Alain Roques *Editor*

Processionary Moths and Climate Change: An Update

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Zoologie Forestière
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Foreword

As this book's introduction clearly illustrates, processionary moths have long been organisms of interest and the subject of research. This is because of the severe skin irritation they cause in both humans and animals, the havoc they wreak on vegetation, and the remarkable social behavior they demonstrate. Very early on, researchers began to study their characteristics, biology, ecology, behavior, population dynamics, and evolution. They also examined their impacts on and risks to human and animal health, as well as the ways in which to control them. In France, and at INRA in particular, many studies have been and continue to be carried out on the pine processionary moth. I wish to dedicate this preface to Guy Démolin, who unfortunately passed away a few weeks ago and who was one of the major researchers in the field at the end of the twentieth century.

Despite the varied and growing amount of research that has been conducted on this topic since the early 2000s, not a single review on processionary moths has been published to date. Indeed, the primary goal of this book is to provide a synthesis of the available literature, in addition to updating our current knowledge. As a consequence, this work includes the most recent findings on processionary moths. The results presented here are the fruit of modern approaches deployed in the fields of population genetics, mathematical modeling, computer simulation, and ecology. Researchers have also exploited up-to-date techniques to examine the moth's evolutionary interactions with tree species, predators, and other members of the insect community; they have predicted and characterized the risks posed by these organisms, particularly in the urban environments they are entering and ever more frequently colonizing.

This book is unique for another reason: it takes into account climate change and, in particular, addresses the future expansion of the processionary moth's range. Studying such biological invasions requires to combine various approaches: empirically observing and monitoring distribution patterns; modeling and predicting range expansion based on current and future changes in the climate, vegetation structure, and anthropogenic activities; dynamically modeling propagation patterns; understanding the specific genetic and demographic processes that are operating within populations on or just behind the invasion fronts, as well as those driving propagation; and examining the effects that this invasion has on biodiversity and the risks it entails for human and animal populations.

I wish to extend my sincere gratitude to Alain Roques and Andrea Battisti, who took the initiative to bring together a large number of experts in this field. They were thus able to report on the work that has been carried out over the last 15 years as a result of national, regional, and pan-European projects. Within INRA, research on the processionary moth draws on an entire network of scientific teams that contribute different skills and expertise, as well as complementary empirical and experimental perspectives. It is clear that the international nature of this research plays a crucial role in its success, and I am pleased to see that this book clearly illustrates that the work being carried out on this insect model system transcends national borders.

President of the French National Institute
for Agricultural Research, INRA
Paris, France
July 8, 2014

François Houllier

Acknowledgments

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We are deeply indebted to the reviewers who devoted considerable time to read the chapters and whose corrections and suggestions largely contributed to improve the quality of this work. We thus thank Sylvie Augustin (INRA Orléans, France), Matt Ayres (Dartmouth College, Hanover, New Hampshire, USA), Thomas Boivin (INRA Avignon, France), Jean-Noël Candau (Canadian Forest Service, Great Lakes Forestry Centre, Sault Sainte Marie, Canada), Marc Kenis (CABI Délémont, Switzerland), Andrew Liebhold (USDA Forest Service, Morgantown, West Virginia, USA), and Géraldine Roux (INRA and University Orléans, France). We also thank Franck Rogeon, INRA Orléans, for his help in the literature review and Louis-Michel Nageilesen (Département Santé des Forêts, Nancy) and György Csóka (Forest Research Institute, Mátrafüred, Hungary) for supplying pictures.

Finally, we also want to thank Jean-Marc Guehl and Thierry Caquet, the successive heads of the department of Forest, Grassland and Freshwater Ecology (EFPA) with INRA, and Jean-Luc Flot, head of the Département Santé des Forêts (Ministry of Agriculture, Paris), who largely facilitated the development of this project.

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Chapter 1
Introduction

Alain Roques and Andrea Battisti

1 Pine Processionary Moth, a Species Known Since the Ancient Times

Pinorum erucae: vis omnium communis erodere, ulcerare (Dioscoride II, 53, in Matthioli 1562): the urticating character of larvae living on pines, called '*pityocampes*', was already noticed in Italy in 77 A.C. in "*De Materia medica*", a treaty by Dioscoride (40–90 A.C.), a Greek doctor having accompanied as a surgeon the armies of the Roman Emperor Néron. The word *pityocampes* referred to *pitus*, the Aleppo pine in ancient greek (*Pinus halepensis*), and to *campa* the larva. Quite at the same time, Pline the Ancient indicated in "*Naturalis Historia*" to use a liquid called "*Sapa*" to treat the urtication due these pine larvae (*Pinorum Erucas quas Pityocampas uocant*- the pine larvae called pityocampes; Livre 23, 30; André, 1971). Actually, the presence of pine processionary larvae had already been shown several centuries ago in Greece. Théophrastos of Eresos (371–286 B.C.), one of the first botanists, thus mentioned in "*Historia Plantarum*" written in 314–313 B.C., that a plant, the Chiron's panacée (*Inula helenium*) was to be used mixed with wine and oil "*against vipers, tarentulas, pine larvae and other reptiles*" (IX, 11, 1; Amigues, 2006). During these ancient times, the law of Rome considered processionary larvae as a violent poison and sentenced to death *pityocampœ propinatores* (*those who encourage to ingest pityocampes*) (Lesser 1745). The Justinien's law or *Digeste* or *Pandectes* (in Greek), published in 534 but in use until the Middle Age, thus included *pityocampes* in its Title VIII of the Cornelia law on assassins and poisoners

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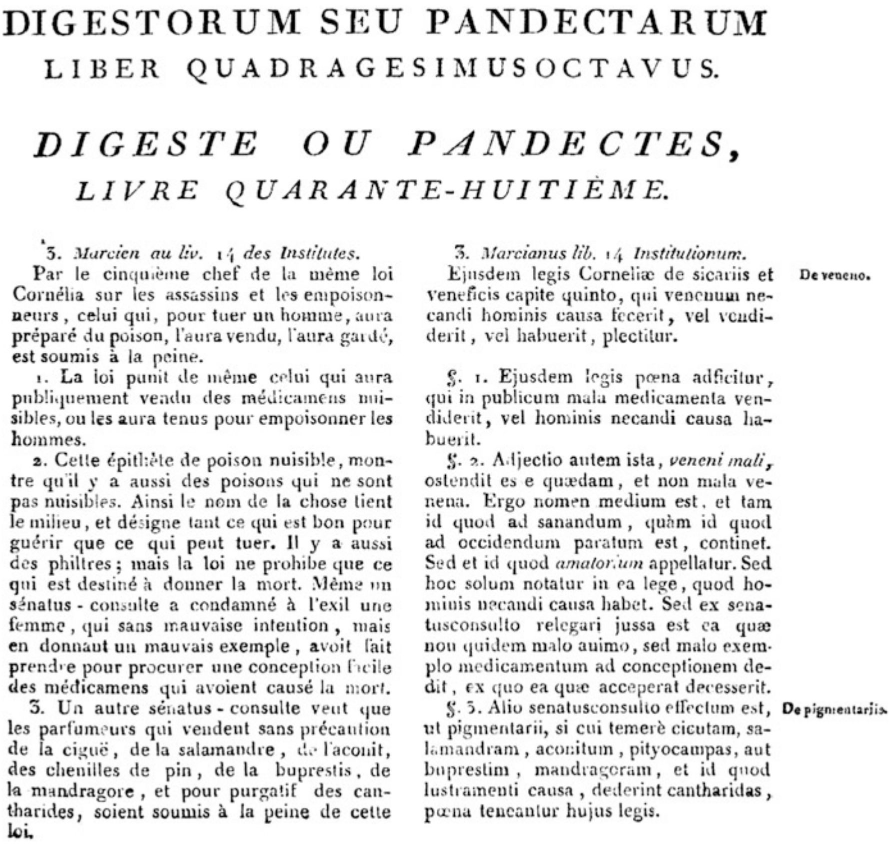


DIGESTORUM SEU PANDECTARUM
LIBER QUADRAGESIMUSOCTAVUS.

DIGESTE OU PANDECTES,
LIVRE QUARANTE-HUITIÈME.

3. *Marcien au liv. 14 des Institutes.*

Par le cinquième chef de la même loi Cornélia sur les assassins et les empoisonneurs, celui qui, pour tuer un homme, aura préparé du poison, l'aura vendu, l'aura gardé, est soumis à la peine.

1. La loi punit de même celui qui aura publiquement vendu des médicamens nuisibles, ou les aura tenus pour empoisonner les hommes.

2. Cette épithète de poison nuisible, montre qu'il y a aussi des poisons qui ne sont pas nuisibles. Ainsi le nom de la chose tient le milieu, et désigne tant ce qui est bon pour guérir que ce qui peut tuer. Il y a aussi des philtres; mais la loi ne prohibe que ce qui est destiné à donner la mort. Même un sénatus-consulte a condamné à l'exil une femme, qui sans mauvaise intention, mais en donnant un mauvais exemple, avoit fait prendre pour procurer une conception facile des médicamens qui avoient causé la mort.

3. Un autre sénatus-consulte veut que les parfumeurs qui vendent sans précaution de la ciguë, de la salamandre, de l'aconit, des chenilles de pin, de la buprestis, de la mandragore, et pour purgatif des cantharides, soient soumis à la peine de cette loi.

3. *Marcianus lib. 14 Institutionum.*

Ejusdem legis Corneliæ de sicariis et veneficis capite quinto, qui venenum necandi hominis causa fecerit, vel vendiderit, vel habuerit, plectitur. **De veneno.**

§. 1. Ejusdem legis pœna adficitur, qui in publicum mala medicamenta vendiderit, vel hominis necandi causa habuerit.

§. 2. Adjectio autem ista, *veneni mali*, ostendit esse quædam, et non mala venena. Ergo nomen medium est, et tam id quod ad sanandum, quàm id quod ad occidendum paratum est, continet. Sed et id quod *amatorium* appellatur. Sed hoc solum notatur in ea lege, quod hominis necandi causa habet. Sed ex senatusconsulto relegari jussa est ea quæ non quidem malo animo, sed malo exemplo medicamentum ad conceptionem dedit, ex quo ea quæ acceperat decesserit.

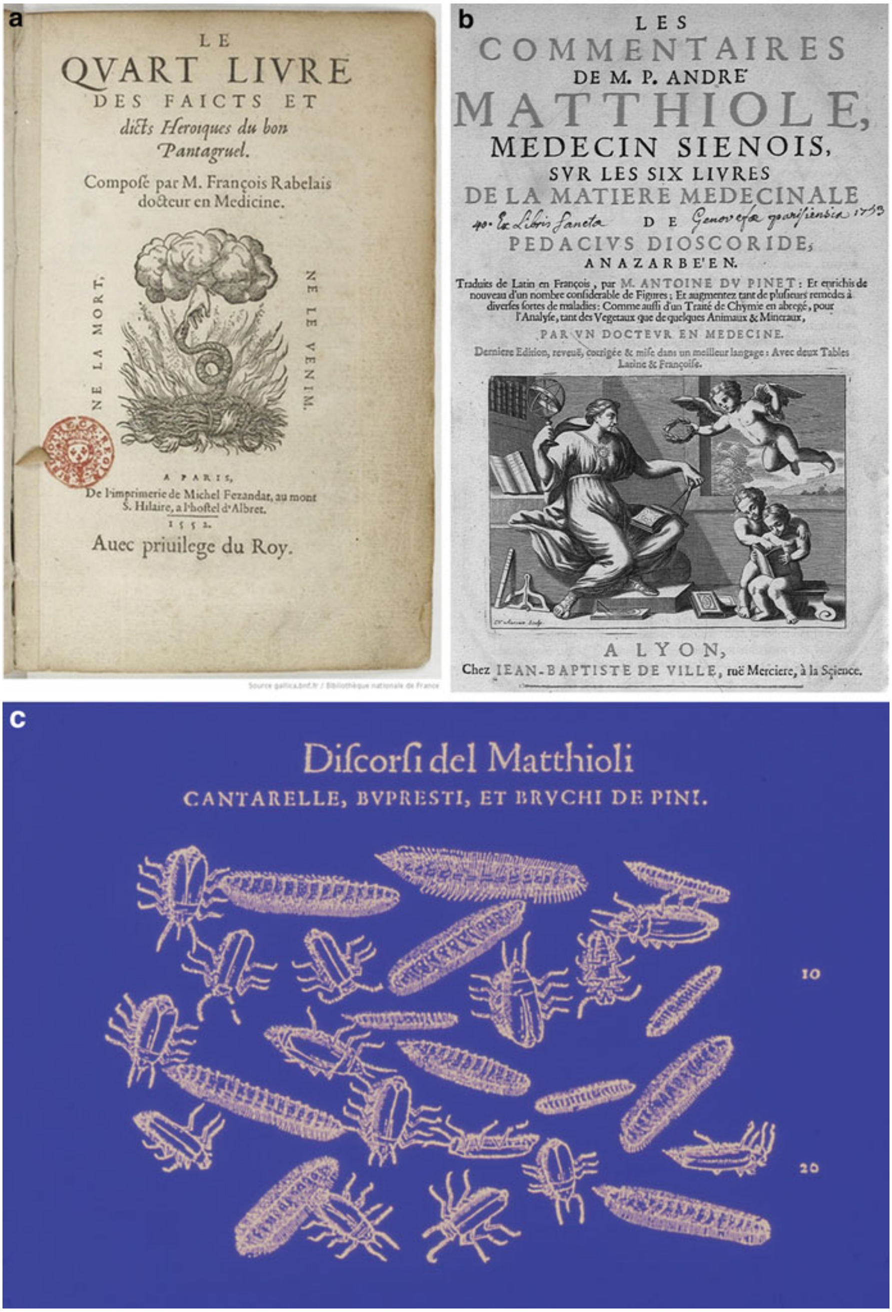
§. 3. Alio senatusconsulto effectum est, ut pigmentarii, si cui temerè cicutam, salamandram, aconitum, pityocampas, aut buprestim, mandragoram, et id quod lustramenti causa, dederint cantharidas, pœna teneantur hujus legis. **De pigmentariis.**

Fig. 1.1 Extract of the Digeste of Justinien from 533 B.C., Title VI Julia law on public violences (Titulus VI, Ad Legem Juliam de Vi Publica) (Translation from Hulot 1803)

(Titulus VIII, *Ad legem Corneliam de Sicariis et veneficis; Marcianus 14 Inst. Lege 3 §3;* Fig. 1.1; Hulot 1803).

Much later, François Rabelais cited "*pityocampes*" in 1552 his list of poisonous animals of *Le quart livre des faicts et dicts Heroiques du bon in Pantagruel* (Fig. 1.2a.; chapter LXIV). Then, in 1562, Pietro Andrea Matthioli (1501–1577), a medical doctor and botanist from Italy, made it known the Dioscoride observations about *pityocampes* larvae in his *Medici Senensis Commentarii, in Libros sex Pedacii Dioscoridis Anazarbei, de Materia Medica, Adjectis quàm plurimis plantarum & animalium imaginibus, eodem authore* (Fig. 1.2b; Matthioli 1562), better known as *Commentarii*. Matthioli was apparently the first to supply a visual representation of processionary larvae. Although schematic, this drawing highlighted the presence of a large number of urticating setae on the larvae (Fig. 1.2c).

Then, the knowledge largely progressed during the eighteenth century with René-Antoine Ferchault de Réaumur. In the second volume of his "*Mémoires pour servir à l'étude des insectes*" published in 1736 (Fig. 1.3a), Réaumur largely



LE
QVART LIVRE
DES FAICTS ET
dicts Heroiques du bon
Pantagruel.
Compoſé par M. François Rabelais
docteur en Medicine.

NE LA MORT,
NE LE VENIM.

A PARIS,
De l'imprimerie de Michel Fezandat, au mont
S. Hilaire, a l'hoſtel d'Albret.
1552.
Auec priuilege du Roy.

