



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  $195 \pm 2.4$  (range  
237 60-336). Fecundity was significantly lower in Tipaza region ( $171 \pm 2.4$ ) compared to Theniet El-  
238 Had ( $208 \pm 3.6$ ) and Ain-Defla ( $207 \pm 4.1$ ) ( $F_{2, 12} = 11.1$ ,  $p = 0.002$ ).

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 ( $18.6 \pm 1.6$ ).  
246 Intermediate values were observed in Theniet El-Had ( $10.7 \pm 0.9$ ) and fewer *B. servadeii*  
247 emerged in Ain-Defla ( $4.7 \pm 0.5$ ). As for *O. pityocampae*, highest numbers per egg batch were  
248 observed in Theniet El-Had ( $7.7 \pm 0.7$ ). In Tipaza and in Ain-Defla the mean numbers of *O.*  
249 *pityocampae* were similar,  $4.2 \pm 0.4$  and  $5.1 \pm 0.5$ , 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  $1.4 \pm 0.2$  tent per tree, observed in one site in Theniet El-Had, up  
261 to  $3.8 \pm 0.4$  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

393 **References**

- 394 Arnaldo, P.S. & Torres, L.M. (2006) Effect of different hosts on *Thaumetopoea pityocampa*  
395 populations in northeast Portugal. *Phytoparasitica*, **34**, 523-530.
- 396 Auger-Rozenberg, M-A., Barbaro, L., Battisti, A., Blache, S., Charbonnier, Y., Denux, O.,  
397 Garcia, J., Goussard, F., Imbert, C-E-, Kerdelhué, C., Roques, A., Torres-Leguizamon, M.  
398 & Vetillard, F. (2015) Ecological responses of parasitoids, predators and associated insect  
399 communities to the climate-driven expansion of pine processionary moth. In Roques, A.  
400 (Ed), *Processionary Moths and Climate Change: An Update*. Springer, Dordrecht. pp.  
401 311-358.
- 402 Barbaro, L. & Battisti, A. (2011). Birds as predators of the pine processionary moth (Lepidoptera:  
403 Notodontidae). *Biological control*, **56**, 107-114.
- 404 Battisti, A. (1989) Field studies on the behaviour of two egg parasitoids of the pine processionary  
405 moth *Thaumetopoea pityocampa*. *Entomophaga*, **34**, 29-38.
- 406 Battisti, A., Stastny, M., Netherer, S., Robinet, C., Schopf, A., Roques, A. & Larsson, S. (2005).  
407 Expansion of geographic range in the pine processionary moth caused by increased winter  
408 temperatures. *Ecological applications*, **15**, 2084-2096.
- 409 Battisti, A., Avci, M., Avtzi, D.N., Jamaa, M.L.B., Berardi, L., Berretima, W., Branco, M.,  
410 Chakali, G., El Fels, M.A., Frérot, B. & Hódar, J. A. (2015) Natural history of the  
411 processionary moths (*Thaumetopoea* spp.): new insights in relation to climate  
412 change. In *Processionary moths and climate change: An update*. Springer,  
413 Dordrecht, (pp. 15-79).
- 414 Battisti, A., Larsson, S. & Roques, A. (2017) Processionary moths and associated urtication risk:  
415 global-change driven effects. *Annual Review of Entomology*, **62**, 323-342.
- 416 Berryman, A.A. (1996) What causes population cycles of forest Lepidoptera? *Trends in Ecology*  
417 *& Evolution*, **11**, 28-32.
- 418 Bouchou L. & Chakali G. (2014) Egg mass analysis of the pine processionary moth,  
419 *Thaumetopoea pityocampa* Schiff. (Lepidoptera, Thaumetopoeidae) in Aleppo pine  
420 forests in semi-arid area (Djelfa - Algeria). *International Journal of Agricultural Science*  
421 *and Research*, **4**, 43-52.

