Effect of habitat type and soil moisture on pupal stage of a Mediterranean forest pest (*Thaumetopoea pityocampa*)

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Abstract

Habitat selection is especially important for pupae of holometabolous insects because this stage is usually immobile and to a certain extent unable to react to environmental changes. In the present study, we analyze how habitat and soil moisture determine the fate of pupae of the pine processionary moth *Thaumetopoea pityocampa*, a defoliator pest in pine woodlands of Europe and the Circummediterranean region. The pine processionary moth pupates buried in the soil and can spend up to 9 years in an extra-long diapause.

We considered the impact that different habitats, as well as the manipulation of soil water conditions in the preferred habitat (i.e. in bare ground with null or sparse herbaceous vegetation), can exert on pupation.

Less than half of the buried larvae successfully pupated, even in the most favourable habitats and soil water conditions, whereas, on average, 2.5% underwent extra-long pupae diapause (2 years after pupation).

Although habitat influenced mainly pupation success and pupal survival, changing moisture conditions in the preferred habitat affected primarily the phenology of emergence, whereas pupal survival remained unaffected.

The results of the present study reveal the importance of both habitat and soil moisture on the pupal stage, providing valuable information with respect to adequately forecasting the effects of changes in climate or land use on the population dynamic of this important forest pest.

Keywords Habitat, moth phenology, Pine processionary moth, pupal diapause, soil moisture.

Introduction

The pupal stage of holometabolous insects is a critical step of their life history. The lack of mobility makes pupae susceptible to high rates of predation, parasitism and/or diseases, and also limits their reaction capacity against extreme abiotic conditions (Cornell & Hawkings, 1995; Hawkins et al., 1997). Thus, larvae often select a protected site before pupation, seeking shelter, camouflage and frequently adding a silk cocoon as protection (Sims & Shapiro, 1983; Ruszczyk, 1996; Stefanescu, 2004; Zheng et al., 2011). A common solution is burrowing into the soil, where temperature changes are tempered and many predators and pathogens are excluded (Hogdson et al., 1998), although there is also a notable risk of flooding, as well as rotting by the action of fungi and bacteria, and specialist predators (Kaya & Haya, 1981; Murray & Zalucki, 1990; Hogdson et al., 1998; Zheng et al., 2011). The pupal period not only imposes spatial immobility, but also allows temporal flexibility to suit the emergence time as an adult to favourable ambient conditions aboveground (Tauber & Tauber, 1976; Hayes, 1982; Tauber, 1986; Denlinger, 2002; Kingsolver et al., 2011).

The extension of the pupation period, beyond the time strictly needed for metamorphosis, can be a result of mere quiescence, a simple arrest of the development lasting until ambient conditions change (e.g. until temperature increases) or diapause, a break of development somewhat independent of ambient conditions, as well as centrally or physiologically controlled (Danks, 1987; for diapause-related terminology, see also Kostál, 2006). In the case of the diapause, the entry in pupal diapause can be promoted by food during the larval period (Liu et al., 2010; Metspalu et al., 2013), as well as photoperiod and/or temperature (Kay, 1982; Sims & Shapiro, 1983; Xiao et al., 2013), and the same applies to the exit (Shimoda & Kiuchi, 1997; Chen et al., 2013). Thus, the beginning and the end of that time period can be partially modulated by environmental conditions, even those with strict...
genetic control (Dehlinger, 2002; but see Menu et al., 2000). For this reason, the habitat selection for pupation is important not only for predation risk or shelter against adverse environmental conditions, but also for conditions of abiotic stimuli perceived by pupae.

In the current context of climate change, many of these abiotic stimuli (e.g. humidity or temperature) are expected to vary substantially. Taking into account the above consideration, we followed a field-experimental approach to analyze how different habitat and climate conditions affect the survival and phenology of a moth species that undergoes pupation in the soil. As a model species, we chose the pine processional moth (PPM) *Thaumetopoea pityocampa*. This species represents an excellent case study because it combines univoltine life cycles with prolonged pupal diapause, and because of its ecological and economic importance as a forest pest (Battisti et al., 2015).

