

# Can climate change drive speciation ?

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**Abstract** — Global climate change has generally been linked with species extinctions, while a possible evolutionary effect of the new environmental conditions was seldom considered. Further, the overwhelming majority of speciation studies focus on population divergence under allopatry, a process resulting from the spatial separation of a group of individuals, that under different selection pressures, later give rise to a new species. Nevertheless, speciation may also take place under sympatry, when some individuals within the population genetically diverge, in spite of remaining in the same, originally occupied area. The very rarely observed process of sympatric speciation, also called adaptive speciation, is here documented through an ongoing study of two populations of a forest insect, the pine processionary moth, *Thaumetopoea pityocampa* (Lepidoptera, Notodontidae), between which gene flow has ceased. One of the populations has undergone a shift of its annual cycle and succeeded to adjust to different, generally warmer, climatic conditions. This population already shows both ecological adaptations, such as a higher temperature niche, as well as some divergence at genetic level. Such findings draw attention to the need of considering the role of species plasticity and of speciation processes, in response to climate change. A thorough interdisciplinary approach is clearly needed, when planning mitigation strategies for biological communities under different scenarios.

**Keywords** - adaptive speciation, temperature niche, population divergence, pine processionary moth.

## 1 INTRODUCTION

Populations are the evolutionary units that make up species and respond to environmental changes. According to classical theory, the genetic and ecological characteristics of a population will determine its dynamics, distribution and fate. However, the role of phenotypic plasticity, that is the capacity of a genotype to originate different phenotypes, has since long been empirically recognized e.g. [1]. More recently it was established that throughout the developmental period of an organism, gene expression does not have a fixed outcome. In fact, the capacity of a genotype to translate into more than one phenotype is driven by environmental pressures, among which climatic and ecological ones e.g. [2].

Additionally, plasticity in one trait can influence selection on linked or correlated traits, among others a phenological alteration may induce physiological changes e.g. [3]. Hence, adaptive phenotypic plasticity may be important in explaining diversification [4]. The presence of new phenotypes will cause divergence within populations and in consequence, divergence among populations may occur, giving rise to new species.<sup>1</sup>

An ongoing, very rarely observed case of divergence between two sympatric (coexisting in the same area) populations of a forest insect is here documented. *Thaumetopoea pityocampa* (Lepidoptera, Notodontidae) the pine processionary moth (PPM), is a conifer (needle trees) defoliator, widely distributed around the Mediterranean basin, where it causes economic damage to forestry and constitutes a health hazard for humans and domestic animals, e.g. [5], due to urticating hairs present in the late larvae. The usual life-cycle of the normal PPM populations comprise a larval stage developing between September and February. The following pupal stage undergoes a diapause (a period when development is delayed) buried in the soil, which lasts until July. Adult emergence, mating and egg laying take place between July and September, e.g. [6].

The discovery of a PPM population divergent from the normal form, presented a unique opportunity for state-of-the-art research to be conducted on two controversial topics: i) The occurrence and unfolding under field conditions, of mechanisms leading to sympatric (or adaptive) speciation and ii)

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The role of climate as driver of population divergence.

Extensive studies of the two divergent populations were performed at genetic, biological and ecological level. An integrated approach to the results obtained for the PPM asynchronous population, provides evidence that a shift of its fundamental ecological niche regarding temperature, *sensu* Hutchinson [7], has already occurred. This new trait can thus enable the potential expansion of the pine pest into areas that, due to climatic characteristics, are beyond limits for colonization by the normal, original population.

## 2 Phenological shift

PPM phenology (life-cycle timing) can be considered uncommon for insects of temperate regions, since the unfavourable winter season is spent in the form of larvae, that is a rather vulnerable stage. However, in August 1997 a unique PPM population having a shifted phenology, was discovered in the coastal area of Mata Nacional de Leiria (MN Leiria) [8], colonizing the same trees and pine plantations as the normal population.

