esa ECOSPHERE

Expansion of elevational range in a forest pest: Can parasitoids track their hosts?

José A. Hódar,[1,†] Luis Cayuela,[2] Daniel Heras,[2] Antonio J. Pérez-Luque,[1,3] and
Lucía Torres-Muros[4]

[1]Departamento de Ecología, Universidad de Granada, E-18071 Granada, Spain
[2]Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, E-28993 Móstoles, Madrid, Spain
[3]Laboratorio de Ecología (iEcolab), Instituto Interuniversitario de Investigación del Sistema Tierra en Andalucía (CEAMA), Universidad de Granada, Avenida del Mediterráneo s/n, 18006 Granada, Spain
[4]Dirección de Educación para la Sostenibilidad de la UNAE- Galápagos, Universidad Nacional de Educación del Ecuador (UNAE), Santa Cruz, Ecuador

Citation: Hódar, J. A., L. Cayuela, D. Heras, A. J. Pérez-Luque, and L. Torres-Muros. 2021. Expansion of elevational range in a forest pest: Can parasitoids track their hosts? Ecosphere 12(4):e03476. 10.1002/ecs2.3476

Abstract. Gradients in elevation impose changes in environmental conditions, which in turn modulate species distribution and abundance as well as the interactions they maintain. Along the gradient, interacting species (e.g., predators, parasitoids) can respond to changes in different ways. This study aims to investigate how egg parasitism of a forest pest, the pine processionary moth (PPM), *Thaumetopoea pityocampa*, vary along an elevational gradient (190–2000 m.a.s.l.) in a mountain range of SE Spain, including areas of recent elevational expansion, for a seven years period (2008–2014). We used generalized linear mixed models to ascertain the effect of both elevation and the winter North Atlantic Oscillation (NAO) index (a proxy of interannual climatic conditions) on the rate of parasitism, and the occurrence probabilities of two parasitoid species: a PPM specialist and a generalist species. Since four pine species are stratified along the elevational gradient, we repeated all the analyses separately for lowlands (190–1300 m. a.s.l.) and uplands (1350–2000 m. a.s.l.). Results showed a decrease in both parasitism rate and probability of occurrence of the two main parasitoid species with elevation, although decline was more severe for the specialist species. The effect of elevation was more conspicuous and intense in uplands than in lowlands. Positive NAO winter values, associated with cold and dry winters, reduced the rate of parasitism and the probability of occurrence of the two main parasitoid species—but particularly for the generalist species—as elevation increases. In a context of climate warming, it is crucial to mitigate PPM elevational and latitudinal expansion. Increasing tree diversity at the PPM expansion areas may favor the establishment of parasitoids, which could contribute to synchronizing host– parasitoid interactions and minimize the risk of PPM outbreaks.

Key words: biological control; elevational gradient; host–parasitoid interactions; North Atlantic Oscillation Index; pest dynamic; pine processionary moth.

Received 15 September 2020; revised 1 December 2020; accepted 15 December 2020; final version received 10 February 2021. Corresponding Editor: T'ai Roulston.

† **E-mail:** jhodar@ugr.es

INTRODUCTION

The mean global temperatures increased 0.60°C over the past 100 yr (IPCC 2013), and the different emission scenarios forecast further increases in global temperature (Rogelj et al. 2012). The effects of global warming can cause ecological imbalances in many ecosystems, from the level of individual species to communities, most notably in the form of temperature-related range shifts (Davis and Shaw 2001, Walther et al. 2002, Thuiller 2004, Malhi et al. 2020). Recent distributional changes have been documented in plants and animals (e.g., migratory birds, temperate-zone butterflies; Walther et al. 2002, Parmesan and Yohe 2003, Wilson et al. 2007).

Distributional changes triggered by climate warming may, however, affect interacting species differently (Harrington et al. 1999). The interspecific relationships among the members of a community are sometimes very complex (Jordano 2016), and most often the result of a sustained contact over time. When the evolutionary context in which two or more species developed a specific interaction disappears, consequences rapidly arise (Turner et al. 2020). This is the case of a shift in a species range (Davis and Shaw 2001, Parmesan and Yohe 2003, Brooker et al. 2007), which can be followed or not by a similar shift in the range of other species. In the case where interacting species do not shift their range similarly as a response to climate warming, this may be detrimental for the species due to the loss of positive interactions, that is, mutualism or facilitation. However, if the previous situation limited its population growth via predation or parasitism, the expansion of a species into a new area may represent an opportunity to succeed in a new environment (Pearson and Dawson 2003, Hódar et al. 2009, Harley 2011).

Insects are highly influenced by global warming: The increase in temperature is causing a shift of their range in many areas of the world, and these shifts can be especially significant for insect pests (Menéndez 2007, Wilson et al. 2007, Netherer and Schopf 2010). The pine processionary moth (*Thaumetopoea pityocampa* ([Denis and Schiffermüller] 1775), Lepidoptera: Notodontidae; hereafter PPM) is a severe pest of *Pinus* species in the Circum-Mediterranean region (Battisti et al. 2015). Temperature has been recognized as the main limitation for the development of the PPM (Buffo et al. 2007, Battisti et al. 2015). This is a key factor determining the outbreak capacity of PPM, since low winter temperatures heavily determine the larval survival of this insect (Battisti et al. 2005, Buffo et al. 2007, Hoch et al. 2009). Several studies found a progression in latitude and/or elevation with respect to the previous distribution of the pest, as well as an increase in outbreak severity, as a consequence of the general rise in temperatures (Hódar et al. 2003, Hódar and Zamora 2004, Battisti et al. 2005, Robinet et al. 2007). The effects that PPM can cause on pines could be amplified in this situation (Battisti et al. 2005).

Apart from temperature, it is known that PPM populations experience food scarcity after massive defoliation (Battisti 1988, Hódar et al. 2004), and they also suffer attacks of predators and larval and egg parasitoids throughout its historical range (Battisti 1989, Barbaro and Battisti 2011, Battisti et al. 2015). Whereas the latitudinal and/or elevational expansion of PPM as a response to global change is now widely documented (Battisti et al. 2005, Robinet et al. 2007, Roques et al. 2015), it is still uncertain whether parasitoids can track its host into the new colonized areas at its pace or with a temporal delay (Colautti et al. 2004, Liu and Stiling 2006). Furthermore, host tracking is mandatory for specialist parasitoids, but generalist ones could even be present before host arrival, living in alternative hosts (Auger-Rozenberg et al. 2015). Previous studies have shown that in areas recently colonized by PPM, the percentage of parasitism is significantly reduced (Alemany et al. 1994, Tiberi et al. 2015). The conquest of a new habitat could thus be fueled by the lack of natural control against PPM, since egg parasitoids have been repeatedly pointed out as main controller of the PPM populations (Tsankov et al. 1996, Zovi et al. 2006, Mirchev et al. 2012).

