

## EXPANSION OF GEOGRAPHIC RANGE IN THE PINE PROCESSIONARY MOTH CAUSED BY INCREASED WINTER TEMPERATURES

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**Abstract.** Global warming is predicted to cause distributional changes in organisms whose geographic ranges are controlled by temperature. We report a recent latitudinal and altitudinal expansion of the pine processionary moth, *Thaumetopoea pityocampa*, whose larvae build silk nests and feed on pine foliage in the winter. In north-central France (Paris Basin), its range boundary has shifted by 87 km northwards between 1972 and 2004; in northern Italy (Alps), an altitudinal shift of 110–230 m upwards occurred between 1975 and 2004. By experimentally linking winter temperature, feeding activity, and survival of *T. pityocampa* larvae, we attribute the expansions to increased winter survival due to a warming trend over the past three decades. In the laboratory we determined the minimum nest and night air temperatures required for larval feeding and developed a mechanistic model based on these temperature thresholds. We tested the model in a translocation experiment that employed natural temperature gradients as spatial analogues for global warming. In all transects we transferred colonies of *T. pityocampa* larvae to sites within zones of historical distribution, recent distribution, and outside the present range. We monitored air and nest temperature, incoming solar radiation, larval phenology, feeding activity, and survival. Early-season temperature effects on phenology were evident, with delayed development of colonies in the more extreme (colder) sites. In the coldest months, our model was consistent with the observed patterns of feeding activity: Feeding was progressively reduced with increasing latitude or elevation, as predicted by the lower number of hours when the feeding threshold was reached, which negatively affected final survival. Insolation raised nest temperature and increased feeding activity on the south but not the north aspect. Prolonged temperature drops below the feeding thresholds occurred at all sites, leading to starvation and partial mortality. Nonetheless, even the most extreme sites still allowed some feeding and, consequently, up to 20% colony survival and successful pupation. Given that the present distribution of the oligophagous *T. pityocampa* is not constrained by the distribution of its actual or potential hosts, and that warmer winters will cause the number of hours of feeding to increase and the probability of the lower lethal temperature to decrease, we expect the trend of improved survival in previously prohibitive environments to continue, causing further latitudinal and altitudinal expansion. This work highlights the need to develop temperature-based predictive models for future range shifts of winter-limited species, with potential applications in management.

**Key words:** climate change; feeding activity; insect pest; larval survival; Lepidoptera; Pinus; range expansion; spatial dynamics; *Thaumetopoea pityocampa*.

### INTRODUCTION

Distributions of organisms are often defined by climatic factors, such as temperature and precipitation. With a mean global temperature increase of ~0.6°C over the past 100 years, and further projected increases (Houghton et al. 2001), widespread climate-related changes in the biosphere, and associated effects on eco-

logical communities, are to be expected. The effects of global warming on living organisms have now been recognized from the level of individual species to communities, most notably in the form of temperature-related range shifts, often assumed to be closely linked to species physiological constraints (Walther et al. 2002, Root et al. 2003). Recent distributional changes have been documented for plants, migratory birds, and temperate-zone butterflies (Parmesan et al. 1999, Walther et al. 2002, Parmesan and Yohe 2003). However, a causal relationship between climatic factors and species range limits is often difficult to determine. Ev-

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PLATE 1. (Top) The larvae of the pine processionary moth are gregarious and develop inside a conspicuous silk nest, which they typically build on a branch or treetop to maximize exposure to the sun. Easy detection of the nests allows collection of accurate data on the distribution and abundance even at low population densities. (Lower left) The moth lays all the eggs in a batch around a needle pair. The eggs are protected by scales deposited by the female during the oviposition. (Lower right) Egg batch of the pine processionary moth laid on *Pinus sylvestris* at an elevation of 1450 m in an expansion site in the Italian Alps (Mont Avic, 3006 m, is visible on the background). Photo credit: A. Battista.

idence may come from demonstrating that conditions exceeding the levels within the present range impose prohibitive mortality or preclude the completion of the life cycle (Gaston 2003).

Many insect species, and phytophagous insects in particular, are expected to show relatively rapid responses to the rising temperatures by shifting their geographic range boundaries poleward or to higher elevations (Solbreck 1993, Hodkinson and Bird 1998, Par-

mesan et al. 1999, Harrington et al. 2001, Bale et al. 2002). Most insects are very sensitive to changes in temperature, which may affect their activity, development, phenology, and survival directly (Karban and Strauss 2004), or indirectly through host phenology shifts or effects of temperature on host chemistry (Yang and Stamp 1995, Masters et al. 1998). At the same time, many phytophagous insects are able to quickly adapt to new environments, provided their host plants

are present (Bale et al. 2002). Switching to new hosts may occur among nonspecialist herbivores, and can be the first consequence of the strong selection on colonizers (Harrington et al. 2001).

Insect species that remain active and continue to feed during winter may be particularly influenced by global warming through increased feeding and survival (Leather et al. 1993). For these species, the critical temperatures for survival (lower lethal temperature, LLT) are often recorded in the winter (Fields and McNeil 1988, Sinclair 1999). Winter warming has reduced the limiting effect of temperature on the survivorship of the butterfly *Atalopedes campestris*, facilitating its latitudinal and altitudinal range expansion (Crozier 2003, 2004). The northern range of the southern pine beetle *Dendroctonus frontalis* in North America is restricted by winter LLT (Ungerer et al. 1999); consequently, an increase of 3°C in minimum temperature could extend its northern distribution limit by 170 km (Williams and Liebhold 2002). Global warming could also affect the establishment of the multivoltine pierid butterfly *Colotis evagore*, whose survival in the disjunct range in southern Spain is limited by winter temperature and winter availability of its host resource (Jordano et al. 1991).

The winter pine processionary moth, *Thaumetopoea pityocampa* (Denis & Schiffermüller) (Lepidoptera, Notodontidae), provides a classic example of an insect that is active in the winter, usually as a larva in the third and fourth instar. Its geographic range in southern Europe lies within limits set by winter temperatures (Androic 1956, Démolin 1969a, Huchon and Démolin 1971). Winter air temperature (mean January minimum above -4°C, LLT -16°C) and annual solar radiation (minimum of 1800 hours) were also used to define its potential range (Démolin 1969a). In the last three decades, a substantial expansion of the outbreak area has taken place near the edge of the range, both latitudinally and altitudinally (Hellrigl 1995, Benigni and Battisti 1999, Goussard et al. 1999, Hódar et al. 2003, Hódar and Zamora 2004). Similar range expansion has been predicted by models on insect life history (e.g., Bale et al. 2002), but few empirical studies exist to support model predictions or suggest mechanisms for range expansion (but see Crozier 2003, 2004).

