

A rapid altitudinal range expansion in the pine processionary moth produced by the 2003 climatic anomaly

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Abstract

Climatic anomalies may produce, or accelerate, geographic range expansions of species limited by temperature or other climatic variables. Most such expansions are only temporary, before the prevailing climatic conditions drive the founder populations extinct. In contrast, here, we report a recent rapid shift of the range limit during the record hot summer of 2003 in southern Europe that has the potential to be both permanent, and to have important implications on species range dynamics in general. The winter pine processionary moth (*Thaumetopoea pityocampa*), an important pine defoliator whose larvae feed in colonies during the winter, is limited in its distribution by winter temperatures. In the last three decades, warmer winters have led to a gradual but substantial expansion of its range both latitudinally and altitudinally. In the summer of 2003, *T. pityocampa* underwent an extraordinary expansion to high elevation pine stands in the Italian Alps; its altitudinal range limit increased by one third of the total altitudinal expansion over the previous three decades. In an experiment, we found flight activity of newly emerged females to increase with temperature. By determining a threshold temperature for flight take-offs under controlled conditions, we calculated that the nights above the threshold temperature were over five times more frequent, and considerably warmer, at the range limit in 2003 than in an average year. We therefore attribute the colonization of extreme, high-elevation sites to increased nocturnal dispersal of females during the unusually warm night temperatures in June – August 2003. Importantly, the colonies established at extreme sites survived the winter and produced offspring in 2004, although the range did not expand further because of low night temperatures that year. We discuss several life-history characteristics of *T. pityocampa* that maximize the likelihood of population persistence at the new range limit. As global warming continues and climatic anomalies are predicted to become more frequent, our results draw attention to the importance of extreme climatic events in the range formation of phytophagous insects.

Keywords: climate change, climatic anomaly, colonization, dispersal, extreme event, flight, forest pest, survival, temperature

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Introduction

The study of species range limits has long been a central theme in ecology. A suite of biotic and abiotic factors,

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ranging from climatic variables and edaphic conditions, to competition, predation and resource distribution, have been invoked to explain the limits in species distributions (Spicer & Gaston, 1999; Gaston, 2003; Parmesan *et al.*, 2005). Still, our understanding of the spatial dynamics at range limits and their underlying factors is far from complete. One uncertainty lies in distinguishing between temporary spatial fluctuations

in range limits, common in many organisms (Ayres & Lombardero, 2000; Gaston, 2003), and directional, ongoing shifts in geographic distributions, leading to a displacement of one or more boundaries of a species' range. Range expansions have been reported for a number of organisms in recent history, and appear to be, at least in part, driven by global climate change (Parmesan *et al.*, 1999; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003; Crozier, 2004; Karban & Strauss, 2004; Hickling *et al.*, 2005; Battisti *et al.*, 2005). The concerns about rapid global warming patterns and the increased frequency of climatic anomalies (Meehl *et al.*, 2000) call for an urgent need to understand the factors that affect species' range limits. While average trends in climate change have intuitive value in predicting long-term range expansions (Hill *et al.*, 2002; Parmesan *et al.*, 2005), stochastic, extreme weather events and climatic anomalies of longer duration represent an important but often overlooked driver that can accelerate spatial shifts in species distributions (Meehl *et al.*, 2000; Parmesan *et al.*, 2000).

An increasingly important question in ecology is whether the rate of species range expansions can track the rapid and potentially stochastic changes in climate. It is well known that many insects disperse into novel geographic regions as a result of unusual climatic conditions (Sparks *et al.*, 2005). However, such events may not, and typically do not, result in successful establishment at the new location (Loxdale & Lushai, 1999). The expansion of geographic range of an insect species beyond the present distribution limit requires a combination of dispersal and a subsequent establishment and long-term persistence of a population. The establishment may depend on, for example, the availability of critical resources, viable effective population size, and climatic factors (Gaston, 2003). Many insect species in the temperate region are believed to be limited in their distribution by low temperature (e.g. Ungerer *et al.*, 1999; Crozier, 2004). Adult dispersal of such temperature-limited species into a new area outside the present range may then not lead to a lasting range expansion if the offspring perish in the following years because of unfavourable climatic conditions. The range may simply expand during unusually warm years and then retract again in years with sudden cold spells or prolonged cold weather, producing spatial fluctuations (Murawski, 1993; Whittaker & Tribe, 1998). If, however, the species life history allows at least a proportion of the subsequent generations to survive during unfavourable years, whether in an active or a dormant stage, the population can persist and effectively extend the species' range.

