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Quaternary history of the pine processionary moth: role of topography and host tree in shaping the population genetic structure

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Introduction The winter pine processionary moth (PPM), *Thaumetopoea pityocampa*, belongs to a circum-Mediterranean species complex associated to pine and cedar species. As its larval development takes place during autumn and winter, this insect is highly sensitive to climate variations. In recent years, this species has expanded to upper latitudes or elevations in several European countries due to increased winter temperatures. This rapid response to current climatic changes due to its cold sensitivity suggests that its past distribution is likely to have been strongly affected by Pleistocene climate changes.

In general, thermophilic species have expanded during warm periods and responded to cold phases by local extinctions in northern and mountainous regions, while arctic and alpine species exhibit opposite responses. However, there is increasing evidence of more complex patterns of response, because many species have intermediate ecological requirements or habitat-generalist traits.

The distribution range and the population dynamics of the pine processionary moth are in fact constrained by both cold winter and high summer temperatures. The sub-mediterranean areas (with relatively mild summers and mild winters) could correspond to its optimal ecological niche. Nevertheless, this insect exhibits some plasticity in the host plant use and the timing of its life cycle that allows the species to adapt to various

environments. *T. pityocampa* occurs from coastal areas and lowlands (with hot summers and mild winters) to mountainous environments (with milder summers and colder winters).

Pinus nigra is the preferred host, but PPM can attack several tree species with very different climatic requirements (*P. halepensis*, *P. pinaster*, *P. pinea*, *P. sylvestris*, *C. atlantica* and several exotic conifers). However, PPM distribution area is more restricted geographically than that of its potential hosts, which include montane or boreal species. In western Europe, regions with continental climate or situated above the 48th parallel, as well as the high-elevation areas of the main mountainous ranges, are not colonized.

Our objectives were to test whether:

[1] the glacial refugia were restricted to the southernmost part of the European peninsula (where the Mediterranean climate persisted during the last glacial maximum)

[2] the unsuitable areas of the Pyrenees, Massif Central and Alps have been effective barriers to gene flow during the Quaternary history of this species (reputed to be a poor disperser)

[3] there are cryptic host strains in this oligophagous defoliating insect.