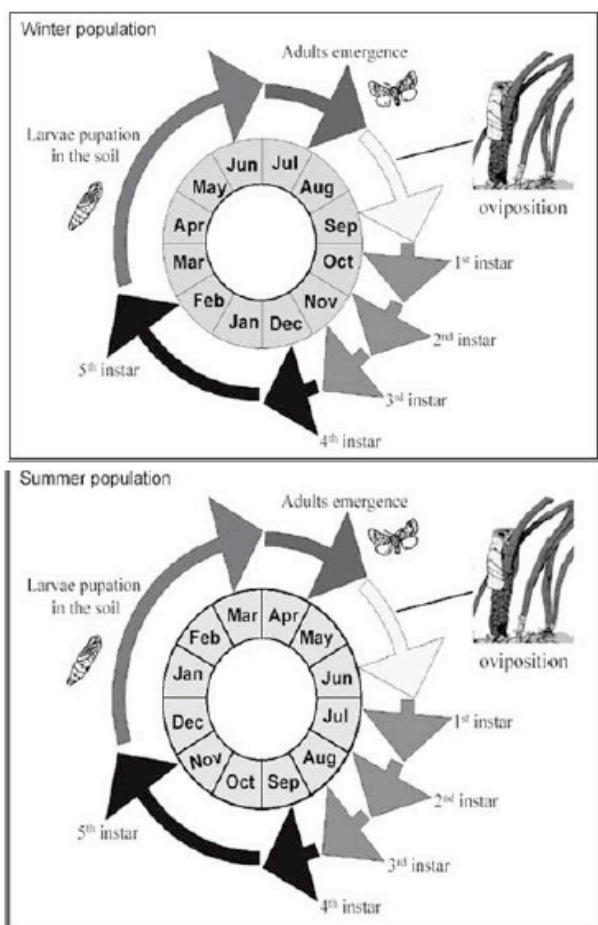


Fig. 1 – Phenology of PPM winter population (WP) and summer population (SP) in MN Leiria, Portugal.

Since the larvae were developing in the summer, instead of in the winter, this population was designated PPM SP (summer population) and complementary, the normal form was called PPM WP (winter population).

Because the reproductive period of both populations is asynchronous (Fig. 1 and Fig. 2), adults of both populations are not simultaneously present in the field. This mechanism consequently acts as a pre-mating isolation barrier.

The flight period of the males of both PPM populations was monitored in MN Leiria and surrounding areas, over five consecutive years, using specific traps baited with the female sex pheromone, so that males only are trapped.

It was concluded that a time gap of two, to three weeks, occurs between the end of the flight of the SP males and the beginning of those of the WP (Fig. 2) [9]. Results lead to the inference that an allochronic differentiation of the two populations has apparently already taken place.

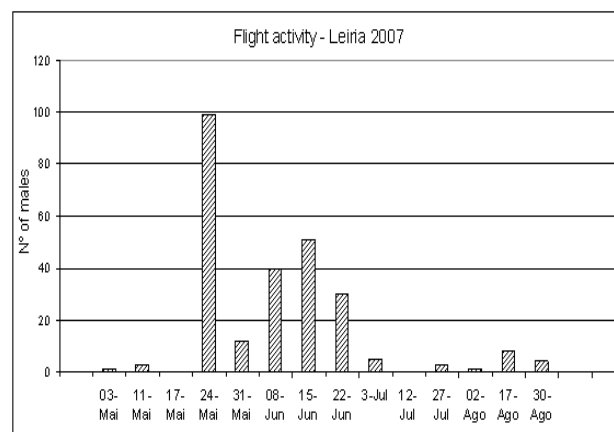


Fig. 2 – Flight period of PPM males in MN Leiria in 2007: summer population (SP): May to June; winter population (WP): end of July to September, Portugal.

## 3 Genetic structure

The genetic structure of the PPM SP was compared with that of other European populations, including the WP, by analysing mitochondrial DNA. It was concluded that in this species, polymorphism is highly structured. Insects of both MN Leiria populations exhibit only endemic haplotypes, one major haplotype being shared between the SP and the WP, thus suggesting that the SP did not disperse from another region, but had instead a local origin [10].

In parallel, the allelic frequencies of six

microsatellite loci were used to genotype SP individuals. Five of these loci, namely MSThpit1, MS-Thpit2, MS-Thpit3, MS-Thpit4 and MS-Thpit5, are described in [10] Rousselet et al. (2004), and MS-Thpit6 in [11]. Sample sizes and the complete data set can be consulted in [12].

It is concluded that markers show evidence of a founder effect (Fig. 3). All alleles present in the SP also occur in the WP, however the SP has a lower allelic richness than the WP, and the frequencies are distorted [12].