Unlike most temperate and Mediterranean Lepidoptera, the PPM has a peculiar 1-year development cycle because the larvae feed over the winter. Pupae spend several months (in spring) undergoing metamorphosis in the soil and moths emerge in early summer to autumn depending on elevation/latitude and temperature. Additionally, prolonged pupal diapause makes the population dynamics rather complex. The information available on the biology of the PPM adult and larva is quickly increasing (Battisti et al., 2005; Stastny et al., 2006; Buffo et al., 2007; Hoch et al., 2009; Dulaurent et al., 2012), whereas knowledge of the pupa remains scarce (Markalas, 1989; Aimi et al., 2006; Dulaurent et al., 2011).

The present study aimed to analyze the effect of habitat on the survival and phenology PPM. Accordingly, we chose a mosaic landscape composed of patches of native forest and degraded habitats (hereafter, Habitat experiment). Selected habitats comprised open areas, shrubland and forest, with the main ones in the Mediterranean mountains, representing the trend towards replacement of cropland and pastures with shrubland and woodland. Moreover, because the present study aimed to determine the effects of climatic variability on the survival and phenology of PPM (hereafter referred to as the Water experiment), we experimentally varied the soil water content that could appear during the coming decades in the Mediterranean area (i.e. drier and wetter summer conditions). We simulated: (i) sporadic wetter conditions during the growing season, based on maximum historical records from the study area (Matías et al., 2011), and (ii) drier climatic conditions during the growing season, in accordance with the A-2 scenario from the Intergovernmental Panel on Climate Change (IPCC).

Thus, the present study aimed to test the effect of different habitats (Habitat experiment) and soil moisture (Water experiment) conditions on: (i) burial success, as indicated by larvae becoming buried without dying in surface soil; (ii) pupation success and pupal survival, as indicated by larvae pupating after being successfully buried and pupae surviving after the first summer, respectively; (iii) extra-long pupal diapause, as indicated by pupae remaining buried after 2 years of the experiment; and (iv) moth emergence and phenology, as indicated by the number of emerged moths and the date by when this is achieved. These two experiments will provide valuable information on how the soil stages of life cycle of PPM will be affected by two important factors related to global change.

Materials and methods

Study area

The study was performed in La Cortijuela Botanical Garden, within Sierra Nevada National Park (1650 m.a.s.l., 37°0′5′′N, 3′28′′W, Granada, SE Spain). This mountain area has a continental Mediterranean climate, with cold winters, and hot and dry summers. Rainfall is 870 ± 70 mm/year, mostly during spring and autumn, and the mean temperatures of coldest and warmest months (January and July, respectively) are 3.0 ± 0.3 and 21.6 ± 0.4 °C, respectively (mean ± SE 1990–2012). The vegetation in the area is composed of patches under different management, namely pine plantations (*Pinus sylvestris* and *Pinus nigra*) with intermingled oaks (*Quercus ilex*), shrublands, open areas and patches of native forest (*P. sylvestris* var. *nevadensis*, *Acer opalus* ssp. *granatense*, *Taxus baccata*). The study lasted 3 years, starting in 2010, when there was a peak in the PPM population cycle, with severe defoliation in the area, whereas 2011 and 2012 had much lower infestations.