In this study we sought a mechanistic understanding of the range expansion in *T. pityocampa*. We studied larval performance during the winter at two expansion areas: one occurring at a latitudinal (central France) and the other at an altitudinal scale (northern Italy). In each area we explored natural temperature gradients as spatial analogues for climate change by rearing cohorts of larvae in three zones along each gradient: the core zone (where the moth has been present for over 30 years), the expansion zone (where recent colonization has occurred), and the external zone (outside its 2003 distribution). This approach allowed us to test a mechanistic model for winter feeding that was developed

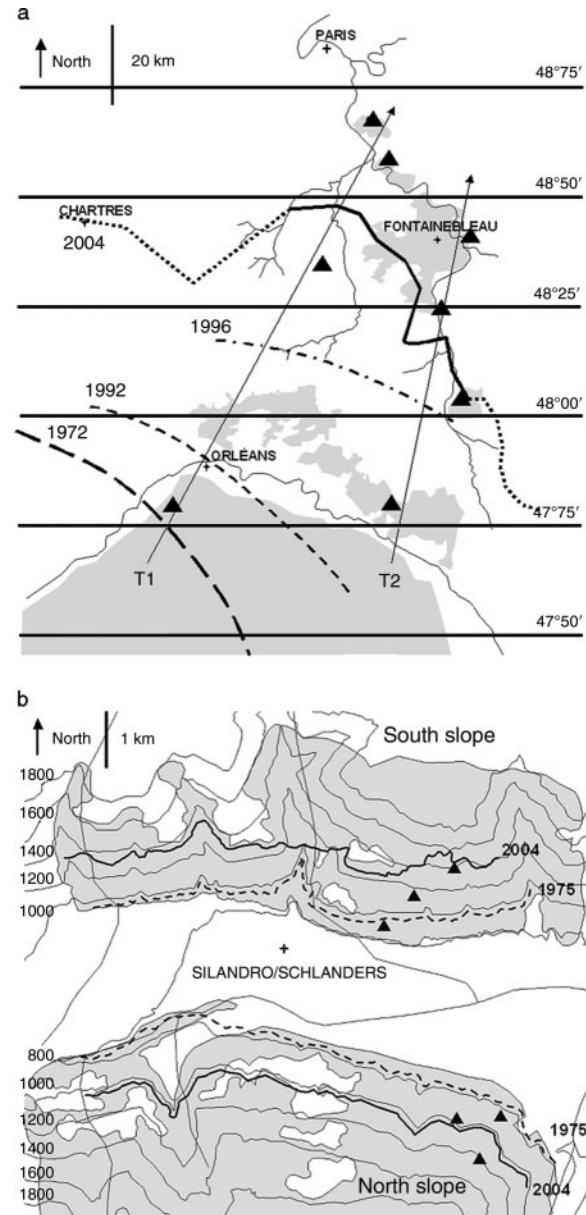


FIG. 1. Expansion of the geographic range of *Thaumetopoea pityocampa* (a) in the Paris Basin, France, from 1972 to present and (b) in Venosta/Vinschgau Valley, Italy, from 1975 to present. Triangles indicate sites used in the translocation experiment. Transects 1 and 2 (T1 and T2, respectively) are described in *Materials and methods; Translocation experiments*. The gray area shows the distribution of suitable host plants. Lines indicate the upper limit of the colonies in different years. The data for the 1972 front are from Abgrall (2001); the 1992 and 1996 fronts are from Goussard et al. (1999). The dotted line in the 2004 front indicates discontinuous assessment. The village of Silandro/Schlanders is located at 46°38' N, 10°43' E; elevation 721 m.

from laboratory data, and to assess the importance of feeding in winter survival. The model is based on the combined effect of daytime nest temperature, which induces feeding, and minimum temperature for night feeding. The observed patterns in feeding and survival confirm the model's ability to explain the trends in temperature-linked range expansion, and highlight the potential of similar approaches in improving our understanding of species range shifts.

#### MATERIALS AND METHODS

##### *Biology of the pine processionary moth*

*Thaumetopoea pityocampa* is a univoltine oligophage on coniferous trees (see Plate 1). Its main hosts in the study areas are *Pinus* spp., but it can also attack *Cedrus* spp. and the introduced *Pseudotsuga menziesii* (Roques et al. 2002). Phenology varies with climatic conditions (Démolin 1969a). In most of its range, *T. pityocampa* lives in areas with a Mediterranean climate, characterized by hot, dry summers. Like other insects with life histories adapted to this climate, it avoids high summer temperatures by having a longer pupal period, thereby postponing adult emergence until late summer when conditions for egg and larval development are more favorable. In more continental climates, on the other hand, the pupal period (aestivation) is shorter and emergence occurs earlier in the summer; such adaptation allows sufficient time for larval development and nest building before temperatures drop to freezing.

The larvae are gregarious and develop inside a conspicuous silk nest, which they typically build on a branch or treetop to maximize exposure to the sun. Larvae feed nocturnally on the needles throughout the winter, as long as the night temperature is above 0°C (Huchon and Démolin 1971). In late winter or spring the larvae form a procession and move to pupate in the soil. A variable proportion of the colony enters an extended diapause, which may last up to six years (Démolin 1969a). Adult emergence is immediately followed by mating and egg laying.

*T. pityocampa* frequently occurs at outbreak densities throughout the Mediterranean basin. Late larval instars can reduce tree growth through complete defoliation (Laurent-Hervouet 1986), and their presence creates a public health risk due to the production of urticating hairs, which may cause allergic reactions (contact dermatitis; Lamy 1990). Because of its economic and medical importance, *T. pityocampa* populations have been monitored for many years, by means of winter-nest censuses and pheromone trapping, as part of pest management programs throughout the Mediterranean region. Easy detection of the nests allows collection of accurate data on the distribution and abundance even at low population densities (Geri and Millier 1983).

##### *Study areas*

Latitudinal and altitudinal expansion areas for experimental studies were selected in the Paris Basin,

south of Paris, France, and in Venosta/Vinschgau Valley near Bolzano/Bozen, northern Italy, respectively. At both study areas the boundary of the expansion zone was defined as accurately as possible using data from past monitoring and detailed surveys of nests at the present range edge.