In this study, we present evidence that climatic anomalies in the form of prolonged unusually warm

weather can lead to a dramatic and potentially permanent range expansion. The winter pine processionary moth, *Thaumetopoea pityocampa* (Denis & Schiffermüller, 1776) (Lepidoptera, Notodontidae), an economically important defoliator of pines in southern Europe, is active in its larval stage throughout winter. Its geographic range limit is governed by low winter temperatures (Démolin, 1969a; Huchon & Démolin, 1971). In the last three decades, a substantial expansion of its geographic range has taken place, both latitudinally and altitudinally (Hellrigl, 1995; Goussard *et al.*, 1999; Benigni & Battisti, 1999; Hóðar *et al.*, 2003; Hóðar & Zamora, 2004; Battisti *et al.*, 2005). Availability of host plants (*Pinus* spp.) does not seem to limit the distribution of this oligophagous herbivore (A. Battisti *et al.*, unpublished results). Moreover, translocation experiments have shown that larvae can successfully complete their development at temperature regimes prevailing outside the present distribution (Battisti *et al.*, 2005).

During the last 30 years, *T. pityocampa* has extended its altitudinal distribution in the Italian Alps upslope by a vertical gain of 110–230 m (Battisti *et al.*, 2005). For most of this period, the upslope expansion has most likely occurred as a continuous process characterized by small increments and occasional temporary reversals. The summer of 2003, the warmest summer in Europe in the last 500 years (Luterbacher *et al.*, 2004), appears to have facilitated unprecedented colonization outside the range limit. In this paper, we aim to explain this expansion into high-elevation sites in the context of the 2003 climatic anomaly, using field-collected data and controlled cage experiments. Specifically, we (1) quantify and contrast the extent of the 2003 expansion to infer female dispersal under anomalous climatic conditions; (2) test whether female flight is enhanced by increased night temperature and (3) evaluate the potential for long-term population persistence by monitoring larval colonies from the 2003 expansion.

Materials and methods

Study system

Larvae of the winter pine processionary moth, *T. pityocampa* (Lepidoptera, Notodontidae), feed gregariously on pine foliage during the winter. Pupation occurs in spring, and adult emergence in summer, which is immediately followed by mating and oviposition. Females during typically live only one night. The insect is distributed throughout the Mediterranean, and has long been known to produce spectacular outbreaks (Matthioli, 1568). Forest inventories generally report a scattered distribution of outbreaks, with usually no

Table 1 Study sites for monitoring the expansion of *Thaumetopoea pityocampa* in the Italian Alps, showing the elevation of the highest-situated nests during the years of monitoring, and the mean gains (\pm SE) in elevation and distance observed in 2003

Site*	Coordinates	Host plants	Historical upper limit (m)†	Upper limit 2002 (m)	Upper limit 2003 (m)	Upper limit 2004 (m)	Elevation gain 2003 (m)	Distance gain 2003 (m)
Avic, Aosta	45°39'N 07°41'E	PN, PS, PU	1000	1310	1430	1430	113.7 \pm 23.0	232.7 \pm 22.4
Venosta/Vinschgau	46°38'N 10°46'E	PN, PS	1150	1350	1415	1380	65.0 \pm 12.3	120.4 \pm 17.2
Perarolo, Cimolais	46°22'N 12°21'E	PM, PN, PS	760	1010	1150	1130	114.3 \pm 25.7	642.2 \pm 70.7
Forni di Sotto, Udine	46°23'N 12°40'E	PM, PN, PS	950	1250	1300	1300	114.5 \pm 41.2	243.1 \pm 67.4
Resia	46°22'N 13°18'E	PN, PM	860	1090	1210	1200	45.6 \pm 11.3	168.8 \pm 55.3

*Weather stations used for reference (see text). Avic, Aosta: Covarey 1300 m, Pré Oursi 1791 m; Venosta/Vinschgau: Silandro 718 m, Lasa 863 m, S. Giovanni Martello 1616 m; Perarolo, Cimolais: Perarolo 532 m, Valle di Cadore 851 m; Forni di Sotto: Enemonzo 408 m, Zoncolan 1740 m; Resia: Coritis 830 m.