Experimental design

To analyze how the habitat affects the survival and phenology of PPM, we chose a mosaic landscape composed of patches of native forest and degraded habitats. The Habitat experiment had three levels: Open, in bare ground with null or sparse herbaceous vegetation; Shrubland, in areas covered by the dominant shrubs at the site (e.g. *Crataegus monogyna*, *Prunus marburi* and *Genista speciosa*); and Woodland, formed by mixed forests of *P. sylvestris*, *P. nigra*, and *Q. ilex*. Each level had three replicates, consisting of plots of 2x2 m, in which the controlled burials of larvae were set. Accordingly, each plot had 11 breathable buried bags: 10 for larval pupation and one for the microclimatic stations. Pine processionary caterpillars in pre-pupation processions were collected to burial into the bags. A total of 50 larvae by bag were buried. Thus, the initial setting was 3 levels × 3 replicates × 10 bags × 50 larvae for habitat experiment, for a total of 4500 larvae (see Supporting information, Fig. S1).

The water experiment also had three levels: Drought, Control and Watering. All levels were set in the same bare-ground area, the preferred burial habitat (Robredo, 1963; Dulaurent et al., 2011), and soil-water input was manipulated. The differentiation in these climate scenarios was based on the study by Matías et al. (2011). The Drought treatment was arranged by means of rain-exclusion shelters (Yahdjian & Sala, 2002) formed by a 2x2 m metal frame supporting V-shaped clear methacrylate bands without ultraviolet filters (Barlocast; Faberplast S.L., covering 35% of the surface, and intercepting the same percentage of natural water supply (rain)). The level for rain exclusion was based on the SRES A-2 model by the IPCC (2007), where a reduction in summer rainfall of 30% is predicted from 1980–1999 to 2080–2099 for Mediterranean areas. Rainout shelters were placed from April to September, simulating drier and longer summers. The control treatment involved squares exposed to natural rainy conditions over the experimental period. In the Watering treatment, the sporadic summer storms characteristic of Mediterranean mountains were simulated. Accordingly, a
Insects used in the experiments

In March 2010, pine processory caterpillars in pre-pupation processions were collected in a forest gap 200 m far from the burial site. All larvae collected were pooled to ensure a mixture of genetic origins. Each bag within each plot, in both experiments, received 50 larvae and was sealed to avoid escapes, allowing the caterpillars to bury themselves. All burials were performed on the same day. Two days after making burials, all bags were checked to count the larvae that remained in the top soil because they failed to bury. The larvae were not replaced, although the number of larvae failing to bury was recorded, to obtain an exact number of the larvae buried in each of the experimental bags.

The initial scheme in each experiment included one bag extraction, randomly selected, per plot and year, before the period of moth emergence (May) to enable pupal survival to be checked. However, several bags in the Open (habitat) and Control (climate) treatments were accidentally damaged after the set-up of the experiment, which reduced the initial number of bags. To maintain a balanced number of bags for moth emergence in all treatments, which moths emerged was estimated as the proportion of moths alive was recorded.

Statistical analysis

Data were recorded and analyzed on a plot basis for climatic data and on a bag basis for burial success, burial depth, pupation survival, moth emergence and moth phenology. Differences between treatments for each variable were analyzed with Tukey’s honestly significant difference (HSD) all-pairwise comparisons.
were analyzed independently, except for pupae survival (see Experimental design).

Climatic data were analyzed with linear mixed models, with a different model being used for each variable. In all models, treatment was considered the fixed factor and the random factor was plot.

Larval burial success and pupal survival were analyzed using a generalized linear mixed model (GLMM) with a binomial response. Pupation depth was analyzed using a linear mixed model and with respect to the number of emerged moths. Differences in the phenology of moth emergence were analyzed with a GLMM with Poisson and Gamma distribution, respectively. In all of these models, the fixed factor was treatment, with the exception of pupal survival data, where the fixed factors were treatment and year. The random factors were bag nested within a plot.

Mixed models were generated using the ‘lme4’ R package (Bates, 2011) and the ‘glmmADMB’ package (Fournier et al., 2012), and a posteriori multiple comparisons were carried out using the ‘multcomp’ R package (Hothorn et al., 2008). All statistical analyses were performed into the open source statistical language R, version 3.0.1 (R Core Team, 2013).