- 422 Bouchou, L. (2015) Les parasitoïdes embryonnaires de la processionnaire du pin,  
423 *Thaumetaupoea pityocampa* Schiff et leur importance dans quelques peuplements de pin  
424 et de cèdre du Nord de l'Algérie. Thèse de Doctorat, ENSA El-Harrach -Alger- Algeria.
- 425 Carcanague, C. (1988) Les chenilles processionnaires du pin et du chêne: risques liés à leurs  
426 envenimations et à leur expansion sur le territoire français, conseils et traitements  
427 associés. Thèse de doctorat : Université de Limoges (France).
- 428 Charbonnier, Y., Barbaro, L., Theillout, A. & Jactel, H. (2014) Numerical and functional  
429 responses of forest bats to a major insect pest in pine plantations. *PloS one*, **9**, e109488.
- 430 Damien, M., Jactel, H., Meredieu, C., Régolini, M., van Halder, I. & Castagneyrol, B. (2016) Pest  
431 damage in mixed forests: Disentangling the effects of neighbor identity, host density and  
432 host apparency at different spatial scales. *Forest Ecology and Management*, **378**, 103-110.
- 433 De La Vega, X., Grez, A.A. & Simonetti, J.A. (2012) Is top-down control by predators driving  
434 insect abundance and herbivory rates in fragmented forests? *Austral Ecology*, **37**, 836–  
435 844.
- 436 Démolin, G., Delmas, J.C. (1967) Les ephippigères (Orthopteres Tettigonidae) prédateurs  
437 occasionnels mais importants de *Thaumetopoea pityocampa* Schiff. *Entomophaga*, **12**,  
438 399-401.
- 439 Dulaurent, A.M., Rossi, J.P., Deborde, C., Moing, A., Menassieu, P. & Jactel, H. (2011)  
440 Honeydew feeding increased the longevity of two egg parasitoids of the pine  
441 processionary moth. *Journal of Applied Entomology*, **135**, 184-194.
- 442 Faria, C.A., Wackers, F.L. & Turlings, T.C.J. (2008) The nutritional value of aphid honeydew for  
443 non-aphid parasitoids. *Basic Applied Ecology*, **9**, 286–297.
- 444 Fick, S.E. & Hijmans, R.J. (2017) Worldclim 2: New 1-km spatial resolution climate surfaces for  
445 global land areas. *International Journal of Climatology*, **37**, 4302-4315
- 446 Hawkins B.A. (1994) Pattern and process in host-parasitoid interactions. Cambridge University  
447 Press, Cambridge UK.
- 448 Imbert, C.E., Goussard, F. & Roques, A. (2012) Is the expansion of the pine processionary moth,  
449 due to global warming, impacting the endangered Spanish moon moth through an induced  
450 change in food quality? *Integrative zoology*, **7**, 147-157.
- 451 Jacquet, J.S., Orazio, C. & Jactel, H. (2012) Defoliation by processionary moth significantly  
452 reduces tree growth: a quantitative review. *Annals of Forest Science*, **69**, 857-866.