†Data for 1982, provided by the Forest Service; in part by Focarile (1984) for Avic, Aosta and by Hellrigl (1995) for Venosta/Vinschgau.

PM, *Pinus mugo*; PN, *Pinus nigra*; PS, *Pinus sylvestris*; PU, *Pinus uncinata*.

more than 2 years of strong defoliation in a row, after which most of the trees recover (Masutti & Battisti, 1990). *T. pityocampa* is considered a noxious insect pest in the region, especially because of the health risk associated with the urticating hairs produced by late-instar larvae (Lamy, 1990).

Climatic variables represent the most important limiting factor for population persistence, as the range limits of *T. pityocampa* in the area are defined by winter temperatures critical for larval feeding and survival (Démolin, 1969a; Huchon & Démolin, 1971; Battisti *et al.*, 2005). Démolin (1969a) estimated the potential distribution based on winter air temperature (mean January minimum above -4°C , lower lethal temperature, LLT, of -16°C) and annual solar radiation (minimum of 1800 hours).

Study sites

We selected five sites ranging in size from 300 to 800 ha, situated on the southern slopes of the Italian Alps (Table 1). The climate is typical of the Southern Alps, with relatively short summers, and is generally much wetter and cooler in the eastern sites. Four pine species are native in these areas: *Pinus mugo* Turra (mountain pine, dwarf form), *P. uncinata* Miller (mountain pine, upright form), *P. nigra* Arnold (Austrian or black pine), and *P. sylvestris* L. (Scots pine). With the exception of *P. uncinata*, they occur almost continuously from low elevation to the timber line, growing in pure stands or intermixed with broadleaf and other conifer species. Plantations of *P. nigra* have extended the distribution of this species in the last century beyond the native eastern area. All four species tend to occur on infertile and steep

slopes, where they are of marginal importance in timber production but serve in soil protection.

Female dispersal in 2003: nest surveys

The winter nests, built by third-instar larvae on the most peripheral, sun-exposed parts of the canopy, conspicuously denote the presence of *T. pityocampa* and can easily be seen from a distance. The larvae live gregariously inside the nest, and their spinning activity increases when the temperature begins to fall substantially below 0°C , causing the nest to enlarge to 20–25 cm in diameter. In our study areas, most nest building occurs in November, and in this period forestry officials scan the forest canopies to assess for the presence of the insect.

Cumulative data from the surveys conducted by the local Forest Service, including the upper limit of the distribution at all five study sites, are available since 1975–1982 (Table 1). A detailed annual survey is available since 1999 for Venosta/Vinschgau only. In addition, we began a detailed monitoring of nests at the range limit in the winter of 2002 (November 2002–April 2003), and repeated the monitoring in the winters of 2003–2004 and 2004–2005. Nest positions were mapped with a GPS, and the distances between nests found at highest elevations (hereafter, extreme nests, and extreme sites) in 2002–2003 and in 2003–2004 were calculated. Distances were defined as the lowest straight distance between two extreme nests in respective years, taking the slope into consideration. Elevation differences were calculated accordingly. Thus, we were able to check whether there was an expansion or a contraction in the distribution of the extreme nests, with respect to the previous year. For the purpose of this paper, we refer to

nests originating from within the 2002 distribution as core nests.

In the period 2001–2004, we surveyed adult emergence time and population density of *T. pityocampa* annually at two sites (Venosta/Vinschgau and Resia) by collecting adult males in funnel traps with pheromone dispensers (Serbios, Badia Polesine, Italy). The traps were located just below the range limit in each respective year (Venosta/Vinschgau: $n = 7$ – 10 ; Resia: $n = 5$), and were checked weekly from June to August. At the other sites, we used pheromone trap ($n = 3$) catches of males to estimate the timing and duration of the adult emergence period in the field in 2002 and 2003. We then defined the female flight period as the 60 days centered around the estimated median of the emergence period at each site (June 10–August 10 at Venosta; June 15–August 15 at Avic and Perarolo; July 1–August 31 at Forni and Resia).