In the Paris Basin, we reconstructed the spatial distribution of *T. pityocampa* through time in collaboration with the Forest Health Department at the French Ministry of Agriculture (Paris, France). We defined the core zone as the area where the moth has been present for at least 30 years (Huchon and Démolin 1971; Fig. 1a). The northward expansion in native *Pinus sylvestris* and introduced *P. nigra* stands has been monitored by annual colony censuses carried out for >30 years (Abgrall 2001). In 2002–2004 the data set was expanded by a GPS-assisted nest census in an area extending 100 km from the core zone.

In the Venosta/Vinschgau Valley (Fig. 1b), we produced a similar reconstruction in collaboration with the Forest Service of the Bolzano/Bozen district. Historical data on population density were available from surveys carried out during pest management efforts (1950–1998; Hellrigl 1995, Minerbi et al. 2001). The Venosta/Vinschgau Valley (hereafter Venosta/Vinschgau) has an east–west orientation with opposite-facing slopes. On the south-facing slope (hereafter “south slope”), a series of plantations of *P. nigra* extends between 750 m and 1250 m and is intermixed with native *P. sylvestris* stands that continue up to ~1500 m. The stands on the north-facing slope (hereafter “north slope”) are composed mainly of native *P. sylvestris*, reaching a maximum elevation of ~1200 m. On each slope, the density of larval colonies was mapped in an area of ~1600 ha. In 2002–2004, colonies at the upper edge of the expansion zones were surveyed by visual observations of the winter nests by binoculars, and their coordinates recorded by a GPS device.

Latitudinal and altitudinal shifts (kilometers and meters per decade, respectively) in the respective areas were assessed using a GIS model by comparing the position of the expansion zone boundary in 1972 (Paris Basin) and 1975 (Venosta/Vinschgau) with the present one. For the latitudinal shift, transects orthogonal to the curve delimiting the core zone were laid out every 10 km, and the distance from the front to the core area was measured. For the altitudinal shift, the difference in elevation between the extremes of transects taken every kilometer was measured.

##### *Determination of feeding thresholds*

We conducted a laboratory experiment to determine how feeding is controlled by low temperatures. In November 2003, colonies of third or fourth larval instars were collected in Venosta/Vinschgau, and kept at +3°C ( $\pm 2^\circ\text{C}$ ) until testing. Nine individual colonies (sum total of 345 larvae) were then transferred to rearing chambers, and allowed to feed on *P. nigra* foliage under

short-day photoperiod (8 L:16 D, light from 08:00 to 16:00) and at constant night temperatures of either +3°C and -3°C. Preliminary data had shown that the larvae feed only if they have experienced a temperature of ~9°C during the previous day, independently of the larval instar. To confirm this threshold, we selected four temperature regimes for the light phase: +3°, +6°, +9°, and +12°C. Each temperature was tested for 2 d with a minimum of five replicates. Feeding was assessed by weighing feces collected automatically every 90 min. Feces production (fresh mass) was summed up for each time interval during 2 d, and divided by the number of larvae in the colony to obtain per capita feces production.

#### Translocation experiments

In both France and Italy, we utilized natural gradients to simulate temperature conditions experienced by the insect, as spatial analogues for climate change. In the Paris Basin, two latitudinal gradients were used: a western transect (T1) from 47°48' to 48°40', and an eastern transect (T2) from 47°48' to 48°25' (Fig. 1a). T2 had to be situated outside the historical range because of the limited availability of sites for colony translocation, but its core site was selected as close to the historical range as possible. Four sites were selected along each of the two transects: two sites within or close to the core zone, three sites in the expansion zone, and three sites in the external zone. Each latitudinal gradient spanned ~90 km. In Venosta/Vinschgau (latitude 46°40' N), two altitudinal gradients were established on the opposite slopes: 960–1450 m on the south slope, and 810–1190 m on the north slope (Fig. 1b). Each gradient involved three sites (on the south slope, 960 m, 1210 m, 1450 m; north slope, 810 m, 1010 m, 1190 m), representing the core, expansion, and external zones, respectively.

Air temperature at each site was recorded with data loggers (Hobo, Onset, Pocasset, Massachusetts, USA, and Tinytag, Gemini Data Loggers, Chichester, UK) between 1 October 2002 and 31 May 2003. Nest temperature was similarly recorded using a probe inserted inside a nest. On the south slope in Venosta/Vinschgau, incoming solar radiation (insolation) was measured by a pyranometer (Star pyranometer, Type 8101; Schenk, Vienna, Austria). The calculated weekly mean of the minimum daily air temperature was used to define the “cold period,” i.e., the period during which the weekly mean of the minimum day air temperature is below 0°C, the postulated threshold for larval feeding (Huchon and Démolin 1971). The recorded hourly temperatures were assigned to day or night according to the length of the light period for each respective calendar day. The period before the cold period is here referred to as the “pre-cold period.”

*T. pityocampa* colonies were collected at the egg stage (Venosta/Vinschgau) or as neonate larvae (Paris Basin) from the natural populations in the respective

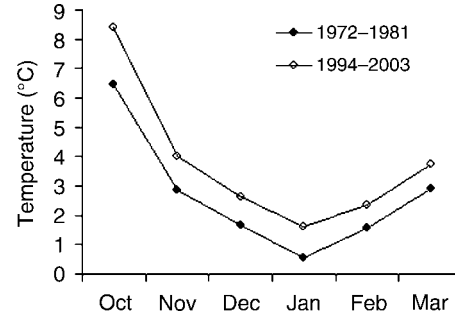


FIG. 2. Monthly mean of minimum temperatures recorded in the expansion area of *Thaumetopoea pityocampa* in the Paris Basin, showing two periods corresponding to different rates of range expansion (see Fig. 1). The overall difference in the mean minimum winter temperature between the two periods is 1.1°C. Data are based on the weather stations in Orléans (Meteo France).

core zones, and established at all sites along each gradient. A single egg mass producing  $191.5 \pm 21.3$  (mean  $\pm$  SD) larvae (Venosta/Vinschgau) or a colony of 200 larvae in the first instar (Paris Basin) was fixed to a branch of each of 20–30 trees of *P. sylvestris*, mostly from natural regeneration. In the Paris Basin, colony survival and larval development were assessed at the beginning and at the end of the cold period. Colonies in Venosta/Vinschgau were checked once every two weeks, noting the larval developmental stage (based on the size of feces visible through the silk), nest size, silk production, recent feeding, and damage to the nests. At the beginning of the cold period, the quality of the nests was assessed by means of a “nest silk index,” based on silk production and defined as follows: 1 = loose nest wall, larvae visible through the wall; 2 = thick nest, larvae not visible, external silk layer sparse; and 3 = very thick nest, larvae not visible, external silk layer dense. Close to pupation, the larvae were collected and weighed, and the colonies were allowed to pupate in cages under outdoor conditions.