- 453 Jactel, H., Barbaro, L., Battisti, A., Bosc, A., Branco, M., Brockerhoff, E. G., Castagneyrol, B.,  
454 Dulaurent, A.-M., Hódar, J. A., Jacquet, J.-S., Mateus, E., Paiva, M. R., Roques, A.,  
455 Samalens, J.-C., Santos, H. & Schlyter, F. (2015) Insect – Tree Interactions in  
456 *Thaumetopoea pityocampa*. In Roques, A. (Ed), Processionary Moths and Climate  
457 Change: An Update. Springer, Dordrecht (p. 265-310).
- 458 Li, S., Daudin, J.J., Piou, D., Robinet, C. & Jactel, H. (2015) Periodicity and synchrony of pine  
459 processionary moth outbreaks in France. *Forest Ecology and Management*, **354**, 309-317.
- 460 Mills, N.J. & Getz, W.M. (1996) Modeling the biological control of insect pests: a review of host  
461 parasitoid models. *Ecological Modeling*, **92**, 121–143.
- 462 Mirchev, P., Schmidt, G.H., Tsankov, G. & Pllana, S. (1999) Egg parasitoids of the processionary  
463 moth *Thaumetopoea pityocampa* (Den. & Schiff.) collected in Albania. *Bollettino di*  
464 *Zoologia agraria e di Bachicoltura*, **31**, 152-165.
- 465 Mirchev, P., Tsankov, G., Douma-Petridou, E. & Avtzis, N. (2010) Comparative analysis of  
466 participation of egg parasitoids of pine processionary moth, *Thaumetopoea pityocampa*  
467 (Den. & Schiff.) (Lep.: Thaumetopoeidae) in northern and southern mainland Greece. *Silva*  
468 *Balcanica*, **11**, 73-97.
- 469 Mirchev, P., Dautbašić, M., Mujezinović, O., Georgiev, G., Georgieva, M. & Boyadzhiev, P.  
470 (2015) Structure of egg batches, hatching rates and parasitoids of pine processionary tree  
471 eggs, *Thaumetopoea pityocampa* (Denis and Schiffermüller, 1775) (Lepidoptera:  
472 Notodontidae). *Acta Zoologica Bulgarica*, **67**, 579-586.
- 473 Mirchev, P., Georgiev, G. & Tsankov, G. (2017) Long-term studies on parasitoids of pine  
474 processionary pine (*Thaumetopoea pityocampa*) eggs in a new locality in Bulgaria.  
475 *Journal of the Entomological Research Society*, **19**, 15-25.
- 476 Perez-Contreras, T. & Soler, J.J. (2004) Egg parasitoids select for large clutch sizes and covering  
477 layers in pine processionary moths (*Thaumetopoea pityocampa*). *Annals Zoologici*  
478 *Fennici*, **41**, 587-597.
- 479 Petrucco-Toffolo, E., Basso, A., Kerdelhué, C., Ipekdal, K., Mendel, Z, Simonato, M. & Battisti  
480 A. (2018). Evidence of potential hybridization in the *Thaumetopoea pityocampa* -  
481 *wilkinsoni* complex. *Agricultural and Forest Entomology*, **20**, 9-17.

- 482 Pimentel, C., Ferreira, C. & Nilsson, J. Å. (2010) Latitudinal gradients and the shaping of life-  
483 history traits in a gregarious caterpillar. *Biological Journal of the Linnean Society*, **100**,  
484 224-236.
- 485 Robinet, C., Baier, P., Pennerstorfer, J., Schopf, J. & Roques, A. (2007) Modelling the effects of  
486 climate change on the pine processionary moth (*Thaumetopoea pityocampa* L.) expansion  
487 in France. *Global Ecology and Biogeography*, **16**, 460-471.
- 488 Roland, J. & Taylor, P. (1997) Insect parasitoid species respond to forest structure at different  
489 spatial scales. *Nature*, **386**, 710–713.
- 490 Rossi, J.P. & van Halder, I. (2010) Towards indicators of butterfly biodiversity based on a  
491 multiscale landscape description. *Ecological Indicators*, **10**, 452–458.
- 492 Samalens, J. & Rossi, J. (2011) Does landscape composition alter the spatiotemporal distribution  
493 of the pine processionary moth in a pine plantation forest? *Population Ecology*, **53**, 287-  
494 296.
- 495 Santos, H., Paiva, M. R., Tavares, C., Kerdelhue, C., & Branco, M. (2011) Temperature niche  
496 shift observed in a Lepidoptera population under allochronic divergence. *Journal of*  
497 *Evolutionary Biology*, **24**, 1897-1905.
- 498 Santos, H.M., Paiva, M.R., Rocha, S., Kerdelhué, C. & Branco, M. (2013) Phenotypic divergence  
499 in reproductive traits of a moth population experiencing a phenological shift. *Ecology and*  
500 *evolution*, **3**, 5098-5108.
- 501 Sheehan, W. (1986) Response by specialist and generalist natural enemies to agroecosystem  
502 diversification: a selective review. *Environmental Entomology*, **15**, 456-461.
- 503 Schmidt, H., Mirchev, P. & Tsankov, G. (1997) The egg parasitoids of *Thaumetopoea*  
504 *pityocampa* in the atlas Mountains near Marrakech (Morocco). *Phytoparasitica*, **25**, 275.
- 505 Schmidt, G.H., Tanzen, E. & Bellin, S. (1999) Structure of egg-batches of *Thaumetopoea*  
506 *pityocampa* (Den. and Schiff.) (Lep., Thaumetopoeidae), egg parasitoids and rate of egg  
507 parasitism on the Iberian Peninsula. *Journal of Applied Entomology*, **123**, 449-458.
- 508 Simonato M, Pilati M, Magnoux E, Courtin C, Sauné L, Rousselet J, Battisti A, Auger-  
509 Rozenberg M-A & Kerdelhué C (2019) A population genetic study of the egg parasitoid  
510 *Baryscapus servadeii* reveals large scale automictic parthenogenesis and almost fixed  
511 homozygosity. *Biological Control*, **139**, 104097.