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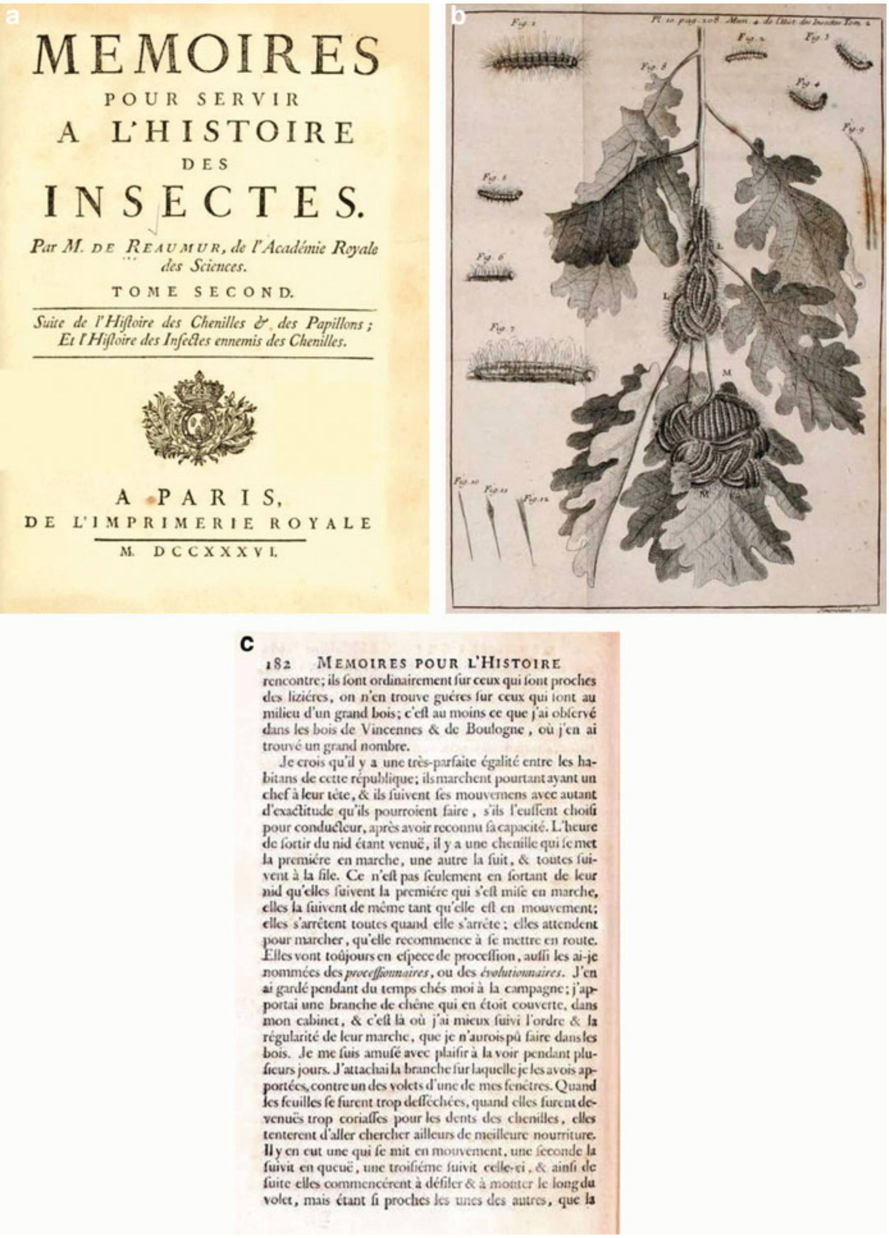
LES
COMMENTAIRES
DE M. P. ANDRE'
MATTHIOLE,
MEDECIN SIENOIS,
SVR LES SIX LIVRES
DE LA MATIERE MEDECINALE
40. Ex Libris Sanctæ DE Genovefæ parisiensis 1753
PEDACIVS DIOSCORIDE,
ANAZARBE'EN.
Traduits de Latin en François, par M. ANTOINE DV PINET: Et enrichis de nouveau d'un nombre conſiderable de Figures; Et augmentez tant de pluſieurs remedes à diverſes ſortes de maladies: Comme auſſi d'un Traité de Chymie en abregé, pour l'Analyſe, tant des Vegetaux que de quelques Animaux & Mineraux,
PAR VN DOCTEVR EN MEDECINE.
Derniere Edition, reveuë, corrigée & miſe dans un meilleur langage: Avec deux Tables Latine & Françoiſe.

A LYON,
Chez IEAN-BAPTISTE DE VILLE, ruë Merciere, à la Science.

Diſcorſi del Matthioli
CANTARELLE, BVPRESTI, ET BRVCHI DE PINI.

Fig. 1.2 (**a**) Front cover of *Le quart livre des faicts et dicts Heroiques du bon Pantagruel* from Rabelais; (**b**) Front Cover of *Medici Senensis Commentarii, in Libros sex Pedacii Dioscoridis Anazarbei* from Matthioli; (**c**) Drawing of processionary larvae and other insects in Matthioli's book



MEMOIRES
POUR SERVIR
A L'HISTOIRE
DES
INSECTES.
Par M. DE REAUMUR, *de l'Académie Royale des Sciences.*
TOME SECOND.
Suite de l'Hiſtoire des Chenilles & des Papillons;
Et l'Hiſtoire des Inſectes ennemis des Chenilles.

A PARIS,
DE L'IMPRIMERIE ROYALE
M. DCCXXXVI.

182 MEMOIRES POUR L'HISTOIRE

rencontre; ils ſont ordinairement ſur ceux qui ſont proches des liziéres, on n'en trouve guéres ſur ceux qui ſont au milieu d'un grand bois; c'eſt au moins ce que j'ai obſervé dans les bois de Vincennes & de Boulogne, où j'en ai trouvé un grand nombre.

Je crois qu'il y a une très-parfaite égalité entre les habitans de cette république; ils marchent pourtant ayant un chef à leur tête, & ils ſuivent ſes mouvemens avec autant d'exactitude qu'ils pourroient faire, s'ils l'euſſent choiſi pour conducteur, après avoir reconnu ſa capacité. L'heure de ſortir du nid étant venuë, il y a une chenille qui ſe met la premiére en marche, une autre la ſuit, & toutes ſuivent à la file. Ce n'eſt pas ſeulement en ſortant de leur nid qu'elles ſuivent la premiére qui s'eſt miſe en marche, elles la ſuivent de même tant qu'elle eſt en mouvement; elles s'arrêtent toutes quand elle s'arrête; elles attendent pour marcher, qu'elle recommence à ſe mettre en route. Elles vont toûjours en eſpece de proceſſion, auſſi les ai-je nommées des *proceſſionnaires*, ou des *évolutionnaires*. J'en ai gardé pendant du temps chés moi à la campagne; j'apportai une branche de chêne qui en étoit couverte, dans mon cabinet, & c'eſt là où j'ai mieux ſuivi l'ordre & la régularité de leur marche, que je n'aurois pû faire dans les bois. Je me ſuis amuſé avec plaiſir à la voir pendant pluſieurs jours. J'attachai la branche ſur laquelle je les avois apportées, contre un des volets d'une de mes fenêtres. Quand les feuilles ſe furent trop deſſéchées, quand elles furent devenuës trop coriaſſes pour les dents des chenilles, elles tenterent d'aller chercher ailleurs de meilleure nourriture. Il y en eut une qui ſe mit en mouvement, une ſeconde la ſuivit en queuë, une troiſiéme ſuivit celle-ci, & ainſi de ſuite elles commencérent à défiler & à monter le long du volet, mais étant ſi proches les unes des autres, que la

Fig. 1.3 *Memoirs of Réaumur*; (**a**) front cover; (**b**) illustration of the life history of oak processionary moth; (**c**) page 182 detailed the gregarious biology, lifecycle and tent structure of the larvae affecting pines (3rd memoir, pages 188–203), but also extended the observations to the larvae showing a similar behavior on oaks (4th memoir, pages 226–250), supplying very precise illustrations (Fig. 1.3b). Having noticed that these larvae always move in a kind of procession, he named them for the first time "*processionaires*" but also "*évolutionnaires*" (Fig. 1.3c), and mentioned he got tents from the Landes forest of Bordeaux and from Montpellier in France. However, the moth's taxonomic description waited until 1776 when Denis and Schiffermüller (1776) named it as *Bombyx pityocampa*, using specimens from southern Tyrol as type material. Then, Amoreux (1789) precised that pine processionary colonies were present in Italy, southern France and part of Switzerland at the end of the eighteenth century (page 159). In 1822, Godart (1822) already recorded it from the Forest of Fontainebleau, in the southern Paris basin.

2 The '*Naturalist*' Knowledge on Processionary Moths Largely Progressed During the Nineteenth and Twentieth Centuries

One has to wait until the late 1800s to get significant progresses in the knowledge of these insects. Looking further Réaumur's studies, Jean-Henri Fabre published in 1899 five outstanding chapters on pine processionary moth in his *Souvenirs entomologiques* (Série VI), entitled egg-laying and hatching (*La ponte, l'éclosion*; Chapter 18), tent and colony (*Le nid, la société*; Chapter 19), procession (*La procession*; Chapter 20), climate (*La météorologie*; Chapter 21), and adult moth (*Le papillon*; Chapter 22). At the same time, the forest engineer Julien-Eugène- Antoine Calas noticed it as a forest pest strongly affecting natural stands and pine plantations (Calas 1897, 1900).

The twentieth century saw the development of a number of studies at national as well as Mediterranean level. Since the 1960s on, an INRA scientist, Guy Démolin, largely developed our knowledge on the biology of the moth in France and other Mediterranean countries (Fig. 1.4). Guy Démolin unfortunately disappeared in June 2014. We greet his memory. Although not all of his results were actually published, these works were of particular significance for the understanding of the population dynamics and the specific life cycle of the pine processionary moth in the different parts of its natural range (Démolin 1962, 1963, 1969a, b, 1971, 1990; Huchon and Démolin 1970, 1971; Démolin et al. 1996). Indeed, the abacus proposed in Démolin (1969a) was largely used from the 1970s on to forecast the moth lifecycle according to latitude and elevation (Fig. 1.5). Additional studies by Abgrall and Bouhot (1990), Battisti (1988), Billioti (1958), Géri (1980, 1983a, b), Masutti and Battisti (1990) and Montoya (1981) allowed to precise other aspects in population dynamics.

Because the processionary moth was considered as the first pine defoliator all over the Mediterranean basin, large-scale experiments were also carried out to test

Fig. 1.4 Guy Démolin looking at a pine processionary procession (Credit: J.-C. Martin)

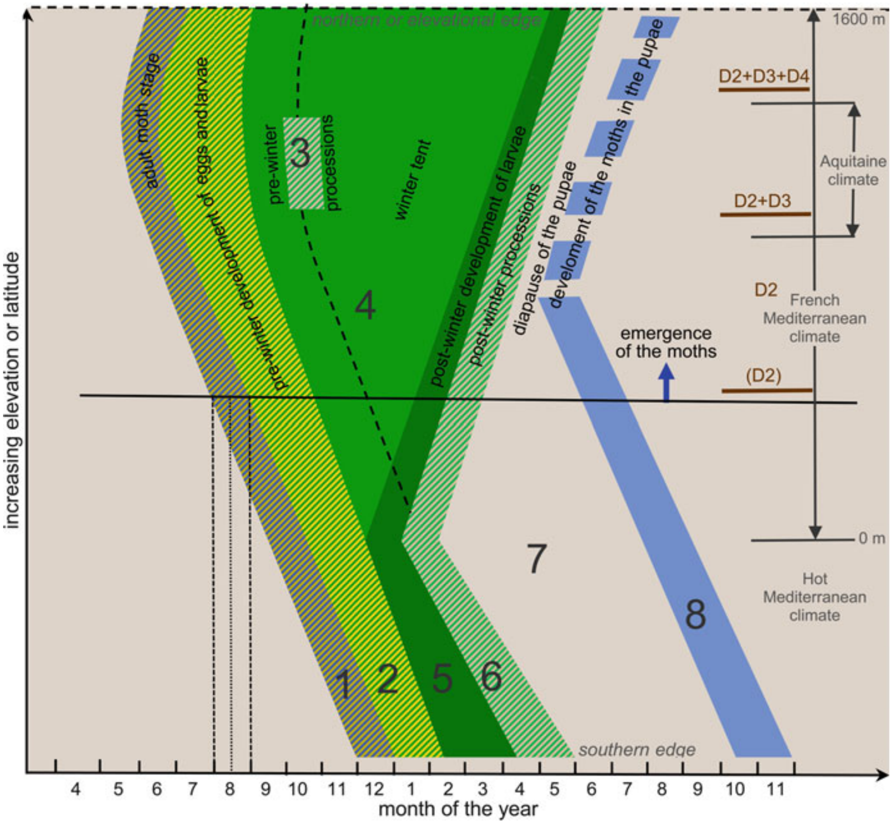


Fig. 1.5 Démolin's Abacus: *1* – moth flight period; *2* – Development of eggs and larvae before winter; *3* – processions before winter; *4* – winter tents; *5* – larval development following winter; *6* – processions following winter; *7* – diapause; 8 – pupal development. D2, D3, D4: prolonged diapause in cycles lasting 2, 3, and 4 years, the *vertical arrows* indicate adult emergence (Modified from Démolin (1969a) and Démolin et al. 1996)

for control methods applicable by forest managers in pine stands (e.g., Grison et al. 1959; Dafauce 1970; Démolin and Millet 1981; Démolin et al. 1993). In parallel, the ecology of some other species of processionary moths began to be studied, but knowledge usually remained much more limited except for oak processionary moth (e.g., Dissescu and Ceianu 1968; Pascual 1988).

Besides, medical doctors and veterinarians developed specific investigations about the urticating properties of the larvae on humans and animals, trying to identify the chemicals susceptible to be involved in such processes (e.g., Lamy 1990; Lamy et al. 1983, 1985; Charmot 1987; Werno and Lamy 1990; Vega et al. 1997, 1999). However, these studies remained rather separated from the ones looking at the insect ecology. Finally, no synthesis has ever been published on pine processionary moth, nor on other species of processionary moths.

3 The Twenty-First Century and the Climate Warming Up: An Urgent Need for an Integrated, Multidisciplinary Approach of Processionary Moths

During the late 1990s, first observations of pine processionary colonies moth in new locations of the Paris basin suggested a possible expansion of the natural range, that could be due to winter warming up favoring the survival of the winter-developing larvae very sensitive to weak variations in temperatures (Benigni and Battisti 1999; Goussard et al. 1999). The occurrence of such an expansion in latitude and elevation was rapidly confirmed during the early 2000s (Battisti et al. 2005). It led this urticating species to penetrate into largely populated human areas, turning from a forest pest to an urban sanitary threat whilst the previous management methods could not be completely adequate to this new environment. In addition, the predictions related to Démolin's abacus progressively appeared less and less consistent, including multiple observations of processions significantly advanced or conversely delayed with regard to the previous situation. This triggered the development of international programs aimed at precising the relationships between climate change and expansion.

A first international project, PROMOTH – *Global change and pine processionary moth: a new challenge for integrated pest management*, was launched in the 5th European Research framework Programme (2002–2005). Its results led the Intergovernmental Panel on Climate Change (IPCC) to retain the pine processionary moth as one of the few model insects used as indicator of global warming (Rosenzweig et al. 2007). PROMOTH was quickly followed by another project funded by the French National Agency for Research entitled URTICLIM-*Anticipation of climate change effects on the environmental and sanitary impacts associated with the expansion of pine processionary moth* (2008–2012), which was aimed as a multidisciplinary project associating entomologists, ecologists, medical doctors, veterinarians, mathematical modelers, and managers from France, Italy and Spain. These two projects allowed large progresses in characterizing the processes underlying past, present and future moth expansion, in precising the adaptive mechanisms acting during expansion, in predicting the risks for specific biodiversity as well as for human and animal populations, and in identifying management methods adapted to the newly colonized urban areas. The focus put on the expansion range in Western Europe was then extended to Southeastern Europe through the development of an ECONET project- *Modeling the expansion of an urticating pest in the Balkans with global warming* (2009–2010), associating scientists from Albania, Bosnia and Herzegovina, Bulgaria, Croatia, Macedonia, Romania, Serbia and Slovenia.

Finally, an international network entitled PCLIM – *International research network about the adaptive response of processionary moths and their associated organisms to global change*- was then founded by INRA in 2011 under the ACCAF program (*Adaptation of agriculture and forestry to climate change*), and also supported by the BCGC international program (*Biological Consequences of Climate Change*) of the International Union of Biological Sciences (IUBS) and the International Society of Zoological Sciences (ISZS). PCLIM's major target was the publishing of a book synthesizing the knowledge on processionary moths, which should absolutely combine all the concerned research fields (entomology, ecology, genetics, mathematical modelling, medical and veterinary science, pest management) in a multidisciplinary approach. The present book results from this initiative. Associating 101 authors from 22 countries of Europe, Minor Asia and North Africa, it presents our current knowledge of the responses of processionary moths, more especially the winter pine processionary moth, to climate change. The chapters successively detail natural history, expansion processes, genetics and phylogeography, models to reconstruct past movements and predict potential ones with future climate change, impacts on both host plants, native biodiversity, humans and animals, and conclude by the proposal of management methods adapted to the newly colonized areas.

4 Processionary Moths: A Dozen of Species in the Genus *Thaumetopoea*

The genus *Thaumetopoea* Hübner *sensu lato* is included in the subfamily Thaumetopoeinae, which was formerly considered as a self-standing family (Thaumetopoeidae), within the Notodontidae family. The cladistics analysis of Notodontidae family (Miller 1991) indicates that Thaumetopoeinae is a basal, homogenous clade in the family. This has been confirmed by a recent molecular phylogeny of the group (Zahiri et al. 2011, 2013). The Thaumetopoeinae comprise 100 species in 23 genera occurring in Africa, the Mediterranean, southern Europe to northern India, Australia, and New Caledonia (Kiriakoff 1970; Schintlmeister 2013). In the cladistic analysis of Miller (1991) the genus *Thaumetopoea sensu lato* is represented by two species (*Traumatocampa pityocampa* and *Thaumetopoea*

Table 1.1 List of *Thaumetopoea* species

Species	Range
pityocampa	Europe, Middle East, North Africa
wilkinsoni	Middle East
pinivora	Europe
bonjeani	North-Western Africa
ispartaensis	Turkey
libanotica	Lebanon
processionea	Europe, Middle East
solitaria	Europe, Middle East
jordana	Northern Africa, Jordan valley
herculeana	Europe, Middle Esat, India
cheela	Pakistan
apologetica	Eastern Africa

processionea) while the African group by one species (*Anaphe panda* (Boisduval)) and the Australian group by one species (*Epicoma melanosticta* (Donovan)).