In this study, we investigated whether the main egg parasitoids of PPM are able to track the elevational expansion of its host. To achieve this goal, we analyzed the response along the elevational gradient in the Sierra Nevada mountain range, southern Spain, of egg parasitism rate, as well as probability of occurrence of the two most common PPM parasitoids in the area: a specialist species feeding exclusively on PPM, *Baryscapus servadeii* (Dom.), and a generalist species *Ooencyrtus pityocampae* (Mercet). The specific objectives of the study were to (1) to quantify changes in parasitism rate and probability of occurrence of the two main parasitoid species along the elevational gradient; and (2) to ascertain the effects of interannual climatic conditions (using the

North Atlantic Oscillation [NAO] Index as a proxy) on parasitoid populations along the elevational gradient.

It is known that parasitism rate decreases as elevation increases along the altitudinal gradient (Hódar 2015). However, we hypothesized that the two parasitoids may differentially respond to PPM expansion, with the specialist species suffering a more pronounced decoupling than the generalist species. Additionally, we expect cold and dry winters (i.e., positive NAO winter index) to have a negative effect on parasitoid populations, particularly in the uplands (Hódar et al. 2012), where extreme climatic conditions can harm the possibilities of parasitoids to overwinter. If parasitoids track the expansion of PPM, then they will contribute to control PPM population densities in these new areas. Conversely, if parasitoids are not able to follow PPM in its elevational expansion, this will imply more eruptive outbreaks of their populations, which could ultimately threaten the pine forests at the areas of recent expansion.

METHODS

Study area and sampling sites

The study area was located in Sierra Nevada and their surroundings, South-eastern Andalusia, Spain (Fig. 1). It has a Mediterranean climate, but conditions are contrasting depending on location. Inland basins and mountains are cold in winter, with frequent frosts. Summers are dry and hot, with maximums often above 35°C. Rainfall comes principally in the cold months. Conversely, the coastal range has a subtropical microclimate (AEMET 2011). The region has experienced a rise of temperatures and a greater variation in precipitation during the last decades (Pérez-Palazón et al. 2015, Pérez-Luque et al. 2016).

Nearly 44,000 km^2 of the 87,300 km^2 comprising Andalusia are forested, with 19% of them covered by pine woodlands (Junta de Andalucía 2010), both natural (around 5%) and afforested. *Pinus pinea*, *P. halepensis*, *P. pinaster*, *P. nigra,* and *P. sylvestris* are the main conifers that dominate the landscape. Non-native species such as *P. canariensis* and *P. uncinata* are also present in some restricted areas. From 2008 to 2014, 11 plots located along the Sierra Nevada mountain range and surrounding inland basins were monitored: 10 were located in the province of Granada, and one (Doña María) in the province of Almería (Fig. 1). The plots were located along an elevational gradient, ranging from 190 to 2000 m.a.s.l., representing a variety of pine forests dominated by different host species. Plots below 1200 m.a.s.l. were dominated by *Pinus halepensis*, whereas *P. pinaster* was found at mid elevations (1200–1600 m), and *P. nigra* and *P. sylvestris* appeared at the top of the gradient. Cerro Gordo and Cerro del Mirador are natural forests, while the remaining plots are afforestations 30–70 yr old, aimed to prevent erosion and never used for timber.

Study species

Thaumetopoea pityocampa ([Denis and Schiffermüller] 1775) (Lepidoptera, Notodontidae) is a moth established in the Mediterranean Basin, where it represents a main insect pest in pine woodlands (Battisti et al. 2015, Ros-Candeira et al. 2019). Moths emerge from soil for a short and nocturnal life, to lay its egg batch around pine needles, covered and protected by scales. In our study area, egg laying occurs in mid-summer (July–August). The larvae emerge *ca*. 1 month later, and the complete larval development requires five instars. PPM requires a specific combination of diurnal–nocturnal temperatures in order to feed and process food, or else they die. When the temperature is extremely low (−17°C), they die from freezing, but sublethal temperatures sustained over time can also kill larvae by making them unable to digest food (despite being able to feed). Therefore, a rainy winter, with relatively mild average temperatures, can kill PPM larvae if they do not manage to get warm and digest food, whereas a dry and sunny winter, with lower minimum temperatures but sunny days, does not freeze the larvae to death and allows them digest food (Hoch et al. 2009). Thus, if the autumn is warm and sunny, the caterpillar can reach the fifth instar in early winter, but usually the development prolongs until late winter or early spring. Larvae spin white silken nests in order to be protected from cold during the day, when they congregate, and to increase the exposure to sun. Once larval development finished, caterpillars abandon the trees in processions and bury to pupate into the soil

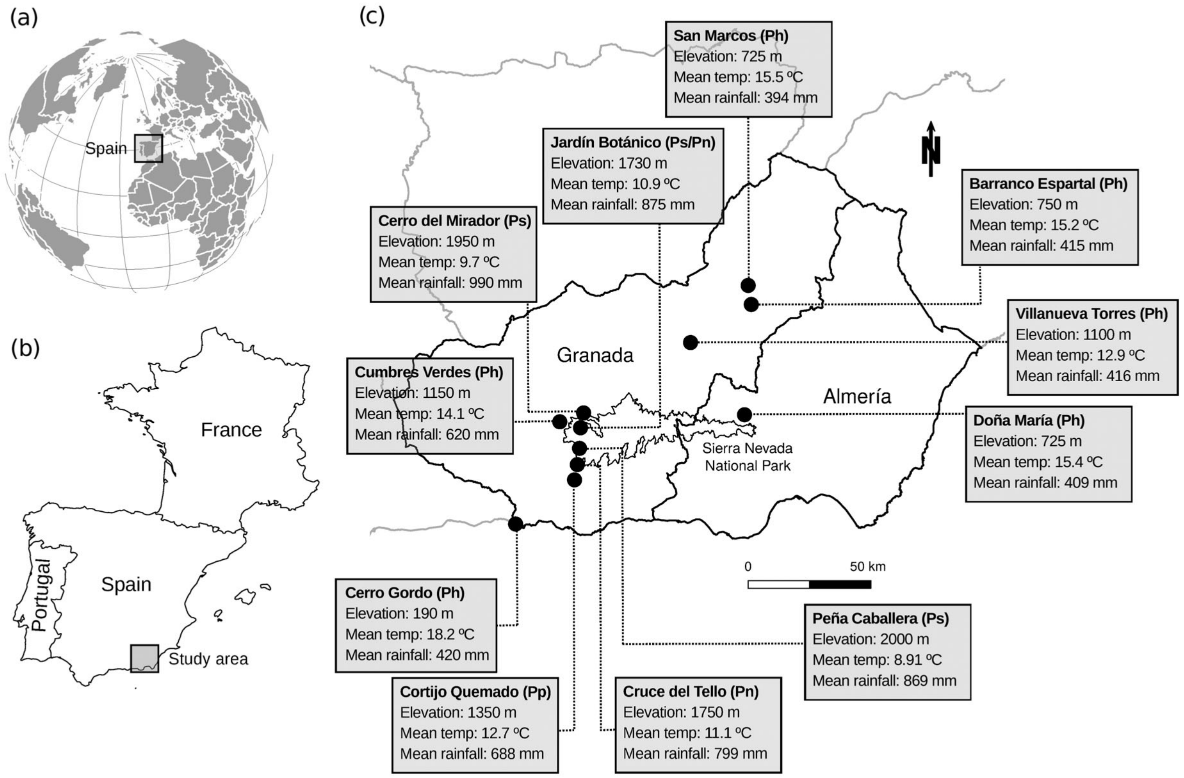

Fig. 1. (a) Location of the study area in the world; (b) within Spain; and (c) location and main characteristics (dominant host tree species, elevation, mean annual temperature, mean annual rainfall) of the 11 sampling plots selected for the monitoring of pine processionary moth egg batches from 2008 to 2014. Abbreviations are Ph, *Pinus halepensis*; Pn, *P. nigra*; Pp, *P. pinaster*; Ps, *P. sylvestris*.

until the next moth emergence. The life cycle of *T. pityocampa* is normally univoltine, but diapause of pupae that burrowed into the soil can be prolonged for several years (Battisti et al. 2015, Torres-Muros et al. 2017).