- 512 Tamburini, G., Marini, L., Hellrigl, K., Salvadori, C. & Battisti, A. (2013) Effects of climate and  
513 density-dependent factors on population dynamics of the pine processionary moth in the  
514 Southern Alps. *Climatic Change*, **121**, 701-712.
- 515 Tiberi, R., Bracalini, M., Croci, F., Tellini Florenzano, G. & Panzavolta, T. (2015) Effects of  
516 climate on pine processionary moth fecundity and on its egg parasitoids. *Ecology and  
517 evolution*, **5**, 5372-5382.
- 518 Tsankov, G. (1990) Egg parasitoids of the pine processionary moth, *Thaumetopoea pityocampa*  
519 (Den. & Schiff.) (Lep., Thaumetopeidae) in Bulgaria: Species, importance, biology and  
520 behaviour. *Journal of Applied Entomology*, **110**, 7-13.
- 521 Tsankov, G., Schmidt, G.H. & Mirchev, P. (1996) Parasitism of egg batches of the pine  
522 processionary *Thaumetopoea pityocampa* (Den & Schiff.) (Lep., Thaumetopoeidae) in  
523 various parts of Bulgaria. *Journal of Applied Entomology*, **120**, 93-105.
- 524 Tsankov, G., Schmidt, G.H. & Mirchev, P. (1998) Studies on the egg parasitism in  
525 *Thaumetopoea pityocampa* over a period of four years (1991–1994) at  
526 Marikostino/Bulgaria. *Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz*, **71**,  
527 1-7.
- 528 Turchin, P., Wood, S.N., Ellner, S.P., Kendall, B.E., Murdoch, W.W., Fischlin, A., Casas, J.,  
529 Mccauley, E. & Briggs, C.J. (2003) Dynamical effects of plant quality and parasitism on  
530 population cycles of larch budmoth. *Ecology*, **84**, 1207–1214.
- 531 Uemura, M., Perkins, L., Battisti A. & Zalucki, M. (2019) Egg mass structure of the  
532 processionary caterpillar *Ochrogaster lunifer* (Lepidoptera: Notodontidae): is the outer  
533 egg layer sacrificed for attack by the egg parasitoid *Anastatus fuligispina* (Hymenoptera:  
534 Chalcidoidea: Eupelmidae)? *Austral Entomology*, **58**, 810–815.
- 535 Valdés-Correcher, E., Van Halder, I., Barbaro, L., Castagneyrol, B. & Hampe, A. (2019) Insect  
536 herbivory and avian insectivory in novel native oak forests: Divergent effects of stand size  
537 and connectivity. *Forest Ecology and Management*, **445**, 146-153.
- 538 Zamoum, M., Guendouz, H., & Deia, D. (2016). Structure des communautés d'ennemis naturels  
539 de *Thaumetopoea pityocampa* Denis & Schiffermüller (Lep., Thaumetopoeidae) sur pin  
540 d'Alep en Algérie. *Entomologica*, **40**, 139-151.
- 541 Zovi, D., Stastny, M., Battisti, A. & Larsson, S. (2008) Ecological costs on local adaptation of an  
542 insect herbivore imposed by host plants and natural enemies. *Ecology*, **89**, 1388-1398.