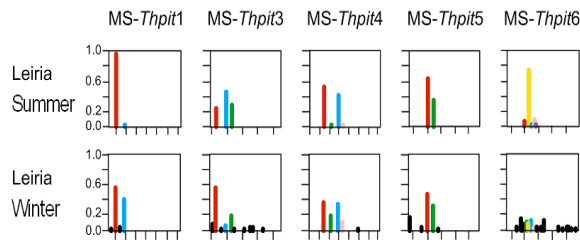


Fig. 3 - Histogram of allelic frequencies of PPM summer population (SP) and winter population (WP) per population, for five loci. MN Leiria, Portugal. Source: modified from [12].

## 4 Ecological divergence

### 4.1 Pheromone composition

Pheromones are mostly volatile substances emitted to transmit a message to an individual of the same species, which will influence either the behaviour, or the physiology of the receiver, e.g. [13]. Insect biocology is, to a large extent, ruled by pheromones and consequently reproductive isolation is often, although not always, linked to the evolution of pheromone differences. In fact, convergent or parallel evolution within pheromone components indicates that pheromone evolution is plastic and might not be congruent with phylogeny [14].

However, the genetic mechanisms by which pheromone signals change during the process of speciation remain largely unknown, e.g. [15].

The mating behaviour of the two PPM populations was studied by analysing the composition of the sex pheromone emitted by SP females, and comparing it with that of WP females. In the laboratory, the volatile emissions of virgin SP females were collected by SPME (Solid Phase Micro Extraction) and the characterization of the volatiles performed by gas chromatography (GC) and mass spectrometry (MS).

The pheromone bouquet of the SP was compared with that of the WP, by using the pheromone standard of the normal PPM winter population identified by Guerrero et al. [16], obtained from Biosani Ltd.. Fig. 4 presents a close up of the

pheromone range for both chromatograms, with major peaks identified. Mass spectra were also performed for the two peaks identified, respectively of the SP and of the WP.

It was concluded that the pheromone composition of the two PPM populations do not differ. Furthermore, similarly to reported for the WP by Quero et al. [17], no additional compounds were identified in the volatile emissions of the SP, that could act in synergism with the sex pheromone. Results clearly indicate that the mechanism of olfactory communication in the two populations, has not diverged regarding sexual attraction, so that cross mating between SP and WP remains possible.

Such findings agree with a pattern of pheromone evolution characterized by large discontinuous leaps, as observed in bark beetles, e.g. [18]. This inference has been corroborated under laboratory conditions, where ongoing experiments succeeded in obtaining progeny from crosses between SP x WP adults.

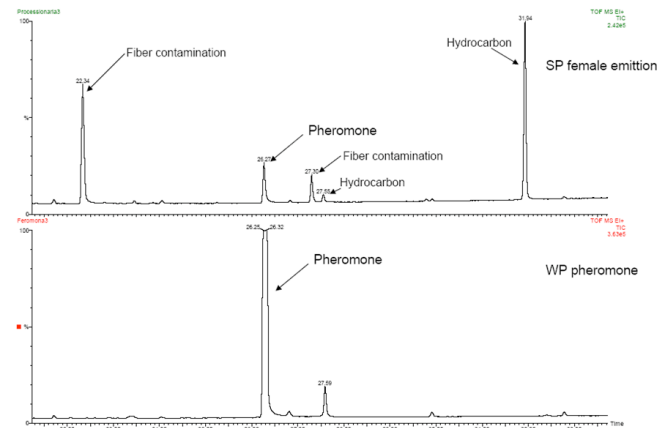


Fig. 4 - Chromatograms obtained by Solid Phase Micro Extraction (SPME) for the volatile emissions of PPM SP females, and for the standard commercially available pheromone of the WP. Laboratories of FCT, UNL, Portugal, 2010.

### 4.2 Temperature thresholds

Particularly in insects, temperature plays a key role among the climatic factors that might limit the establishment and expansion of a new population with a phenology different from that of the original one, e.g. [19].

Literature references generally indicate that larvae of the normal PPM winter populations would not be able of surviving at temperatures in the range of those recorded in the summer, in areas of Mediterranean climate. For France, Démolin [20] indicated that larvae stopped growing at temperatures above 30°C, and did not survive at 32°C.