The genus *Thaumetopoea* Hübner *sensu lato* includes a dozen of species in the Palaearctic region, and one in the Afrotropical region (Agenjo 1941; Kiriakoff 1970; Schintlmeister 2013; Table 1.1). It has been split into two genera (*Thaumetopoea* Hübner *sensu stricto* and *Traumatocampa* Wallengren) by de Freina and Witt (1982), with a further separation of the new genus *Heliantocampa* de Freina & Witt from *Traumatocampa* (1987) using morphological traits of the adults. According to these authors, solely *Thaumetopoea processionea* (Linnaeus, 1758) and *Thaumetopoea solitaria* (Freyer, 1838) belong to the *Thaumetopoea* genus while all the other species belong to *Traumatocampa* (*T. apologetica* Strand, 1909; *T. bonjeani* (Powell, 1922); *T. cheela* Moore, 1883; *T. jordana* (Staudinger, 1894); *T. libanotica* Kiriakoff & Talhouk, 1975; *T. pinivora* (Treitschke, 1834); *T. pityocampa* (Denis and Schiffermüller 1755); *T. wilkinsoni* Tams 1925), with the only exception of one species assigned to the new genus *Heliantocampa* (*H. herculeana* (Rambur, 1840)). Another species was described from Arabic peninsula (Oman) as *Thaumetopoea dhofarensis* Wiltshire and not included in the revision of de Freina and Witt (1982). According to Wiltshire (1980), *T. dhofarensis* belongs to the *apologetica* group and thus fits into *Traumatocampa*. Furthermore, three new species were described later from Turkey and assigned to the *Traumatocampa* genus. They are *Traumatocampa ispartaensis* Doğanlar & Avci (Doğanlar and Avci 2001), *Traumatocampa sedirica* Doğanlar and *Traumatocampa torosica* Doğanlar (Doğanlar et al. 2005). Finally, new taxonomic issues arose from the genetic analysis of the most studied species (*T. pityocampa* – *T. wilkinsoni* group, Salvato et al. 2002; Simonato et al. 2007; Kerdelhué et al. 2009), indicating that the group actually consists of three species with a different geographic distribution. *T. pityocampa* is present in Europe and north-western Africa, *T. wilkinsoni* lives in the Middle East, and a new clade provisionally called *T. pityocampa* ENA (eastern-north Africa) occurs between Libya and eastern Algeria.

A recent molecular phylogeny (Simonato et al. 2013a, b, see Kerdelhué et al. 2014, Chap. 4, this volume) strongly supports a parallel evolution of the morphological traits used to divide *Thaumetopoea* in the three distinct genera *Traumatocampa, Heliantocampa* and *Thaumetopoea sensu stricto*. This result suggests that all species should be treated as members of a single genus *Thaumetopoea sensu lato*. Further systematic revision should be delayed until a complete taxonomic coverage becomes available and the phylogenetic relationships among all species are fully resolved.

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Chapter 2
Natural History of the Processionary Moths (*Thaumetopoea* spp.): New Insights in Relation to Climate Change

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1 Introduction

It is difficult to find a genus of Lepidoptera showing the high variability of life history traits observed in *Thaumetopoea*. Within the genus there are typical summer-feeding close to winter feeding species, and in one special case a recent switch has been detected even within one species, the pine processionary moth, indicating that the natural history traits are constantly evolving at a fast rate. There are species adapted to cold conditions of high mountains and high latitude close to truly Mediterranean and sub-desert region species (Fig. 2.1). The life cycle is

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typically annual but some species may spend up to 9 years of prolonged diapause as a pupa in soil, as a possible way to spread the risk of experiencing too harsh conditions for survival. On top of this, all species have a remarkable gregarious behaviour through all the egg (Fig. 2.2) and larval (Fig. 2.3) stages, and are well protected against vertebrate predators by billions of urticating setae they may release when disturbed. Because of all these features, they were called '*Thaumetopoea*', which means the [insect that] 'makes wonderful things' [likely originating from the Greek words "θαύμα" that means "miracle" and "ποιώ" that means "do"] such as shining silk tents on top of trees or long head-to-tail processions at the time of pupation (Figs. 2.4, 2.5, 2.6). Here we summarize the information available for the life history of the most common species, with the general aim of finding what makes a few of them very good indicators of climate change.

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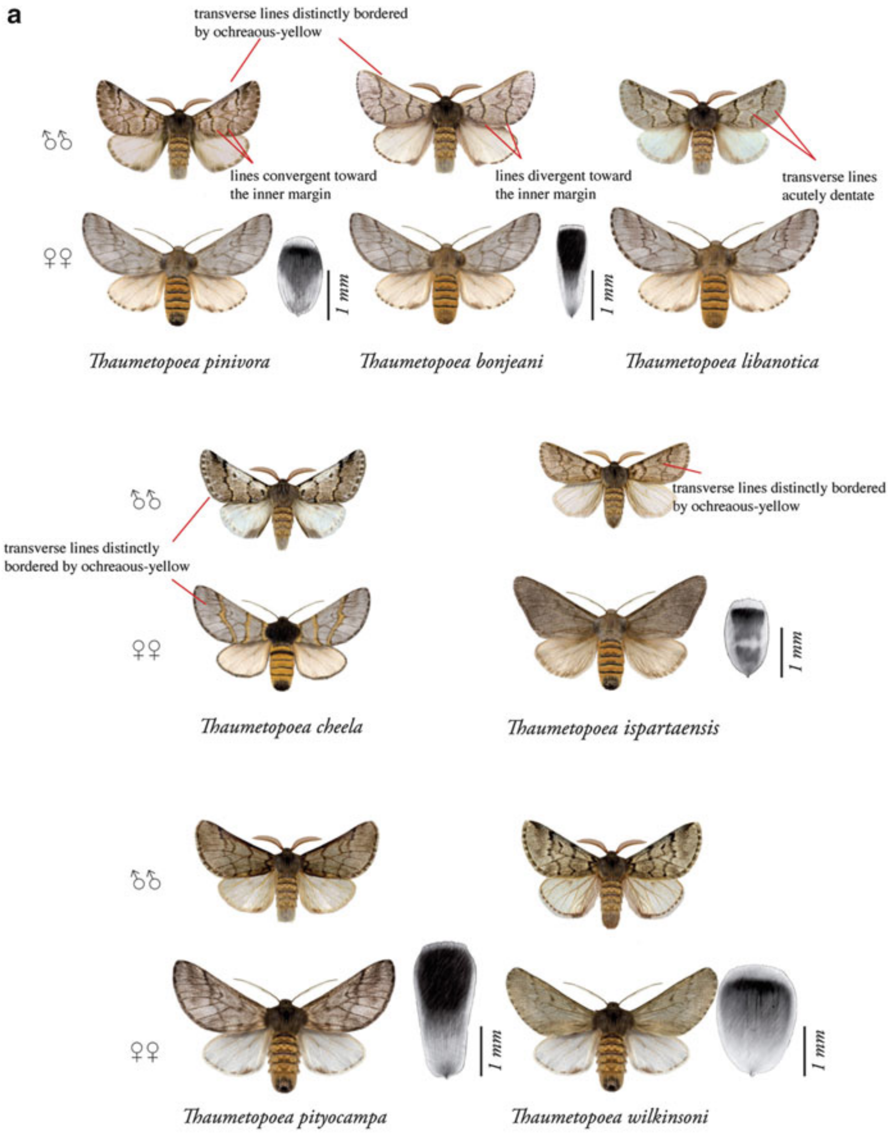

Fig. 2.1 (**a**) Adults of *Thaumetopoea* and related species with the indication of discriminant morphological traits and detail of scales of forewings: *T. pinivora* (♂ – ♀ coll. Zoologische Staatssammlung München); *T. bonjeani* (♂ – ♀ coll. Witt, München); *T. libanotica* (♂ Liban – Bscharre emerged Beirut, coll. Zoologische Staatssammlung München; ♀ coll. Witt, München); *T. ispartaensis* (♂ – ♀ Isparta – Senirkent, coll. Padua Univ.); *T. cheela* (♂ Afghanistan, Sarobi, coll. Zoologische Staatssammlung München; ♀ redrawn from Moore, 1883); *T. pityocampa* (♂ Veneto, Padova, Colli Euganei; ♀ Alto Adige, Val Venosta, coll. Padua Univ.); *T. wilkinsoni* (♂ – ♀ Turchia, Sarkikaragas and coll. Witt, Munchen). (**b**) Adults of *Thaumetopoea spp*. and related species with the indication of discriminant morphological traits and detail of scales of forewings: *T. processionea* (♂ Romagna, Forlì; ♀ coll. Witt, Munchen); *T. herculeana* (♂ – ♀ ex larvae, Portogallo, Vigo, Cabo Home, coll. Padua Univ.); *T. solitaria* (♂ http://www.nature-of-oz.com; ♀ coll. Witt, Munchen); *T. jordana* (♂ – ♀ Palestina, Jerusalem; coll. Zoologische Staatssammlung München); *T. apologetica* (♂ S. Rhodesia, Bulawayo, Glenville; ♀ Ofcolaco Tvl; coll. Schintlmeister); *T. dhofarensis* (♂ – ♀ Oman, Dhofar, prov. Jebel, Samhan M.ts 900–1,100 m, Tawi Attair; region; coll. Witt, München); *Anaphe panda* (♂ – ♀ Africa, coll. Oxford University Museum of Natural History); *Ochrogaster lunifer* (♂1 – Australia, 85 km SE of Broome (Len Willan and CSIRO Entomology); ♂2, ♂♀ 3) Australia, coll. Padua Univ.; ♀ Australia, 5 km E of Broome (Len Willan and CSIRO Entomology)

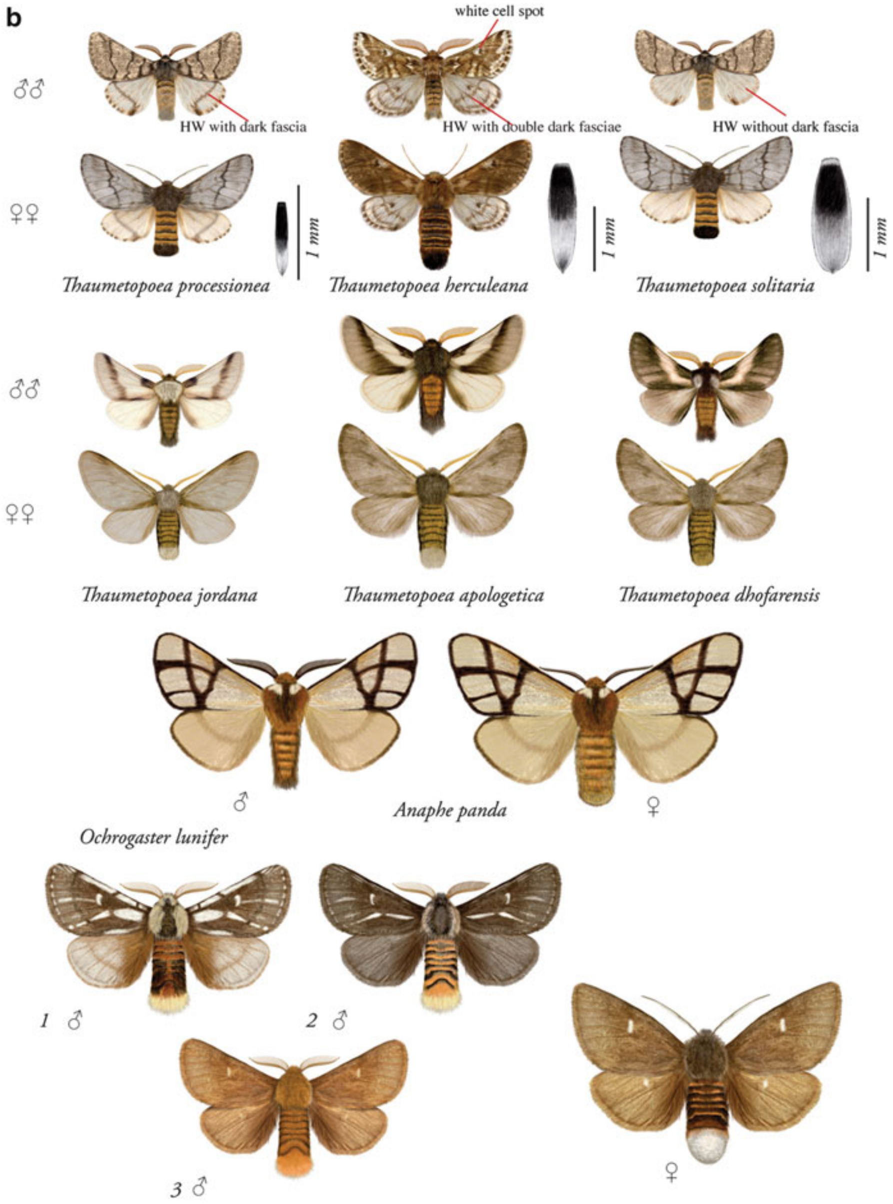

Fig. 2.1 (continued)

Fig. 2.2 Adults and egg batches of processionary moths, *Thaumetopoea* (**a**) ovipositing female of *T*. *pityocampa* on *Pinus nigra*; (**b**) ovipositing female of *T*. *pinivora* on *Pinus sylvestris*; (**c**) *T*. *processionea* (Credit: L.M. Nageilesen); (**d**), (**e**) *T*. *pityocampa* on *Pinus halepensis* (Credit: A. Roques)

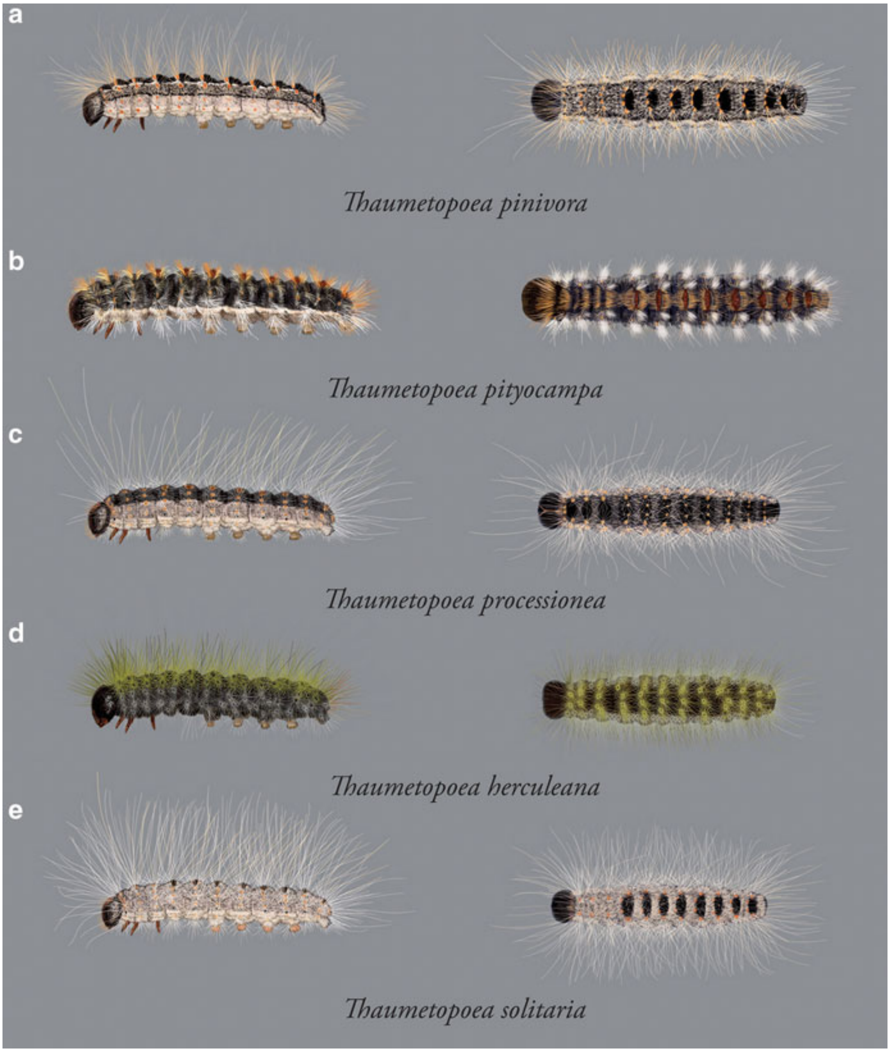

Fig. 2.3 Larvae of processionary moths, *Thaumetopoea* (**a**) *T. pinivora*; (**b**) *T. pityocampa*; (**c**) *T. processionea*; (**d**) *T. herculeana* (Portugal, Vigo, Cabo Home); (**e**) *T. solitaria*; (**a**–**c**, **e**) redrawn from http://www.lepiforum.de; http://www.pyrgus.de; Carlos Gomez de Aizpúra (1986); (**d**) Credit: L. Berardi

Fig. 2.4 (**a**) Larval colonies and tents of processionary moths, *Thaumetopoea* (*a*) *T. pinivora*; (*b*) *T. bonjeani*; (*c*) *T. pityocampa*; (*d*) *T. processionea* (Credit: L.M. Nageilesen); (*e*) *T. herculeana*. (**b**) Tents of *T. pityocampa* on unusual host plants: (*f*) Himalayan cedar (*Cedrus deodara*); (*g*) True fir (*Abies* sp.); (*h*, *i*) Douglas-fir (*Pseudotsuga menziesii*); (*j*) Eastern White pine (*Pinus strobus*); (*k*) European larch (*Larix decidua*) (Credit: A. Roques)

Fig. 2.4 (continued)

2 Natural History of the Pine Processionary Moth, *Thaumetopoea pityocampa*

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2.1 Host Plants and General Distribution

Thaumetopoea pityocampa is oligophagous on *Pinus* and *Cedrus* species, both native and introduced. Occasionally it can be found on other conifer species, including those of the genus *Pseudotsuga*. It typically occurs on isolated trees and stand edges,

Fig. 2.5 Processions of *Thaumetopoea* for pupation. (**a**) *T. pityocampa*; (**b**) *T. processionea* (Credit: L.M. Nageilesen)

although inner parts of the stands may also be colonised during outbreaks. The geographic range extends from northern Africa to southern Europe (see Roques et al. 2014, Chap. 3, this volume), from the Atlantic coast to the western part of Turkey.

