijmans, 2017), based on the geographical coordinates of
177 each collection sites. These data are produced by modelling data recorded from 1970-2000
178 (<https://www.worldclim.org/data/index.html>).

179

180 *Land-use - Land-cover data spatial analysis*

181 A Geographic Information System (GIS) was used to compute, store and organize all the Land-
182 use Land-cover (LULC) data. The LULC data were obtained using five classes representing: 1)
183 urban surfaces, including artificial and industrial areas, mines; 2) roads; 3) bare soil, including
184 sparsely herbaceous areas, rocky and bare ground areas; 5) agriculture, including arable intensive
185 irrigated and non-irrigated areas, vineyards, fruit trees, and olives groves; 4) forest, including
186 natural and semi-natural, managed and unmanaged broadleaved, mixed, and coniferous forest,
187 scrublands and transitional woodland-scrubland areas.

188 A circular buffer with 300 m radius was first positioned surrounding the centre of each forest
189 stand, using the GPS coordinates, according to methodology applied in Samalens & Rossi (2011).
190 Inside the circular buffer, the LULC patches were manually digitalized by visual classification of
191 high-spatial resolution World Imagery layer (ArcGIS Online data, Copyright © Esri), obtained in
192 2016 with a spatial resolution of 50 cm (Fig. 2). Buffer featuring has been previously identified
193 as an important methodological approach for the identification of landscape–species relationships
194 (Rossi & Halder, 2010; Samalens & Rossi, 2011). The spatial analyses were conducted for a
195 single buffer size (radius = 300 m) which allowed not overlapping buffer radius among nearest

196 sampling points. LULC variables were evaluated as the percentage of the area occupied by each
197 class, in the total buffer area. Elevation, slope and slope orientation were obtained for each site
198 based on the SRTM 1 Arc-Second Global Digital Elevation Model, with 30 m of spatial
199 resolution (available at <https://earthexplorer.usgs.gov/>) using the geographic coordinates of the
200 sites. Orientation was calculated using the aspect function while slope was extracted as percent
201 slope using the surface toolbox in ArcGIS 10.5 (ArcGIS, Copyright © Esri). Distribution maps
202 were made using ESRI ArcGis® 10.3 software.

203 Forest land-use dominated all the studied sites, with the highest values (92.9%) observed in
204 the national park of Theniet El-Had (Table 2). Agricultural areas were common in Tipaza region
205 (15.7%) and in several sites included in the dataset of Bouchou (2015). In addition, the average
206 size of the forest patches was higher in the Theniet El-Had (32.5 ha), followed by Tipaza (18.8
207 ha), Ain-Defla (15.6 ha) and the sites surveyed by Bouchou (2015) (14.5 ha).

208

209 *Data analysis*

210 The distribution pattern of each parasitoid species was studied by fitting the Poisson model
211 (random) and negative binomial model (clustered) through generalized linear models (GLM).
212 Site was considered as a random factor. Goodness of fit was evaluated by the deviance
213 information criterion (DIC).

214 For the sampling surveys conducted in the three regions (Tipaza, Ain-Defla, and Theniet El-
215 Had) during 2017-2019, the percentage of parasitism was analysed using GLM with binomial
216 distribution, considering the proportion of eggs parasitized from the total number of eggs per egg
217 batch. The total number of parasitoids emerged for each species was also compared using GLM
218 with negative binomial distribution. The site factor was nested within the region. We analysed
219 both the numbers of parasitoids emerging from the egg batches and the percentage parasitism, as
220 we found a high variability on the number of eggs per egg batch, which influenced the percentage
221 of parasitism. The number of eggs per egg batch was tested as a relevant predictor for the
222 selection by the parasitoids using GLM and binomial negative distribution model. Fecundity, that
223 is the number of eggs per egg batch, was compared among regions using generalized mixed
224 linear model considering site as random variable. Correlations were analysed using Pearson, r ,
225 and Spearman's rho, s_r coefficients.