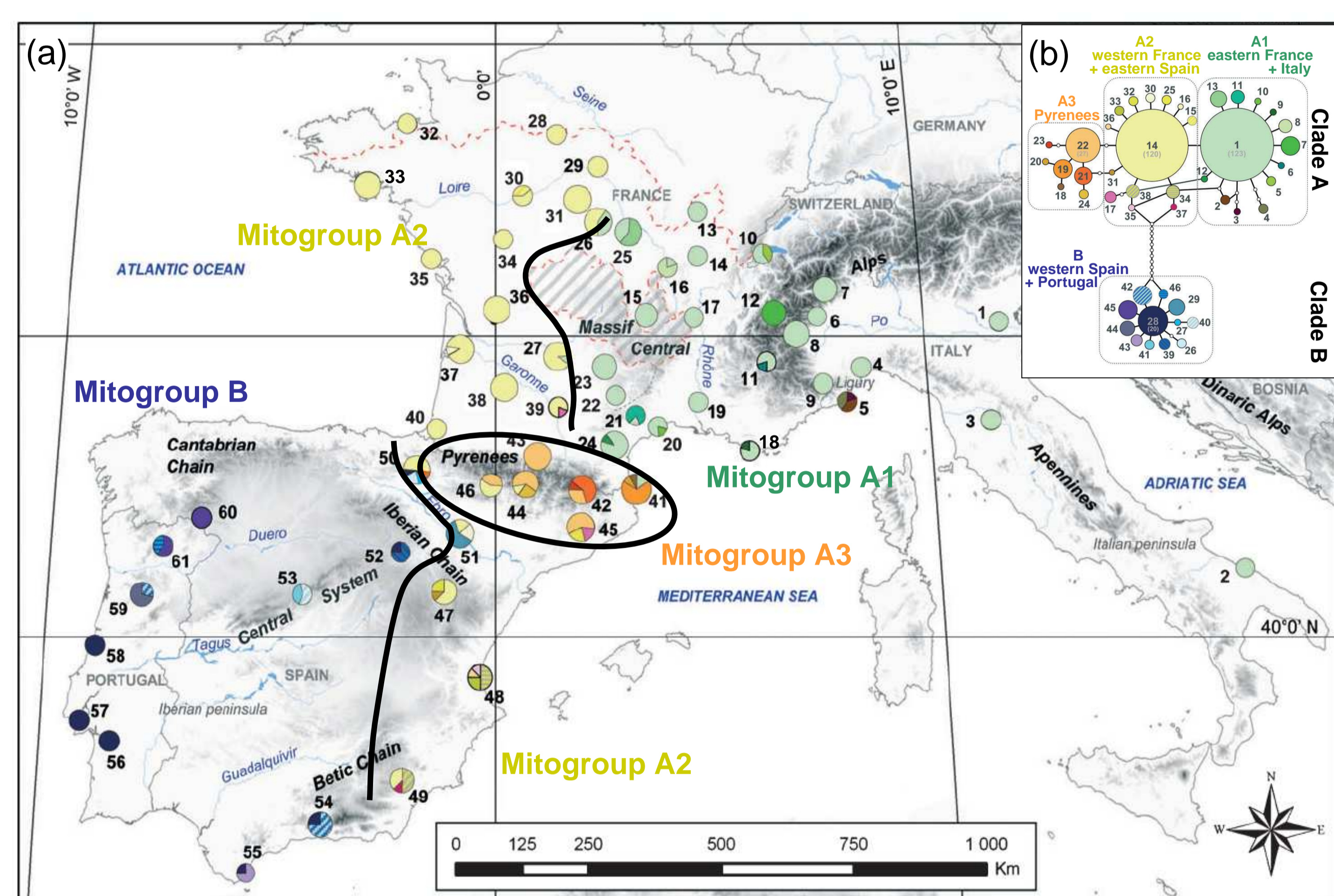


Figure 1 Haplotype network and geographic distribution of the 46 COI haplotypes of *T. pityocampa* among the 61 sites sampled in western Europe. (a) geographic distribution; the total area of each circle is proportional to the sample size and haplotype frequencies are represented by the area of the circle occupied; the red dotted line indicates the present-day northern limit of *T. pityocampa* in France and the hatched area indicates the uncolonized part of the Massif Central; the northern limit in Italy and the Balkans (not represented) corresponds to the southern side of the Alps and Dinaric Alps, respectively. (b) haplotype network; each circle represents a different haplotype (numbered from 1 to 46 and identified by a different colour); haplotype frequencies are represented by the area of the circle. Each line between circles corresponds to a mutational step and each small empty circle to a missing intermediate haplotype.

Discussion In western Europe, we identified four genetic lineages that are strongly geographically structured, but surprisingly they are not isolated by the unsuitable high elevation areas of the main mountain ranges. Conversely, the mountainous areas from the Betic Chain to the eastern Pyrenees, and maybe up to the Massif Central and the Alps, appear to have offered suitable environmental conditions along the slopes during the ice ages, and the current distribution reflects expansion from these refugial populations exhibiting a higher genetic diversity.

The western and central Iberian clade (B) did not contribute to the northward post-glacial recolonization of Europe. The present delimitation between clades A and B is south-north oriented and definitely does not correspond to the Pyrenees. However, it might correspond to major Iberian drainage basins toward the Mediterranean sea and the Atlantic Ocean respectively. Interestingly, the distributions of several Iberian endemic plant and animal species suggest a similar east to west polarity, with a trend for the areas of endemism to coincide with the largest mountain ranges (García-Barros *et al.*, 2002).

Surprisingly, the Pyrenean Chain hosts an endemic lineage having managed to survive the ice ages in Catalonia. This refugial area is located much more northerly than expected, but neither contributed to the northward postglacial expansion.

The only Iberian lineage occurring north to the Pyrenees is mitogroup A2, which originated from refugial areas located more southerly (eastern Iberian or Betic Chains).

The different contributions of the identified refugia to post-glacial expansion might be explained by differences in host plant species richness and the relative plasticity of this insect in host plant use.

No genetically differentiated host strains were observed within clade A (and the apparent host effect detected in the whole data set is likely due to the strong spatial structure of the host trees; Table 1). *P. sylvestris* and particularly *P. nigra* are the preferred host plants and they probably persisted in all the glacial refugia of this insect. The Iberian lineages of these mountain pines did not contribute to the northward post-glacial recolonization of Europe (Cheddadi *et al.*, 2006; Afzal-Rafii & Dodd, 2007).

P. nigra and *P. sylvestris* were probably the main continuously available hosts in the eastern Pyrenees, while *P. pinaster* was also probably present and abundant in the eastern Iberian Chain. Consequently, the Pyrenean lineage of the pine processionary moth could have been trapped elevationally by tracking mountain pines, while the eastern Iberian lineage could have expanded latitudinally by tracking thermophilic lowland pine species (Fig.3). Interestingly, the expansion pathway from eastern Spain to southwestern France corresponds to one of the migration routes suggested for *P. pinaster* (Salvador *et al.*, 2000), which would be consistent with the moth following the migration route of one of its hosts.