Fig. 2.6 Cocoons and emerging adults of processionary moths, *Thaumetopoea* (**a**, **b**) *T. pinivora*; (**c**, **d**) *T. processionea*

2.2 Life Cycle

Thaumetopoea pityocampa has a very peculiar one-year development cycle, which is reversed compared to the other species of the genus and to most of other defoliating insects, because the larvae feed across the winter. As a result the adult emergence timing is largely affected by temperature (Démolin 1969a; Huchon and Démolin 1971; Zamoum and Démolin 2005; Pimentel et al. 2010). At colder sites (high elevation or high latitude), adults emerge as early as June whereas emergence can be delayed until September at warmer sites. In individual with annual development, this is regulated by a different length of the summer pupal diapause, which may extend into prolonged diapause under specific circumstances. On the mountains of Corsica Island the development cycle is semivoltine, i.e. with one generation over 2 years (Géri 1983a, 1983b). Figure 2.7 show typical life cycles observed in different parts of the range. In general, females are short lived, probably living for only 1 or 2 days, while males live longer (Zhang and Paiva 1998).

The dispersal capacity of the female is limited although a few individuals may fly more than 10 km (see Sect. 2.5), whereas the males disperse over much longer distances. Females lay about 150–350 eggs, depending on environmental conditions that may affect also egg size (Zovi et al. 2008; Pimentel et al. 2012). Populations from the very southern edge of the natural range (Eastern Morocco and Saharan Atlas Algeria) have a lower fecundity (105–150 eggs/batch) although they do not differ in the other natural history traits (Zamoum 1998; Zamoum and Démolin 2005; El Alaoui El Fels unpublished data). The eggs are laid in batches on pine needles or twigs shortly after moth emergence and are covered with scales produced by the female. The eggs hatch in July at colder sites and in October at warmer sites. Groups of neonate larvae are full siblings, but larval groups commonly merge at later instars, sometimes forming aggregates of several hundred individuals. Larvae build silk tents right after they hatch from the eggs, and leave them empty when they move to more sun-exposed parts of the tree. The shape and thickness of the silk tent (Fig. 2.4) depends on the number of individuals, host plant, and climate. One colony of larvae can build 2 or 3 of such tents before establishing the final one where larvae stay until the end of their development, which goes through five instars. Initially larvae feed on current-year needles near the oviposition site, but soon after they switch to old needles for the rest of the development. They can go back to current-year needle only when the old ones have been eaten. Feeding mostly occurs at night. Larvae of the third to fifth instar feed when temperature is above 0 °C provided that the colony temperature during the day before has reached 9 °C inside the tent (Battisti et al. 2005). From the third instar larvae develop urticating setae about 0.2 mm in length, situated in groups on the dorsal parts of the abdomen. When larvae are disturbed, setae are actively released, and can cause severe allergic reactions to humans (see Moneo et al. 2014, Chap. 8, this volume). Larvae leave trees in typical head-to-tail processions to search for suitable sites in soil for cocoon spinning as early as December at warmer sites and years, but more typically between February and May. When a suitable site is found, such as open areas and forest edges (Démolin 1971), larvae join in digging through the soil down to a depth of 5–20 cm. Cocoons remain in soil for the next one to a few months until the emergence of moths. A certain proportion of the cocoons enter a prolonged diapause which can be extended over several years (Géri 1983a, 1983b; Démolin 1990).

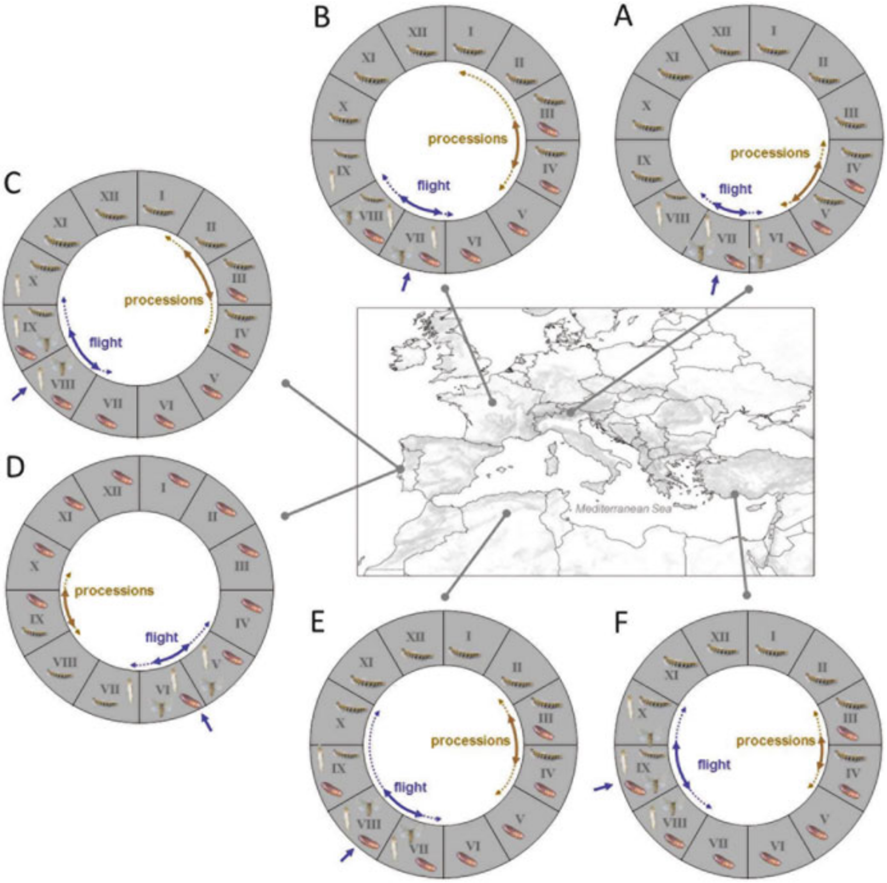

Fig. 2.7 Schematic representation of typical life cycles of the pine processionary moth, *Thaumetopoea pityocampa*, in different biogeographic zones of France as defined by Huchon and Démolin (1970), Bouhot-Delduc (2005): (**a**) Italian Alps; (**b**) expansion area in north-central France = degraded oceanic climate; (**c**) south oceanic climate; (**d**) summer population in Portugal; (**e**) Algeria; (**f**) southern Turkey (*T. wilkinsoni*); (**g**) oceanic climate; (**h**) endemic areas in the northern coast of the Mediterranean sea and Corsican littoral; (**i**) Corsica mountains; (**j**) continental climate; (**k**) north oceanic climate. Only the dominant annual cycle is figured although possibilities of prolonged diapause exist (Abgrall 2001), except for population (**i**) where prolonged diapause is obligatory. Dates of 50 % emergence are only indicative because depending on the annual variations in weather conditions.

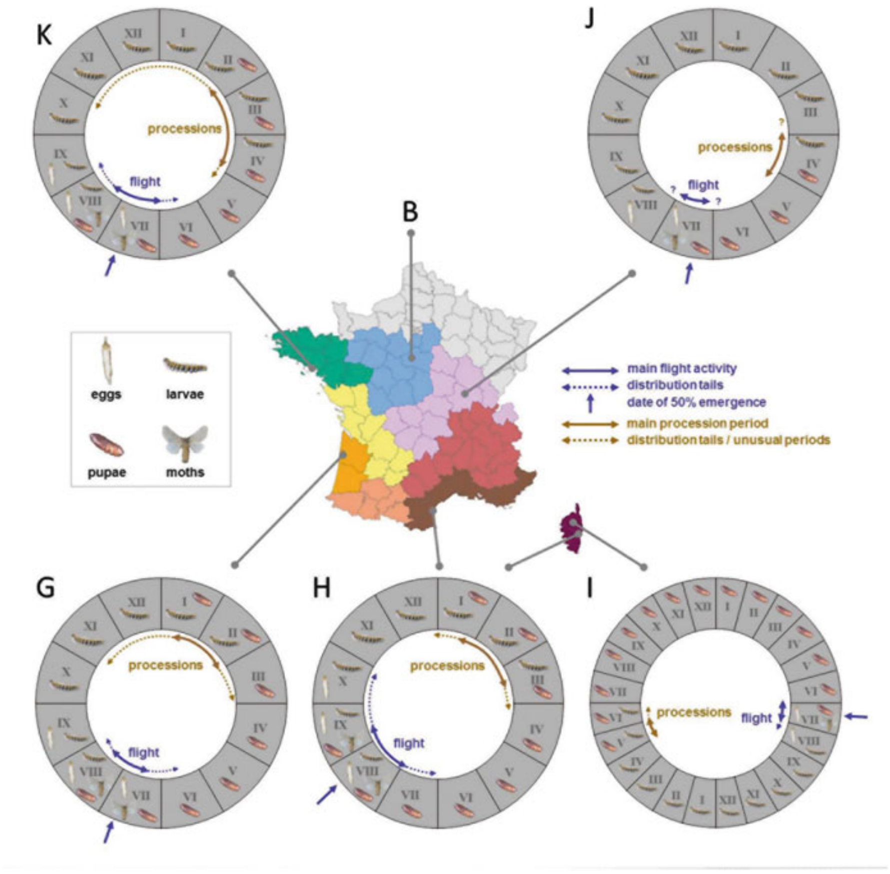

Fig. 2.7 (continued)

2.3 Natural Enemies

The natural enemies of *T. pityocampa* have been firstly reviewed by Biliotti (1958) and since then considered in several studies. A complete list is given in Tables 2.1, 2.2, and 2.3, with additional information on their importance in a Mediterranean country where they have been extensively studied (Zamoum 1998). Figure 2.8 presents some of the parasitoids and predators.

The eggs are mainly parasitized by *Baryscapus servadeii* and *Ooencyrtus pityocampae*, while a few other polyphagous species may occur as well. *Baryscapus servadeii* is restricted to conifer-feeding *Thaumetopoea* species, on which it develops one generation per year, which is well synchronized with the availability of the host eggs (Battisti 1989). *O. pityocampae* is polyphagous and has several generations per year on various hosts. The overall parasitism can locally reach up to 45 % (Tsankov et al. 2006).

Table 2.1 List of insect parasitoids of developmental stages of *T. pityocampa*. Periods of activity and maximum values or estimates of the mortality rate based on 20 years of observations in Algeria (1983–2003) in various forest types are also given (Zamoum et al. 2006). No parasitoids are known for the adult stage

Stage	Parasitoid species	Period of activity (month)	Maximum mortality (%)
Egg	*Baryscapus servadeii* (Hym., Eulophidae)	VI–IX	20
	Ooencyrtus pityocampae (Hym., Encyrtidae)	IV–VI and VII–X	8
	Anastatus bifasciatus (Hym., Eupelmidae)	VI and IX	0.5
	Trichogramma embryophagum (Hym., Trichogrammatidae)	V–VI and VII	0.1
	Pediobius bruchicida (Hym., Eulophidae)	III and IV	0.03
	Eupelmus (Macroneura) seculata (Hym., Eulophidae)	V–VI–VII	0.1
	Eupelmus (Macroneura) sp. (Hym., Eulophidae)	V–VI–VII	1
	Eupelmus (Macroneura) vesicularis (Hym., Eulophidae)	Not available	Not available
Larva	*Phryxe caudata* (Dipt., Tachinidae)	IX–X and II–III–IV	10
	Compsilura concinnata (Dipt., Tachinidae)	IV–V	7
	Exorista segregata (Dipt., Tachinidae)	IV	5
	Erigorgus femorator (Hym., Ichneumonidae)	I–II–III	17
	Cotesia vestalis (Hym., Braconidae)	IX–X–XI	4
	Pteromalus chrysos (Hym., Chalcididae)	IV	Not available
	Dibrachys lignicola (Hym., Chalcididae)	IV	Not available
Pupa	*Villa brunnea* (Dipt., Bombyliidae)	VIII–IX	35
	Coelichneumon rudis (Hym., Ichneumonidae)	V–VI	5
	Conomorium pityocampae (Hym., Pteromalidae)	VI–VI	0.1

Larvae are parasitized after the third instar by the tachinid fly *Phryxe caudata*, which completes two generations per year, with the first emerging in spring from mature larvae and the second in summer-autumn from pupae (Buxton 1990). A number of other species of larval and larval-pupal parasitoids (Diptera and Hymenoptera) have been reported at lower frequencies. Mortality from generalist arthropod predators can be locally high (e.g. the syrphid fly *Xanthandrus comtus*) and several predators are found inside larval tents (Branco et al. 2008). In contrast, larvae seem to be well protected against vertebrates (Barbaro and Battisti 2011). A number of pathogenic organisms have been described to affect the larvae, the most frequent being cytoplasmic and nuclear viruses (Vago 1959) and entomopathogenic nematodes (Triggiani and Tarasco 2002).

Pupae are parasitized by a number of specialized insects such as the bombylid fly *Villa brunnea*, the ichneumonid *Coelichneumon rudis*, and the pteromalid *Conomorium pityocampae*, which may interfere with the most common predator, the hoopoe *Upupa epops* (Battisti et al. 2000; Barbaro et al. 2008). They are often

Table 2.2 List of predators of developmental stages of *T. pityocampa*. Periods of activity and estimates of the mortality rate based on 20 years of observations in Algeria (1983–2003) in various forest types are also given (Zamoum et al. 2006)

Stage	Species	Period of activity (month)	Mortality
Egg	Orthoptera	VIII	Medium
Larva	*Xanthandrus comtus* (Dipt., Syrphide)	X–XI	Medium
	Scolopendra sp. (Myriapoda)	IV–VII	Low
	Sphodromantis sp. (Mantidae)	IX	Low
	Coccinella septempunctata (Coccinellidae)	IX–X	Low
	Formica rufa (Hym. Formicidae)	Not available	Not available
	Linepithema humile (Hym., Formicidae)	Not available	Not available
	Calosoma sycophanta (Col. Carabidae)	Not available	Not available
	Parus spp. (Paridae)	III–IV	Low
Pupa	*Upupa epops* (Aves, Upupidae)	V–VI	Low
	Sus scrofa (Mammalia, Suidae)	Not available	Not available
Adult	*Vespa germanica* (Hym., Vespidae)	VII–IX	Low
	Crematogaster scutellaris (Hym., Formicidae)	VII–IX	Low
	Leptothorax recedens (Hym., Formicidae)	VII–IX	Low
	Paraechinus sp. (Erinaceidae)	VI–IX	Medium

Table 2.3 List of pathogens of developmental stages of *T. pityocampa*. Estimates of the mortality rate based on 20 years of observations in Algeria (1983–2003) in various forest types are also given (Zamoum et al. 2006)

Stage	Species	Mortality
Egg	Unidentified fungus	Low
Larva	*Smithiavirus pityocampae* (Virus)	up to 80 %
	Borrelina pityocampae (Virus)	up to 80 %
	Clostridium sp. (Bacteria)	Low
	Beauveria bassiana (Fungus)	5–20 %
	Nematode	Not available
Pupa	*Beauveria bassiana* (Fungus)	5–20 %
	Poecilomyces fumoso-roseus (Fungus)	Low
	Metarrhizium anisopliae (Fungus)	Low
	Verticillium sp. (Fungus)	Low

contaminated by entomopathogenic fungi, with *Beauveria bassiana* being the most common one (Battisti et al. 2000).