We selected two variables to characterize the cold period in more detail. First, we calculated the number of hours during which a threshold nest temperature, responsible for inducing subsequent night feeding, was reached. We refer to this threshold as the “activation temperature” (AT). For the respective days, we then calculated the number of hours during which the night air temperature was above 0°C, and thus allowed larval feeding (Huchon and Démolin 1971). We refer to this threshold as the “potential feeding temperature” (PFT). Finally, using AT and PFT, we determined the total number of hours during which both conditions were met, i.e., night air temperature was above 0°C and the preceding daytime nest temperature was above AT. This final parameter, hereafter referred to as the “realized feeding threshold” (RFT), represents the number of hours during which feeding may have occurred, assuming that at least one hour of day and night tem-

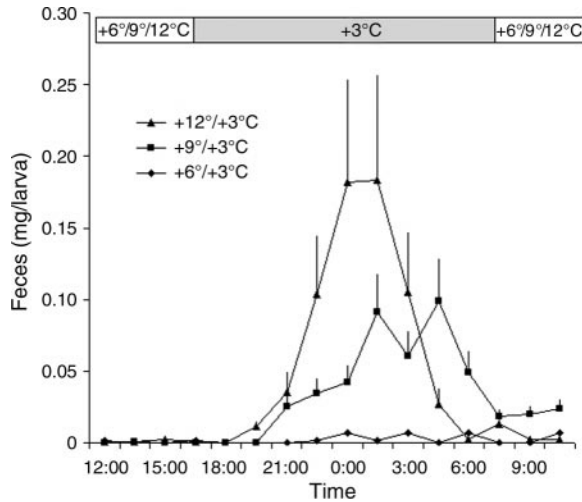


FIG. 3. Mean feeding activity of *Thaumetopoea pityocampa* colonies under different temperature regimes, measured as feces production. Thermal responses of third- and fourth-instar larvae did not differ, and the graph shows pooled data. For clarity, only the upper standard deviation is shown for each value of activation temperature (AT). Each test was conducted for 48 h, and the amount of feces shown at each 1.5-h step represents the total of the feces produced at that time during the test. Temperature was changed through steps of 0.3°C/min at the switch of the photoperiod (08:00 and 16:00, show as white/gray changes in horizontal bar at top). The treatment +3°/+3°C (see *Materials and methods; Determination of feeding thresholds*) is not shown, as no feeding activity was recorded.

perature above the respective threshold is sufficient. Both AT and RFT were also calculated as the number of days, to assess a possible skew in the distribution of hours of AT or RFT.

#### Statistical analyses

The effects of different day and night temperature in the laboratory feeding experiments were tested in a repeated-measures ANOVA. We used the  $\chi^2$  test with sequential Bonferroni correction for multiple tests (Rice 1989) to compare the frequency of colonies surviving in the different periods and their larval instar. The log-likelihood test was used instead of the  $\chi^2$  test whenever the number of observations predicted by the  $H_0$  hypothesis was lower than five (Sokal and Rohlf 1995, Zar 2001). For Venosta/Vinschgau, among-site differences in nest silk index were tested in a factorial analysis of covariance, using the larval stage (instar) as a covariate. The number of larvae per colony at the end of the translocation experiment was tested in a factorial analysis of variance, and correlations among variables were tested by Pearson's  $r$ . In all cases, ANOVA assumptions were met, and all variables were left non-transformed.

## RESULTS

### Range assessment

Recent expansion of *Thaumetopoea pityocampa*'s distribution was documented at both study areas. In the

Paris Basin, the edge of the distribution has shifted by 86.7 km between 1972 and 2004, with an accelerated shift in the last decade (Fig. 1a). This corresponds to a latitudinal shift of  $27.1 \pm 1.34$  km (mean  $\pm$  SD) per decade, with a significant acceleration during the last 10 years ( $55.6 \pm 5.39$  km). The change in altitudinal distribution in Venosta/Vinschgau varied with slope aspect (Fig. 1b). The mean upper distribution on the south slope advanced from an elevation of 1150 m in 1975 to 1380 m in 2004, equivalent to  $70.1 \pm 12.01$  m per decade. On the north slope, the shift corresponded to  $29.4 \pm 4.19$  m per decade, from 920 m to 1030 m. At both study areas, a substantial increase in mean of daily minimum temperatures in winter (21 December–23 March) was recorded in the last three decades; overall, the 1947–1972 period and the 1973–2003 period differ by 0.94°C and 1.5°C in the Paris Basin (Paris; Klein Tank et al. 2002) and in Venosta/Vinschgau (Silandro/Schländers; Forest Service of Bolzano/Bozen District, unpublished data), respectively. In the Paris Basin, the shift of the last decade was coupled with a considerable temperature increase (Fig. 2).

### Determination of feeding thresholds

Laboratory experiments confirmed that temperature thresholds for larval winter activity exist both with respect to induction of feeding and actual night feeding. A daytime nest temperature above 6°C (i.e., activation temperature, AT) was necessary to induce feeding during the following night; if this condition was not met, the larvae did not feed even if the feeding conditions at night were favorable. The magnitude of induction varied with day temperature; larvae fed significantly more when the nest reached higher daytime temperatures (repeated-measures ANOVA,  $F_{2,109} = 4.95$ ,  $P < 0.01$ ; Fig. 3). At night, feeding was observed only when the air temperature was above 0°C (i.e., potential feeding temperature, PFT). No feces were produced when the night temperature was  $-3^\circ\text{C}$  (data not shown). Daytime feeding was scarce and limited to early hours (09:30–11:00); the larvae did not feed during the day even when they were prevented from feeding during the night due to low temperature (data not shown). Thus, two temperature thresholds control larval feeding: feeding occurs when night air temperature is above 0°C, but only if the nest experienced temperatures above 6°C the preceding day. We decided to use 9°C as a conservative value of AT, in order to be sure that the larvae experienced induction for at least one hour.

### Larval performance during the pre-cold period

Colony survival during the pre-cold period, during which starvation usually does not occur, varied among sites within each study area but showed no clear relationship with latitude or elevation (Table 1). In Venosta/Vinschgau larval growth rate was higher at the core sites than those in the expansion zone and the external zone, as shown by the percentage of larvae

TABLE 1. Results of the translocation experiments of the pine processionary moth, *Thaumetopoea pityocampa*, in 2002–2003 in the Paris Basin, France, and in Venosta/Vinschgau, Italy.