226 The relationships between land cover types, environmental variables and average percentage
227 parasitism rates were analysed using GLM with Gaussian distribution. Two sampling surveys
228 were used, the one conducted between 2017 and 2019, and the one conducted in 2012 by
229 Bouchou (2015). The factor sampling survey was considered to account for differences between
230 surveys. Each parasitoid species was analysed separately. Parasitism data was log transformed.
231 Data are presented in the form of average values \pm standard error (SE).

232

233 Results

234

235 Fecundity

236 Overall, the mean number of eggs per batch in the three regions surveyed was 195 ± 2.4 (range
237 60-336). Fecundity was significantly lower in Tipaza region (171 ± 2.4) compared to Theniet El-
238 Had (208 ± 3.6) and Ain-Defla (207 ± 4.1) ($F_{2, 12} = 11.1$, $p = 0.002$).

239

240 Parasitism

241 Two parasitoid species emerged from the egg batches, *B. servadeii* and *O. pityocampae*.
242 Distribution of both species was best fitted by the negative binomial model (deviance=1.33 and
243 1.75, respectively). The number of *B. servadeii* and *O. pityocampae* differed significantly among
244 the three regions (Wald $\chi^2 = 105.3$, $df = 2$, $p < 0.001$, and Wald $\chi^2 = 23.6$, $df = 2$, $p < 0.001$,
245 respectively). On average, more *B. servadeii* per egg batch emerged in Tipaza (18.6 ± 1.6).
246 Intermediate values were observed in Theniet El-Had (10.7 ± 0.9) and fewer *B. servadeii*
247 emerged in Ain-Defla (4.7 ± 0.5). As for *O. pityocampae*, highest numbers per egg batch were
248 observed in Theniet El-Had (7.7 ± 0.7). In Tipaza and in Ain-Defla the mean numbers of *O.*
249 *pityocampae* were similar, 4.2 ± 0.4 and 5.1 ± 0.5 , respectively.

250 The number of emerged *B. servadeii* (Wald $\chi^2 = 1.03$, $df = 1$, $p < 0.310$) or *O. pityocampae*
251 (Wald $\chi^2 = 3.096$, $df = 1$, $p = 0.079$) were not correlated with the fecundity.

252 At site level, from the 15 sites surveyed in 2017-2019, overall parasitism ranged from 2.8%, in
253 one site located in the region of Ain-Defla, to 25.5% in one site located in Theniet El-Had.
254 Parasitism rates differed among the three regions (Wald $\chi^2 = 849.77$, $df = 2$, $p < 0.001$), being
255 higher in Tipaza, $15.8 \% \pm 0.2$ then in Theniet El-Had, $13.3 \% \pm 0.2$, and Ain-Defla, $7.6 \% \pm 0.1$.

256 Overall parasitism rate by each species was 8.7 % for *B. servadeii* and 3.6 % for *O. pityocampae*.
257 Parasitism by *B. servadeii* surpassed that by *O. pityocampae* in 13 out of the 15 sites.

258

259 *Tent density*

260 The density of tents varied from 1.4 ± 0.2 tent per tree, observed in one site in Theniet El-Had, up
261 to 3.8 ± 0.4 in one site in Tipaza. From the survey on 2017-2019 percentage parasitism by *B.*
262 *servadeii* were negatively correlated with tent density in the same sites and year ($r = -0.608$,
263 $p=0.016$; $s_r = -0.657$, $p=0.008$, $n=15$) (Fig. 3). In contrast, the correlation between parasitism by
264 *O. pityocampae* and tent density was not significant ($r = -0.331$, $p=0.227$; $s_r = -0.225$, $p=0.420$,
265 $n=15$).