2.3.1 Population Dynamics

The literature often reports periodic outbreaks of *T. pityocampa*, although periods may have different lengths. This has been observed on pine in French

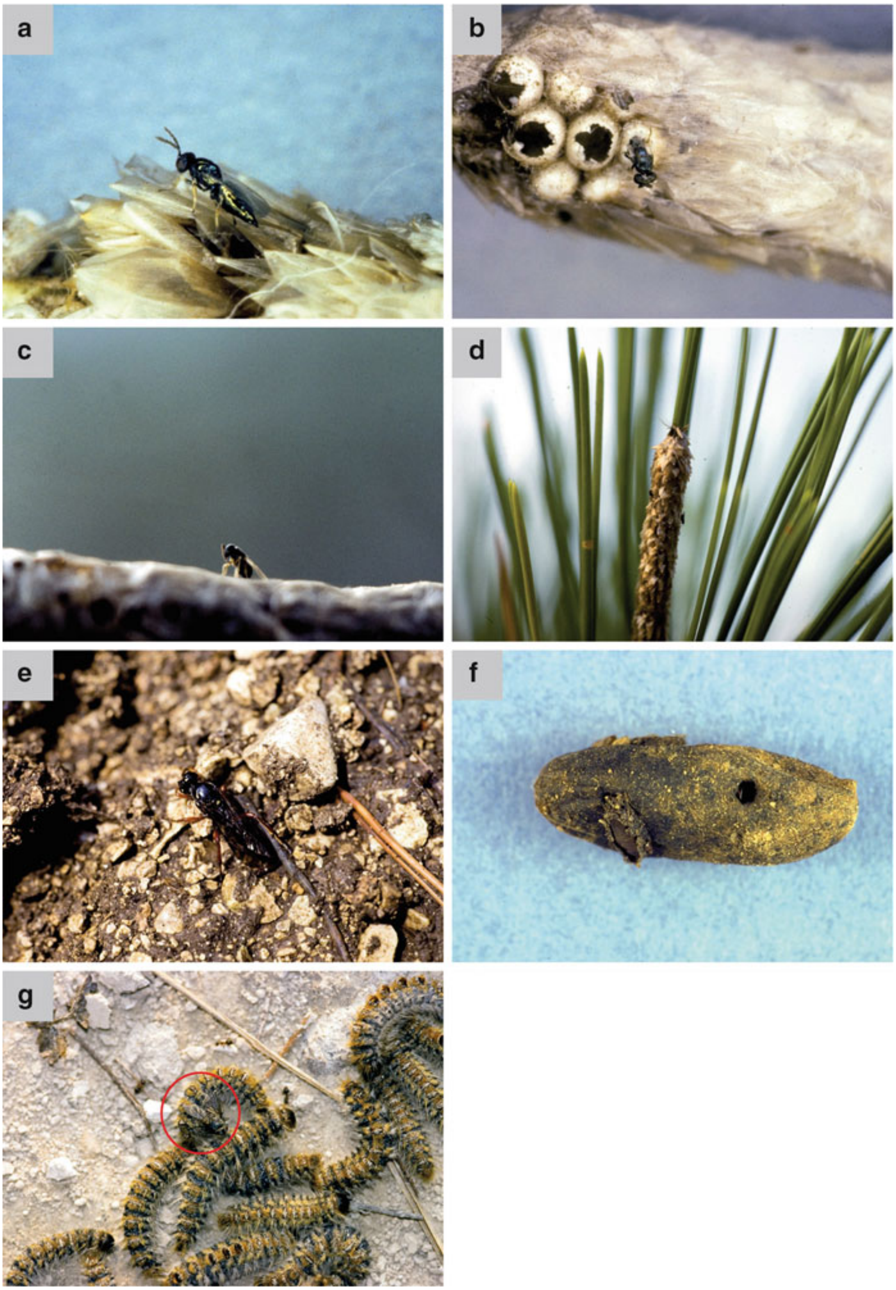

Fig. 2.8 Natural enemies of pine processionary moth. (**a**–**e**): egg parasitoids (*a*, *b*, *c* – *Baryscapus* sp.; *d*, *e* – *Ooencyrtus* sp.); (**e**, **f**) – pupal parasitoid, *Coelichneumon* sp. (*e* adult; *f* adult emergence hole on cocoon); (**g**) adult of a Tachinidae fly ovipositing on larva; (**h**) larval colony killed by virus; (**i**) pupae killed by fungi; (**j**) predation of pupae by hoopoe; (**k**, **l**) other signs of predation on pupae

Fig. 2.8 (continued)

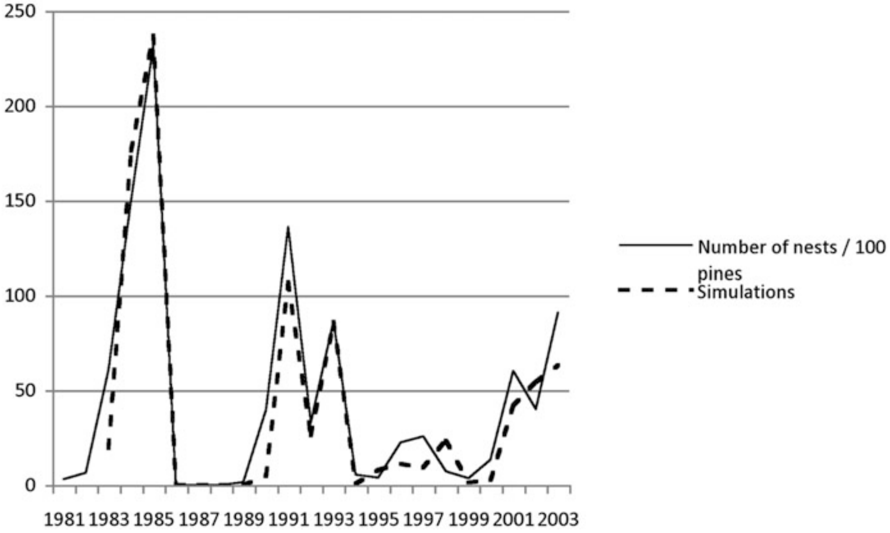

Fig. 2.9 Observed outbreak cycle (*thick line*) in pine stands of two areas of north-central France (Loiret; Cher) compared to simulations (*dashed line*) resulting from a delayed Ricker model accounting for temperatures (Modified from Robinet 2006)

mountains (from 1959 to 1982, Géri et al. 1985), in the Italian Alps (from 1950 to 2011, Hellrigl 1995; Tamburini et al. 2013), and on pine and cedar in Algeria (Zamoum et al. 2007; Sbabdji and Kadik 2011) and in Morocco (El Alaoui El Fels, unpublished data). The analysis of long-term series (>30 years) of population density, based on the annual survey of tent numbers in endemic French stands which were not treated with any pesticides, tended to indicate the existence of a rough 6-year cycle when a delayed Ricker model is applied (Fig. 2.9; Robinet 2006). Other datasets from Algeria, France, and Spain point to the same direction but still have to be analysed. Pest control and tree growth are important confounding factors and for this reason it is difficult to draw conclusions.

Potential factors involved in the population dynamics of *T. pityocampa* have been seldom studied using long-term data. Tamburini et al. (2013) found that a negative density dependent feedback with a 1-year lag emerged as the most important factor driving the population dynamics in the Southern Alps. Potential mechanisms explaining the observed negative density feedback include deterioration of host quality, increased mortality caused by pathogens, and increase of prolonged diapause as an adaptive mechanism to escape adverse conditions as explained above. Little information is available on the density dependence of natural enemies, which may possibly drive the periodicity in the outbreaks. Some small scale studies have indicated that outbreaks usually result in a deterioration of food quality and a decrease of food quantity that seem to be important factors responsible for the collapse of the population (Avtzis 1986; Battisti 1988; Hódar et al. 2004). Considering the natural enemy species associated with *T. pityocampa*, a relatively large number of predators and parasitoids are expected to respond numerically to moth density potentially producing negative density feedback on host populations (Zovi et al. 2008). Due to the gregarious behaviour of the larvae, high population density during outbreaks is further expected to trigger the spread of viral diseases with potential negative effect on its populations. In addition, the mechanism of prolonged diapause of the pupae, which may extend up to 8 years under mountain conditions (Battisti unpublished data), is causing an additional noise in the dynamics and in the relationships that the insect may establish with the complex of the natural enemies. All this makes the population dynamics of the pine processionary moth rather unpredictable at the global scale, while locally it may well result that a periodicity may exist.

2.4 Relationships with Climate Change

Several climatic parameters are expected to affect moth population dynamics. Winter temperatures were found to be the main limiting factor for the moth development and range expansion mainly in the northern part of the pest geographical distribution (Huchon and Démolin 1971; Battisti et al. 2005). During the last decades, temperature warming has affected the natural distribution of the pine processionary moth, which has expanded its range both in latitude and in elevation (Hódar and Zamora 2004; Battisti et al. 2005; Buffo et al. 2007; Robinet et al. 2007, 2013). Warmer temperatures may contribute to an improvement of larval performance, and therefore winter survival, in concert with to a decreased probability of occurrence of lethal temperatures (Hódar et al. 2003). The improved performance results from the combined effect of night temperature permissive of feeding ($T > 0$ °C) and day temperature allowing food digestion when the larvae rest in the tent ($T > +9$ °C). The high day temperature is obtained through exposure of the larval tents to solar radiation, even when air temperature is far below the threshold of +9 °C (Battisti et al. 2005). The improved larval performance has resulted in a progressive colonization of areas outside of the core range. Furthermore, moth mobility has been found to be favoured by the increase in temperature, as warmer summer nights allow a more frequent achievement of the flight threshold temperature (Battisti et al. 2006). In addition, human-inadvertent translocation of the insect, likely as pupae in the soil of ornamental trees, has overcome the natural dispersal limitation and resulted in the establishment of populations outside of the range, possible because of the improved thermal conditions (Robinet et al. 2011, 2013). A recent long-term study (Tamburini et al. 2013) indicates that both summer temperatures and rainfall significantly affected population growth rate, with different outcomes depending on the local conditions. Although previous studies indicated that low winter temperatures have negative effects on insect performance, these analyses did not show any negative impact on population dynamics. Other potential important climatic factors are rainfall (Pimentel et al. 2011; Hódar et al. 2012) and summer temperatures affecting adult dispersal (Battisti et al. 2006). Extreme events of high temperatures during summer may further contribute to high mortality of early instar larvae (Santos et al. 2011a, 2011b; Robinet et al. 2013) and locally reduce populations. Despite the clear effect of climate on range expansion, its effect on population dynamics and outbreak propensity has not been fully elucidated yet. A recent study (Hódar et al. 2012) has investigated the response of *T. pityocampa* defoliation to the atmospheric pattern called NAO (North Atlantic Oscillation) finding significant correlations between this global climate index and pest damage. However, it would be important to further evaluate the relative importance of single climatic variables and to consider their effect in combination with endogenous, density-dependent factors.

The scarce knowledge about the drivers of population dynamics is currently preventing to predict large-scale response of the species to climate change. Even if the temperature effects on insect physiology are well known, the influence of the single climatic variables on the population dynamics is still largely unclear (but see Pimentel et al. 2011; Tamburini et al. 2013). This is probably due to the paucity of studies based on long time-series that are able to give a comprehensive view of the moth dynamics and interaction with exogenous factors. The study of Hódar et al. (2012) has been a first step in this direction showing the potential for a good predictive power of climatic models to forecast forest defoliation by *T. pityocampa*.

2.5 Morphological, Physiological and Behavioural Adaptations of Pine Processionary Moths in the Expanding Areas

Daniel Sauvard and Annie Yart

Insect range expansion related to climate change (Parmesan 2006; Hill et al. 2011) has often been associated with increased dispersal capacities (Hill et al. 1999, 2011; Thomas et al. 2001), generally explained by the selection during expansion of insects with higher dispersal capacities. Studies carried out during the recent years within the Urticlim project supplied information about the possible changes in the biology of the pine processionary moth in the Paris basin (France) where the species is expanding northwards since the late 1980s. The characteristics of the moth populations were compared along a gradient of decreasing duration of the insect presence, from endemic, core areas (presence observed about a century ago or more), to newly-colonized zones (presence since 15–20 years) and front edge (presence since 5 years at most) (see Fig. 3.7). Not yet invaded zones, located beyond the expansion front, were also used to test experimentally the survival potential of the moth under those conditions. This section briefly presents their main results, which will be extensively published soon.

In 2008, preliminary studies have shown changes in the phenology and quantity of urticating setae (Battisti et al. unpublished data). Bred in the same conditions, populations from the expansion areas developed faster than those from the core area, with a 2-day advance in the adult emergence peak. Meanwhile, larvae from the expansion areas appeared to release about twice as many urticating setae as those from the core area.

In 2009 and 2010, cross-translocation experiments of larval colonies between the different areas of the expansion gradient in the Paris basin were realized in order to assess adult traits, especially those related to dispersal. During autumn, a total of 80 colonies of early-instar larvae (2nd larval stage) were simultaneously collected per site in the core, newly-colonized and front areas (see Fig. 3.7). Each tent lot was then divided into four groups of 20 tents, and one group from each sampled area was translocated and grafted on pines (one larval tent per tree) in the two other areas of the expanding gradient. The two groups remaining per lot were either grafted on the sampling site (control) or in a non-invaded site beyond the front edge. The larvae were allowed to continue their development on the grafted pines until spring, when the mature tents were collected just before the larvae begin to process for pupation. The collected colonies were then stored at the same location, in an outdoor insectary at Orléans, France, where they were put in individual containers filled with soil allowing pupation. Further development was surveyed until the adult emergence. Emerging adults from each combination of sampled/translocated and development areas were used to test for the relative importance of population and environmental effects by comparing morphological (thorax width, wing size), physiological (energy resources) and behavioural (flight capabilities) variables among the different insect groups. Energy resources usable for flight (carbohydrates and fat content) were quantified according to the methods described by Van Handel and Day (1988). Flight capacities were tested in laboratory using flight mills (Fig. 2.10), made up with a horizontal carbon fibre arm plugged on a vertical axis using a ball bearing. Tested insects were plugged on the

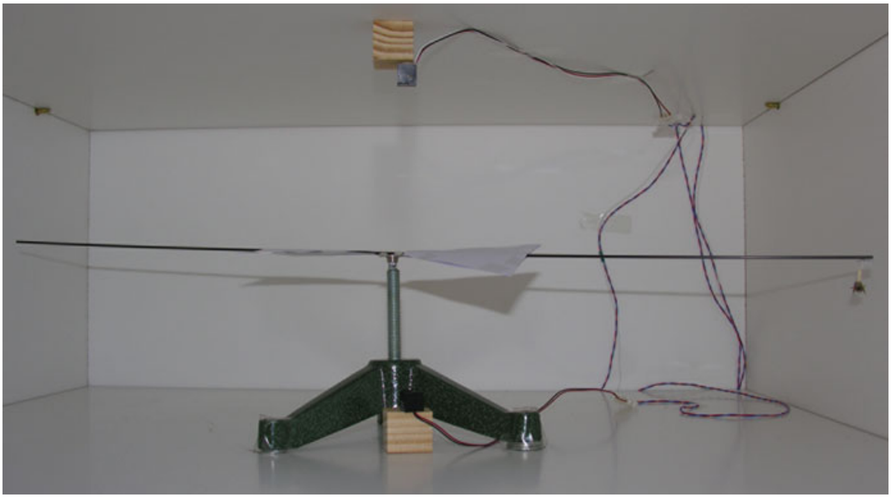

Fig. 2.10 An adult of the pine processionary moth plugged on a flight mill for measuring flight capabilities

end of the arm. When flying, they dragged the arm, each revolution of which being detected with an IR transmitter-receiver set and recorded on a computer, allowing to measure the total distance travelled by the insect and other parameters of the flight. Each insect was tested during 24 h. The experiment was repeated during 3 years, from 2008 to 2011.

The dispersal potential of *T. pityocampa* measured on flight mill appeared significantly more important than the estimations of previous studies based on empirical observations or rough experiments of release-recapture. In 2008–2009, the mean distance covered by males and females were 10.9 km (up to 41 km) and 1.9 km (up to 10.5 km), whereas female flight was considered as very limited, from a few dozen meters up to 2 km (Démolin 1969b). The values observed during the two following years were even much more important with a mean distance averaging 17 and 24 km for males, with flights up to 61 and 56 km in 2009–2010 and 2010–2011, respectively. In the same years, female flight averaged 5.6 and 5.1 km, with maximum values up to 27 and 24 km, respectively. Although measured in a very artificial environment, these data were consistent with the observed expansion speed of the moth (about 5 km a year; Battisti et al. 2005), so they could be representative of the actual flight capabilities of females in the field.

Interestingly, two clines in morphological variables were also observed in 2008–2009. First, the adults originating from the newly-colonized area were smaller, whatever the place they were translocated, than those originating from the core area. Second, those obtained from larvae which had developed in colder areas at the front edge and beyond the front were smaller, whatever their primary origin, than those which had developed in warmer areas (core and recently-colonized areas). These differences were observed in both males and females and for all size variables. Carbohydrates and fat contents were also lower in females originating from the front edge than in those originating from the core area. A similar trend was noticed for female (but not male) flight capabilities, which were less important in females from the front edge or which had developed in colder areas. However, this trend remained not significant statistically. Moreover, these clines were not observed during the two following years which were characterized by unusually severe climatic conditions resulting in very low winter survival and emergence rates.

According to these preliminary studies, moth expansion may be associated to changes in insect features such as phenology, urticating power, size, and partially energy resources and perhaps flight capabilities. The shift in the adult phenology can be integrated in its known variation in the range, where it has been observed that adult flights occur earlier in its northern part (Démolin 1969a). This variation is interpreted as an adaptation to colder climates, with the early flight allowing an earlier larval development, so that the larvae can enter winter in its more cold-resistant fourth larval instar. The clines observed (or suspected) in size and related variables (energy resources, flight capabilities) in relation with population origin and development environment combine their effects in the field, both resulting in smaller insects in the expansion area. The environmental cline may result from a decreasing fitness in the northern areas due to harder climatic conditions. This cline tends to reveal an adaptation of moth populations to the expansion area, and suggests that small and short-dispersing insects may be selected during the expansion process. Similar clines have been observed in species with fragmented range (Hill et al. 2011). It could be due to an Allee effect which reduces the fitness of long-dispersing insects at the range margins. However, contrasting results obtained in the second and third year of the experiment indicate that the expression of the two clines may depend of environmental factors and could for example depend on unusual climatic conditions.

3 Recent Occurrence of a Summer Population of *Thaumetopoea pityocampa* in Portugal

Helena Santos, Manuela Branco, and Maria-Rosa Paiva

3.1 Host Plants and General Distribution

The summer population of *Thaumetopoea pityocampa* was found originally in Portugal in a plantation of maritime pine*, Pinus pinaster,* which is, to date, the sole host species known for this atypical population. However, since the summer population is expanding to other areas, it can be expected to colonize other conifer species in the future.

3.2 Life Cycle

The life cycle of the atypical summer population has been studied since its discovery (Pimentel et al. 2006; Santos et al. 2007; Pimentel et al. 2010) (Fig. 2.11). Adults start emerging from the soil by the end of April and mate just after emergence. Usually females die after egg laying, but males can persist for 3–4 days. In laboratory experiments both males and females showed a good flight capacity (H. Santos, personal observation). Fecundity was demonstrated to be lower in the summer population, when compared to winter populations, either sympatric or originating from other regions (Santos et al. 2013).