Area and site	Latitude	Elevation (m)	No. colonies translocated	Pre-cold period (Aug–Nov)		
				Colony survival (%)†	Colonies with 4th instar (%)	Nest silk index (±SD)
Paris Basin						
T1 core	47°79′		10	90 <sup>a</sup>	100	
T1 expansion	48°34′		10	60 <sup>a</sup>	100	
T1 external	48°59′		20	70 <sup>a</sup>	100	
T2 core	47°80′		10	100 <sup>a</sup>	100	
T2 expansion	48°25′		20	95 <sup>a</sup>	100	
T2 external	48°41′		10	100 <sup>a</sup>	100	
Venosta/Vinschgau						
South core		920	22	59 <sup>a</sup>	69.2	2.3 <sup>a</sup> ± 0.8
South expansion		1200	22	64 <sup>a</sup>	35.7	2.0 <sup>a</sup> ± 0.4
South external		1450	23	39 <sup>a</sup>	0.0	1.3 <sup>a</sup> ± 0.4
North core		900	21	29 <sup>a</sup>	16.7	2.7 <sup>a</sup> ± 0.6
North expansion		990	21	48 <sup>a</sup>	10.0	1.8 <sup>a</sup> ± 0.9
North external		1040	15	68 <sup>a</sup>	0.0	1.6 <sup>a</sup> ± 0.5

Notes: T1 and T2 refer to the two transects in the Paris Basin, as shown in Fig. 1; South and North refer to the slope aspect in Venosta/Vinschgau. Cold period is defined in *Materials and methods; Translocation experiments*. Data from replicated sites within the external (T1) and expansion (T2) zones in the Paris Basin were pooled. Different letters indicate significant differences in the pairwise comparison of survival rates (*G* test,  $P < 0.05$ ) and of the means (Tukey's test,  $P < 0.05$ ).

† Colony survival with reference to the initial number of colonies for both pre-cold and post-cold periods.

‡ Pupa time is arbitrarily defined as the median date of the pupation period in outdoor cages. Julian date is the number of days from January 1.

that had reached the fourth instar at the end of the pre-cold period (south slope,  $\chi^2 = 8.71$ ,  $df = 2$ ,  $P = 0.01$ ; north slope,  $\chi^2 = 12.67$ ,  $df = 1$ ,  $P < 0.01$ ; Table 1). When developmental stage was taken into account, nest silk index did not differ between slopes and among sites (ANCOVA), and was significantly correlated with the larval stage (Pearson's  $r = 0.61$ ,  $P < 0.05$ ; Table 1). Overall, colony survival was higher and phenology was more advanced in the Paris Basin than in Venosta/Vinschgau (Table 1), likely due to the higher mean night temperatures in the former area (October–November, 6.3°C vs. 5.5°C).

#### Larval performance during the cold period

As expected, larval performance during the cold period differed among sites within areas, with the core sites generally showing the highest performance, followed by the expansion sites and the sites outside the present range. The proportion of colonies that survived to pupation gradually decreased from core sites for all transects (Table 1). Highest mortality was observed at the most extreme sites; significant differences were found for two sites on the north slope in Venosta/Vinschgau (log likelihood  $G = 7.16$ ,  $df = 2$ ,  $P = 0.027$ ), and for transect 2 in the Paris Basin (log likelihood  $G = 6.51$ ,  $df = 2$ ,  $P = 0.038$ ). In 48 out of 53 cases, the larvae were found dead inside the nest, with no signs of predation or parasitism. The number of larvae per colony at the end of the cold period was significantly lower in the external zones of transect 1 in the Paris Basin and on both slopes in Venosta/

Vinschgau (Table 1). Using the data from the six Venosta/Vinschgau sites only, larval instar at the beginning of the cold period was a good predictor of survival during the cold period (regression of the percentage of larvae in the fourth instar on percentage of colony survival;  $R^2 = 0.66$ ,  $F_{1,4} = 7.7$ ,  $P = 0.05$ ). On the south slope, 66.7% fourth-instar colonies survived ( $n = 9$ ), whereas only 22.2% of third-instar colonies survived ( $n = 18$ ). On the north slope, survival was 60% ( $n = 5$ ) and 18.2% ( $n = 11$ ), respectively. The date of pupation for colonies from Venosta/Vinschgau clearly differed among sites: Pupation occurred 10–20 days and 35 days earlier at the core sites than at the sites in the expansion zone and external zone, respectively (Table 1). Differences in termination of the larval period were less pronounced in the Paris Basin.

During the cold period, most of the recorded mortality did not appear to be caused by extreme temperatures. In fact, the lower lethal temperature (LLT =  $-16^\circ\text{C}$ ; Démolin 1969a) was reached only at one of the two expansion sites of the eastern transect in the Paris Basin ( $-16.7^\circ\text{C}$ ), where it resulted in total mortality. However, colonies in the Paris Basin also suffered extensive mortality in mid-January through a combination of rain followed by a quick temperature drop from a daily mean of  $11.5^\circ\text{C}$  to  $-7.4^\circ\text{C}$  within a few days.

#### Temperature effects on feeding activity in the field

The cold period (weekly mean of the minimum daily air temperature below  $0^\circ\text{C}$ ) lasted from 1 January until

TABLE 1. Extended.

Cold period (Dec–Feb)	Post-cold period (Mar–May)			Pupation time (Julian date)‡
	Final colony survival (%)†	No. larvae/ colony (±SD)	5th instar in March (%)	
78 <sup>a</sup>	70 <sup>a</sup>	70.4 <sup>a</sup> ± 46.1	97.6	
83 <sup>a</sup>	50 <sup>a</sup>	17.6 <sup>b</sup> ± 16.5	67.0	
64 <sup>b</sup>	45 <sup>a</sup>	27.8 <sup>b</sup> ± 30.5	35.1	
100 <sup>a</sup>	100 <sup>a</sup>	54.2 <sup>a</sup> ± 33.7	96.9	
42 <sup>b</sup>	40 <sup>b</sup>	57.0 <sup>a</sup> ± 26.3	99.6	
20 <sup>b</sup>	20 <sup>b</sup>	37.0 <sup>a</sup> ± 28.3	100.0	
54 <sup>a</sup>	32 <sup>a</sup>	119.9 <sup>a</sup> ± 41.1		110
29 <sup>a</sup>	18 <sup>b</sup>	57.2 <sup>b</sup> ± 30.2		120
44 <sup>a</sup>	17 <sup>b</sup>	22.6 <sup>b</sup> ± 3.5		145
83 <sup>a</sup>	24 <sup>a</sup>	81.7 <sup>a</sup> ± 73.9		125
18 <sup>b</sup>	10 <sup>b</sup>	36.5 <sup>b</sup> ± 7.3		145
10 <sup>b</sup>	7 <sup>b</sup>	31.3 <sup>b</sup> ± 0.0		160