266 Tent density differed with topographic orientation (Wald $\chi^2 = 20.52$, $df=5$, $p=0.001$) as it
267 was higher on sites oriented to South, Southwest and Northwest compared to sites oriented to
268 North, East and Northeast. Topographic orientation was not a significant predictor variable for
269 parasitism by *B. servadeii* (Wald $\chi^2 = 4.86$, $df= 5$, $p=0.433$) or *O. pityocampae* (Wald $\chi^2 =$
270 2.42 , $df=5$, $p=0.788$). Slope was not a significant predictor of parasitism by *B. servadeii* (Wald
271 $\chi^2 = 1.761$, $df=1$, $p=0.184$) or *O. pityocampae* (Wald $\chi^2 = 0.4828$, $df=1$, $p=0.488$).

272

273 *Large scale study and land cover*

274 When the sites studied by Bouchou (2015) were added, a dataset of 27 sites was obtained, which
275 covers most of the north of Algeria (Fig. 1). Overall, parasitism by *B. servadeii* and *O.*
276 *pityocampae* was significantly correlated with each other ($r= 0.432$, $p=0.024$). By comparing data
277 from 2017-2019 with those of Bouchou (2015), we found that percentage parasitism did not
278 differ between the two sampling surveys (Wald $\chi^2 = 2.502$, $p=0.114$ and Wald $\chi^2 = 2.996$,
279 $p=0.083$, for *B. servadeii* and *O. pityocampae*, respectively).

280 The proportion of forest cover in the surrounding landscape did not explain the differences in
281 parasitism rates by *B. servadeii* (Wald $\chi^2 = 0.115$, $p=0.735$) while it did for *O. pityocampae*
282 (Wald $\chi^2 = 7.230$, $p=0.007$). Parasitism by *O. pityocampae* increased with forest cover in a
283 non-linear form (Fig. 4). Also, the proportion of agriculture land cover did not explain parasitism
284 by *B. servadeii* (Wald $\chi^2 = 0.206$, $p=0.650$) whereas it did for *O. pityocampae* (Wald $\chi^2 =$
285 6.833 , $p=0.009$), with which it was positively correlated. The proportion of urban area, roads and
286 bare soil were not correlated with parasitism for any species.

287

288 *Climate*

289 For the larger dataset, the average parasitism rates and the average of maximal temperatures of
290 the three summer months, for the 1970-2000 period, were not significantly correlated (parameter
291 estimate $B = -0.044 \pm 0.073$, $p = 0.553$, $n = 27$).

292

293 **Discussion**

294 Analysing how top-down regulation of forest insect pests is affected by host density, landscape
295 structure and composition, and climate is important to understand drivers of population dynamics
296 and management actions that may prevent outbreaks. This study focused on egg parasitism rate of
297 the pine processionary moth in a Mediterranean country (Algeria) poorly studied in this concern.
298 Egg parasitism in this pest species has been discussed in many papers and summarized in Auger-
299 Rozenberg *et al.* (2015). It typically ranged from 6 to about 40% in studies conducted in Southern
300 Europe (Mirchev *et al.*, 1999; Schmidt *et al.*, 1999; Tsankov *et al.*, 1996, 1998). Data from
301 Algeria presented in this study fall in the lower part of the interval, ranging from 3 to 25.5% in
302 the 15 sites studied in 2017-2019 and from 2.1 to 15.6% in the 12 sites studied in 2012. As data
303 were collected in different years, there could be a year effect. Still, overall differences between
304 the two samplings were not significant. The pooled average parasitism from the 27 sites was less
305 than 10%. The data appear to be similar to those observed in the Djelfa region of Algeria by
306 Zamoum *et al.* (1998). Similarly low parasitism rates were found in studies from northern Africa
307 and southern Mediterranean countries close to Algeria, namely Morocco (21%) (Schmidt *et al.*,
308 1997), southern Spain (4-15%) (Perez-Contreras & Soler, 2004), Portugal (2-29%) (Arnaldo &
309 Torres, 2006; Santos *et al.*, 2013). Higher parasitism rates were observed from cooler geographic
310 areas, i.e. Bulgaria (38.9%) (Tsankov *et al.*, 1996; Tsankov *et al.*, 1998), and Greece (44.3%)
311 (Mirchev *et al.*, 2010), although a strong variation was observed among years, as for example in
312 France (5-43%) (Auger-Rozenberg *et al.*, 2015).