A great variety of species can parasite PPM eggs, yet in our study area two species were dominant: *Baryscapus servadeii* (Domenichini) (Hymenoptera, Eulophidae) and *Ooencyrtus pityocampae* (Mercet) (Hymenoptera, Encyrtidae). *B. servadeii* is a specific parasitoid, and a primary oophagous of PPM egg clutches. Thus, synchronization is vital for this hymenopteran (Halperin 1990). It has a solitary life with one or two generations per year. Its occurrence varies from very low rates to a parasitism up to 45% of the eggs (Tsankov et al. 2006). *B. servadeii* may also behave as a hyperparasitoid of other parasitoids' eggs, such as *O. pityocampae* (Zovi et al. 2006), the other main parasitoid of PPM. Although *O. pityocampae* was first considered a specific parasitoid of PPM, it was later demonstrated that it could feed on other species (Battisti 1989, Samra et al. 2015). This species typically emerges one month before PPM lays its eggs, and, until emergence from pupation of PPM, it parasites other hosts, totaling two or three generations per year. Due to its searching strategy and polyvalence, this parasitoid may survive in low-density populations of *T. pityocampae*. *O. pityocampae* can be a hyperparasitoid of other parasitoid species (Zovi et al. 2006). For both parasitoid species, the last generation enters diapause overwinter and emerges as an imago the next spring (usually from May to June).

Data sampling

Sampling took place during a seven years period (2008–2014), including a severe outbreak in 2009–2010, so this time span is likely to embed a

PPM full 6-yr cycle (Robinet 2006, Hódar et al. 2012). Every year, trained people searched for egg batches laid in the previous year (July–August) in each of the study plots. This search was conducted usually in February–March, after the coldest part of the winter was over, in order to ensure that the parasitoids had undergone the minimum winter temperatures, before the spring flush of parasitoids. Up to 30 PPM egg clutches were collected in each plot every year, depending on their availability. Once in the laboratory, clutches were stored individually in sealed transpirable cellophane bags, until the end of the emergence of parasitoids (4–6 months after collection). Egg batches were then examined with the help of an electronic lens. The scales covering the eggs were removed, and the number of hatched, parasitized, and unhatched eggs were counted. Hatched and parasitized eggs were easily identifiable by the different size and shape of the exit holes. Emerged parasitoids were then identified on the basis of the organic leftovers of the hatching and the carcasses of adult parasitoids (Alemany et al. 1994).

Statistical analyses

Three response variables were calculated: (1) parasitism rate (i.e., percentage of eggs per batch with evidence of parasitism); (2) probability of occurrence of *B. servadeii*; and (3) probability of occurrence of *O. pityocampae*. The parasitism rate was negatively correlated ($r = -0.488$) with percentage of reproductive success (i.e., percentage of eggs per batch that had clutched), so the latter variable was not used in this study. We used generalized linear mixed models (GLMMs), with a binomial error distribution, to analyze the change of these three response variables along the elevational gradient while accounting for the effect of interannual climatic conditions using Hurrell's winter North Atlantic Oscillation (NAO) index (Hurrell 1995; see Hódar et al. 2012 for a similar application of this index). The interaction between elevation and NAO was also statistically tested, where a significant effect would indicate that the slope of the relationship between the response variable and elevation might change depending on the value of NAO. Explanatory variables were scaled by dividing their mean by their standard deviation to avoid singularity and convergence problems during model fitting. Plot was included as a random factor in the models to account for potential autocorrelation in the data analyzed, as the same locations sampled in different years might have a similar response over time due to particular features of the plot, such as land-use history, topography, or plant diversity, that might have a strong effect on parasitoid abundance. We also included an additional observation-level random-effects (OLRE) factor (Harrison 2014) to account for overdispersion in GLMMs of the parasitism rate. The OLRE factor considers each data point as a single level of a random effect and can offset overdispersion due to aggregated data.

To test for the statistical significance of fixed effects, we used likelihood-ratio tests (LRTs) of reduced versus full models based on the ratio of their likelihoods. LRTs are generally used to compare two nested models—that is, in situations where one of the models is a special case of the other—using the chi-squared distribution, with the null hypothesis that the data are drawn from the simpler of the two models. Model residuals were explored using a simulation-based approach to create readily interpretable scaled (quantile) residuals for the fitted GLMMs (Hartig 2019). Following Nakagawa and Schielzeth (2013), we calculated two components of R^2 for GLMMs: (1) a marginal R^2 (R^2_{m}) that only takes into account the variability explained by fixed effects; and (2) a conditional R^2 (R^2_{c}) that accounts for the variability supported by both the fixed and random effects.

Due to a strong correlation between pine species and elevation, it proved difficult to ascertain whether an effect of elevation on any of the response variables was attributable to changes in the climatic conditions or to host-mediated responses (potential confounding effects). Therefore, we repeated all the analyses for a subset of plots dominated by a single host, *Pinus halepensis*. This species occupies a broad range in our study area on a gradient from 120 to 1150 m.a.s.l. (hereafter lowlands). Additionally, we repeated all the analyses for all other pine species lumped together (*P. pinaster, P. nigra, P. sylvestris*), which have similar habitat requirements and occupy the upper level part of our elevational gradient from 1350 to 2050 m.a.s.l. (hereafter the uplands).

All the analyses were performed in R (R Core Team 2020), using the packages lme4 (Bates et al. 2015), glmmADMB (Fournier et al. 2012), and DHARMa (Hartig 2019).

RESULTS

A total of 1558 egg batches were sampled over the study period. All the samples, pooled along the elevational gradient over the entire time period, averaged of 186.5 eggs per batch (ranging from 27 to 321 eggs), with 10.9% of eggs per batch parasitized (ranging from 0.0 to 62.7%; Table 1), 17.6% of eggs per batch unhatched (ranging from 0.0 to 100.0%), and 71.5% of eggs per batch that successfully hatched (ranging from 0.0 to 100.0%). The largest clutch size was found in Cortijo Quemado, at 1350 m.a.s.l., whereas Barranco del Espartal, at 750 m.a.s.l., had the smallest (Table 1).

Out of the total number of clutches examined, 73.7% contained parasitoids, either *O. pityocampae* (present in 48.1% of egg clutches) or *B. servadeii* (present in 55.5% of egg clutches; Table 1). No competitive exclusion was found, as some batches contained both parasitoids (representing a 29.8% of all clutches, and 40.5% of the parasitized batches).