Results of a comparative study performed using larval stages of the SP and WP, subjected to different heat treatments [21], showed that SP larvae survived significantly better at all temperatures tested than WP larvae, except those of 2<sup>nd</sup> instar at 36°C, for which no significant differences between populations were found (Table 1, Fig. 5).

Table 1 – Comparison between PPM summer population (SP) and winter population (WP) survival of the 1<sup>st</sup> and 2<sup>nd</sup> instar larvae, after the 1<sup>st</sup> instar was subjected to three days of heat treatment. Larvae form MN Leiria, Portugal, 2008.

Temperature	L1		L2	
	Chi-Square	p	Chi-Square	p
36°C	50,632	0,000	1,172	0,279
38°C	39,828	0,000	25,168	0,000
40°C	23,643	0,000	148,663	0,000
42°C	67,728	0,000	40,177	0,000

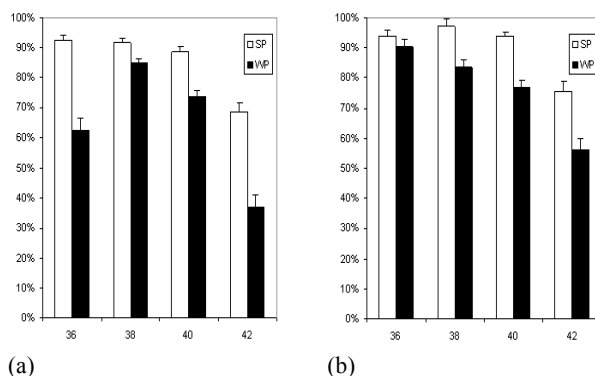


Fig. 5. Percentage of PPM summer population (SP, white bars) and winter population (WP, black bars) larval survival, after three days of heat treatment of the: (a) - 1<sup>st</sup> instar . (b) – 2<sup>nd</sup> instar. Larvae form MN Leiria, Portugal.

Furthermore, 1<sup>st</sup> instar larvae are, in general, more susceptible to high temperatures than 2<sup>nd</sup> instars. However, for the SP both instars survived in similar high percentages at 36°C and 38°C (Fig. 5).

## 5 Discussion and conclusions

For the PPM in Leiria area, evidence shows that a new population (SP) evolved in consequence of a

phenological shift and is developing under ecological conditions characterized by high summer temperatures, thus indicating ecological niche divergence in relation to the original WP. Since PPM polymorphism is highly structured [12] and high temperature tolerance might be considered a polymorphic trait, enabling selection to act, the observed allochronic differentiation apparently constitutes a first step along an ongoing process of adaptive speciation.

This inference is supported by e.g. [22], considering that once sympatric divergence has reached the level of incipient speciation, full speciation will be inevitable, as assortative mating factors make the evolutionary return journey unlikely, or impossible. Furthermore, different ecological selection scenarios can give rise to selection pressures under which adaptive speciation is theoretically possible and likely to occur [23].

Although the causal mechanisms underlying temporal variation in the strength, direction and form of selection are still insufficiently understood, variation in environmental conditions driven by climatic fluctuations appear to be common and important. Additionally, evidence that stress induces adaptive mutations in individuals has been growing, e.g. [1].

Nevertheless, most studies concerning the effect of climate on populations generally take into account the species present ecological requirements, in particular the thresholds of their realized niches. Niche conservatism is thus implicitly hypothesized [24] and the inherent capacity of the species to rapidly evolve and adapt to new conditions disregarded. This simplistic approach has been empirically proved unsuitable, as documented by the expansion of insect species towards geographical regions of more extreme climatic conditions, namely the Alps and Northern France, as observed for PPM winter populations [25].

From the case study here presented it may be inferred that: i) Additionally to promoting selection at phenotypic level, a second role of the environment must be considered in evolutionary studies: the capacity to generate plasticity among individuals; ii) Credible scenarios forecasting the impact of climatic factors on the future of biodiversity, require an understanding of the evolutionary theory and of the forces that shape responses to environmental change. As recognized by e.g. Visser [26], predictive models for species geographical retractions, extinctions or expansions, must be based upon eco-evolutionary dynamic models, incorporating ecological, genetic and physiological characteristics of the populations under study. Unfortunately, such insights seem only rarely to reach other relevant fields, not to mention the general public and policy makers [27].



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