313 Several factors may explain why egg parasitism is lower in the southern part of the range of
314 the pine processionary moth. First, mean realised fecundity of the host is also lower at the
315 southern edge of the range than at higher latitudes (Pimentel *et al.* 2010), resulting in a reduced
316 availability of eggs per egg batch, which may limit the access of the parasitoids to the resources
317 (Mills & Getz, 1996). Second, egg batches from the southern populations of the pine

318 processionary moth are characterized by a different type of scales covering the eggs (Petrucco-
319 Toffolo *et al.*, 2018), which may negatively affect the activity of the egg parasitoids that are
320 known to respond to the quality of the eggs (Uemura *et al.*, 2019, Zovi *et al.*, 2008). Third, the
321 climate at the southern edge of the range can make it difficult for parasitoids to exploit the
322 resources, because of a bad synchronisation between parasitoid emergence and moth oviposition
323 (Auger-Rozenberg *et al.*, 2015) or because of a higher probability to be exposed to excessively
324 high temperatures.

325 In a study conducted by Tiberi *et al.* (2015), with a 9-years' time series observed in Monte San
326 Michele, Florence, Italy, the average parasitism varied inter-annually from 4 to 26%. It was
327 proposed that daily temperatures above 30°C would explain lower parasitism rates in years with
328 hot summers. Assuming this hypothesis, the parasitism rates in the present study should be
329 extremely low as the average temperature of summer month in the studied locations was above
330 30°C, and, in many sites, temperatures in the studied year in the date of collection, were
331 frequently above 40°C. As the relationship between maximum temperature of the summer months
332 and parasitism was not significant in this study, temperature should be excluded as a major driver
333 of observed parasitism rates. To explain this outcome, an adaptation of the parasitoid species to
334 the high summer temperatures observed in this region can be hypothesized. Likewise, but at the
335 herbivore scale, the summer form of the pine processionary moth shows an adaptation of the
336 larvae to survive at higher temperatures than those experienced by the winter form, even above
337 38°C (Santos *et al.*, 2011).

338 Nevertheless, more studies based on wider spatial and temporal scales would be useful to
339 disentangle the diverse factors affecting the egg parasitism across geographic/climatic gradients.
340 They should be ideally combined with mechanistic studies on the effect of climate, and
341 particularly climate change, on the performance of the egg parasitoids, following the indications
342 provided by Auger-Rozenberg *et al.* (2015).

343 The two major egg parasitoid species found in this study, *B. servadeii* and *O. pityocampae*, are
344 the same observed all over the Mediterranean basin, although in variable proportions (e.g.
345 Tsankov *et al.*, 1998, Schmidt *et al.*, 1997; Mirchev *et al.*, 2010; Tiberi *et al.*, 2015, Perez-
346 Contreras & Soler, 2004, Arnaldo & Torres, 2006). In the present study, overall parasitism by *B.*
347 *servadeii* was higher than that of *O. pityocampae*, with slight differences among sites. Both

348 species showed an aggregated distribution pattern, best explained by a negative binomial model,
349 as previously shown by Battisti (1989).

350 The abundance of the two parasitoid species could be explained by different factors. As *B.*
351 *servadeii* is a specialist parasitoid (Simonato *et al.*, 2019), a density-dependent response is
352 expected (Mills and Getz, 1996). Such a relationship has been shown by the negative correlation
353 between parasitism and tent density in the same year, meaning that the parasitoid may effectively
354 act as a regulator of the host density. It is also probable to display a density-dependent response
355 with a time lag. A 2-year lag between the host density and the parasitoid response would produce
356 negative correlation relationship. Further, a second-order feedback typically observed for many
357 forest defoliator species seems to be strongly leading to cyclic outbreaks (Berryman, 1996).
358 Effectively, some studies indicate the existence of periodic outbreaks in the pine processionary
359 moth (Tamburini *et al.*, 2013; Li *et al.*, 2015), corroborating the hypothesis of host-parasitoid
360 interaction with time lag. In a long-term study on pine processionary moth egg parasitoids,
361 Mirchev *et al.* (2017) observed that maximum parasitism values were observed two years after
362 outbreak and declined thereafter. The availability of a temporal series for the southern edge of the
363 range would allow testing if a density-dependent relationship is driving the population dynamics
364 in this area.