Results

Microclimatic conditions

From April to September, mean surface and soil temperatures, as well as minimum soil temperatures, were significantly different between treatments in the Habitat experiment (Fig. 1a,b), being higher in Open and lower in Woodland. This was also the pattern for irradiance, with the lowest value for Woodland, although this was similar to Shrubland (see Supporting information, Table S1), and with Open having the highest record, as well as being significantly different from the other two habitats (Tukey’s HSD: both \( P < 0.0001 \), see Supporting information, Table S1). With respect to soil VWC, there were significant differences between habitats (see Supporting information, Table S1). Open and Woodland showed similar values, whereas the lowest values were in Shrubland (Tukey’s HSD: Shrubland-Woodland, \( P = 0.01 \); Open-Shrubland, \( P < 0.02 \)) (Fig. 2a). Regarding treatments in the Water experiment, no differences were found, either for surface or for soil temperatures (in all cases, \( P > 0.16 \) (Fig. 1c,d; see also Supporting information, Table S1), whereas differences were found for soil VWC, with this being lowest in Drought and highest in Watering (Tukey’s HSD: Drought-Control, \( P = 0.384 \);
regardless of the Habitat (to pupate was found to be quite similar between treatments, but the number of pupae remaining alive varied much between treatments. It was higher in Open/Control (39.4 ± 6.5%) and Watering treatments (34.0 ± 2.3%) and somewhat lower in Drought (30.0 ± 6.4%). Climate treatments did not significantly differ ($F_{2,7} = 0.119, P = 0.091$).

In both experiments, from the initial proportion of larvae that successfully pupated, the number of pupae remaining alive declined over time as a result of moth emergence and also because some of the pupae died during the extended diapause (Fig. 3). At the beginning of the third season, the number of pupae remaining alive in extended diapause varied between 5.3% in the Control/Open treatment and 0.7% in Woodland (Fig. 3b).

Figure 2 Soil volumetric water content (%) mean ± SE) over time in the Habitat (a) and Water (b) experiments. Bars represent the amount of natural rainfall. The dotted line in (b) indicates the period of water addition in the Watering treatment and also that of rain exclusion in the Drought treatment.

Drought-Watering, $P = 0.008$; Control-Watering, $P = 0.323$ (Fig. 2b). Therefore, these results indicate an effect of applied treatments on the climatic variables.

**Burial success**

Approximately 94.6% of the larvae (8512 out of 9000) buried successfully. There were differences between habitats in burial success ($F_{2,5} = 12.113, P < 0.001$). For the Habitat experiment, 100% of larvae buried successfully in Woodland and Shrubland, whereas 96.7 ± 0.1% did so in Open, which significantly differed from the other treatments (Tukey’s HSD: Open-Woodland and Open-Shrubland, $P < 0.001$; Woodland-Shrubland, $P = 0.999$). For the Water experiment, the lowest success was in Drought (84.8 ± 0.1%) and the highest was in Watering (94.5 ± 0.1%), with Control being intermediate (90.7 ± 0.1%). In this case, there were no statistically significant differences between treatments ($F_{2,5} = 1.952, P = 0.221$). The depth at which larvae buried to pupate was found to be quite similar between treatments, regardless of the Habitat ($F_{2,6} = 2.018, P = 0.1309$) or Water experiments ($F_{2,6} = 0.390, P = 0.672$). Almost all pupae (97.4%) were found at a depth between 4 and 10 cm, with more than half (56.2%) at a depth in the range 6–8 cm.

**Pupation success and pupae survival**

For Habitat experiment, the initial proportion of larvae that successfully pupated greatly varied between different treatments ($F_{2,5} = 19.226, P < 0.0001$) (2010 data in Fig. 3). Pupation rate was much higher in Open/Control (39.4 ± 6.5%; see Experimental design) than in Shrubland and Woodland (2.7 ± 0.7% and 0.7 ± 0.7%, respectively). Overall, significant differences were found between the Open and the other two habitats (Tukey’s HSD: $P < 0.001$) but not between Shrubland and Woodland (Tukey’s HSD: $P = 0.999$) (Fig. 3a).