Changes of parasitism along the elevational gradient

Both elevation and NAO index affected all three response variables (Table 2a, Fig. 2). Additionally, the interaction between the predictors influenced both the parasitism rate and the occurrence of *O. pityocampae* (Table 2a). In models for parasitism rate and the occurrence of *O. pityocampae*, the amount of variability explained by fixed effects was relatively small (10.9% and 12.0%, respectively), whereas for probability of occurrence of *B. servadeii* the amount of variability was much higher (52.5%, Table 2a).

When we focused only on lowlands (plots dominated by *P. halepensis*), we found the effect of elevation on all three response variables to be considerably diluted, as shown by (1) the non-significant effect of elevation on the parasitism rate (Table 2b, Fig. 2b); (2) a positive effect of elevation on the probability of occurrence of *O. pityocampae* (Table 2b, Fig. 2d); (3) a weak negative effect of elevation on the occurrence of *B. servadeii*; and (4) a decrease in the estimated explained variance of both fixed and random effects in all response variables (Table 2b).

By contrast, when we focused on the uplands, which were dominated by *P. pinaster, P. nigra,* or *P. sylvestris*, we found the results to be more consistent with the overall patterns revealed when all pine species were analyzed. Elevation had an effect on all three response variables, and the NAO index influenced the rate of parasitism and the probability of occurrence of *B. servadeii* (Table 2c); in addition, the amount of variability explained by fixed effects was generally higher than for the lowlands (Table 2c).

Model predictions showed a decrease in the parasitism rate (Fig. 2a), and in the probability of occurrence of the two main species of parasitoids (Fig. 2c, e) along the elevational gradient. The parasitism rate declined from ~0.5 in the lowlands to less than 0.1 in the uplands (Fig. 2a). The probability of occurrence of *B. servadeii* (Fig. 2e) declined more severely in the uppermost part of the gradient—dropping almost to zero at the highest elevation—than probability of occurrence of *O. pityocampae* (Fig. 2c). For the lowlands, the relationship of the parasitism rate with elevation did not change (Fig. 2b), while the probability of occurrence of *O. pityocampae* increased moderately with elevation (Fig. 2d), and the probability of occurrence of *B. servadeii* decreased evenly with elevation, but in all cases remained high (Fig. 2f). For the uplands, the parasitism rate clearly decreased with elevation (Fig. 2b), showing the probability of occurrence of *O. pityocampae* declining (Fig. 2d), and the probability of occurrence of *B. servadeii* falling abruptly (Fig. 2f).

Relationship between parasitism and NAO

The NAO index had a statistically significant effect on all three response variables when all plots were considered (Table 2a). When only the lowland plots were considered, the NAO affected the parasitism rate but not the probability of occurrence of the two parasitoids (Table 2 b), whereas in the uplands NAO influenced both the parasitism rate and the occurrence of *B. servadeii* (Table 2c). Overall, positive NAO winter values, associated with cold and dry winters, reduced the parasitism rate and the probability of occurrence of the two main parasitoid species

Table 1. Number of batches, average clutch size (eggs number), rate of parasitism, abortion and reproductive success, and number and proportion (%P, in brackets) of batches with presence of *Ooencyrtus pytiocampae*, *Baryscapus servadeii*, or any of these two parasitoids by year and plot.

Year and plot	No. batches	Clutch size (no. eggs)	Parasitism (%)	Abortion (%)	Reproductive success (%)	No. (%P) *O. pityocampae*	No. (%P) *B. servadeii*	No. (%P) any parasitoid
2008	292	190.9 53–275	4.5 0.0–42.8	16.8 0.0–100.0	78.7 0.0–100.0	136 (46.6)	107 (36.6)	183 (62.7)
2009	291	181.8 50–285	6.2 0.0–40.0	23.5 0.0–85.2	70.3 0.0–100.0	165 (56.7)	161 (55.3)	233 (80.1)
2010	320	184.0 62–279	16.5 0.0–55.5	18.0 0.0–96.8	65.5 0.8–100.0	200 (69.0)	217 (74.8)	271 (93.4)
2011	282	177.6 27–321	16.8 0.0–62.6	17.4 0.0–94.5	65.9 0.0–100.0	76 (26.9)	158 (56.0)	173 (61.3)
2012	161	201.9 58–319	8.4 0.0–48.5	10.9 0.0–79.7	80.7 0.9–100.0	42 (32.1)	59 (45.0)	71 (54.2)
2013	113	196.9 101–274	9.2 0.0–41.7	15.4 0.0–83.3	75.4 15.0–100.0	55 (48.7)	39 (34.5)	80 (70.8)
2014	99	183.6 112–244	14.5 0.0–45.9	15.5 0.9–74.7	70.0 12.9–99.1	46 (46.5)	90 (90.9)	93 (93.9)
Cerro Gordo	210	192.7 27–299	15.2 0.0–62.7	20.4 0.0–95.4	64.4 4.5–100.0	77 (36.7)	185 (88.1)	196 (93.3)
San Marcos	121	184.0 79–261	7.4 0.0–36.7	20.5 0.9–93.6	72.2 0.0–99.1	83 (68.6)	98 (81.0)	116 (95.9)
Doña María	90	178.3 99–279	18.5 0.0–58.6	19.3 0.0–78.6	62.2 0.0–99.5	38 (42.2)	85 (94.4)	87 (96.7)
Bco. Espartal	149	160.2 57–224	12.9 0.0–53.8	24.9 1.3–94.5	62.2 0.0–95.5	100 (67.1)	141 (94.6)	148 (99.3)
Villanueva Torres	121	136.4 50–233	12.7 0.0–52.9	24.5 1.4–100.0	62.7 0.0–98.6	80 (66.1)	80 (66.1)	111 (91.7)
Cumbres Verdes	113	171.7 67–265	18.6 0.0–57.9	23.9 0.5–96.8	57.4 0.8–99.5	59 (52.2)	82 (72.6)	93 (82.3)
Cortijo Quemado	170	206.5 89–321	8.5 0.0–34.0	18.9 0.0–83.3	72.5 0.9–100.0	66 (38.8)	18 (10.6)	69 (40.6)
Jardín Botánico	116	204.7 125–273	11.7 0.0–54.0	13.6 0.0–56.4	74.7 29.5–100.0	37 (31.9)	82 (70.7)	94 (81.0)
Cruce de Tello	152	194.7 62–319	9.1 0.0–48.0	14.7 0.0–100.0	76.2 0.0–100.0	103 (67.8)	38 (25.0)	108 (71.1)
Cerro del Mirador	145	205.7 32–275	8.4 0.0–48.5	10.9 0.0–46.1	80.7 34.4–100.0	44 (30.3)	21 (14.5)	48 (33.1)
Peña Caballera	171	197.3 53–285	1.3 0.0–20.2	5.5 0.0–96.9	93.2 0.0–100.0	33 (19.3)	1 (0.6)	34 (19.9)
Total	1558†	186.5 27–321	10.9 0.0–62.7	17.6 0.0–100.0	71.5 0.0–100.0	720 (48.1)†	831 (55.5)†	1104 (73.7)†

Note: The range for each variable (minimum–maximum) appears below the mean values.
† There were only a total of 1498 batches for which it was recorded the presence of *O. pityocampae* and *B. servadeii*.

—but particularly for the generalist—in the uplands (Fig. 3).