Hourly temperature data for the female flight period of *T. pityocampa* at the study sites were obtained from weather stations (Table 1) located inside or near the pine stand, and from data loggers (HOBO[®]) at the extreme sites of Avic and Venosta. When temperature data for extreme sites were not available, we estimated them using a temperature/elevation gradient of $0.66\text{ }^{\circ}\text{C}/100\text{ m}$ (SD 0.08), calculated for the 4 years using data from local weather stations, and based on estimations available for the Alps (Mennella, 1967). For our purposes, the night was defined as the period during which the female moths are active: usually from 21:00 hours to 5:00 hours. When hourly temperature data were not available for the entire period of interest (1982–2004), we used minimum daily temperatures instead. A longer temperature record was obtained from the meteorological station of Verona Villafranca ($45^{\circ}23'\text{N}$, $10^{\circ}5'\text{E}$, 68 m), which is located in the same geographic region as all our sites, and is included in the European Climate Assessment database (Klein Tank *et al.*, 2002).

Temperature and female flight: cage experiment

To test for the influence of temperature on flight activity of *T. pityocampa* females, we used data from an experiment carried out in large outdoor cages during June 25–July 20, 2004 at the campus of the University of Padova, Italy. Adults of four populations (Venosta, Cimolais, Forni di Sotto, and Resia) were allowed to emerge undisturbed in separate net cages (dimensions $6 \times 4 \times 2.7\text{ m}$). We estimated their flight activity from the number of females caught on six sticky traps (dimensions $7 \times 14\text{ cm}$) attached to each of four potted *P. nigra* trees about 2 m in height. The trees were rotated daily among fixed positions in the cage to minimize position effects. Female emergence was checked every

morning by counting both live and dead insects present inside the cage, in addition to those caught on the traps. Temperature was recorded every 2 h by data loggers hung on the trees (HOBO[®]). The threshold temperature for female flight (see Results) obtained from the cage experiment was then compared with the mean night temperature during the female flight period, calculated, respectively, for each extreme site in each of the 4 years.

Population persistence: colony monitoring

A sample of nests ($n = 9$ – 28 per site, the number which could be collected at each site in 1 day of field work) was collected before pupation in April 2004 from extreme nests and from core nests located 200–300 m (in elevation) below. In the laboratory, we recorded the nest diameter, counted the number of larvae, and determined their instar. Performance of the larvae was estimated by weighing 10 individuals sampled randomly from each nest. The colonies were reared under outdoor conditions until pupation, and the pupae were weighed.

In the spring 2005, we visited the sites again and at each we randomly collected a sample of extreme nests to check colony survival during the winter 2004–2005. These nests were then used for rearing without any detailed analysis as done in 2004.

Statistical analyses

The annual rates of expansion (distances between nests found at highest elevations in 2002–2003 and in 2003–2004 within the same site) at different sites were averaged for the years for which data were available, and regressed against the temperature difference between each year and the mean for the 1982–2004 period.

To explore the relationship between female flight activity in the cage experiment and temperature, we regressed the number of females caught on the sticky traps, divided by the total number of female moths present on each night, against the mean of hourly temperature records for each night (21:00–05:00 hours). As the regressions did not differ among populations, we pooled the catch results for all populations tested, with each night as a separate replicate in the regression to avoid pseudoreplication. For all regressions we used untransformed data as the statistical assumptions were met.

With the exception of larval instar, differences between core and extreme sites for all colony parameters (nest diameter, larvae per nest, larval weight, pupal weight) were tested in a factorial ANOVA. We used a nonparametric Friedman ANOVA to analyze larval instar data, as the assumption of normality was not satisfied

after transformation. Trap catches of males in pheromone traps in 2001–2004 were tested in a repeated measures ANOVA blocked by site. All tests were carried out with Statistica software (StatSoft Italy, 2003).

Results

Female dispersal in 2003

We observed a rapid mean upslope expansion (99 m, SE 17.4, $n = 5$ sites) in the altitudinal range limit of *T. pityocampa* in the Italian Alps during 2003–2004. This event represents about 38% of the expansion during the last 30 years, and contrasts dramatically with a relatively gradual range shift from 1982 (1975 in one case) to 2002, during which the altitudinal distribution expanded, on average, by 8.6 m yr^{-1} (SE 0.7, $n = 5$). Most of the extreme distribution resulting from the 2003 to 2004 range expansion persisted into 2004–2005; the altitudinal range contracted, on average, only by 13 m (SE 6.2) among the five sites (Table 1) between 2003–2004 and 2004–2005.