Conversely, in the Water experiment, pupation success did not vary much between treatments. It was higher in Open/Control (39.4 ± 6.5%) and Watering treatments (34.0 ± 2.3%) and somewhat lower in Drought (30.0 ± 6.4%). Climate treatments did not significantly differ ($F_{2,7} = 0.119, P = 0.091$).

In both experiments, from the initial proportion of larvae that successfully pupated, the number of pupae remaining alive declined over time as a result of moth emergence and also because some of the pupae died during the extended diapause (Fig. 3). At the beginning of the third season, the number of pupae remaining alive in extended diapause varied between 5.3% in the Control/Open treatment and 0.7% in Woodland (Fig. 3b).

Moth emergence and phenology

A total of 771 moths emerged during the 3 years of study; of these, 764 emerged the first summer (2010) and thus we restricted our analysis to these data.

In the Habitat experiment, most of the moths were recorded in Open, registering the highest emergence rate (12.3 ± 1.9%) in this treatment. Interestingly, this proportion was found to decrease with an increasing vegetation habitat. Thus, just a few emerged in Shrubland (4.8 ± 1.1% of successfully buried larvae) and no moths emerged in the Woodland treatment. The differences were significant between treatments ($F_{2,5} = 7.426, P = 0.0183$). Furthermore, emergence in the Shrubland treatment was much later in the season, with the difference in emergence pattern being significant (Tukey’s HSD: Open-Shrubland, $P < 0.001$) (Fig. 4a).

In the Water experiment, there were no differences between treatments in the number of emerged moths ($F_{2,5} = 0.033; P = 0.967$). Moth emergence was slightly higher in the Drought treatment (16.7 ± 2.2%), although differences with respect to other treatments were negligible (Control: 16.4 ± 1.4%, Watering: 15.3 ± 1.5%; $P$ values in the range 0.996–0.966). This was not the case for the emergence pattern ($P < 0.001$) (Fig. 4b), being earliest in the Drought treatment, intermediate in Control and latest in Watering (Tukey’s HSD: Watering-Control and Watering-Dry, both $P < 0.001$; Control-Drought, $P = 0.4$).

Discussion

The results of the present study provide strong evidence indicating that the different soil moisture scenarios and the type of habitat significantly affect the emergence phenology and pupal survival, respectively. Furthermore, an important effect was also found regarding the phenology of moth emergence. These results offer valuable insights into how the life cycle of this forest pest can be conditioned by climate, providing relevant information about the differences in survival of pupae and moth emergence among the main habitats. In a context of global climate change, the results of this study could help in predicting and managing the impact of this forest pest on forest ecosystems.
change in the Mediterranean region, with land use and climatic change as major drivers (Doblas-Miranda et al., 2015), the study of the effect of these environmental conditions has even more importance.

Burial and pupation success

Burial depth was quite constant in our field experiments, irrespective of treatment. Dulaurent et al. (2011) also failed to find significant differences between habitats, although they did not report the usual depth for burial, as was also unreported by Markalas (1989). Montoya and Hernández (1998) stated that burial depth depends on soil structure (for Spodoptera exigua, see Zheng et al., 2011), whereas Battisti et al. (2015) place this variation at between 5 and 20 cm. A deeper burial provides greater protection against predators and soil abiotic conditions (e.g. see differences between $T_i$ and $T_e$ in Supporting information, Table S1). Nevertheless, a deeper burial also represents a major handicap for moth emergence (Capinera, 2008) such that, in hard clay soils, as is the case in the present study, this could be disadvantageous.