Material and Methods Maternal genetic structure was investigated using a 802 bp-long fragment of the mitochondrial cytochrome c oxidase subunit I (COI) gene. We analysed 412 individuals from 61 locations. DNA extraction, PCR amplifications and sequencing followed the protocol described in Rousselet *et al.* (2010).

Results A strong phylogeographic pattern was found (NST=0.880±0.036 > GST=0.689±0.038, p<0.001; Fig. 1a) with two deeply divergent clades (Fig.1b). These clades were distributed from the Italian Peninsula to eastern Iberia (clade A) and from central to western Iberia (clade B).

Clade A consisted of three shallowly divergent lineages (mitogroups A1, A2, A3; Fig. 1b) that exhibited strong geographic structure (Table 1) and independent population expansions (Table 2). The three identified lineages occurred: (A1) from the western Massif Central to Italy, (A2) from eastern Iberia to western France, with a higher genetic diversity in the south (A3) on both sides of the Pyrenean range, with more genetically diverse populations in the east (see Figure 1). Admixture areas were found at the foot of the Pyrenees and Massif Central.

No significant host effect was observed within clade A (Table 2). The haplotypes 1, 11, 14, 19, 21, 22, 28, 43 were found on different host-plants (Fig. 2). All the others were private haplotypes occurring once or found in samples collected on a single host species.



Figure 2 Host plant species mapped onto the haplotype network. For each haplotype, pie-charts represent the proportion of individuals found on each host plant sampled. The four groups used for the AMOVA are indicated in the legend (numbers 1-4).