The insect population density, estimated from pheromone trap catches of males, did not vary significantly among sites (ANOVA: $F_{(1,45)} = 1.65$, $P = 0.20$) or among years (ANOVA: $F_{(3,45)} = 2.23$, $P = 0.10$) in the period considered, with mean values ranging from 51 (SE 10) to 129 (SE 27) males per trap in 2003.

Temperature and female flight

Flight activity of females in the outdoor cages was positively and significantly correlated with the mean night temperature for the two populations tested (Fig. 1). Hardly any emerging females were caught on sticky traps in flight until the mean night temperature exceeded 14°C , suggesting a temperature threshold for take-off.

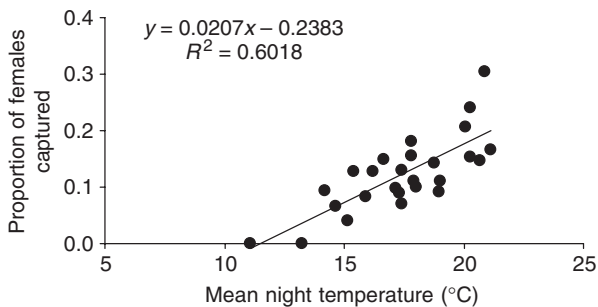


Fig. 1 Relationship between flight activity of female *Thaumetopoea pityocampa* in the outdoor rearing cage (number of females caught on sticky traps/total number of females) and the mean night temperature.

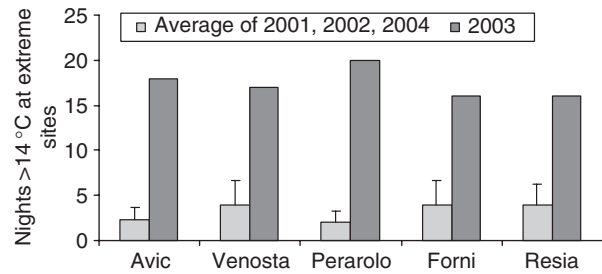


Fig. 2 Number of nights above the take-off threshold (14°C) for female *Thaumetopoea pityocampa* flight at the expansion edge in 2003 compared with the mean of 2001, 2002 and 2004, for the five study sites.

Assuming the take-off threshold for female flight of 14°C , we then calculated the number of nights with the mean temperature above this threshold for the respective female flight periods in the years 2001–2004, for each site. At the range limit, the temperature during the female flight period in 2003 was $2.4\text{--}3.5^\circ\text{C}$ higher than the mean of the other 3 years considered, resulting in, on average, 5.3 times more nights above the threshold (Fig. 2). In addition, the nights with mean temperatures above the threshold in 2001, 2002 and 2004 had values just above 14°C , whereas in 2003, 71% of the nights with the mean temperature above the threshold recorded mean values above 17°C .

To check for a relationship between temperature and the annual altitudinal range expansion, we plotted the mean deviation in temperature from the long-term mean during the emergence period for each year against the mean expansion for each year during the period 1999–2004 (Fig. 3). Temperature deviation was a strong predictor of expansion ($R^2 = 0.92$), and the year 2003 is distinct as an extreme observation for both expansion and temperature deviation. The long-term data set (1951–2004) for Verona Villafranca also confirms the year 2003 as a temperature anomaly in this region (see inset graph, Fig. 3). It is noteworthy that even when the year 2003 is excluded, the period 1999–2004 was warmer than the average, making our comparison of 2003 with the average of 1999–2004 (without 2003) conservative.

Population persistence

Colonies established during the 2003 colonization (extreme nests) showed similar larval survival and performance as lower-elevation colonies (core nests) in the same year (Table 2). Larvae were more advanced at core than at extreme sites when colonies were sampled in April 2004, and there were significant differences among sites. However, the subsequent rearing of larvae