Eggs are mostly laid in the field between the end of April and early July, when adult emergence usually ceases. The oviposition period may slightly vary from year to year (for more detail about the ecology of the summer population see Kerdelhué et al. 2014, Chap. 4, this volume). Hatching starts about one month later. The young larvae are gregarious and start hatching and feeding on *P. pinaster*, between the end of May and the beginning of July, preferring 1 year old needles. The early instars spin small temporary tents and change location several times. When multiple egg batches are laid on the same tree, colonies can merge in a single tent. Like the typical *T. pityocampa* populations, from the third instar onwards larvae produce urticating setae and spin definitive, loose tents that will be used until the end of larval development.

In this atypical population, larval development is much faster than in the typical, winter populations, probably because it takes place during the warmer months. By the

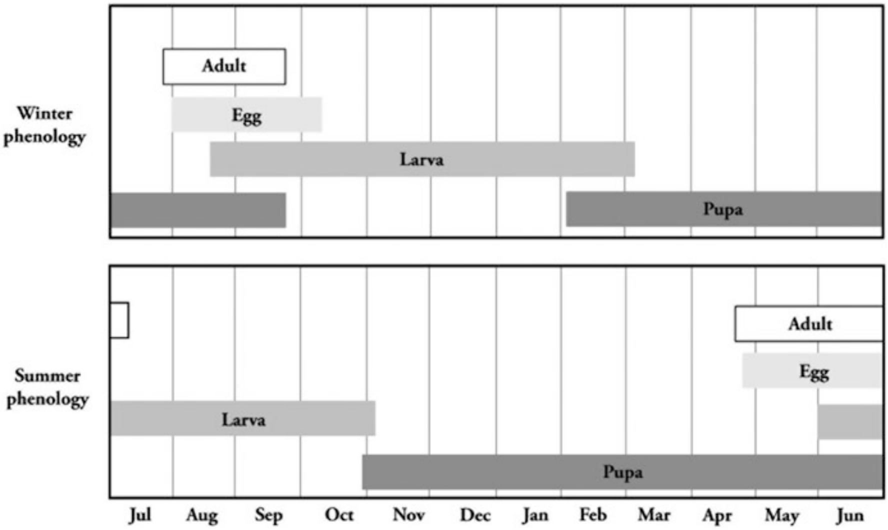

Fig. 2.11 Typical phenology observed for *T. pityocampa* summer and winter populations, in Leiria, Portugal

end of September the larvae have reached the fifth instar and descend from the trees in processions, searching for a suitable place to bury in the soil. Larvae bury between 5 and 15 cm deep where they pupate. The pupae enter a winter diapause, which is just the opposite of the summer diapause of the typical form. It is not clear if the summer population may have prolonged diapause such as in the typical form.

3.3 Natural Enemies

Egg parasitoids attacking the summer population belong to the same species known for the winter populations (Fig. 2.8), although their frequencies are different. *Ooencyrtus pityocampae* (Hymenoptera, Ooencyrtidae) and *Trichogramma embryophagum* (Hymenoptera, Trichogrammatidae) are the two main species, followed by *Baryscapus servadeii* (Hymenoptera, Eulophidae). Eggs are predated by orthopteran species of the family Tettigoniidae.

Larvae are mostly parasitized by *Phryxe caudata* (Diptera, Tachinidae). Ants, particularly the Argentine ant *Linepithema humile* (Hymenoptera, Dolicoderinae), are important predators of the summer population, since they can consume up to 100 % of the larvae of an infested tree (Way et al. 1999). Birds from the genus *Parus* are known to prey on late instar larvae (Pimentel and Nilsson 2009). The fungus *Beauveria bassiana* (Moniliales, Moniliaceae) is another factor of mortality for the larvae and pupae of the summer population. Parasitoids of the pupal stage so far recorded are *P. caudata*, *Erygorgus femorator* (Hymenoptera, Ichneumonidae) *Villa* *brunnea* (Diptera, Bombyliidae) and *Coelichneumon rudis* (Hymenoptera, Ichneumonidae), the three last species being found in very small numbers.

3.4 Population Dynamics

When it was discovered in 1997, the summer population was in an outbreak situation having caused very severe damage to a 10–15 year old pine plantation. The affected area has since expanded northwards and southwards, currently extending about 80 km along the coast line. Within the plantation area, plots with trees over 40–50 years old were not attacked. In urban and peri-urban areas isolated pines, or small tree aggregates, have also been colonized. In the core area, infestation levels remained high, i.e. 25–75 % defoliation, between 1997 and 2005 when they started decreasing, reaching the low levels of damage presently observed, while spots of high density can be found in the expansion area.

3.5 Relationships with Climate Change

Although the expansion range of the summer population has progressed both northwards and southwards in relation to the initial core area, it is still confined to a geographical region with similar climatic conditions. However, under a scenario of global warming, an increase of the maximum temperatures might be limiting for the survival of the larval stage of this population, since it takes place during the summer, consequently precluding its expansion. Yet, an adaptation of this population to hot summers is also plausible (Santos et al. 2011a, 2011b).

4 Natural History of the Eastern Pine Processionary Moth, *Thaumetopoea wilkinsoni*

Mustafa Avcı, Kahraman İpekdal, and Zvi Mendel

4.1 Introduction

The eastern pine processionary moth, *Thaumetopoea wilkinsoni*, was described as a new species by Tams (1925), who studied specimens found in Cyprus and compared their male genitalia with those of *T. pityocampa*. Démolin (1969a) found significant morphological overlapping between populations of these two taxa (Fig. 2.1); and, furthermore, both use the same female sex pheromone: (Z)-13 hexadecen-11-ynyl acetate (e.g., Frérot and Démolin 1993). Recent genetic studies (e.g., Salvato et al. 2002) indicated the existence of strong genetic differentiation between the two species, which became separated before the Quaternary ice ages (see Chap. 4). Therefore, we consider it as a separate species although more analyses in the contact zone of western Turkey are needed in order to define the overlapping area and potential introgression.

4.2 Host Plants and General Distribution

Thaumetopoea wilkinsoni develops on native and introduced *Pinus* spp. in the East Mediterranean, from western Turkey to Israel, and occasionally colonizes *Cedrus* spp., especially *C. atlantica* (Halperin 1990a, 1990b). In Turkey, mainly *P. nigra*, *P. brutia brutia*, *P. halepensis*, *P. pinea*, and *P. radiata* are colonized (Çanakçıoğlu and Mol 1998); according to İpekdal and Çağlar (2012), *T. wilkinsoni* preferred *P. nigra* in a multiple choice experiment. In Israel, *T. wilkinsoni* occurs mainly on *P. canariensis, P. halepensis*, and *P. brutia brutia*; on wet sites it is observed in high densities also on *P. brutia eldarica* and on *P. radiata*. In mixed stands the moth seems to prefer the exotic *P. canariensis, P. radiata* and *P. brutia eldarica* to the native *P. halepensis* and *P. brutia brutia* (Mendel 1988). Two other common exotic species in Israel, *P. pinea* and *P. pinaster*, are rarely attacked by the moth. In Cyprus, the moth primarily attacks the native pine, *Pinus brutia brutia*, the dominant tree species on the island, and, less frequently, *P. nigra pallasiana*; it also attacks the exotic pine species *P. canariensis* and *P. halepensis,* but not *P. pinea* (Ciesla 2004).

4.3 Life Cycle

Thaumetopoea wilkinsoni has a 1-year development cycle, which is similar to that of *T. pityocampa* (Fig. 2.7). The first comprehensive study of the moth was conducted by Wilkinson (1926). The adult females fly short distances (<2 km) while males may travel long distances (>50 km) in open areas, and they are strongly attracted to the sex pheromone of the female. Mating may occur on the ground before the female concludes its wing spread. Five instar larval development occurs in autumn and winter, and its duration depends mainly on temperature. At colder sites (high elevation or high latitude) the adults emerge in late July; at warmer sites, in October. In Israel these extremes are manifested by early flight (from late August to mid-September) in the Upper Galilee, and late flight (from late September to mid-October) in the western Negev. Observations in Lebanon (Houri and Doughan 2006) and Israel (Mendel, unpublished) suggested that emergence is triggered by the first significant rainfall. The females survive for 1–2 days and lay about 200 eggs on needles (and rarely on twigs during outbreaks). The eggs hatch in August at colder sites and in November at warmer sites. Özkazanç (2002) recorded a 1-month difference in the beginning of the larval stage, over an 800 m elevation difference (earlier at the higher elevation). The larvae are gregarious, and construct silken tents throughout their development: 2 or 3 fragile temporary webbing during the first two instars, and a permanent massively webbed tent for the last three instars. Studies in Israel suggest that an average tent harbour brood of 2–4 females. The two early instars feed during the day; the older ones pass the day in tents and feed during the night. From the third instar onward the larvae are covered with urticating setae which reach their highest density in the fifth instar. The larvae descend from trees to the ground in a typical procession during spring, until early May. Pupation takes about 4–5 months; possibly shorter at high elevations. Mendel (unpublished data) observed the processions of larvae descending for pupation in mid-July in the Shuff Mountains in Southern Lebanon. Summer pupal diapause can be prolonged up to 9 years (Halperin 1990a, 1990b).

4.4 Natural Enemies

The most common natural enemies are shared with *T. pityocampa* (Fig. 2.8), starting from the egg parasitoids *Ooencyrtus pityocampae* and *Baryscapus servadeii*. In Israel the populations of the former species develop during the summer in the eggs of the caper bug *Stenozygum coloratum* (S. Samra, personal communication). Three other egg parasitoids of the moth, *Pediobius bruchicida*, *Anastatus bifasciatus*, and *Trichogramma embryophagum*, are usually much less common. Overall, parasitism can be as high as 52 % locally (Avcı 2000; Avcı and Oğurlu 2002; Mirchev et al. 1998, 2004; Pekel 1999; Tsankov et al. 1998), and close to 80 % in extreme cases in Israel, where the parasitism level in urban areas is much lower than in the forests (Mendel unpublished data). The parasitic fly *Phryxe caudata* attacks the larvae in southern populations (unpublished data). *Formica rufa* and *Calosoma sycophanta* are known as larval predators of the eastern pine processionary moth and are used in biological control projects in Turkey (Avcı 2000). The hoopoe *Upupa epops* and the boar *Sus scrofa* and several forest bird species, especially *Parus major,* are known to feed on larvae and/or pupae. On wet sites significant pupal mortality is caused by the entomopathogenic fungi, *Beauveria bassiana* and *Metarhizium anisopliae*.

4.5 Population Dynamics

On an area basis *T. wilkinsoni* is the dominant forest pest in the Middle East, and the major pine defoliator. Outbreaks of *T. wilkinsoni* have been observed in the area since the late nineteenth century in Cyprus and the early twentieth century in Turkey (Schimitschek 1944), with the first record of high population density in İstanbul in 1904 (İpekdal 2012). Another recorded outbreak was from İzmir in 1949 (Acatay

1953), and a synchronized outbreak was recorded throughout Turkey between 1996 and 1997 (Gabir 1998). In Israel outbreaks became frequent since the 1950s, with the establishment of large areas afforested with *P. halepensis* (Halperin 1990a, 1990b).

The number of tents on a single tree can be as high as 100 during outbreaks in southern regions of Turkey (Mol and Küçükosmanoğlu 2002). Low winter temperatures seem to play an important role in the build-up of the moth population at high elevations and high latitudes. In dry areas in Israel outbreaks occur after rainy winters that follow several years of drought. Defoliation of pine forest mainly happens in young stands, and colonization is observed as early as the third year after planting or regeneration after a fire, and reaches its peak about 10 years later. In adult stands the population is low, with only trees on the margin of the plots being lightly infested; heavy thinning coupled with rainy winters encourages population build-up in adult stands. In Israel the moth is also a severe pest of ornamental pine trees in urban areas, where mature trees are prone to attack. This susceptibility in urban habitats is the consequences of continuous tree growth, thanks to ample water supply, via either irrigation or root penetration of sewage systems. City pine trees may be heavily infested year after year, unlike the typical dynamic in the forest, where heavy defoliation results in poor performance of the larvae in the first and second year after a major outbreak.

The urticating setae located on the back of the late instar larvae (see Moneo et al. 2014, Chap. 8, this volume) form the major reason for needing to control the moth population. The moth is a great nuisance both to residents in urban areas, especially children on playgrounds, and to visitors and travellers camping on infested sites (Solt and Mendel 2002). Successful management of the moth is accomplished by aerial application of microbial insecticides based on *Bacillus thuringiensis* formulations. To prevent *T. wilkinsoni* infestation on ornamental pine trees, systemic insecticides are applied via stem injection. Since 2006 the use of Monocrotophos (a very effective organophosphate compound) formulations has been banned in Israel. Stem injections to control *T. wilkinsoni* are applied successfully with commercial products of Emamectin benzoate or Azadirachtin (Mendel, unpublished results).

4.6 Relationships with Climate Change

İpekdal and Çağlar (2012) showed that rising temperatures blur host preferences of *T. wilkinsoni*, and thus may bring new threats to additional *Pinus* species in a warmer future. The question whether duration of pupal diapause will be influenced by frequent drought periods is still open (Halperin 1990a, 1990b). The prolonged diapause may also favour the establishment of the moth in loosely managed forests on a warming globe. However, more data are needed to enable development of general inferences to use in future afforestation works and management plans. Simonato et al. (2007) found that the spreading of the moth from the initial range was contiguous, indicating a great ability to colonise areas which become suitable for insect survival. However, in the East Mediterranean the moth already occupies all potential habitats in the infested areas, while it can still expand in the northeast. İpekdal and Beton (2013) showed a possibility of range expansion at the northern edge in Turkey towards Caucasus between 2050 and 2080. In light of the thriving of the moth population in pine plantation in semi-desert areas in Israel, it is suggested that global warming will not cause the retraction of the range at the southern edge of *T. wilkinsoni*.

5 Natural History of the Northern Pine Processionary Moth, *Thaumetopoea pinivora*

Stig Larsson and Andrea Battisti

5.1 Host Plants and General Distribution

Thaumetopoea pinivora is monophagous on Scots pine *Pinus sylvestris*, but is occasionally found also on black pine, *Pinus nigra*, and mountain pine, *Pinus mugo*. Typical habitats include light stands on poor soil, and populations are scattered from south-western Europe (Iberian Peninsula) to northern Europe (around the Baltic Sea).

5.2 Life Cycle

The following is a summary of what is currently known mainly based on field observations in Sweden (Aimi et al. 2008; Ronnås et al. 2010), and from what is known from mostly older literature data from Germany and Spain (Koch 1953; Hering 1970; Montoya and Robredo 1972). *Thaumetopoea pinivora*, at least in northern Europe, has a 2-year development cycle (Fig. 2.12). In Sweden, adults emerge from the cocoons in the soil in July–August (Figs. 2.1 and 2.6). Females are short lived, probably living for only one or a few days. The dispersal capacity of the female is limited, as indirectly shown by molecular markers (Ronnås et al. 2011), whereas the male can disperse over much longer distances. Females develop about 100–200 eggs. The eggs are laid in batches on the pine needles shortly after female emergence and are covered with scales produced by the female. The eggs are laid in the opposite direction compared to those of *T. pityocampa*, i.e. the female is pointing to the needle base (Fig. 2.2). The eggs hatch in late April the following year. Groups of neonate larvae are full siblings, but larval groups commonly merge at later instars, sometimes forming aggregates of up to 1,000 individuals. Larvae do not build tents, in contrast to *T. pityocampa* and *T. processionea*. The larvae go

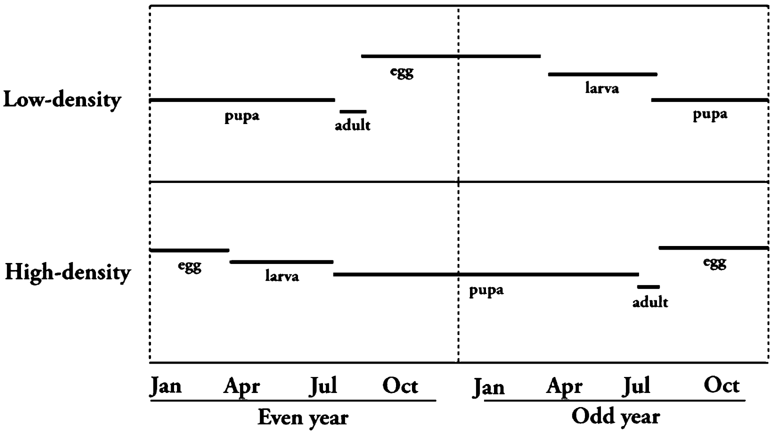

Fig. 2.12 Life history characteristics of *Thaumetopoea pinivora* on Gotland Island, south Sweden. *Thaumetopoea pinivora* has a 2-year life cycle with parallel year classes. High population densities of larvae occur in even years

through five instars and feed until late July (Fig. 2.4). The larvae feed on mature needles, even in later instars when current-year needles have developed. The feeding mostly occurs during the night.

First and second instar larvae have a distinct basking behaviour, forming dense clusters at the tip of branches directed towards the sun and thus accumulate heat during the rather cold days in early spring (Ronnås et al. 2010; Battisti et al. 2013). Late-instar colonies, however, hide on the trunk or on a major branch supposedly in order to reduce overheating. From the third instar larvae develop urticating setae about 0.1 mm in length, situated in groups on the dorsal parts of the abdomen. When the larvae are disturbed setae are actively released, and can cause severe allergic reactions in humans (Holm and Larsson 2006). When ready to spin cocoons the larvae leave the trees in typical head-to-tail processions to search for suitable sites in the soil. When a suitable site is found the larvae join in digging through the soil down to a depth of 5–20 cm. The cocoon overwinters and stays in the soil for most of the following summer before emerging in late July. A certain proportion of the cocoons have a prolonged diapause. The Swedish *T. pinivora* population on Gotland Island has discrete year classes with high larval densities in even years, whereas much lower densities occur in odd years (Larsson et al. 2006) (Fig. 2.12).