**543 Acknowledgments**

544 This study received support from European Union's Horizon 2020 Program for Research and  
545 Innovation under grant agreement no. 771271 'HOMED' and from Forest Research Centre  
546 (CEF). We thank H. Jactel (INRAe, France) for helpful comments. CEF is a research unit funded  
547 by Foundation for Science and Technology (FCT), Portugal (UID/AGR/00239/2019 and  
548 UIDB/00239/2020). MRF was supported by national funds via FCT – Fundação para a Ciência e  
549 a Tecnologia, I.P., under "Norma Transitória DL57/2016/CP1382/CT0019. The authors also  
550 gratefully acknowledge DGF (General Forestry Direction) and DGRSDT (General Direction for  
551 Research and Technology development) for facilities and assistance. The authors have no conflict  
552 of interest. There are no disputes over the ownership of the data presented in the paper. All  
553 contributions have been attributed appropriately via co-authorship and acknowledgements.

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.

For Review Only

563 Table 1

Region	Site	Longitude E	Latitude N	Elevation (m)	Topographic orientation	Slope (%)	Tree height (m)
<b>Data survey 2017-2019</b>							
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
<b>Data survey 2012</b>							
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

For Review Only

565 Table 2

Designation	Tipaza (n <sub>SU</sub> =31)	Ain-Defla (n <sub>SU</sub> =27)	Theniet El-Had (n <sub>SU</sub> =19)	Several (Bouchon ) (n <sub>SU</sub> =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**

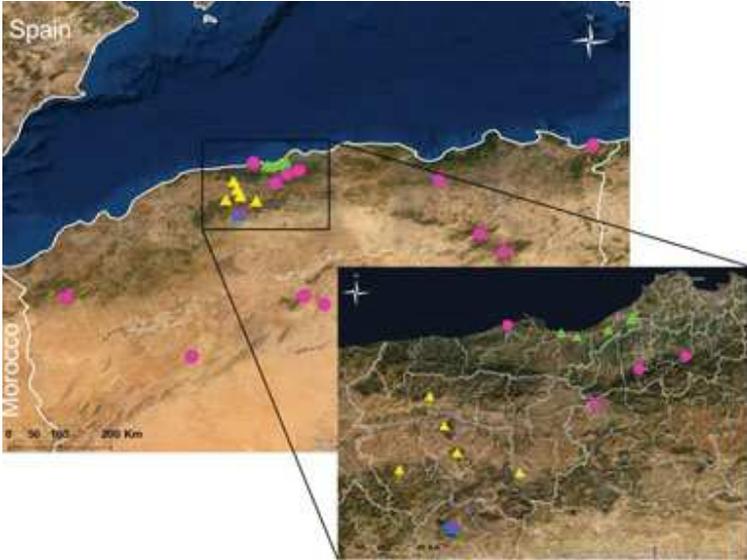
568  
569 **Figure 1** Sampling sites (triangles: data 2017-2019, circles: data 2012 from Bouchou, 2015) in  
570 northern Algeria. Green triangles represent Tipaza, yellow triangles Ain-Defla and blue triangles  
571 Theniet El-Had regions.