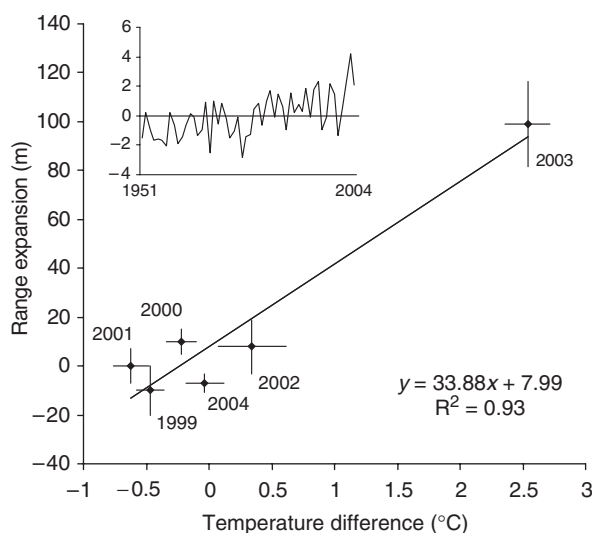


Fig. 3 Relationship between the annual expansion of *Thaumetopoea pityocampa* in the Italian Alps and the temperature difference between the mean night temperature of the female flight period in each year and the corresponding average of the last 30 years. Vertical and horizontal bars show the SE for each variable. For the years 1999–2001, only the data from Venosta/Vinschgau were available. Inset: The record of deviations from the mean temperature for the female flight period during 1951–2004 at Verona Villafranca, which is central to all sites and included in the ECA database (Klein Tank *et al.*, 2002).

from two of the sites (Venosta and Resia) showed that no significant differences between core and extreme sites remained with regard to pupal weight. All the extreme nests sampled in the spring 2005 contained living larvae, which pupated successfully in the rearing.

Discussion

We have documented a rapid altitudinal expansion of the range limit of *T. pityocampa* at several sites in the Italian Alps during 2003, the warmest summer in Europe since at least 1500 (Luterbacher *et al.*, 2004), far exceeding previous annual expansions. While a number of studies have linked changes in species distributions to warming trends (e.g. Hill *et al.*, 2002; Crozier, 2004; Hickling *et al.*, 2005), range expansion in response to a short-term climatic fluctuation has not been reported, to our knowledge. We argue that the colonization event in *T. pityocampa* appears to have been driven by a climatic anomaly, and is unlikely to be only temporary. We detected a threshold night temperature below which short-lived females of *T. pityocampa* rarely fly — a likely limiting factor at the range limit. The record high temperatures of the summer of 2003 resulted in an over fivefold increase in the number of nights above this threshold compared with an average year, allowing

Table 2 Nest characteristics and larval performance of *Thaumetopoea pityocampa* (mean ± SE) at core and extreme sites in the Italian Alps in spring 2004, with the summary results of the ANOVAS

Population	Nest no.		Nest diameter (cm)		Larval instar*		Larvae/nest		Larval weight (mg)		Pupal weight† (mg)	
	Core	Ext	Core	Ext	Core	Ext	Core	Ext	Core	Ext	Core	Ext
Avic	12	10	8.3 ± 2.2	4.8 ± 2.1	4.7 ± 0.5	3.6 ± 0.9	25.3 ± 12.8	23.4 ± 10.1	393.3 ± 107.3	360.0 ± 100.3	—	—
Venosta	25	28	8.9 ± 2.7	6.8 ± 2.9	4.6 ± 0.5	4.3 ± 0.7	68.1 ± 37.0	42.8 ± 35.1	420.3 ± 102.4	390.8 ± 98.7	447.1 ± 97.2	422.6 ± 112.9
Perarolo	9	12	9.4 ± 2.3	7.2 ± 0.3	4.9 ± 0.3	4.3 ± 0.6	74.9 ± 31.5	61.7 ± 41.4	514.1 ± 184.6	379.8 ± 81.4	—	—
Forni	17	23	7.9 ± 2.2	9.4 ± 1.3	4.7 ± 0.5	4.7 ± 0.5	53.9 ± 28.4	111.0 ± 23.4	620.5 ± 173.8	595.4 ± 219.9	—	—
Resia	15	19	7.0 ± 1.9	7.9 ± 2.6	4.6 ± 0.6	3.7 ± 0.4	42.4 ± 26.2	75.9 ± 41.9	495.1 ± 121.6	121.6 ± 76.7	419.4 ± 117.4	448.3 ± 144.2
Origin (core-ext)			$F_{(1,8)} = 1.7,$	$P = 0.23$	$F_{(1,8)} = 7.4,$	$P = 0.03$	$F_{(1,8)} = 0.34,$	$P = 0.57$	$F_{(1,8)} = 1.9,$	$P = 0.20$	$F_{(1,109)} = 2.6,$	$P = 0.12$
Site			$F_{(4,160)} = 4.2,$	$P < 0.01$	$F_{(4,160)} = 5.3,$	$P < 0.01$	$F_{(4,160)} = 15.6,$	$P < 0.01$	$F_{(4,160)} = 21.8,$	$P < 0.01$	$F_{(1,109)} = 2.4,$	$P = 0.11$
Origin × site			$F_{(4,160)} = 7.6,$	$P < 0.01$	$F_{(4,160)} = 4.5,$	$P < 0.01$	$F_{(4,160)} = 7.2,$	$P < 0.01$	$F_{(4,160)} = 5.9,$	$P < 0.01$	$F_{(1,109)} = 0.9,$	$P = 0.77$

*Mean of the larval instar (3–5) at sampling time.