27 February 2003 in the Paris Basin, and from 3 December 2002 until 4 March 2003 in Venosta/Vinschgau. In both areas, among-site differences in the duration of the cold period were negligible, while differences in the total number of hours during which the realized feeding threshold (RFT) was reached were evident particularly between the sites in the core zone and the remaining sites (Table 2, Fig. 4). The relative contribution of activation temperature (AT) and potential feeding temperature (PFT) in the total number of RFT hours varied due to site-specific factors. We were able to confirm most feeding events by observation of fresh feces in the nest and adjacent branches during the pe-

riodic checks of the sites. When expressed in days, the pattern and distribution of AT and RFT in time corresponded proportionally to the number of hours above these thresholds; consequently, we use the number of hours as a more precise estimation of larval activity.

The topographic uniformity of the Paris Basin allowed us to assess the effect of latitude on AT, PFT, and RFT. The total number of RFT hours decreased with increasing latitude for both transects, at a rate of 1.5 and 2.4 hours per degree of latitude for transect 1 and 2, respectively. The distribution of RFT hours during the cold season showed similar patterns for both transects, with relatively short breaks in feeding activity in the core zone, and considerably longer periods of starvation interrupted only by very short periods of feeding in the expansion and external zones. The two transects were expected to show similar insolation and, consequently, nest temperature; however, the number of hours with daytime nest temperature above AT was higher in transect 1 ( $t$  test,  $t = 5.14$ ,  $df = 2$ ,  $P = 0.036$ ; Table 2). In contrast, similar number of hours at which night air temperature was above PFT was recorded for the two transects. When both variables were combined, the final number of hours corresponding to RFT was higher in transect 1 ( $t$  test,  $t = 6.71$ ,  $df = 2$ ,  $P = 0.021$ ), clearly due to differences in AT hours.

In Venosta/Vinschgau, the colonies on the south slope experienced a markedly higher number of RFT hours than the north slope (for all sites combined RFT equaled 1187 vs. 366 hours, respectively). Differences among the sites were also more pronounced on the south slope: The number of RFT hours in the core zone on the south slope was almost twice as high as in the external zone because of favorable night temperatures

TABLE 2. Temperature conditions experienced by the colonies at the different sites in the “cold period” (defined in *Materials and methods; Translocation experiments*), expressed as the total number of hours during the cold period.

Area and site	AT, feeding induced		PFT, feeding conditions favorable (hours)	RFT, feeding induced and conditions favorable		AT without PFT, feeding induced but conditions not favorable (hours)	PFT without AT, conditions favorable but feeding not induced (hours)
	Days	Hours		Days	Hours		
Paris Basin							
T1 core	31	213	468	22	273	48	195
T1 expansion	21	135	504	16	201	24	303
T1 external	24	153	492	16	201	48	291
T2 core	21	135	456	17	228	21	228
T2 expansion	14	96	489	13	165	3	324
T2 external	14	96	453	11	141	15	312
Venosta/Vinschgau							
South core	52	323	664	55	476	49	188
South expansion	54	245	625	54	446	38	93
South external	46	269	388	46	265	29	123
North core	9	32	576	10	97	0	479
North expansion	15	41	589	17	133	0	456
North external	20	55	442	21	106	13	336

*Notes:* AT (activation temperature) is the number of days/hours at which daytime nest temperature exceeded 9°C; PFT hours (potential feeding temperature) is the number of hours at which night air temperature exceeded 0°C; RFT (realized feeding threshold) is the number of days/hours at which both AT and PFT occurred in a single day, i.e., night air temperature was above 0°C and the preceding daytime nest temperature was above 9°C. The last two columns show conditions under which RFT is not met, i.e., feeding does not occur.

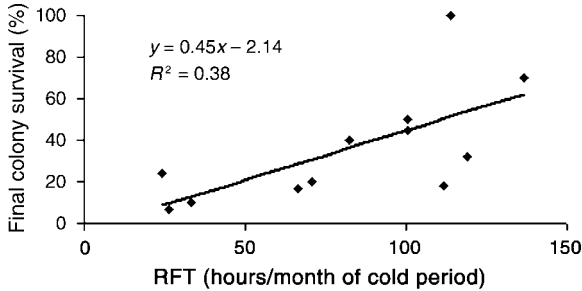


FIG. 4. Regression of the final percentage of colony survival observed at 12 experimental sites against the number of hours above the realized feeding threshold (RFT), standardized for the two regions per length of the cold period in months (Paris Basin, RFT/2; Venosta/Vinschgau, RFT/4). See Tables 1 and 2 for details.

(Table 2, Fig. 4). Furthermore, insolation had a significant effect on the number of AT hours. Even though daytime air temperature at this site was above AT during only 82 hours, the nest temperature reached AT during 323 hours out of 864 (Table 2), because of a significant correlation between daytime nest temperature and insolation (Pearson's  $r = 0.73$ ,  $P < 0.01$ ). Indeed, remarkable temperature gains were observed when the nests received direct sun: Insolation levels of 50–200 W/m<sup>2</sup> raised the nest temperature by 5°–20°C (data not shown). Our temperature-based model of feeding activity estimated that although feeding occurred throughout the cold period, it alternated with starvation periods of ~10 days (data not shown), during which feeding was either not induced because daytime nest temperatures were below AT, or, less frequently, induced but not possible because night air temperature remained below PFT.

Insolation to a large extent determined total AT hours, which then drove between-slope differences in total RFT hours (compare “PFT without AT” vs. “AT without PFT,” Table 2). Insolation was about six times lower on the north slope than on the south slope, due to the shading by the mountain ridge. Our model estimated that feeding occurred only at the end of the cold period, when the sun angle allowed direct insolation (note that this effect was more evident in the external zone because of its more exposed position). Apart from an isolated and brief (28 hours) feeding event, triggered by an abrupt rise in temperature due to the warm Föhn wind (A. Battisti, *personal observation*), the cold period on the north slope was characterized by starvation lasting >50 days. Feeding would have been possible because night air temperature frequently exceeded 0°C, but was not induced as the lack of insolation during the day prevented the nests from reaching AT.