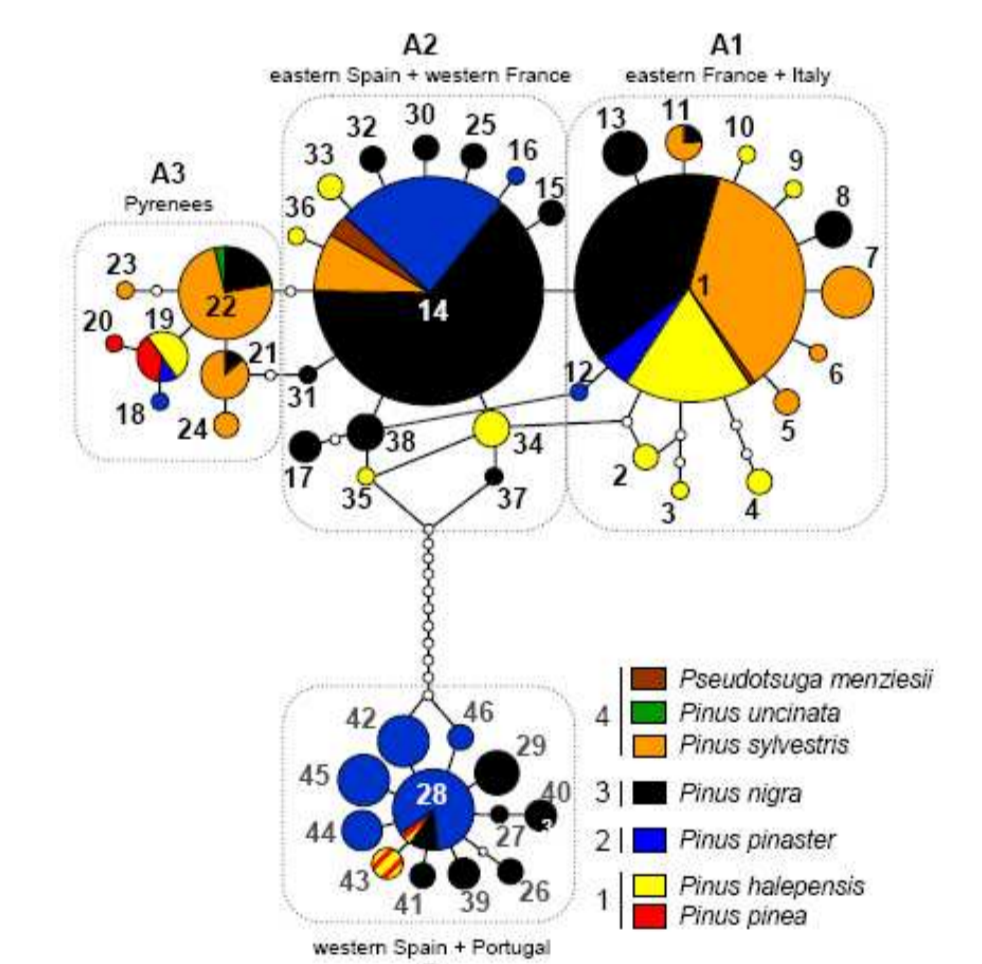


Table 1 Analyses of molecular variance (AMOVA) among populations of *T. pityocampa*. The populations were grouped either by geographical location or by host species. Geographical groups were defined on the basis of the distribution area of the lineages identified with phylogenetic and parsimony network analyses. Samples corresponding to putative secondary contact zones (i.e. sampling sites containing haplotypes from different lineages) were treated using two options. When samples were grouped by geographical regions, the results always showed that a large and significant proportion of the variance was found among groups. When they are grouped by host species, most of the genetic diversity was found among populations within groups. A significant part of the variance was found among groups for the whole data set, but not within clade A.

Structure	Source of variation	Whole data set (Clade A + B)			Clade A		
		Variance (%)	Fixation indices	P-value	Variance (%)	Fixation indices	P-value
Grouping by geographical regions I*	Among groups	78.52	$\Phi_{CT} = 0.78534 < 0.001$	53.00	$\Phi_{CT} = 0.53002 < 0.001$		
	Among populations within groups	8.80	$\Phi_{SC} = 0.60995 < 0.001$	15.68	$\Phi_{SC} = 0.33362 < 0.001$		
	Within populations	12.67	$\Phi_{ST} = 0.87328 < 0.001$	31.32	$\Phi_{ST} = 0.68881 < 0.001$		
Grouping by geographical regions II**	Among groups	91.54	$\Phi_{CT} = 0.91540 < 0.001$	72.90	$\Phi_{CT} = 0.72904 < 0.001$		
	Among populations within groups	4.06	$\Phi_{SC} = 0.48043 < 0.001$	11.49	$\Phi_{SC} = 0.42416 < 0.001$		
	Within populations	4.40	$\Phi_{ST} = 0.95604 < 0.001$	15.60	$\Phi_{ST} = 0.84397 < 0.001$		
Grouping by hosts***	Among groups	21.36	$\Phi_{CT} = 0.2136 < 0.001$	4.58	$\Phi_{CT} = 0.04581 < 0.001$		
	Among populations within groups	43.26	$\Phi_{SC} = 0.08045 < 0.001$	16.29	$\Phi_{SC} = 0.09478 < 0.001$		
	Within populations	15.38	$\Phi_{ST} = 0.8462 < 0.001$	29.12	$\Phi_{ST} = 0.70876 < 0.001$		