365 Conversely, no correlation between tent density and parasitism rate was observed for the
366 generalist parasitoid *O. pityocampae*, as expected based on the specialist/generalist parasitoid
367 hypothesis (Hawkins, 1994). An interesting result was the finding of a positive correlation
368 between the proportion of agriculture and forest cover with the parasitism by *O. pityocampae*.
369 This may be explained by this species being a generalist parasitoid, i.e. finding a higher
370 probability of alternative host species in sites where more diversity of hosts is expected (Sheehan,
371 1986). The need to find alternative hosts during periods when the eggs of the pine processionary
372 moth are not available does not allow to show a direct response to the host density, although
373 locally parasitism can be high when for some reasons a high abundance of parasitoids coincides
374 with availability of host eggs (Hawkins, 1994).

375 Other landscape characteristics may be also important in order to understand the spatial
376 distribution of the parasitism in the pine processionary moth system. Patch richness density, an
377 indicator of landscape diversity, as well as the proportion of different land uses, have been found
378 to correlate negatively with the host population density in France (Samalens & Rossi, 2011). The

379 referred study also identified a positive correlation between pine forest cover and pine
380 processionary moth tent density, although the landscape diversity was more important. The
381 presence and abundance of the egg parasitoids may be also influenced by the landscape diversity
382 (Roland and Taylor, 1997). For instance, Faria *et al.* (2008) showed that the regulatory action of
383 parasitoids may be supported when additional sugar-rich food is available, which is more likely
384 to occur in highly heterogeneous landscape when compared with monoculture forest areas. In
385 addition, it is known that egg parasitoids of the pine processionary moth do respond to the
386 availability of sugar-rich food (Dulaurent *et al.*, 2011). In this study, a positive correlation
387 between the proportion of agricultural areas and the parasitism by *O. pityocampae* was found, but
388 a test for the importance of landscape diversity could not be done. Further studies regarding
389 forest composition and landscape characteristics at different spatial scaled would be needed to
390 test this hypothesis.

391

392

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554 **Table captions**

555

556 **Table 1** Main environmental characteristics of the studied sites surveyed in 2017-2019 and in
557 2012 (Bouchou & Chakali, 2014).

558

559

560 **Table 2** Land-use types in the studied regions. Mean (standard deviation) of land-use patches in
561 the 300 m-buffer. Total number of land-use patches (n_{SU}) contributing for each land-use type in
562 each region.

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563 Table 1

Region	Site	Longitude E	Latitude N	Elevation (m)	Topographic orientation	Slope (%)	Tree height (m)
Data survey 2017-2019							
Tipaza	Kolea North	2.795089	36.645925	113	East	8.1	2 - 6
	Attatba	2.690203	36.598186	216	Northeast	13.2	6 - 8
	Kolea South	2.791331	36.637197	103	South	18.2	2 - 6
	Tipaza	2.480361	36.589036	67	North	31.1	7 - 10
	Sidi-Rached	2.550094	36.573828	251	South	11.3	2 - 7
Ain-Defla	Djemaa O. Chikh	2.015763	36.135899	508	West	9.7	3 - 5
	Oued Djemaa	2.295372	36.059944	437	Northeast	10.9	2 - 5
	Djebel Doui	1.959523	36.237487	548	Northwest	33.7	2 - 5
	Annab	1.893689	36.349358	813	North	42.8	6 - 10
	El Mayenne	1.758825	36.070772	625	North	15.6	6 - 11
Theniet El-Had	Centre	1.969208	35.858728	1643	East	11.8	6 - 20
	North High	2.007728	35.853194	1510	North	56.7	6 - 20
	North Low	2.002942	35.858811	1368	Northeast	23.6	6 - 20
	South High	1.996332	35.849708	1391	West	24.0	6 - 20
	South Low	1.987008	35.841908	1283	West	16.2	6 - 20
Data survey 2012							
Several (Bouchou and Chakali 2014	Batna	6.209925	35.567356	1203	South	6.09	NA
	Bouarfa	2.825119	36.451228	605	Northwest	13.29	NA
	Chr�ea	2.633333	36.316667	1400	East	10.20	NA
	Chr�ea2	3.033333	36.500000	1400	Northwest	45.86	NA
	Cherchell	2.240200	36.615783	200	Northwest	25.82	NA