5.3 Natural Enemies

Very little specific information is available on natural enemies of *T. pinivora*. The eggs of Spanish populations share the parasitoids *Baryscapus servadeii* and *Ooencyrtus pityocampae* with *T. pityocampa* in the areas where the two species coexist (Sierra de Guadarrama, Battisti unpublished data) whereas no egg parasitoids have been found in the Swedish population despite thorough searches. Egg predation by birds has been observed in Sweden during winter, accounting for about 20 % of egg loss (Ronnås unpublished data). The larvae of late instars in both Spain and Sweden are parasitized by the tachinid fly *Blondelia pinivorae*, which complete the development in pupae (Agenjo 1941; Bergstrom and Bystrowski 2011). No population estimates are available, but patch parasitism on Gotland Island can be as high as 20 % (Larsson, unpublished data). In Sweden, mortality from generalist arthropods predators (spiders, ants) can be quite high in young instars (Aimi et al. 2008; Ronnås et al. 2010). The pupae have been found to be infested by fungi but no precise information is available on mortality rates. Occasional cocoon predation by birds has been observed in Sweden, but is most likely of minor importance for the population dynamics. No information on adult predation is available.

5.4 Population Dynamics

Outbreaks of *T. pinivora* have been documented from central and northern Europe but never over large areas. There are no outbreaks recorded from southern Europe. The first record of high population density was in Germany in 1891 (Altum 1895, 1896). Quantitative estimates of outbreak size are available from Germany (2,500 ha) in 1947–1949 (Gäbler 1951, 1954), Poland: Hel (1,200 ha) in 1952–1960, Leba (1,100 ha) in 1956–1960 (Hajduk 1963); Stegna (940 ha) in 1956–1960, Darzlubie (150 ha) in 1961–1970 (Sliwa 2002), and Russia (Kaliningrad, a few hundred ha) (Maksymov 1978). The outbreak in Sweden on Gotland Island is more recent and started in 2004. The highest density was found on the southernmost tip of the island where about 3,000 ha had high population densities in 2006 (defined as >10 colonies found within a 30 min search). The density slowly declined, but spots with high density still (2014) occur. Despite several years of monitoring of the population we still have no clear picture of what factors are most important in controlling the population. The spatial distribution, and the local character, of the outbreak were tentatively explained by predation from generalist arthropods; plant quality did not seem to be important (Aimi et al. 2008). It should be noted that the outbreak area is characterized by slow-growing pine trees at low density of trees, similar to populations in Kaliningrad and Spain (pers. obs.). It is interesting that there has been virtually no exchange of individuals between the outbreak area and seemingly suitable sites on Gotland Island distant from the outbreak (Ronnås et al. 2011 see also Kerdelhué et al. 2014, Chap. 4, this volume).

5.5 Relationships with Climate Change

Thaumetopoea pinivora belongs to the group of the summer processionary moths, which are generally adapted to high elevation and, in the specific case of *T. pinivora*, to high latitude. Precise information about the responses of these species to climate change is missing. The natural occurrence of well-established populations at the northern edge of the range in Sweden (Aimi et al. 2008; Ronnås et al. 2011) does not support the hypothesis of a recent range expansion in relation to climate change, as observed in the group of winter processionary moths, and especially *T. pityocampa*. More work is required in order to understand the effect of climate change on *T. pinivora* and to the other species of summer processionary moths.

6 Natural History of the Cedar Processionary Moth, *Thaumetopoea bonjeani*

Noureddine Rahim, Gahdab Chakali, Wahiba Berretima, and Andrea Battisti

6.1 Host Plants and General Distribution

Thaumetopoea bonjeani is monophagous on Atlas cedar *Cedrus atlantica* Manetti in the relic stands of north-western Africa (Algeria and Morocco).

6.2 Life Cycle

Thaumetopoea bonjeani is one of the most serious pests of *Cedrus atlantica* forests in Algeria (Gachi et al. 1986; Démolin 1988). The larvae feed on the needles of cedar trees and have urticating setae that cause contact dermatitis after the third instar. Adults (Fig. 2.1) appear from the beginning of August to mid-September. The wingspan of the males and females is 25–33 mm and 30–39 mm, respectively. Mating and oviposition occur at night soon after emergence. Females oviposit on the underside of *C. atlantica* twigs. Egg batches are covered by greyish brown scales, similar to the colour of the bark and therefore the batches are inconspicuous. The number of eggs per egg batch varies between 44 and 340 (mean 150). Eggs hibernate almost for 8 months and hatch in spring (between late March and late April) of the following year. Unlike the pine processionary moth, *T. bonjeani* does not make structured tent and lives in colonies combined in a form of ball with a very light weave (Fig. 2.4). The mature larvae are the most destructive ones and may cause serious infestation resulting in the complete defoliation of vast areas of cedar forests. The pupation takes place in the first decade of June to the first half of July (Rahim, unpublished data).

6.3 Natural Enemies

Three parasitoid species emerged from *T. bonjeani* eggs: *Ooencyrtus pityocampae* (Hym.: Encyrtidae) and *Trichogramma sp.* (Hym.: Trichogrammatidae) (Démolin 1988). Two tachinid parasitoid are reported from larvae and pupae: *Compsilura concinnata* and *Exorista segregata*. The larvae and pupae have been found to be infected by fungi but no precise information is available. Among the predators listed in Djurdjura cedar forest (Algeria) are the carabid beetle *Calosoma sycophanta* and the staphilinid beetle *Ocypus olens* (Rahim, unpublished data).

6.4 Population Dynamics

Outbreak populations of *T. bonjeani* were observed in Algeria first in 1982 and two major outbreaks were recorded, the first between 1982 and 1990 in Belzma over about 500 ha (Démolin 1988), and the second between 2009 and 2011 in Djurdjura over about 150 ha (Rahim, unpublished data). In Morocco an outbreak was recorded in Kétama (Central Rif) over 120 ha in 1989 (El Alaoui El Fels, unpublished data). More work is certainly required to understand the population dynamics of the species. Defoliation by *T. bonjeani* most certainly contributes to the decline of the relic cedar stands in the Algerian mountains.

6.5 Relationships with Climate Change

Although outbreaks have been observed only recently and at the southern edge of the range, there is not a clear link between climate change and the performance of *T. bonjeani*. More work is required to address the effect of climate change on *T. bonjeani* and to the other species of summer processionary moths.

7 Natural History of the Eastern Cedar Processionary Moth, *Thaumetopoea ispartaensis*

Mustafa Avcı and Kahraman İpekdal

7.1 Host Plants and General Distribution

Thaumetopoea ispartaensis is monophagous on Taurus cedar *Cedrus libani* (Doğanlar and Avcı 2001) in relic stands of Taurus Mountains (southern Turkey).

7.2 Life Cycle

Thaumetopoea ispartaensis (described as *Traumatocampa ispartaensis* by Doğanlar and Avcı in 2001) is one of the most serious pests of *Cedrus libani* forests in Isparta region and on Taurus Mountains in southern Turkey. All the information reported here comes from the original description (Doğanlar and Avcı 2001). The elevational range is between 1,250 and 1,650 m. The larvae feed on the needles of cedar trees and have urticating setae that cause contact dermatitis after the third instar. The wingspan of the males and females is 26–29 mm and 34–37 mm, respectively. Adults (Fig. 2.1) appear from mid-August to the end of September, earlier at lower elevation. Mating starts a few hours after adult emergence and oviposition occurs during the same night. Females oviposit on the underside of *C. libani* twigs. Egg batches are covered by greyish brown scales, similar to the colour of the bark and therefore the batches are inconspicuous. The number of eggs per egg batch varies between 39 and 245 (mean 121). Eggs hibernate for almost 7 months and hatch in spring (between late March and late April) of the following year. The larvae live together in greyish silky tents until the fifth final instar, which is reached in 2.5 months, generally between end of April and mid-July. The silk tents are quite loose in comparison to those of the pine processionary moth. The mature larvae are the most destructive ones and may cause serious infestation resulting in the complete defoliation of vast surfaces of cedar forests. Pupation takes place in the first half of July, at a depth of 5–15 cm of soil, in sunlit cedar forest floors, especially along roadsides. Pupae develop in grey-brown cocoons (Avcı 2003). There is no observation about the occurrence of prolonged diapause of the pupae.

7.3 Natural Enemies

Avcı (2003) reported three parasitoid species reared from *T. ispartaensis* eggs: *Ooencyrtus pityocampae* and *Ooencyrtus* sp. (near *masii*) (Hym.: Encyrtidae), both solitary species, *Trichogramma brassicae* (Hym.: Trichogrammatidae), a gregarious species. *O. pityocampae* was found to be the most abundant species, followed by *O.* sp. near *masii* and *T. brassicae*. Parasitism in *T. ispartaensis* eggs varied between 7.4 % and 11.3 % in 1999 and 2000, respectively.

Avcı and Kara (2002) reported six tachinid parasitoid species for *T. ispartaensis* larvae and pupae: *Blondelia nigripes, Carcelia iliaca*, *Compsilura concinnata, Exorista segregata*, *Pales processioneae*, *Phryxe caudata*. *Blondelia nigripes* was reported to be the most common one, parasitizing up to 4.6 % of the pupae.

A few vertebrate and invertebrate predators have been observed, the most important being *Formica rufa* (Avcı and Carus 2005). More observations are required to produce a complete list of both parasitoids and predators.

7.4 Population Dynamics

Thaumetopoea ispartaensis population in Isparta has been studied since 1998 and an outbreak was recorded between 1999 and 2003 (Avcı and Carus 2005), but it was impossible to see even a single colony in some years such as 2012. We do not know if this is a pattern of regular fluctuation or just irregular outbreaks, as possibly indicated by a dendro-ecological analysis (Avcı and Carus 2005). More work is certainly required to understand population dynamics of the species.

7.5 Relationships with Climate Change

As *T. pinivora, T. ispartaensis* belongs to the group of the summer processionary moths adapted to high elevation. So far, no study has been carried out about its specific response to climate change.

8 Natural History of the Lebanon Cedar Processionary Moth, *Thaumetopoea libanotica*

Andrea Battisti and Nabil Nemer

8.1 Host Plants and General Distribution

Thaumetopoea libanotica is monophagous on Lebanon cedar *Cedrus libani* in relic stands of Lebanon Mountains at high elevation (around 1,900 m) (Kiriakoff and Talhouk 1975).

8.2 Life Cycle

Thaumetopoea libanotica is generally found at low density and the information is scarce. In the original description of the species, Kiriakoff and Talhouk (1975) reported that a single colony was found on a cedar tree in May and the larvae were in the second instar. They were taken to the laboratory and reared until pupation, which happened at the end of June with the larvae in the fifth instar. Adults (Fig. 2.1) emerged in August.

8.3 Natural Enemies

No information is available.

8.4 Population Dynamics

No information is available.

8.5 Relationships with Climate Change

No information is available.

9 Natural History of the Oak Processionary Moth, *Thaumetopoea processionea*

Nicolas Meurisse, Axel Schopf, Traian Manole, Irina Ionescu-Mălăncuş, and Andrea Battisti

9.1 Host Plants and General Distribution

Thaumetopoea processionea feeds on *Quercus* species across Europe and the Near East. In Europe, its preferred species are *Q. cerris*, *Q. pubescens Q. petraea*, *Q. pyrenaica*, and *Q. robur* (Dissescu and Ceianu 1968; Pascual 1988; Stigter et al. 1997). In the Near East, it is also found on Q. boissieri and on the evergreen Q. callyprinos (Démolin and Nemer 1999; Halperin and Sauter 1999). Typical habitats for this thermophilic species in the northern part of its range are urban and avenue trees, forest edges and open forests (Stigter et al. 1997; Offenberg 2000). Colonisations of closed canopy oak stands may occasionally occur, leading to tree dieback after repeated defoliation over several years, or making trees more vulnerable to secondary pests or pathogens (Dissescu and Ceianu 1968; Maksymov 1978; Pascual 1988; Baker et al. 2009; Lobinger 2010).

A population restricted to the mountainous area surrounding the Dead Sea Transform was first identified as the subspecies *T. processionea pseudosolitaria* (Halperin and Sauter 1999). A recent morphological study examined the external and internal characters of a large variety of specimens from all over Europe and the Middle East; it was concluded that all populations from Europe and the Middle East belong to *T. processionea* (Groenen 2010).

9.2 Life Cycle

Thaumetopoea processionea has a 1-year development cycle. The following is a summary of its life cycle observed in most European countries. Moths (Fig. 2.1) emerge from the cocoons on the trunks (old tents) from mid-July to mid-September (Dissescu and Ceianu 1968; Pascual 1988; Wagenhoff and Delb 2011; Williams et al. 2013). Emergences from cocoons are observed from the late afternoon (c.a. 4 p.m.) to the mid of the night (c.a. 2 a.m.) (Dissescu and Ceianu 1968; Pascual 1988; Lobinger 2012). These are usually followed, in the next hours, by an important flight activity (Dissescu and Ceianu 1968).

Observations performed at the edge of the distribution range allowed to deduct that the dispersal ability of females is 5–20 km per year (Stigter et al. 1997; Groenen and Meurisse 2012). Males may disperse over distances of 50–100 km, and are occasionally captured in light traps in areas where the species is not established (Denmark: Lovgren and Dalsved 2005; Franzen and Johannesson 2005; southern coast of Sweden: Skule and Vilhelmsen 1997; island of Jersey and south and southeastern coasts of England: Wedd 2002; Waring et al. 2003; Clancy 2008; Townsend 2009). The eggs (Fig. 2.2) are laid shortly after female emergence on the terminal branches of oak trees, preferably on the tallest part of the tree and on diameters usually comprised between 3.5 and 10 mm (Dissescu and Ceianu 1968; Bin and Tiberi 1983). Egg batches contain about 50–200 eggs, depending on the nutritional conditions of the larval stages (Dissescu and Ceianu 1968). All eggs are covered with scales produced by the female. Shortly after the egg mass is deposited, embryogenesis begins. In autumn, already fully-developed first instar larvae are found within the shells of the eggs (pharate larvae). At midwinter time, these pharate larvae become highly freeze-tolerant and can withstand temperatures as low as −30 °C (Meurisse et al. 2012).

The eggs hatch in April or early May of the following year, mainly depending on the local temperature regime in the preceding weeks (Pascual 1988; Custers 2003; Wagenhoff and Delb 2011; Meurisse, et al. 2012; Wagenhoff et al. 2012). Hatching is usually well synchronized with the time of the specific oak bud flushing (Stigter et al. 1997; Wagenhoff and Veit 2011). Neonates are able to withstand starvation periods of up to 3 weeks, reflecting the species' close adaptation to variable inter-annual, between-tree and within-tree budburst phenology (Wagenhoff and Veit 2011; Meurisse et al. 2012; Wagenhoff et al. 2012). Groups of neonate larvae consist of full siblings, but larval groups commonly merge at later instars, sometimes forming aggregates of up to 1,000 individuals.

The larvae usually go through six instars and feed until mid-June or early July, depending on the local conditions (Pascual 1988; Wagenhoff and Delb 2011). In Rumania the whole larval development takes 96–100 days in the field and 76–79 days in the laboratory at a temperature of 20–22 °C (Dissescu and Ceianu 1968). Feeding and movements of young larvae may occur during daytime, presumably taking advantage of higher day temperatures (Wagenhoff et al. 2012).

Older larvae are active at night, and congregate during the day to rest in a silk tent at branches or on the trunk (Fig. 2.4). The typical big communal tents on the lower part of the trunks are constructed by the fifth or sixth instars (Maksymov 1978). The tents are bag-shaped and consist of an assemblage of silk, hairs, faeces and old larval skins. The larvae pupate in the tent (Fig. 2.6). Tents can be partly in the ground under warm and dry weather conditions such as in Romania (Dissescu and Ceianu 1968) and, more recently, in the Netherlands and Germany (Hellingman, personal communication).

From the third instar onwards, larvae develop urticating setae on specific organs situated on the dorsal parts of the abdomen. Setae are harpoon-shaped and about 50–400 μm in length (Lamy and Novak 1987; Lamy 1990; Battisti et al. 2011; Petrucco Toffolo et al. 2014). They are actively released in the air when the larvae are disturbed, then causing intense irritation, ocular and respiratory problems, as well as severe allergic reactions in nearby animals and humans (Lamy 1990; Maier et al. 2003; Spiegel et al. 2004).