After burial, survival was much higher in Open, and conspicuously low in Shrubland and, particularly, Woodland. Larvae buried themselves easily in these two habitats but, once buried, they were unable to pupate, as indicated by the number of pupae still alive being extremely low 2 months after burial (Fig. 3a). Presumably this pattern is directly linked to soil temperature (Fig. 1a, b), with low temperatures limiting pupation success, as well as delaying moth emergence (for the effect of temperature on moth emergence, see Branco et al., 2016). Bare soil has been previously described (Robredo, 1963; Démolin, 1969; Huchon & Demolin, 1970; Dulaurent et al., 2011) as the most optimal habitat for pupation, and the percentage of survival on it (approximately 40%) is within the range of that reported in similar studies (37–62.7%; Dulaurent et al., 2011; 44–90%: López-Sebastián, 2014). By contrast, the easy burial on Woodland and Shrubland contrasts with the high mortality on these habitats, which were nevertheless systematically avoided by natural processions (Robredo, 1963), suggesting that some strong source of pupal mortality (presumably fungus such as Beauveria bassiana; López-Sebastián, 2014; Battisti et al., 2015) operates on them more intensely than in bare soil. Within the Water experiment, there was a lower burial success in Drought treatment and a higher in success in Watering, although burial success differences between the two extreme treatments were less than 10%. Moreover, these differences are not significant, which indicates that bare soil is the best habitat for burial of the pine processionary larvae, regardless of soil moisture.

Prolonged pupal diapause

The proportion of pupae entering prolonged diapause was low. Approximately 15% of initial larvae in Control/Open were alive.
as diapausing pupae at the beginning of the second season and, by the third season, the live pupae comprised approximately 1–5%, depending on the treatment (Fig. 3). These values are not so different from reported by Abgrall (2001) (6.7±1.6%) and Dulau-
rent et al. (2011) (5.1±0.7%) in France and López-Sebastián (2014) (3.6% and 19.7% in two different locations) in Eastern Spain, although they contrast sharply with the findings of the study by Aimi et al. (2006) (50–100%) in the Italian Alps. The entry into pupal diapause has been attributed not only to the time spent by larvae in nonfeeding and silk-weaving activities (Démolin, 1969; Masutti & Battisti, 1990), but also to low temperatures during the pupal stage (12–14°C: Démolin, 1974; Géri, 1980). Moreover, it is unlikely that soil moisture determines extra-long diapause, although it could affect the survival of extra-long-diapausing pupae (Turnock et al., 1983; Leather, 1984; Markalas, 1989) and the exit of diapause, as previously induced by those other variables (Beck, 1980; Saunders, 1982; Tauber, 1986; Danks, 1987; Kostál, 2006).

Independently of the exact factor determining the engagement in extra-long diapause, the low proportion of pupae showing this strategy suggests that our population is basically univoltine, and that diapausing pupae might represent a reserve for the periods of very low population. It should be noted that the proportion of dia-
pausing pupae is low but the entry into diapause happens during a population peak, such that the absolute number of pupae engag-
ing in extra-long diapause is not low at all. The number of pupae remaining in extra-long diapause in the soil appears to be sufficiently high to allow the local populations to persist during the low infestation phases, which recur in this area every 5–6 years (Hódar et al., 2012). Aimi et al. (2006) found prolonged diapause as the usual strategy in two zones of the Southern Alps, acting as an adaptive mechanism to escape adverse conditions. Also in the Alps, Tamburini et al. (2013) failed to show any negative effect of temperature on the PPM population dynamics and, conversely, found a negative density-dependent feedback with a 1-year lag as the main factor driving the population dynamics in both regions. This relationship was attribute to a deterioration of host quality and increased mortality caused by pathogens. In our case, the low level of extra-long diapause would explain the rather direct response that the population of PPM shows to climatic effectors (Hódar & Zamora, 2004; Hódar et al., 2012). With a high pro-
portion of pupae in extra-long diapause, producing high stocks of moth year after year, the responses to these climatic events should be necessarily smoothed or hidden (Tamburini et al., 2013). However, when this response is based on the survival and reproductive success of the previous generation, as a result of the predominating univoltine strategy, the effect on the population is clear and direct (Hódar & Zamora, 2004; Hódar et al., 2012).