Discussion

Our study reveals that the parasitism rate in our system decreases as elevation increases. This result agrees well with previous studies (Tsankov et al. 1999, Auger-Rozenberg et al. 2015, Hódar 2015). However, we found a high variability among sites and from one year to another, depending on climatic conditions, with cold and dry winters (positive NAO) negatively affecting the populations of PPM parasitoids, particularly at higher elevations.

Although highly variable in space and time, the parasitism rate typically ranges from 6% to 40% in historical PPM distribution areas (Auger-Rozenberg et al. 2015, and references therein), and from 7% to 12% in recently colonized areas (Alemany et al. 1994, see also Auger-Rozenberg et al. 2015). This is consistent with the range of

Table 2. Estimated coefficients (and standard error, in brackets) of fixed effects in generalized linear mixed-effects models (GLMMs) for rate of parasitism, and probability of occurrence of *Ooencyrtus pityocampae* and *Baryscapus servadeii*.

			Probability of occurrence of			
	Rate of parasitism		*Ooencyrtus pityocampae*		*Baryscapus servadeii*	
Fixed effects	Estimate	LRT	Estimate	LRT	Estimate	LRT
(a) All plots						
Intercept	−1.378 (0.159)		−0.449 (0.367)		0.091 (0.421)	
Elevation	−0.774 (0.172)	<0.001	−0.512 (0.397)	<0.001	−2.249 (0.467)	<0.001
NAO	−0.243 (0.038)	<0.001	−0.567 (0.066)	0.2021	−0.873 (0.099)	<0.001
Elev:NAO	−0.190 (0.040)	<0.001	−0.304 (0.063)	<0.001	. . .	0.258
R^2_m	0.109		0.120		0.525	
R^2_c	0.475		0.383		0.695	
(b) Lowland plots						
Intercept	−0.611 (0.066)		−0.363 (0.287)		1.095 (0.565)	
Elevation	. . .	0.670	−0.340 (0.309)	<0.001	−0.908 (0.575)	<0.001
NAO	−0.026 (0.050)	0.019	. . .	0.122	. . .	0.158
Elev:NAO	. . .	0.558	. . .	0.101	. . .	0.589
R^2_m	0.001		0.037		0.076	
R^2_c	0.332		0.070		0.192	
(c) Highland plots						
Intercept	−1.212 (0.363)		−0.362 (1.002)		0.006 (1.516)	
Elevation	−1.152 (0.418)	<0.001	−0.648 (1.145)	<0.001	−2.751 (1.799)	<0.001
NAO	−0.431 (0.055)	0.027	. . .	0.586	0.036 (0.375)	0.155
Elev:NAO	. . .	0.583	. . .	0.298	−1.180 (0.459)	0.008
R^2_m	0.074		0.018		0.302	

Notes: Statistical significance was based on likelihood-ratio tests (LRTs). When the interaction was significant, main effects were also interpreted as significant regardless LRTs. When LRTs were nonsignificant estimated coefficients and their standard errors were not shown. Two components of R^2 were estimated for each GLMM: (1) a marginal R^2 (R^2_m) that only takes into account the variability explained by fixed effects; and (2) a conditional R^2 (R^2_c) that accounts for the variability supported by both the fixed and random effects. GLMMs were fit for all plots (a), and plots dominated solely by *Pinus halepensis* (b), or *Pinus pinaster*, *Pinus sylvestris*, and *Pinus nigra* (c).

values reported in the present study (1.3–18.6%, Table 1) in the context of a new expansion. Parasitoids seem to have exerted less influence as the elevation rose, in agreement with the results reported by Tsankov et al. (1999) in Bulgaria and Auger-Rozenberg et al. (2015) in two elevational gradients in France showing that *O. pityocampae* emerged to a lesser extent at higher elevations. These results imply a certain decoupling in the relationship between host and parasitoids, representing a positive feedback on the expansion of PPM (Hódar et al. 2004), since the lower parasitism rate raised the number of overwintering larvae in the silken nest, which is known to increase the probability of survival to low temperatures (Huchon and Démolin 1971). PPM is freeze tolerant but does suffer time/temperature-related mortality due to cumulative chill injury (Hoch et al. 2009), so milder winters promote PPM adult and larval survival (Battisti et al. 2005), and a lower parasitism rate promotes this expansion, even more.

The probability of occurrence of the two main parasitoids also diminished with elevation, but *B. servadeii* responded more sharply (Fig. 2e) to elevational changes than did *O. pityocampae* (Fig. 2c). This can be explained in two non-mutually exclusive ways. First, the greater susceptibility of *B. servadeii* to frost (Masutti 1964) would limit its performance above a certain elevation in favor of *O. pityocampae*. Second, *O. pityocampae* reportedly emerges three weeks to one month sooner than PPM moths, while in *B. servadeii* this lags approximately one week (Dulaurent et al. 2011). The advance in the emergence time may serve *O. pityocampae* to parasitize other hosts, reaching a higher population at the time when PPM egg batches are available (Battisti et al. 1988, Samra et al. 2015).

Elevation becomes less important when only *Pinus halepensis* data are analyzed, while a key