To summarize the effects of feeding (or conversely, starvation) on survival among sites, we standardized RFT for the two regions by dividing the total RFT by the length of the respective cold period expressed in

months (Paris Basin, RFT/2; Venosta/Vinschgau, RFT/4) and regressed it against the percentage of colony survival. We found that RFT allowed predicting colony survival to some extent ( $R^2 = 0.38$ ,  $F_{1,10} = 6.23$ ,  $P = 0.03$ ; Fig 4). The hours of RFT were distributed among all the months of the cold period at both areas (data not shown).

## DISCUSSION

### *Range expansion and global warming*

We demonstrate that the pine processionary moth, *Thaumetopoea pityocampa*, whose larvae develop continuously throughout the winter, shows a consistent trend of range expansion along its recent historical range boundary. Our results suggest that the observed range shift is largely due to a rise in average winter temperatures, allowing the insect to survive in more northerly latitudes and at higher elevations. Survival is possible because winter feeding, which is tightly controlled by temperature thresholds, increases with rising winter temperatures. More frequent feeding and, in turn, shorter starvation periods, then accelerate development and enhance survival in areas with previously prohibitive climatic conditions.

The magnitude of expansion in *T. pityocampa* is consistent with, or exceeds, the general predictions of responses to climate change (Parmesan et al. 1999, Hill et al. 2002, Walther et al. 2002, Parmesan and Yohe 2003). Parmesan et al. (1999) reported a poleward shift of 35–240 km for 65% of European butterflies within the last 30–100 years, juxtaposed with a 120-km poleward displacement of isotherms in Europe during the 20th century (Houghton et al. 2001). In a meta-analysis of birds, butterflies, and alpine herbs, range shifts were estimated at  $6.1 \pm 2.4$  km per decade or m per decade poleward or upward, respectively (Parmesan and Yohe 2003). These estimates are surpassed by the recent shifts in the northern and upper boundary of the distribution of *T. pityocampa*, which we estimated at  $27 \pm 1.3$  km per decade poleward (corresponding to  $0^\circ 27'$  of latitude), and  $70 \pm 12.0$  m per decade (south slope) and  $29 \pm 4.2$  m per decade (north slope) upward. Given that a shift in one degree of latitude roughly corresponds to a rise of 122 m in altitude (Hopkins 1938), the estimate of latitudinal expansion is consistent with that of altitudinal expansion on the north slope, which is mostly shaded during winter. The proportionally greater expansion on the south slope can be explained by the pronounced effect of insolation during winter; insolation does not decrease with altitude as it does with latitude.

Several other examples of shifting range boundaries have been reported recently (Hodkinson and Bird 1998, Parmesan et al. 1999, Harrington et al. 2001, Bale et al. 2002, Karban and Strauss 2004). Yet, few other studies have attempted to explain range shifts in mechanistic terms. Bryant et al. (1997) demonstrated that

the distribution of temperate nymphalid butterflies is constrained by degree-day requirements. Crozier (2004) showed such temperature-driven physiological constraints on the range of the generalist butterfly *Atalopedes campestris*, via a combination of acute- and chronic-cold stress. Although temperature appears to have a dominant effect on range boundaries of several species, a study of the introduced southwestern corn borer *Diatraea grandiosella* has found that winter temperatures did not consistently explain distribution limits across the range (Baskauf and McCauley 2001).

The above-cited examples deal with species that are winter inactive, overwintering in a diapausing or quiescent stage. Consequently, an increase in temperature may enhance their feeding and growth during the summer, while reducing the probability that the lower lethal temperature (LLT) or other limiting variables will be reached during the winter (Gaston 2003). Species that are active in the winter, or have plastic winter life histories, however, are even more likely to respond to global warming, as the increases in average minimum temperatures have been outpacing increases in average maximum temperatures (Easterling et al. 1997). This is the case of the southern pine beetle *Dendroctonus frontalis*, whose northern range boundary coincides with the isoline of high probability of the lower lethal temperature of  $-16^{\circ}\text{C}$  (Ungerer et al. 1999). While LLT is an important determinant of geographic ranges of some species, one complication is that, unlike mean temperatures, extreme temperatures that cause direct mortality (LLT) are a more stochastic measure based on probability of occurrence, and, hence, not as suitable for predictive models alone. In contrast, mean winter temperatures can have a lasting, cumulative influence on the feeding, survival, fitness, and ultimately the range boundary of winter-active species. Our results demonstrate that the recent warming has been responsible for the expansion of the range of *T. pityocampa*, a defoliator actively feeding throughout the winter, by accelerating larval development in the early instars, increasing the frequency of feeding during the coldest months, and reducing exposure to LLT.

At least two other winter-feeding pierid butterflies could also be affected by global warming. Further establishment of the North African *Colotis evagore* in southern Spain is expected, as both insect growth and persistence of green leaves on the host plant *Capparis spinosa* are limited by winter temperature (Jordano et al. 1991). Range expansion is also likely in the case of the montane pierid *Eucheira socialis*, which lives gregariously in a silk nest and feeds above  $0^{\circ}\text{C}$ , just like *T. pityocampa* does (Fitzgerald and Underwood 2000).

#### *Temperature effects on feeding and survival*

Temperature conditions during both the pre-cold period and the cold period influenced growth and survival of *T. pityocampa* at the expansion sites. By the end of

the pre-cold period, developmental stage was more advanced at warmer sites (i.e., lower latitudes or elevations), likely through an effect of temperature on larval growth since hatching. This result is concordant with the general predictions of temperature-based models of insect development (Chapman 1998). More advanced colonies may then have a higher probability to survive the following cold period, because they are able to construct larger nests, which provide better protection against low temperatures and bird predation (Démolin 1969a, Geri 1983, 1984). Data from Venosta/Vinschgau showed that nest silk index did not differ significantly among sites, but was positively and significantly correlated with larval instar. Because spinning is induced by low temperatures, it started earlier and extended over a longer period of time at the cooler sites, where most larvae were in the third instar. However, the larger fourth instar larvae at the warmer sites spun more silk, which resulted in comparable silk indices.

While temperature during the pre-cold period significantly influences colony survival, it may have an even more important role during the cold period. It is possible to separate the two effects only for three of the sites of Venosta/Vinschgau: the site in the external zone on the south slope, and those in the expansion and external zones on the north slope. At all three sites, at least 90% of the larvae in each of the colonies entered the cold period in the third instar (Table 1), and hence, the differences in the subsequent colony survival and pupation time can be attributed to the conditions during the cold period. Based on the threshold model, feeding was predicted to occur during 265 hours, 133 hours, and 106 hours at the three sites, respectively (Table 2), and was supported by the corresponding colony survival (17.4%, 9.5%, and 6.7%, respectively). However, pupation time of the survivors did not show such a clear relationship, probably due to an additional effect of night air temperatures in the post-cold period, controlled primarily by elevation (data not shown).