Moth phenology

We found contrasting results for the phenology of nondiapausing moth emergence. With respect to habitat, moth emergence was strongly determined by the pupal survival, although habitat also changed the phenology of emergence, with this being delayed in Shrubland by approximately 3 weeks with respect to Open (Fig. 4a). Regarding the different watering scenarios, the proportion of emerging moths was similar between treatments, although phenology varied from early in Drought to late in Watering (Fig. 4b). These results show that soil-water content and temperature can operate as a cue for moth emergence.

Previous studies concerning the effect of habitat and/or soil moisture on moth emergence (Markalas, 1989; Dulau-
rent et al., 2011) have analyzed only the number of moths that emerged and not moth phenology, which prevents comparisons. These issues are pivotal because the time of moth emergence determines the time available for early-instar larvae in autumn before winter arrives (Arnaldo et al., 2011) and, consequently, the fate of these young larvae. Our field experiments suggest that the drier the soil, the sooner the moth emerges (Fig. 4b). Thus, taking into account the aridification trends for the Mediterranean basin, we would expect an early oviposition and more time under optimal climatic conditions for the development of young larvae. This would be an advantageous scenario for the pest to survive during winter.

Conclusions

Our experimental results reveal the critical implications that the pupal stage of the insect’s life cycle may have with respect to determining future population dynamics, and thus pupa-
tion in the PPM. An open and dry pupation site promotes an earlier emergence of moths, whereas vegetation cover or higher soil moisture delays emergence. According to the pre-
dictions of the future climate-change scenarios, a good part of the Mediterranean basin will undergo higher temperatures and lower rainfall, and woodlands will also be replaced by shrublands (Gibelin & Déqué, 2003; Christensen et al., 2007; Matías et al., 2012), which would be advantageous for pupae in open soils, at least when the low moisture does not prevent the moth emergence. Thus, a lower soil moisture, and the landscape changes resulting from this moisture change, could a priori favor this pest. Conversely, changes in land use caused by land abandonment may foster the recovery of the native vegetation cover (Peña et al., 2007), potentially hampering the development of this pest. Therefore, two possible scenarios arise: (i) where aridification exerts a greater influence than land-use changes, the processionary moth will have more places to bury itself successfully, finding more open areas for an advanced moth (and larval) phenology, and (ii) where changes in land use are more important than climate, thus increasing the soil cover by shrubs and trees, the processionary will be less successful at this life stage. The PPM has displayed great demographic plasticity in contrasting situations, from quasi-univoltine strategy to preferential prolonged diapause, also being influenced by the local characteristics of the habitat (open, shrub, forest). All of these options represent a spatiotemporal complex scenario for the PPM interactions in the future (Arnaldo et al., 2011), highlighting the need to consider all phases within the life cycle of an organism to adequately forecast the effects of global change.

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Supporting information
Additional Supporting information may be found in the online version of this article under the DOI reference: 10.1111/afe.12188

Table S1. Climatic description of the different treatments: mean ± SE values of soil surface temperature $T_s$, soil (depth 10 cm), radiation (Rad) and % volumetric water content (%VWC) in the summer and winter for each experiment (Habitat and Water experiments). Units: °C, temperature; W/m², radiation. Summer comprises the period April to September (except %VWC, May to September); winter comprises the period December to February. F- (analysis of variance) and P-values are also shown. Furthermore, different lowercase letters indicate statistically significant differences between treatments (Tukey’s test).

Fig. S1. Schematic showing the experimental design. Upper: the three treatments for the habitat experiment (Open, Shrubland and Woodland). Lower: the three treatments for the watering experiment (Control, Drought and Watering); all them were in open habitat. All treatments had three replicates in both experiments.

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