Chéla	6.617825	35.302356	1933	Northeast	20.31	NA
El bayadh	1.164981	33.728017	1200	Northwest	47.33	NA
El Kala	8.181283	36.874786	200	Southeast	2.92	NA
Moudjbara	3.481503	34.510575	1055	Southwest	2.92	NA
Sétif SF	5.493631	36.365592	804	Northeast	24.65	NA
Senalba	3.134353	34.637978	1306	Northwest	8.10	NA
Theniet El Had	2.002036	35.855456	1465	Northeast	21.75	NA
Tlemcen	-1.030711	34.613600	1141	East	4.05	NA

564 NA- Not available

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565 Table 2

Designation	Tipaza (n _{SU} =31)	Ain-Defla (n _{SU} =27)	Theniet El-Had (n _{SU} =19)	Several (Bouchon) (n _{SU} =80)
	Land-use cover (%)	Land-use cover (%)	Land-use cover (%)	Land-use cover (%)
Urban	4.1 (4.7)	0.04 (0.08)	0.8 (1.2)	3.2 (8.5)
Roads	3.2 (2.6)	2.2 (1.1)	1.2 (0.9)	2.5 (1.9)
Bare soil	4.8 (2.7)	4.36 (1.6)	2.7 (0.7)	14.3 (5.8)
Agriculture	15.7 (18.6)	9.9 (21.0)	2.4 (5.3)	17.8 (31.1)
Forest	72.2 (21.4)	83.5 (19.8)	92.9 (9.6)	62.2 (35.9)

567 **Figure captions**

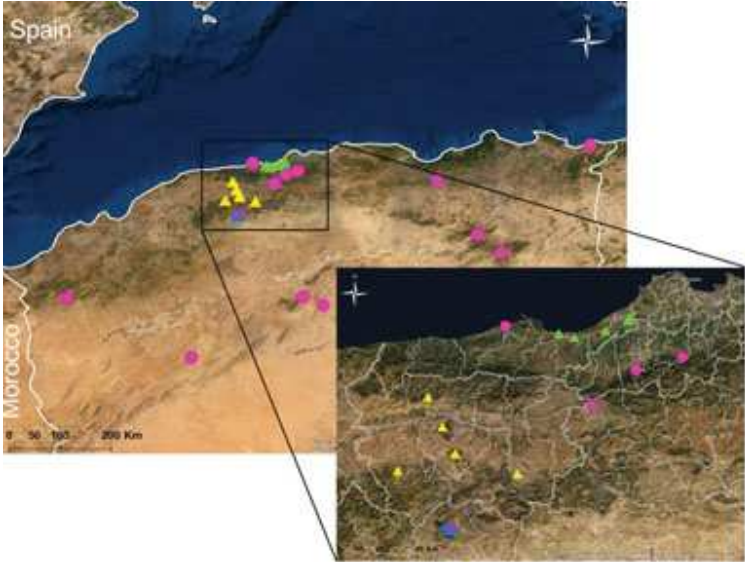
568
569 **Figure 1** Sampling sites (triangles: data 2017-2019, circles: data 2012 from Bouchou, 2015) in
570 northern Algeria. Green triangles represent Tipaza, yellow triangles Ain-Defla and blue triangles
571 Theniet El-Had regions.