†Pooled data per population.

greater numbers of females to disperse to more extreme sites. The new populations survived through 2004 and, given several life-history characteristics of *T. pityocampa*, appear to be predisposed to persist and possibly expand in the future. Our results imply that the role of stochastic climatic anomalies in driving range dynamics is often underestimated. In addition, we show that some species may have an inherent ability to respond positively and permanently to rapid changes or fluctuations in climate. An emphasis on long-term, slow change in climatic variables may then be insufficient in predicting species responses to climate change, especially in light of the forecasted rise in stochasticity of global climate dynamics.

Female dispersal and range expansion in T. pityocampa

Our previous work shows that *T. pityocampa* has benefited from global warming through increased winter survival, and has been expanding its range for at least the last three decades (Battisti *et al.*, 2005). The rapid range shift observed in 2003, however, was unprecedented and constituted more than one-third of the recorded expansion over a period of 25–30 years. We hypothesized that the 2003 expansion occurred because of an unusual increase in dispersal of *T. pityocampa* females, which may have been caused by atypical warm nights during emergence; air temperature controls flight and dispersal activity in a number of moth species (e.g. Ishiguri & Shirai, 2004).

Indeed, our cage experiments showed a significant positive correlation between the mean night temperature and the flight activity of females. We also detected an approximate temperature threshold (14 °C) below which females rarely took off. Therefore, dispersal of the short-lived *T. pityocampa* females at the upper range limit may be strongly limited by the prevailing climatic regime, under which few nights are sufficiently warm during the emergence period. The extreme climatic anomaly of the summer 2003 facilitated conditions under which the take-off threshold could be met, or exceeded, far more often than usual. Our calculations show that in 2003 there were, on average, 17.4 nights of potential flight conditions at the upper range limit, compared with only 3.3 nights, on average, in the other 3 years from which data were available. In 2003, then, a considerably higher number of females could have successfully taken off, and more dispersal could have occurred, compared with an average year. An increased number of females flying could also likely lead to more long-distance dispersal events, which constitute a small fraction of dispersal events (i.e. occupy the tail of dispersal distributions) in nonmigrant organisms, but often drive spatial spread and colonization rates

(Nathan *et al.*, 2003). The recruitment success of such events depends crucially on the total number of dispersing individuals (Trakhtenbrot *et al.*, 2005).

Temperature may affect the dispersal in *T. pityocampa* females not only by increasing the probability of take-off, but possibly also by increasing the actual distance flown. Higher temperatures have been shown to increase the length of flight of moths attached to a rotating device (flight mill) in laboratory experiments (Ishiguri & Shirai, 2004), and have been associated with increased long-distance migration of Lepidoptera (Sparks *et al.*, 2005); unfortunately, space constraints prevented us from examining this hypothesis in our cage experiment. The mean distance gain observed in 2003 in the study areas (281 m, SE 93) was close to the mean distance flown by female moths under optimal conditions (about 300 m, maximum 1000 m) in a release-recapture experiment (Démolin, 1969b). Finally, directionality of dispersal may be as important as its duration in producing range expansion. The flight of *T. pityocampa* in a mountain terrain is generally upslope (Démolin, 1969b). In this environment, flying upslope during the night means invariably flying upwind, against the descending cold air (mountain breeze; Menella, 1967), which complies with our observations and with general models of moth orientation (Mafra-Neto & Cardé, 1994). Therefore, the net dispersal of females would be directed uphill, beyond the present range limit.

The pheromone trap data showed no differences in density among years for any of the sites, and the mean values observed were well below the catch usually observed in outbreak areas (Zhang & Paiva, 1998). Thus, it is very unlikely that the expansion in 2003 was caused by a density-dependent process that forced the insects to leave a nearby overpopulated area (Wolfsberger, 1971).