In general, colony survival in both expansion areas was reduced at sites with a lower number of hours of predicted feeding, showing the importance of winter feeding for *T. pityocampa*. The regression of standardized RFT (RFT per month of cold period) on the percentage of colony survival allowed us to summarize this relationship across all sites (Fig. 4). As the hours of RFT approach zero, the final colony survival tends to zero as well, and this simple relationship can be used to model the potential range of *T. pityocampa* (assuming that dispersal is not limiting). Survival will then occur at sites where RFT (and LLT) is not limiting, as supported by the results of our translocation of colonies outside the range. Given this relationship, we could estimate the width of the potential expansion belt accordingly for the present mean temperatures. Still, it is best to consider this relationship in each area individually, as the general climatic conditions differ dramatically between the Paris Basin and Venosta/Vinsch-

gau, as well as between north and south slopes in the latter area. For example, the low colony survival in the Paris Basin, in spite of the relatively high RFT hours, can be attributed to the incidental high mortality related to the weather anomaly in January (see *Results*). In Venosta/Vinschgau, the relatively high survival of colonies at the core site on the north slope, in spite of the lower RFT hours, is presumably due to the fact that some colonies had reached the fourth larval instar before the cold period, and hence, were able to better withstand starvation (see *Results*).

Nonetheless, in Venosta/Vinschgau, some colonies survived even after a starvation period of nearly three months, interrupted only by a brief 27-hour episode of feeding in late January. In the expansion and external zones in the Paris Basin, feeding did not cease until the end of December, but the starvation period still lasted nearly two months, during which there was a single event of feeding for 30–45 hours, also in late January. It is difficult to assess the relative importance of these single events of feeding in ensuring colony survival; nonetheless, the ability of *T. pityocampa* to endure long periods of starvation is remarkable. Although the larvae may become quiescent during prolonged periods without feeding, thereby greatly reducing their metabolism (Leather et al. 1993), they will face metabolic demands whenever their activity is induced by nest temperature reaching AT. Consequently, unless the night temperatures rise above 0°C (PFT) to allow feeding, activated larvae are forced to starve until they enter quiescence. Larval activity of *T. pityocampa* at temperature around 0°C was also observed by Fitzgerald and Blas (2003), who monitored the movement events under field conditions and showed that, in induced colonies, larvae leave the nest with the onset of darkness and return in the morning as long as the temperature is near 0°C.

Stochasticity in weather may affect larval survival even without reaching LLT (see *Results*). The predicted increase in the frequency of extreme weather events (Parmesan et al. 2000, Bale et al. 2002), which can cause massive mortality in young or starved larvae (Démolin 1969a, Huchon and Démolin 1971), may then complicate predictive models of *T. pityocampa* expansion based on average minimum winter temperatures. On the other hand, such local extinction events could be offset by recruitment of diapausing individuals from the previous years. Therefore, it is reasonable to assume that the geographic range of *T. pityocampa* will continue to expand in response to increasing mean temperatures. One factor limiting the northward expansion could be insufficient insolation, preventing the nest from reaching AT, thus precluding winter feeding beyond certain latitude. According to our calculations based on data from the transects in the Paris Basin, which represent the northernmost limit of the present range, areas approximately two degrees farther north cannot support winter feeding. In contrast, we show

that insolation is less important than night temperature as a limiting factor for the expansion on southern slopes of mountains. Other climatic factors, such as precipitation and cloud cover, are expected to decrease up to 1% per decade in southern Europe (European Environment Agency 2004), likely with negligible influence on the present range. Climate-based models that combine mean day and night temperatures, probability of LLT, and insolation, are likely to provide the best predictive power in range dynamics of *T. pityocampa*.

#### *Shifts and adaptations*

In the core parts of the range, *T. pityocampa* is known to shift its phenology in relation to elevation, with adults emerging from mid to early summer (Démolin 1969a, Geri 1983). Early emergence should be selected for in the expansion areas in order for the larvae to reach an advanced stage before the temperatures begin to drop in the fall. Indeed, such a phenology shift has been observed in several expansion areas in the Alps and in the Paris Basin (Benigni and Battisti 1999, Gousard et al. 1999). However, since larvae can feed on mature needles if the young needles have not yet fully developed (A. Battisti, *personal observation*), phenology shifts in *T. pityocampa* should be largely decoupled from its host. Consequently, global warming is unlikely to lead to increasing asynchronization, in contrast with predictions for many phytophagous insects on herbs, deciduous trees, and flowers or seeds (Baltensweiler 1993, Buse and Good 1996, Peñuelas et al. 2002).

Host plant distribution does not restrict the present range of *T. pityocampa* (Hóðar et al. 2002), nor its poleward and upward expansion. Many present or potential host species, which allow the larvae to complete their development, grow in areas where the insect is currently absent. For instance, *P. sylvestris*, documented to be a suitable host plant (Démolin 1969b), is common across Europe, including the present expansion areas (Hóðar et al. 2003). In addition, *T. pityocampa* readily adopts novel hosts, and has caused outbreaks in several expansion areas, most notably on *Pinus mugo* in northern Italy (Benigni and Battisti 1999), and on *Pseudotsuga menziesii* in tree plantations of France (Roques et al. 2002). A considerable level of plasticity in feeding is likely to be maintained, especially in areas with multiple host species, or in populations characterized by greater gene flow (Salvato et al. 2002, Gaston 2003). Consequently, if the climatic conditions become favorable in higher latitudes or at higher elevations, the insect may expand its range to these areas, often coupled with host switching. Although we do not have recent estimates on the southern range boundaries of *T. pityocampa*, especially in North Africa, these are already constrained by the distribution of suitable hosts (Démolin 1969b). Thus, the northward and upward range boundary shifts in southern Europe reflect an expansion of the geographic range of *T. pityocampa*. Because the warming trends are predicted

on a global scale, species similar to *T. pityocampa*, with a wide geographic range that is relatively unconstrained by host distribution, are most likely to rapidly respond to these changes by shifting their range boundaries. Yet, in general, many species, and insects in particular, have specific temperature requirements that may render them sensitive to new temperature regimes. Therefore, our ability to predict changes in species distributions and their potential community impacts, as well as to evaluate suitable management strategies, would benefit from focusing on the mechanisms that drive correlations between climatic factors and survival of organisms.

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