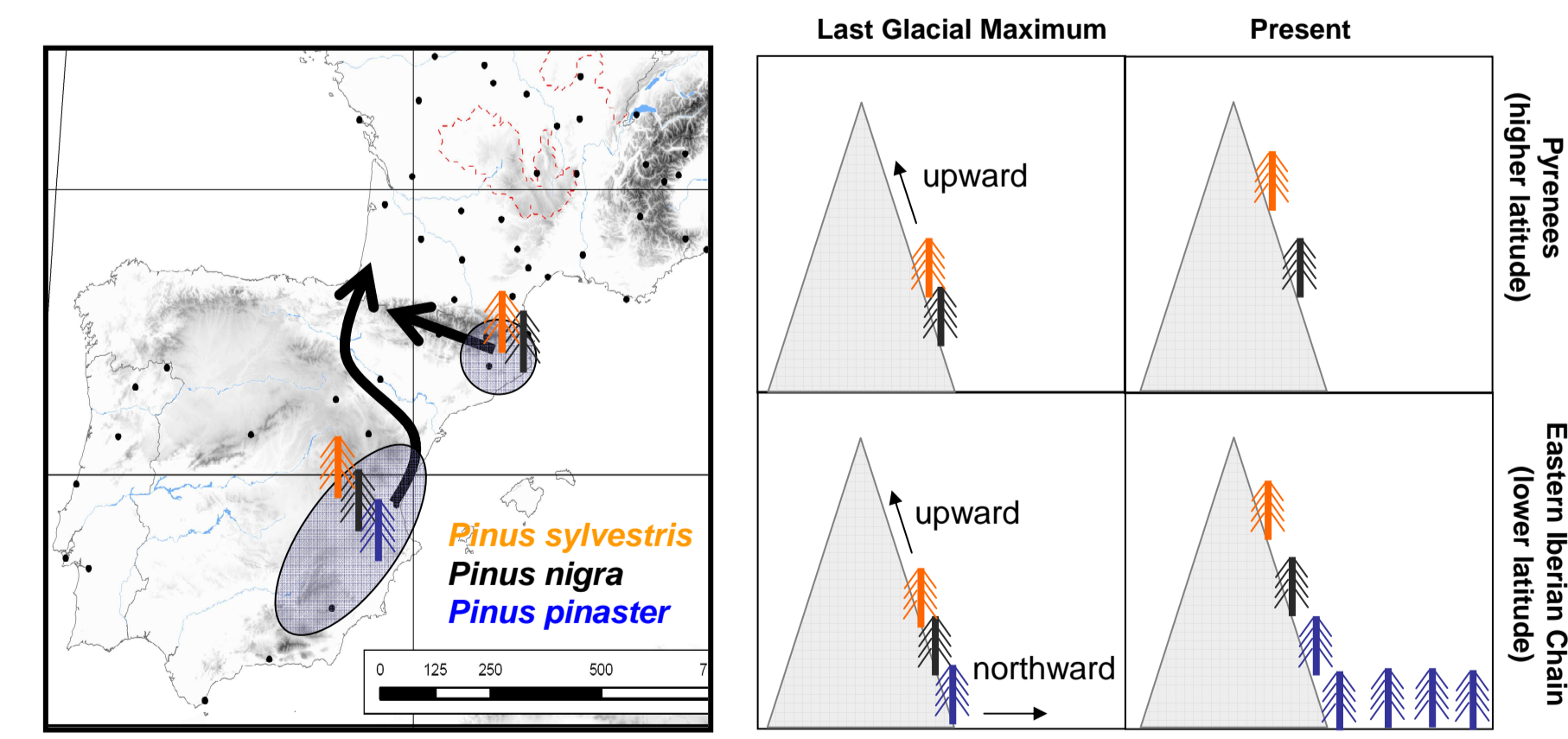
* Grouping by regions I (data from southern contact zones entirely attributed to one of the geographical groups - see Rousselet *et al.*, 2010 for more details); group 1: Italy and western France (samples 1-10); group 2: western France and eastern Spain, including the Ebro Valley (samples 20-40, 47-51); including contact zones 26, 27 and 50, 51; group 3: Pyrenees (samples 41-46); including contact zones 41 and 44-46; group 4: western Spain and Portugal (samples 52-61); clade B, the same three first groupings but without samples 50, 51 and 52-61.
 ** Grouping by regions II (sites from putative contact zones removed from the data set) - same regional grouping as I but samples 26, 27, 41, 44-46, 50 and 51 (all the putative contact zones) were removed from the data set.
 *** Grouping by hosts: group 1: *Pinus halepensis* and *P. pinea* (samples 1, 5, 18-20, 24, 41, 48, 55); group 2: *P. pinaster* (samples 24a, 30b, 37-38, 40, 41a, 54, 56-61); group 3: *P. nigra* (samples 1, 5, 11a, 13-14, 16, 21-23, 25, 26, 27b, 28, 30a-30c, 36a, 38, 40, 47, 48-53); group 4: *P. sylvestris*, *P. uncinata*, *Pseudotsuga menziesii* (4, 7-10, 12, 15, 17, 27b, 29, 42-44, 46); samples collected on several host trees were divided into subsamples (a, b) attributed to the corresponding groups; clade A, the same four groups without individuals from clade B.

Table 2 Results of mismatch distribution and neutrality tests against population growth for each mitogroup. For the northernmost mitogroups A1 and A2, all tests indicated population expansion. For the pyrenean mitogroup A3, only the goodness-of-fit test suggested population growth. For the western Iberian mitogroup B, only Fu's F_s test indicated a departure from neutrality expected with population expansion.

Goodness-of-fit test	A ₁	A ₂	A ₃	B
	SSD	0.00114	0.00145	0.01566
P-value	0.63800	0.62100	0.67400	0.01300
Expansion	OK	OK	OK	NO
Tests of selective neutrality				
	Fu's F_s	-12.39260	-15.83490	-2.38929
P-value	0.00000	0.00000	0.07621	0.01003
Expansion	OK	OK	NO	OK
R_2	0.01907	0.0199	0.0276	0.0392
P-value	0.04266	0.02612	0.13155	0.09548
Expansion	OK	OK	NO	NO

SSD: sum of squared deviations, R_2 : Ramos-Onsins and Rozas' R_2 .

Figure 3 : Putative scenario of post-glacial expansion



Conclusions – perspectives Rather than showing that mountains acted as physical barriers to dispersal, our results suggest that topography played a major role in shaping the distribution of maternal lineages of the moth through the demographic history of its main host plants.

Moreover, the evolutionary history of the maternal lineages of the pine species is often blurred by past and present-day pollen gene flow at large scale and a too low mitochondrial variability. Our results also suggest that the phylogeographic pattern of insect species exhibiting a strong genetic structure could help to reconstruct it.