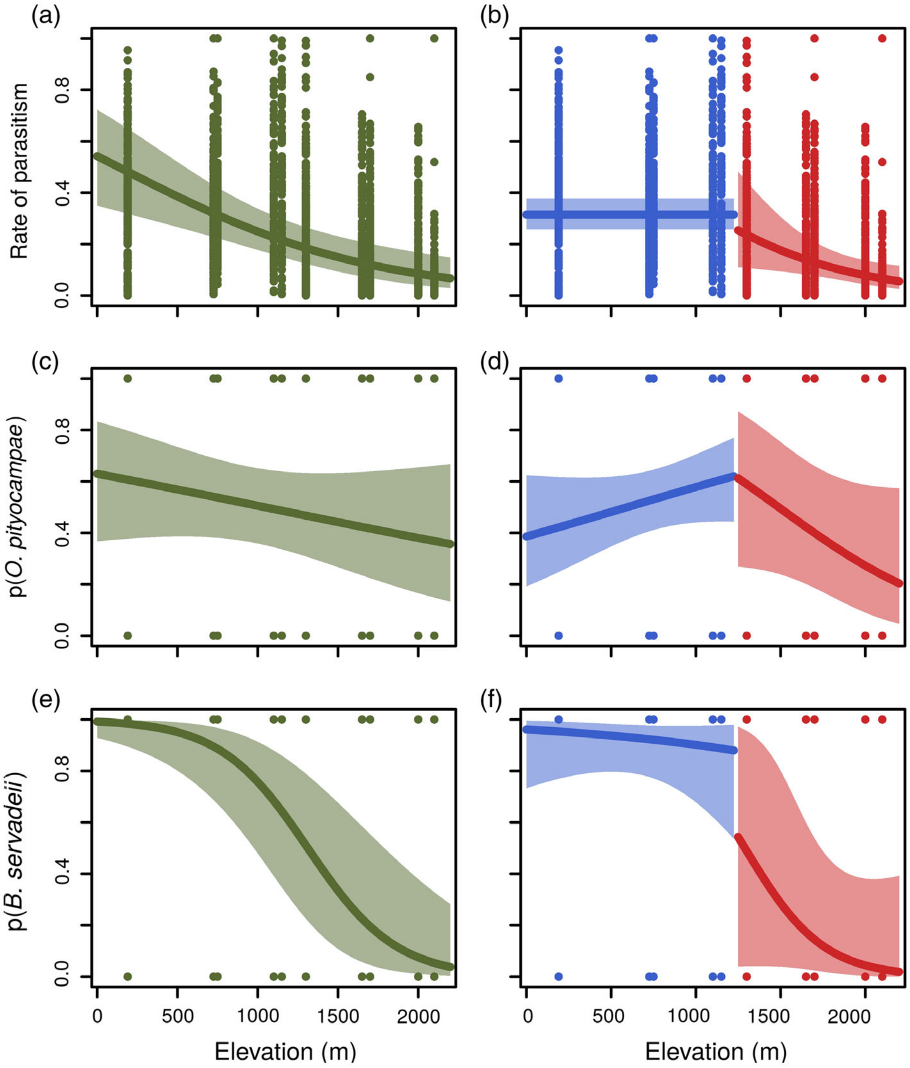

Fig. 2. Model predictions and 95% confidence intervals of parasitism (a, b), probability of occurrence of *Ooencyrtus pityocampae* (c, d), and probability of occurrence of *Baryscapus servadeii* (e, f) as a function of elevation for all plots (a, c, e, in green, Table 2a), and plots dominated solely by *Pinus halepensis* (blue lines, Table 2b), or *P. pinaster*, *P. nigra,* or *P. sylvestris* (red lines, Table 2c), respectively (b, d, f). In those models where the NAO index was significant (Table 2), its value was set to 0 for model predictions. For probability of occurrence of the two parasitoid species, observed data were aggregated at each elevational belt, and mean values (dots) and 95% confidence intervals (bars) were shown instead of raw values (0, 1) to improve visualization.

factor concerns data *Pinus* only above 1300 m (uplands data). With the average clutch size remaining stable along the elevational gradient but parasitism hardly affected by elevation, parasitism becomes the key factor determining PPM reproductive success in the lowlands. In a previous work, Hódar et al. (2012) suggested that PPM incidence was chronic at lower elevations, with more diverse and developed populations of predators and parasitoids than at high-mountain sites, thus leading to more efficient PPM biological control in the lowlands while PPM at medium-high elevations was determined more by climate (Hódar et al. 2012). Our results in the present work point in the same direction: In the lowlands, where the dominant tree is *P. halepensis*,

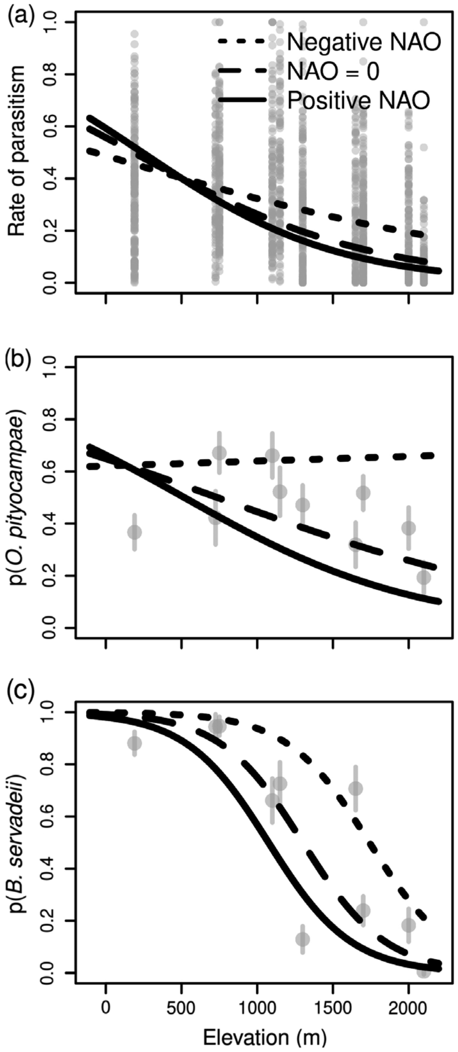

Fig. 3. Model predictions of rate of parasitism (a), probability of occurrence of *Ooencyrtus pityocampae* (b), and probability of occurrence of *Baryscapus servadeii* (c) as a function of elevation for different NAO values. Negative and positive NAO values represent the range of observed NAO values in our study. For probability of occurrence of the two parasitoid species, observed data were aggregated at each elevational belt, and mean values (dots) and 95% confidence intervals (bars) were shown instead of raw values (0, 1) to improve visualization.

PPM is mainly under biological control (egg parasitoids among them), while above ~1300 m, biological control becomes more dependent on climatic conditions. Higher winter temperatures favor the survival of overwintering parasitoids in diapause, resulting in a second flush in spring. Thus, a warm and wet winter (negative NAO values) boosts the parasitism rate and presence of parasitoids, while a cold and dry winter (positive NAO values) has the opposite effect (Fig. 3). The trend is clear for the entire gradient, but the effect of elevation vanishes when lowland plots are considered (Fig. 3), a result consistent with the less harmful winter conditions in the lowlands. By contrast, the influence of the NAO persists at medium-high elevations: A positive NAO at high elevations leads to a low probability of occurrence of the two main parasitoids (Fig. 3b, c), and a dip in the parasitism rate (Fig. 3a). Notably, the winter NAO shows opposite effects for PPM and parasitoids: A negative winter NAO enhances overwinter survival of parasitoids but harms PPM larval development and thus reduces defoliation intensity (Hódar et al. 2012). Although the NAO is a global driver, the local characteristics of the site greatly modulate the effect (Bojariu and Giorgi 2005), and the NAO is known to have a major influence on mountain climatic conditions (López-Moreno et al. 2011).

The capacity of pupae to prolong their diapause underground for several years enables PPM to cope with harsh winter conditions and produce viable populations during warmer winters at higher elevations. This, in combination with the low parasitism rate in the uplands, empowers a rapid expansion of PPM into new warming areas (Hoch et al. 2009, Auger-Rozenberg et al. 2015). At these elevations, the opposite effects of the winter NAO on the survival of parasitoids and PPM prompt more eruptive PPM dynamics, since PPM can quickly expand its population in years with adequate climatic conditions, while PPM control by parasitoids remains weak. The recent nature of the PPM expansion hinders the coupling of the dynamic between host and parasitoid. The direct consequences of climate warming and land-use changes for parasitoids remain unknown (Auger-Rozenberg et al. 2015), hampering predictions concerning parasitoid–host interactions in these expansion areas. However, it is well known that a more diverse and heterogeneous environment (e.g., increasing tree diversity) mitigates the virulence of PPM defoliations (Jactel and Brockerhoff 2007, Cayuela et al. 2011, Castagneyrol et al. 2014, Régolini et al. 2014) and enhances parasitoid survival by providing food sources and alternative hosts (Dulaurent et al. 2011). Therefore, adequate habitat management becomes crucial for promoting the stability of PPM predators and parasitoids, to minimize outbreaks in new expansion areas.