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)

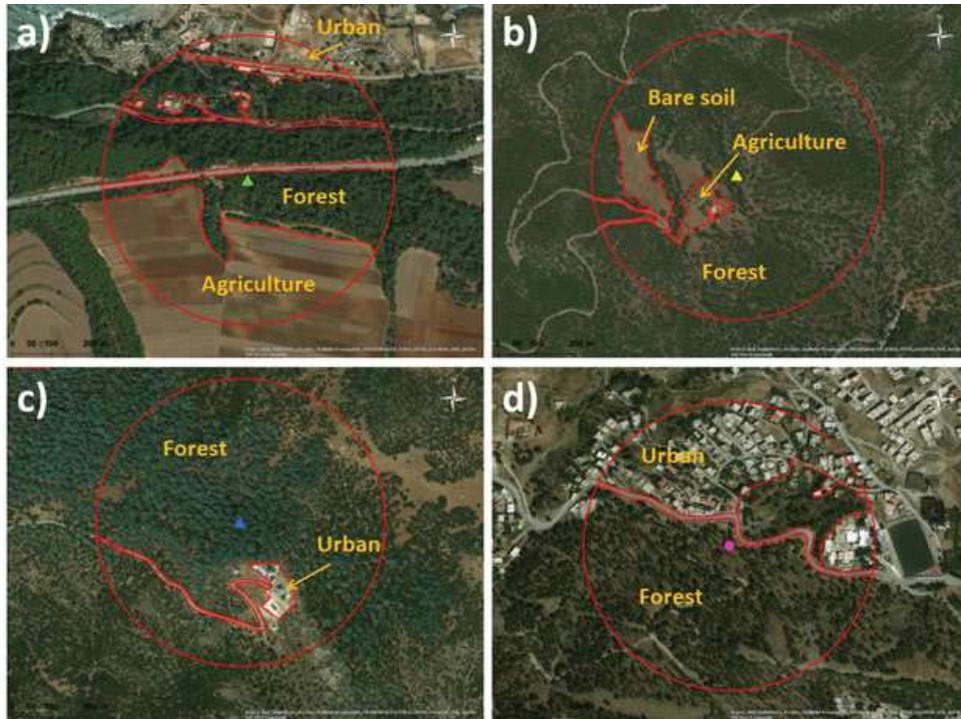
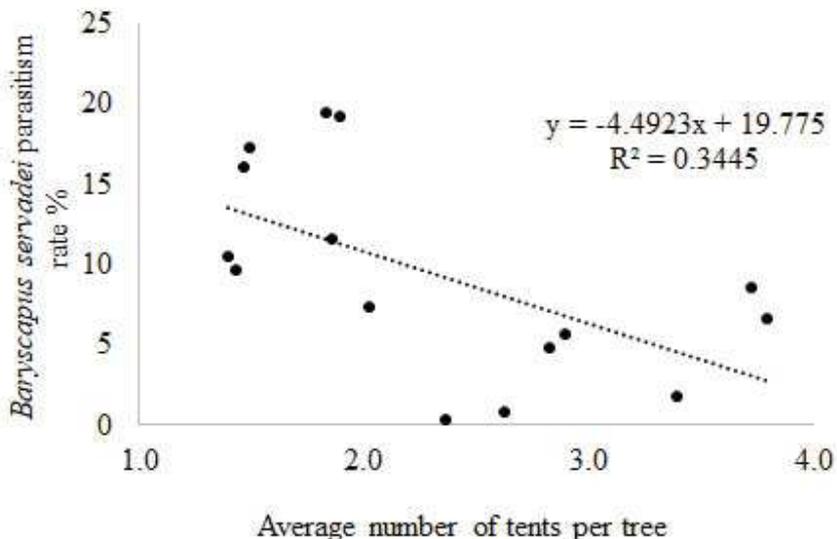