Population persistence and range expansion in T. pityocampa

Colonization of a novel environment does not guarantee that the resulting population will be able to persist there (Loxdale & Lushai, 1999). In the case of *T. pityocampa*, particularly unfavourable winters (sudden cold spells below LLT, or climatic anomalies) still present a potential risk at the extreme sites colonized in 2003, and long periods of monitoring would be required to provide conclusive empirical support for population persistence in such a temporally stochastic environment. We suggest, however, that *T. pityocampa* possesses two broad life history traits that allow it to remain at the new range boundary in spite of adverse climatic conditions.

First, existing adaptations of the larvae to feed at low temperatures allow them to survive winters beyond the range where they have occurred before the recent climate change (Battisti *et al.*, 2005). In this study, the newly established colonies at the extreme sites survived the winter of 2003–2004 (colder than the mean of the previous decade: mean of minimum daily temperature December–February 1.03 °C in 2003–2004 at Verona Villafranca, compared with 1.20 °C, mean of winters 1993–2003; Klein Tank *et al.*, 2002 and web update), and pupated successfully. Colonies also survived the winter 2004–2005, when the mean of minimum daily temperature was even lower than 2003–2004 (–1.39 °C December–February at Verona Villafranca; Klein Tank *et al.*, 2002 and web update). The lower lethal temperature of –16 °C (Huchon & Démolin, 1971) was not reached at any of the extreme sites, and the number of feeding hours during the winter was sufficient to ensure survival (Battisti *et al.*, 2005), suggesting that even at these elevations direct climate-related mortality is a sporadic phenomenon occurring only in some years. Translocation experiments carried out at Venosta/Vinschgau in previous years allowed us to detect colony survival under more extreme conditions than those experienced after the 2003 range expansion (Battisti *et al.*, 2005). Our data from 2003–2004 (see Table 2) show that in spite of delayed phenology at extreme sites, pupal weight of the extreme and core populations was similar, suggesting that the extreme populations were able to produce a comparable adult size and, presumably, attain similar fitness (Nylin & Gotthard, 1998).

Second, the life history of *T. pityocampa* includes a bet-hedging strategy – a proportion of the pupae enters a prolonged diapause of up to of 5–7 years (Démolin, 1969a). Its induction is poorly understood, but it may be reinforced by temperatures unfavourable for larval development (Démolin, 1969a). The population effect of the prolonged diapause is an insurance against local extinction: even if lethal temperatures or starvation kill all the colonies in an unfavourable year, other members of the same cohort can survive in the diapausing pupal bank in the soil, and, by chance, some of them may emerge in favourable years. Thus, the plasticity of the life history allows *T. pityocampa* to survive and reproduce at locations previously outside its geographic range. It is possible that, in spite of dispersal limitation of short-lived females, these habitats could be reached over time simply by gradual expansion in small, variable increments. However, in unusually warm summers, when night temperatures favour flight activity, the insect is able to colonize new areas at a much faster rate, and persist there thanks to its physiological and behavioural adaptations to a cooler climate.

Conclusions

A rapid range expansion in *T. pityocampa* appears to be driven by a combination of two mechanisms that are controlled by temperature: adult female flight during the summer emergence, and larval survival during winter. In spite of possible periodic extinctions in unfavourable years, populations can be maintained at sites outside the continuous range by emergence of individuals surviving as pupae in prolonged diapause. Based on the projections of climate change in the next decades (Houghton *et al.*, 2001; Anonymous, 2004), it is highly likely that *T. pityocampa*, and other organisms with distributions determined in part by temperature, will continue expanding their geographic range. While the projected mean rise in winter and summer temperatures could be used to approximate the rate of such expansions, this study also highlights that such forecasting will underestimate the contribution that stochastic climatic anomalies may have in changing species distributions (Parmesan *et al.*, 2000). The inherent unpredictability of marked deviations from the prevailing climatic regime will clearly pose a challenge in applied decisions, such as pest management or conservation of rare species. Yet, incorporating these effects in a quantitative, predictive framework combined with monitoring could prove practical. For instance, in the case of *T. pityocampa*, management strategies could anticipate the measures needed to protect the forest ecosystem and public health following a climatic anomaly. Therefore, we argue that our understanding of changes in the biosphere can benefit from paying more attention to rapid responses of species to climatic anomalies.

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