Acknowledgments

We are thankful to Karim Senhadji and Ramón Ruiz-Puche for their help during the field work, and to Sara García Morato for her contribution to quantifying rates of parasitism in PPM clutches at the laboratory. Two anonymous referees contributed to improve the manuscript. This study was supported by projects PROPINOL (PN22/2008), GESBOME (P06-RNM-1890) from Junta de Andalucía, REMEDINAL TE-CM (S2018/EMT-4338) from Comunidad de Madrid, ADAPTAMED (LIFE14 CCA/ES/000612) from LIFE program, and GILES (PCIN-2016-150) from the ERA-NET-LAC H2020 Programme.

Literature Cited

AEMET. 2011. Iberian climate atlas. Air temperature and precipitation (1971–2000). AEMET, Agencia Estatal de Meteorología, Ministerio de Medio Ambiente y Medio Rural y Marino, Madrid, Spain.

Alemany, A., M. A. Miranda, and P. Morell. 1994. Primeros resultados del estudio sobre parasitismo en huevos de *Thaumetopoea pityocampa* (Den. and Schif.), en Baleares. Boletín De Sanidad Vegetal. Plagas 20:679–685.

Auger-Rozenberg, M.-A., et al. 2015. Ecological responses of parasitoids, predators and associated insect communities to the climate-driven expansion of the pine processionary moth. Pages 311–357*in* A. Roques, editor. Processionary moths and climate change: an update. Springer, Netherlands and Éditions Quæ, Versailles, France.

Barbaro, L., and A. Battisti. 2011. Birds as predators of the pine processionary moth (Lepidoptera: Notodontidae). Biological Control 56:107–114.

Bates, B., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Battisti, A. 1988. Host-plant relationships and population dynamics of the Pine Processionary Caterpillar *Thaumetopoea pityocampa* (Denis and Schiffermuller). Journal of Applied Entomology 105:393–402.

Battisti, A. 1989. Field studies on the behaviour of two egg parasitoids of the pine processionary moth *Thaumetopoea pityocampa*. Entomophaga 34:29–38.

Battisti, A., et al. 2015. Natural history of the processionary moths (*Thaumetopoea* spp.): new insights in relation to climate change. *Thaumetopoea pityocampa*. Pages 15–80*in* A. Roques, editor. Processionary moths and climate change: an update. Springer Netherlands and Éditions Quæ, Versailles, France.

Battisti, A., S. Colazza, P. F. Roversi, and R. Tiberi. 1988. Alternative hosts of *Ooencyrtus pityocampae* (Mercet) (Hymenoptera: Encyrtidae) in Italy. Redia 71:321–328.

Battisti, A., M. Stastny, S. Netherer, C. Robinet, A. Schopf, A. Roques, and S. Larsson. 2005. Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. Ecological Applications 15:2084–2096.

Bojariu, R., and F. Giorgi. 2005. The North Atlantic Oscillation signal in a regional climate simulation for the European region. Tellus 57:641–653.

Brooker, R. W., J. M. J. Travis, E. J. Clark, and C. Dytham. 2007. Modelling species' range shifts in a changing climate: the impacts of biotic interactions, dispersal distance and the rate of climate change. Journal of Theoretical Biology 245:59–65.

Buffo, E., A. Battisti, M. Stastny, and S. Larsson. 2007. Temperature as a predictor of survival of the pine processionary moth in the Italian Alps. Agricultural and Forest Entomology 9:65–72.

Castagneyrol, B., M. Régolini, and H. Jactel. 2014. Tree species composition rather than diversity triggers associational resistance to the pine processionary moth. Basic and Applied Ecology 15:516–523.

Cayuela, L., J. A. Hódar, and R. Zamora. 2011. Is insecticide spraying a viable and cost-efficient management practice to control pine processionary moth in Mediterranean pine woodlands? Forest Ecology and Management 261:1732–1737.

Colautti, R. I., A. Ricciardi, I. Grigorovich, and H. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? Biology Letters 7:721–733.

Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary Climate Change. Science 292:673–679.

Dulaurent, A. M., J. P. Rossi, C. Deborde, A. Moing, P. Menassieu, and H. Jactel. 2011. Honeydew feeding increased the longevity of two egg parasitoids of the pine processionary moth. Journal of Applied Entomology 135:184–194.

Fournier, D. A., H. J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. Maunder, A. Nielsen, and J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software 27:233–249.

Halperin, J. 1990. Natural enemies of *Thaumetopoea* spp. (Lep., Thaumetopoeidae) in Israel. Journal of Applied Entomology 109:425–435.

Harley, C. D. G. 2011. Climate change, keystone predation, and biodiversity loss. Science 334:1124–1127.

Harrington, R., I. Woiwod, and T. Sparks. 1999. Climate change and trophic interactions. Trends in Ecology and Evolution 14:146–150.

Harrison, X. A. 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. PeerJ 2:e616. https://doi.org/10.7717/peerj.616.

Hartig, F. 2019. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package 0.2.4

Hoch, G., E. P. Toffolo, S. Netherer, A. Battisti, and A. Schopf. 2009. Survival at low temperature of larvae of the pine processionary moth *Thaumetopoea pityocampa* from an area of range expansion. Agricultural and Forest Entomology 11:313–320.

Hódar, J. A. 2015. Incidencia de la procesionaria del pino como consecuencia del cambio climático: previsiones y posibles soluciones. Pages 295–302 *in* A. Herrero and M. A. Zavala, editors. Los Bosques y la Biodiversidad frente al Cambio Climático: Impactos, Vulnerabilidad y Adaptación en España. Ministerio de Agricultura, Alimentación y Medio Ambiente, Madrid, Spain.

Hódar, J. A., J. Castro, and R. Zamora. 2003. Pine processionary caterpillar *Thaumetopoea pityocampa* as a new threat for relict Mediterranean Scots pine forests under climatic warming. Biological Conservation 110:123–129.

Hódar, J. A., J. R. Obeso, and R. Zamora. 2009. Cambio climático y modificación de interacciones planta-animal. Pages 287–299 *in* R. A. Medel, M. A. Aizen and R. Zamora, editors. Ecología y evolución de interacciones planta-animal. Editorial Universitaria, Santiago de Chile, Chile.

Hódar, J. A., and R. Zamora. 2004. Herbivory and climatic warming: a Mediterranean outbreaking caterpillar attacks a relict, boreal pine species. Biodiversity and Conservation 13:493–500.

Hódar, J. A., R. Zamora, J. Castro, and E. Baraza. 2004. Feast and famine: previous defoliation limiting survival of pine processionary caterpillar *Thaumetopoea pityocampa* in Scots pine *Pinus sylvestris*. Acta Oecologica 26:203–210.

Hódar, J. A., R. Zamora, and L. Cayuela. 2012. Climate change and the incidence of a forest pest in Mediterranean ecosystems: can the North Atlantic Oscillation be used as a predictor? Climatic Change 113:699–711.

Huchon, H., and G. Démolin. 1971. La bioécologie de la processionaire du pin. Dispersion potentielle – Dispersion actuelle. Phytoma 23:11–20.

Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. Science 269:676–679.

IPCC. 2013. Summary for policymakers. *In* T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, editors. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Jactel, H., and E. G. Brockerhoff. 2007. Tree diversity reduces herbivory by forest insects. Ecology Letters 10:835–848.