572
573 **Figure 2** Illustration of the delimitation of the land-use types, in the 300 m buffer, using ArcGis
574 World Imagery layer, for a) Tipaza site (Tipaza region), b) Djebel Doui site (Ain-Defla region),
575 c) North High site (Theniet El-Had region) and d) Sétif SF site (as an example for Bouchou
576 (2015) dataset).

577
578 **Figure 3** Relationship between percentage parasitism by *B. servadeii* and tent density, expressed
579 in the average number of tents per tree (n=15 sites, data 2017-2019), with regression equation and
580 R^2 .

581
582 **Figure 4** Relationship between parasitism rate by *O. pityocampae* and forest cover (n=27 sites,
583 15 sites from 2017-2019 indicated by black circles and 12 sites from Bouchou, 2015 indicated by
584 triangles). Data fitted by an exponential model. $y=0.7757e^{0.0149x}$; $R^2 = 0.285$, $P=0.04$.

585
586
587 **Supplemented Material Figure 1** Illustration of the sampled sites in three selected regions



Sampling sites (triangles: data 2017-2019, circles: data 2012 from Bouchou, 2015) in northern Algeria. Green triangles represent Tipaza, yellow triangles Ain-Defla and blue triangles Theniet El-Had regions.

32x24mm (300 x 300 DPI)

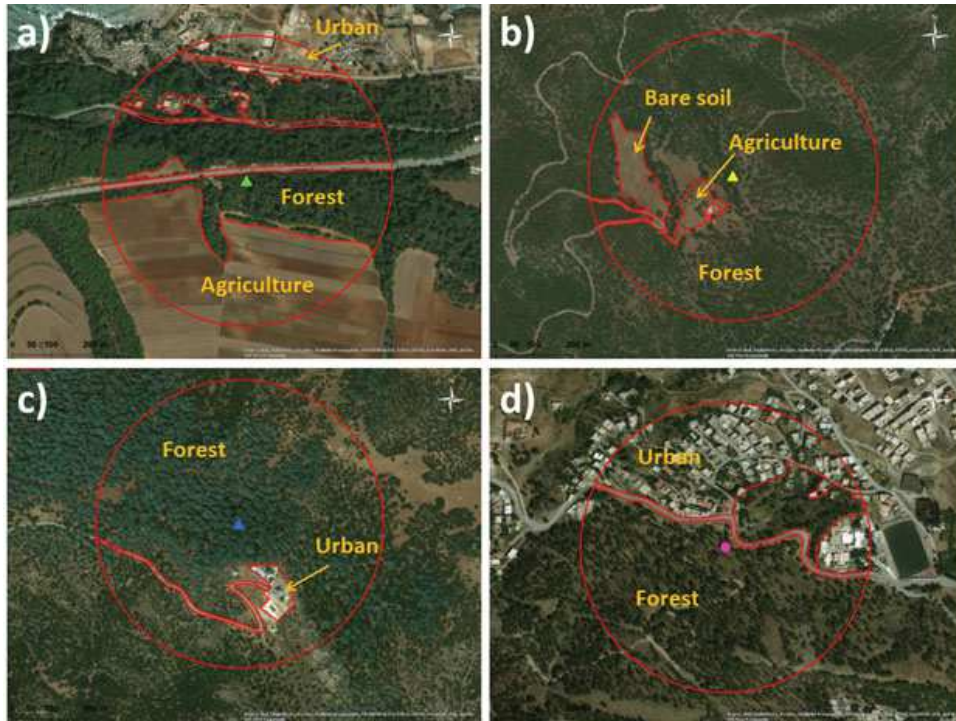
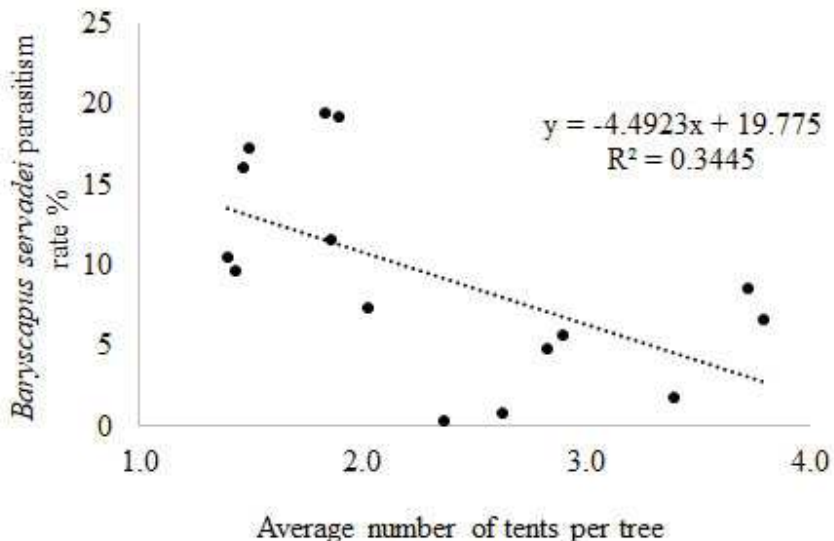