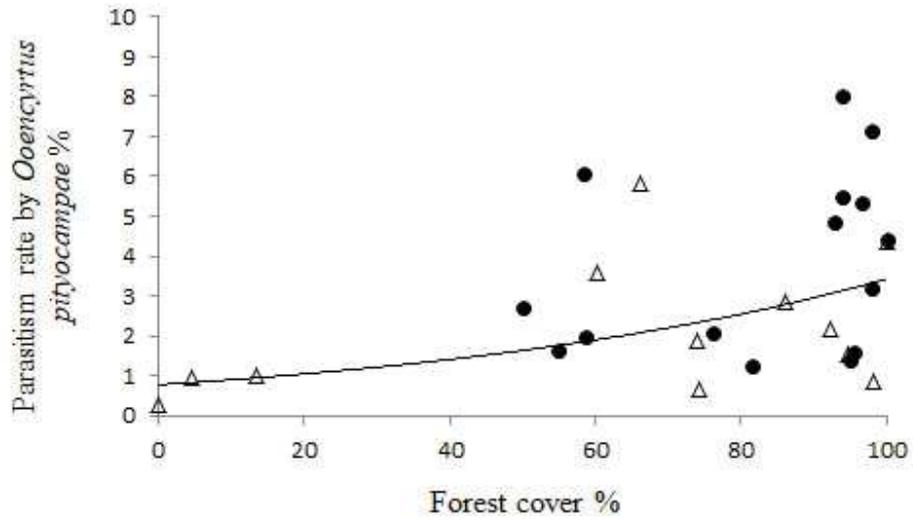
Illustration of the delimitation of the land-use types, in the 300 m buffer, using ArcGis World Imagery layer, for a) Tipaza site (Tipaza region), b) Djebel Doui site (Ain-Defla region), c) North High site (Theniet El-Had region) and d) Sétif SF site (as an example for Bouchou (2015) dataset).

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)

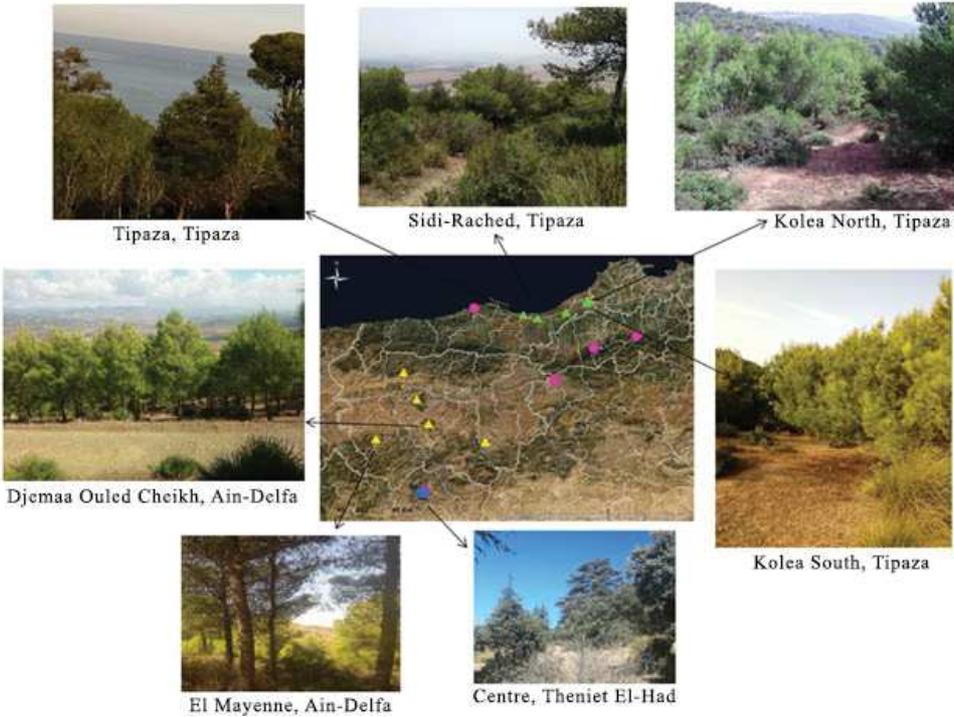


Illustration of the sampled sites in three selected regions.

53x39mm (300 x 300 DPI)