Jordano, P. 2016. Chasing ecological interactions. PLoS Biology 14:e1002559.

Junta de Andalucía. 2010. Tercera adecuación del Plan Forestal Andaluz. Horizonte 2015. http://www.juntadeandalucia.es/medioambiente/site/portalweb/menuitem.7e1cf46ddf59bb227a9ebe205510e1ca/?vgnextoid=fb705d3e12007210VgnVCM1000001325e50aRCRD&vgnextchannel=e2ae4e5bf01f4310VgnVCM1000001325e50aRCRD

Liu, H., and P. Stiling. 2006. Testing the enemy release hypothesis: a review and meta-analysis. Biological Invasions 8:1535–1545.

López-Moreno, J. J., S. M. Vicente-Serrano, E. Morán-Tejeda, J. Lorenzo-Lacruz, A. Kenawi, and M. Beniston. 2011. Effects of the North Atlantic Oscillation (NAO) on combined temperature and precipitation winter modes in the Mediterranean mountains: observed relationships and projections for the 21st century. Global and Planetary Change 77:62–76.

Malhi, Y., J. Franklin, N. Seddon, M. Solan, M. G. Turner, C. B. Field, and N. Knowlton. 2020. Climate change and ecosystems: threats, opportunities and solutions. Philosophical Transactions of the Royal Society B 375:20190104.

Masutti, L. 1964. Ricerche sui parassiti oofagi della *Thaumetopoea pityocampa* Schiff. Annali Del Centro Di Economia Montana Delle Venezie 4:205–271.

Menéndez, R. 2007. How are insects responding to global warming? Tijdschrift Voor Entomologie 150:355–365.

Mirchev, P., G. Georgiev, P. Boyadzhiev, and M. Matova. 2012. Impact of entomophages on density of *Thaumetopoea pityocampa* in egg stage near Ivaylovgrad, Bulgaria. Acta Zoologica Bulgarica 4:103–110.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed effect models. Methods in Ecology and Evolution 4:283–294.

Netherer, S., and A. Schopf. 2010. Potential effects of climate change on insect herbivores in European forests. General aspects and the pine processionary moth as specific example. Forest Ecology and Management 259:831–838.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12:361–371.

Pérez-Luque, A. J., R. Pérez-Pérez, and F. J. Bonet-García. 2016. Climate change over the last 50 years in Sierra Nevada. Pages 24–26 *in* R. Zamora, A. J. Pérez-Luque, F. J. Bonet-García, J. M. Barea-Azcón, and R. Aspizua, editors. Global change impacts in Sierra Nevada: challenges for conservation. Consejería de Medio Ambiente y Ordenación del Territorio, Junta de Andalucía, Granada, Spain.

Pérez-Palazón, M. J., R. Pimentel, J. Herrero, C. Aguilar, J. M. Perales, and M. J. Polo. 2015. Extreme values of snow-related variables in Mediterranean regions: trends and long-term forecasting in Sierra Nevada (Spain). Proceedings of the International Association of Hydrological Sciences 369:157–162.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Régolini, M., B. Castagneyrol, A. M. Dulaurent-Mercadal, D. Piou, J. C. Samalens, and H. Jactel. 2014. Effectof host tree density and apparency on the probability of attack by the pine processionary moth. Forest Ecology and Management 334:185–192.

Robinet, C. 2006. Mathematical modelling of invasion processes in ecology: the pine processionary moth as a case study. Thesis. École des Hautes Études en Sciences 378 Sociales, Paris, France.

Robinet, C., P. Baier, J. Pennerstorfer, A. Schopf, and A. Roques. 2007. Modelling the effects of climate change on the potential feeding activity of *Thaumetopoea pityocampa* (Den. and Schiff.) (Lep., Notodontidae) in France. Global Ecology and Biogeography 16:460–471.

Rogelj, J., M. Meinshausen, and R. Knutti. 2012. Global warming under old and new scenarios using IPCC climate sensitivity range estimates. Nature Climate Change 2:248–253.

Roques, A., et al. 2015. Climate warming and past and present distribution of the processionary moths (*Thaumetopoea* spp.) in Europe, Asia Minor and North Africa. Pages 81–162 *in* A. Roques, editor. Processionary moths and climate change: an update. Springer Netherlands and Éditions Quæ, Versailles, France.

Ros-Candeira, A., A. J. Pérez-Luque, M. Suárez-Muñoz, F. J. Bonet-García, J. A. Hódar, F. Giménez de Azcárate, and E. Ortega-Díaz. 2019. Dataset of occurrence and incidence of pine processionary moth in Andalusia, south Spain. ZooKeys 852:125–136.

Samra, S., M. Ghanim, A. Protasov, M. Branco, and Z. Mendel. 2015. Genetic diversity and host alternation of the egg parasitoid *Ooencyrtus pityocampae* between the pine processionary moth and the caper bug. PLOS ONE 10:e0122788.

Thuiller, W. 2004. Patterns and uncertainties of species' range shifts under climate change. Global Change Biology 10:2020–2027.

Tiberi, R., M. Bracalini, F. Croci, G. Tellini, and T. Panzavolta. 2015. Effects of climate on pine processionary moth fecundity and on its egg parasitoids. Ecology and Evolution 5:5372–5382.

Torres-Muros, L., J. A. Hódar, and R. Zamora. 2017. Effect of habitat type and soil moisture on pupal stage of a Mediterranean forest pest (*Thaumetopoea pityocampa*). Agricultural and Forest Entomology 19:130–138.

Tsankov, G., E. Douma-Petridou, P. Mirchev, G. Georgiev, and A. Koutsaftikis. 1999. Spectrum of egg parasitoids and rate of parasitism of egg batches of the pine processionary moth *Thaumetopoea pityocampa* (Den. and Schiff.) in the northern Peloponnes/Greece. Journal of the Entomological Research Society 1:1–8.

Tsankov, G., P. Mirchev, and M. Matova. 2006. Egg parasitoids, rate of parasitism and structure of egg batches of *Thaumetopoea pityocampa* (Den. and Schiff.) (Lep., Thaumetopoeidae) from the region of Ochrid (Republic of Macedonia). Silva Balcanica 7:77–87.

Tsankov, G., G. H. Schmidt, and P. B. Mirchev. 1996. Parasitism of egg-batches of the pine processionary moth *Thaumetopoea pityocampa* (Den. and Schiff.) (Lep., Thaumetopoeidae) in various regions of Bulgaria. Journal of Applied Entomology 120:93–105.

Turner, M. G., et al. 2020. Climate change, ecosystems and abrupt change: science priorities. Philosophical Transactions of the Royal Society B 375:20190105.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Wilson, R. J., D. Gutierrez, J. Gutierrez, and V. J. Monserrat. 2007. An elevational shift in butterfly species richness and composition accompanying recent climate change. Global Change Biology 13:1873–1887.

Zovi, D., A. Battisti, K. Hellrigl, and S. Minerbi. 2006. Egg parasitoids of the pine processionary moth and their occurrence in Venosta/Vinschgau. Forest Observer 2–3:81–88.

DATA AVAILABILITY

The dataset analyzed in this study is available in the Figshare repository: https://doi.org/10.6084/m9.figshare.13385333.