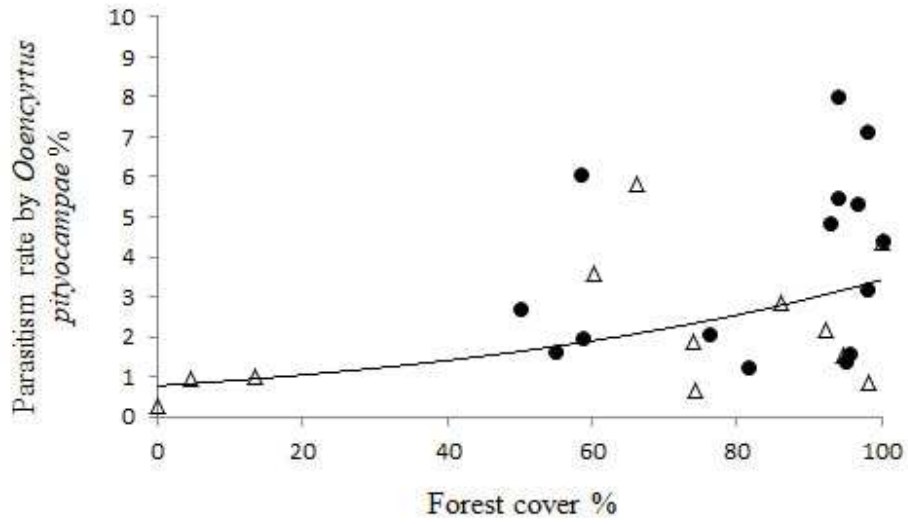
Illustration of the delimitation of the land-use types, in the 300 m buffer, using ArcGis World Imagery layer, for a) Tipaza site (Tipaza region), b) Djebel Doui site (Ain-Defla region), c) North High site (Theniet El-Had region) and d) Sétif SF site (as an example for Bouchou (2015) dataset).

53x39mm (300 x 300 DPI)



Relationship between percentage parasitism by *B. servadeii* and tent density, expressed in the average number of tents per tree (n=15 sites, data 2017-2019), with regression equation and R2.

38x24mm (300 x 300 DPI)



Relationship between parasitism rate by *O. pityocampae* and forest cover (n=27 sites, 15 sites from 2017-2019 indicated by black circles and 12 sites from Bouchou, 2015 indicated by triangles). Data fitted by an exponential model: $y=0.7757e^{0.0149x}$; $R^2 = 0.285$, $P=0.04$.

40x24mm (300 x 300 DPI)



Illustration of the sampled sites in three selected regions.

53x39mm (300 x 300 DPI)