9.3 Natural Enemies

Little specific information is available on natural enemies of *T. processionea*. Eggs are parasitized by chalcidoid parasitoids (Hymenoptera) such as the eupelmid *Anastatus bifasciatus* and the encyrtid *Ooencyrtus masii,* but at relatively low rates of about 15 % (Biliotti 1952; Dissescu and Ceianu 1968; Maksymov 1978; Bin and Tiberi 1983; Mirchev et al. 2003). Late instar larvae and pupae are mostly impacted by the tachinid flies *Carcelia iliaca* and *Pales processionea* (Fig. 2.8). High rates of parasitism relating to these two species, up to 76 %, have been observed in Belgium, in the Netherlands and in France (Grison 1952; Tschorsnig 1993; Stigter et al. 1997; Meurisse, unpublished data). In Bavaria and Baden-Württemberg, the macrotype tachinid *Phorocera grandis* parasitized up to 70 % of mature larvae (Lobinger 2010; Tschorsnig and Wagenhoff 2012). Other tachinids (*Blondelia nigripes, Compsilura concinnata, Pales pavida, Phryxe semicaudata, Zenillia libatrix*) and the braconid species *Meteorus versicolor*, as well as ichneumonids (*Pimpla processionea*, *P. rufipes*, *Coccygomimus turionellae*, *Theronia atalantae*) and pteromalids (*Dibrachys cavus*, *Psychophagus omnivorus*, *Pteromalus puparum*) (Hymenoptera), have been observed as larval or pupal parasitoids (Maksymov 1978; Bogenschütz et al. 1988; Tiberi and Bin 1988; Tiberi et al. 1991; Tschorsnig 1993; Stigter et al. 1997; Zeegers 1997; Kara and Tschorsnig 2003; Cerretti and Freidberg 2009; Zwakhals 2005). Little is known, however, regarding their numerical impacts on *T. processionea* populations. All instars are actively preyed by the larvae and the adults of *Calosoma inquisitor* and, more significantly, *C. sycophanta*. High predation levels have been observed in France, Germany, and Romania (Dissescu and Ceianu 1968; Koch, pers. Obs.;

Table 2.4 List of insect parasitoids of developmental stages of *T. processionea*, with an indication of their activity in Rumania

Stage	Parasitoid species	Maximum mortality (%)
Egg	*Anastatus bifasciatus* (Hym., Eupelmidae)	15
	Ooencyrtus masii (Hym., Encyrtidae)	
	Pleurotropis pyrgo (Hym., Eulophidae)	
	Trichogramma embryophagum (Hym., Trichogrammatidae)	
Larva/ pupa	*Blondelia nigripes* (Dipt., Tachinidae)	
	Carcelia processioneae (Dipt., Tachinidae)	51
	Compsilura concinnata (Dipt., Tachinidae)	38
	Eucarcelia excisa (Dipt., Tachinidae)	
	Masicera cuculliae (Dipt., Tachinidae)	
	Pales pavida (Dipt., Tachinidae)	
	Phorocera agilis (Dipt., Tachinidae)	
	Phorocera assimilis (Dipt., Tachinidae)	
	Phryxe semicaudata (Dipt., Tachinidae)	
	Phryxe vulgaris (Dipt., Tachinidae)	
	Winthemia speciosa (Dipt., Tachinidae)	
	Zenillia dolosa (Dipt., Tachinidae)	
	Zenillia libatrix (Dipt., Tachinidae)	
	Apanteles ruficrus (Hym. Braconidae)	
	Meteorus spp. (Hym. Braconidae)	13
	Rogas geniculator (Hym. Braconidae)	
	Pteromalus puparum (Hym., Chalcididae)	
	Angitia vestigialis (Hym. Ichneumonidae)	
	Cubocephalus germari (Hym. Ichneumonidae)	
	Phobocampe pulchella (Hym. Ichneumonidae)	
	Pimpla spp. (Hym. Ichneumonidae)	
	Schizoloma amictum (Hym. Ichneumonidae)	
	Theronia atalantae (Hym. Ichneumonidae)	

Meurisse, pers. Obs.). Adults of the silphid *Xylodrepa quadripunctata*, the reduviid bugs *Rhinocoris iracundus* and *R. annulatus* as well as *Troilus luridus* (Pentatomidae) were observed as larval predators (Maksymov 1978). Furthermore, larval mortality by generalist arthropods predators (spiders, ants), or by birds (cuckoo, hoopoe, tits) has been reported (Gäbler 1954; Wagenhoff et al. 2012), but no precise information is available. Late instar larvae and pupae have also been found to be infected by microsporidia infecting midguts and fat bodies (Hoch et al. 2008). From surveys performed in Belgium, France, the Netherlands and Germany, *Endoreticulatus* spp. was found to be as the most widespread species (Hoch and Meurisse, unpublished data). The more aggressive *Vairimorpha* and *Nosema* spp. were less common (Table 2.4).

9.4 Population Dynamics

All over its range, *T. processionea* is known for the unpredictable nature of its outbreaks (Agenjo 1941; Gómez-Bustillo 1978; Maksymov 1978; Furth and Halperin 1979; Pascual 1988; Krehan 1993; Tomiczek and Krehan 1996; Jans and Franssen 2008). Epidemics, however, are highly synchronized locally, over distances of ca. 30 km. Synchronization rapidly decreases at larger distances, but still remains significant at large spatial scales of several hundred kilometres (Meurisse, unpublished). A striking outbreak, for instance was simultaneously observed in France, Belgium, the Netherlands and Germany in 1995–1996, and followed by an important decline in the same countries in 1997 (Groenen and Meurisse 2012). From 2000 to 2009, a heavy outbreak of *T. processionea* was observed in oak forests in Bavaria (Germany) causing oak tree mortality of 10–15 % mainly due to secondary infestations by buprestids and *Armillaria sp.* (Lobinger 2011).

Underlying factors for outbreaks and collapses are not known in detail, and there is still controversy if *T. processionea* outbreaks are either cyclic or eruptive (Wagenhoff and Veit 2011). Analysis of recent outbreaks in northern France indicates a possible 9–10 year periodicity (Meurisse, unpublished), while epidemics in Germany are reported to be rather chronic (Lehmann 2009).

9.5 Relationships with Climate Change

Well-established populations of *T. processionea* are known from the nineteenth century in most parts of Europe, with no evidence of any long-term latitudinal shift related to climate change (Groenen and Meurisse 2012). However, it is noticeable that, in recent years, outbreaks developed with an increasing frequency and intensity in many parts of Europe (Lempke 1989; Stigter and Romeijn 1992; Stigter et al. 1997; Maier et al. 2003; Jans and Franssen 2008; Wagenhoff and Delb 2011; Groenen and Meurisse 2012). Nowadays, the latitudinal distribution of *T. processionea* is still more restricted than that of its host-tree *Q. robur*, so that the permanent establishment of the species in Northern Europe could be restricted by climatic factors. Specific mechanisms, however, are not well known. Hypotheses include severe late winter conditions affecting the eggs, or temperature conditions in early spring, as they possibly affect neonate survival through high mismatching between hatching and budburst (Wagenhoff and Veit 2011; Meurisse et al. 2012; Wagenhoff et al. 2012). In Hungary, it was shown that a dry and hot May-July period favours *T. processionea* densities, particularly if it lasts 2–3 consecutive years (Klapwijk et al. 2013).

10 Natural History of the Pistachio Processionary Moth, *Thaumetopoea solitaria*

Zvi Mendel and Alex Protasov

10.1 Host Plants and General Distribution

Thaumetopoea solitaria is oligophagous on several pistachio species, both wild and cultivated, in south-eastern Europe and in the Near East. It occurs mainly on *Pistacia palaestina*, *P. terebinthus* (both named "terebinth" in English), *P. atlantica* (Mt. Atlas mastic tree or Persian turpentine tree) and *P. vera* (pistachio nut). There are single records of the moth on *P. lentiscus* and other related Anacardiaceae such as *Schinus* and *Rhus* species (Halperin 1983). Single references on members of other tree families (such as *Cupressus sempervirens* and *Fraxinus*) (De Freina and Witt 1987) are doubtful. Freyer (1838) suggested that the larvae displayed solitary behaviour, which led the moth to be labelled with the name '*solitaria*', which is inappropriate as indicated by Rauber (1858–1866) and Agenjo (1941).

10.2 Life Cycle

Information about the biology of the pistachio processionary moth was supplied mainly by Davatchi (1958) in Iran, Serafimovski (1975) in Macedonia, Halperin (1983) and the present authors in Israel, Mourikis et al. (1998) in Greece, Mart et al. (1995) and Karadağ et al. (2007) in Turkey, and Mirchev et al. (2012) in Bulgaria. Detailed adult descriptions were supplied by Agenjo (1941) and by Doğanlar and Doğanlar (2005). Agenjo (1941) noticed clear morphological differences between adults from the Mediterranean area and those named *T. solitaria* var. *iranica* collected in Iran.

The main flight period occurs between the second half of August and early November, but sampling of egg clusters in the Golan heights suggested that flight may occur even in December. However, monitoring emergence from collected pupae in Israel and Turkey suggested that the major flight period was in mid-September. The sex ratio is about 1:1. Both sexes display grey forewing and white hind wing, most conspicuously in the males. The wingspan is 20–28 mm for males and 25–35 mm for females. The males start to emerge in the late afternoon, the females a little later, and both complete emergence by around 10 p.m. The female sex pheromone differs from those of other studied processionary moths, in having 18 carbons and 2 double bonds in the 13 and 15 positions of the chain (Z13, Z15-18Al; Frérot and Démolin 1993). Mating was observed during the first half of the night. The females live for 1–2 days and the males may survive for a day longer.

The eggs are initially yellow and turn grey eventually. They are glued to branches of 3–18 mm in diameter, with the preferred diameter being 4–7 mm

(Mirchev et al. 2006). The clusters contain 80–260 eggs in one layer comprising 5–12 rows. Reports on female fecundity vary between areas. The clusters are covered with dark grey scales that closely mimic the colour of the outer bark of the branch. The females tend to concentrate the eggs clusters on particular trees and on certain branches within each tree, so that the clusters clearly display a clumped distribution. The eggs pass through an obligatory diapause, and hatching is usually synchronized with bud swelling and leaf bursting; for example, February–March in Israel and March–April in Turkey.

The neonate larva is 1.6–1.8 mm in length, and the mature fifth instar larva 25–35 mm. Larvae are covered with conspicuous long grey hairs and display a gregarious behaviour during feeding and resting periods. During the first two instars, larvae feed on young leaves and rest along thin branches close to the feeding sites. Older, more advanced instar larvae consume more mature foliage, on which they feed only during darkness, usually in the evenings, and they tend to rest deep inside the canopy. Whereas the early instars are usually active under spring low temperatures the more mature larvae favour periods of high temperature. When fed on semi- or fully grown leaves the young instars gnaw the margin of the leaf, whereas from the third instar onward the larvae consume the entire leaf tissue. The later instars tend to feed on the high canopy, therefore larva-infested spots can be detected by the occurrence of top growth (flags) where most or all of the leaves were consumed. Silk strands with larval faeces and larval exuviae attached to them are usually found close to the resting spots. In Israel, the feeding period lasts 50–60 days for those hatched in February (Halperin 1983). Karadağ et al. (2007) showed that relative humidity had a significant effect on the duration of the development period: for example at 26 °C, at 50 or 75 % RH the feeding period was 34 or 25 days, respectively. The threshold temperature for larval development is about 6.5 °C, and 564–570 degree-days are required for larval development from hatching to pupation (Karadağ et al. 2007).

Pupation occurs in litter and upper soil, usually not deeper than 10 cm below the surface in Israel. In Iran, however, pupation was reported to occur at 15–25 cm deep (Davatchi 1958). The pupae are enclosed in delicate silk webbing. The diapause lasts 141–180 days; some pupae may exhibit diapause prolongation by 1–2 additional years (Halperin 1983). Laboratory observations suggest that adults that emerged after prolonged diapause tend to appear earlier in the season than those that passed only one season in diapause.

10.3 Natural Enemies

Karadağ et al. (2007) showed that high relative humidity adversely affected the survival of advanced-instar larvae. Little information is available on the natural enemies of the eggs and larvae. Egg mortality was addressed mainly by Mirchev et al. (2006): in Bulgaria successful hatching ranged from 75 to 81 %, in Israel it was over 95 %. Mirchev et al. (2006) reported on activity of egg parasitoids (9.5 %) and egg predation (about 3 %) but supplied no information regarding the species involved.

No sign of egg parasitism was observed in Israel. Mirchev et al. (2012) reported that 5.6 % of newly hatched neonates died because of *Beauveria bassiana* fungal infection, and Halperin (1990a, 1990b) found that about 9 % of pupating larvae in the laboratory were killed by this fungus. Kugler (1979) reported on five species of parasitic flies (Diptera; Tachinidae), all of which are considered highly polyphagous; *Drino imberbis* was by far the most dominant species in Israel (Halperin 1983).

10.4 Population Dynamics

Intense defoliation of the infested wild trees is rarely widespread in any area. In Israel the species is a major concern because of the urticating setae of the larvae (see Chap. 8), which are a serious nuisance to foresters, visitors and, especially, to hiking and camping travellers: usually the signs of infestation are inconspicuous, therefore contact with the larval setae while passing though infested vegetation – usually during the summer – is often inevitable. In Turkey and Iran outbreaks occur in pistachio plantations and may cause serious economic damage, especially in mature plantations, where heavy defoliation of young foliage occurs and many of the fruitlets are damaged by the larvae (Anonymous 1995). Although major outbreaks in either forest areas or pistachio plantations are not frequent, when they do occur they may continue for several years. The larvae of *T. solitaria* are highly susceptible to *Bacillus thuringiensis* formulations, but their susceptibility decreases progressively with further moults (Er et al. 2007; Gindin et al. 2008).

10.5 Relationships with Climate Change

No information is available on the impact of global warming on the geographic range of *T. solitaria*.

11 Natural History of Thaumetopoea jordana

Andrea Battisti and Zvi Mendel

11.1 Host Plants and General Distribution

Thaumetopoea jordana is monophagous on *Rhus tripartita*, a species of Anacardiaceae of the Saharo-Arabian region (Furth and Halperin 1979), and was found on this host for the first time in the lower part of the Jordan River valley and the Dead Sea (Jordan and Israel) (Trougth 1954). In captivity, the larvae complete their development when fed with another Anacardiaceae, *Schinus terebinthifolius* (Halperin 1990a, 1990b), but pupae did not survive. It has been found later also in the Asir Mountains of Saudi Arabia, where it was thought to live on the same host plant (Wiltshire 1982).

11.2 Life Cycle

All the information comes from the papers of Trougth (1954), Furth and Halperin (1979), and Halperin (1990a, 1990b). The moth main flight period and oviposition occurs in October-December. However, emergence may happen also through the summer (May–September) (e.g. Aharoni 1912; Amsel 1935). The eggs are glued to the bark, in clusters 18–32 mm in length and 5–14 mm in width. Egg clusters laid on thin twigs are cylindrical whereas those laid on thicker branches are flat. The clusters are covered with shiny gold-brown scales. The incubation period lasts about 6 weeks and the mean number of eggs per cluster is 197 (min 105, max 258). Larvae raised at constant temperatures of 20, 25 and 30 °C complete their development in 70, 48 and 40 days, respectively, while those raised outdoors, in November-March, on trees of *Schinus terebinthifolius*, require about 150 days for full development. The larvae of *T. jordana* do not build a tent and moulting takes place in groups on branches, or in the soil beneath the host plant. When disturbed, the larvae fall from the tree and try to get back to it. The larvae generally bask in the sun during daytime and feed during night, searching for the leaves still on the twigs of *R. tripartita*. The larvae have a silver and black appearance because of the long silver hairs that cover the black integument and the mirrors carrying the urticating setae. Pupation occurs in March–April in the soil and a prolonged diapause of 1–2 years may occur.

11.3 Natural Enemies

High mortality was observed in rearing but the factors were not identified. Only the parasitoids *Ooencyrtus* sp. (close to *masii*) (Hymenoptera, Encyrtidae) and *Palesisa aureola* (Diptera, Tachinidae) emerged from eggs and larvae, respectively (Furth and Halperin 1979). The tachinid was reclassified according to Cerretti and Freidberg (2009), and *T. jordana* seems to be its only host known so far (Cerretti, personal communication).

11.4 Population Dynamics

The species is rare and associated with relic areas of *Rhus tripartita*, which generally occur in clumps of few shrubs.

11.5 Relationships with Climate Change

There are no data about the potential impact of climate change on *T. jordana*, although it has become less abundant in the recent years and repeated surveys in Wadi Qilt conducted in the springs of 2010–2012 failed to find egg clusters or larval colonies.

12 Natural History of Thaumetopoea herculeana

Mauro Simonato, Laura Berardi, Andrea Battisti, and Juan Pino

12.1 Host Plants and General Distribution

Thaumetopoea herculeana is associated with open areas covered with low natural vegetation of truly Mediterranean type of the Iberian Peninsula and on the southern rim of the Mediterranean basin until the Near East. The larvae feed on Geraniaceae (*Erodium moschatum* and *E. arborescens*), and Cistaceae (*Helianthemum vulgare*, *H. croceum* and *Cystus salviaefolius*), which are not crop plants.

12.2 Life Cycle

There is large uncertainty about the life cycle of this species. According to Gómez-Bustillo (1979), the moth's flight period extends from June in the northern and central Spain to September/October in Andalusia. Agenjo (1941) reported moth catches in May, August, September, and October. Larvae are reported to be present from October to April (Gomez de Aizpura 1986). During our small survey in coastal NW Spain, larvae of different instars (second to fifth) were found in April and gave origin to adults emerged in July under laboratory conditions, while in the field moths have been observed between July and September (unpublished data). It is thus possible that the life cycle depends on local weather patterns and host plant phenology. Moths lay eggs on low plants, grouping them in cylindrical batches. Larvae show a gregarious behaviour as they stay in groups of about 20–30 individuals piled up on the ground, forming a small cluster without silk (Fig. 2.4). A silk protection is reported just in the northern and central part of Spain, but not in Andalusia (Gómez-Bustillo 1978). In the sunny days they move in processions with a triangular shape, separating to feed on the low vegetation around, and regrouping again after it. They usually feed during the night and in the morning.

Larvae have a bluish grey appearance, and are covered by hairs of the same colour during the first two instars; in the next larval instars yellow-green tufts interspersed with grey appear on the back until the last moulting, probably to mimic the surrounding vegetation (for example *Ulex europaeus*). Larvae pupate in the ground at a low depth between March and April in the south of Spain. Larvae were not reported to be irritant (Agenjo 1941) although they carry urticating setae as in the other species of the genus (unpublished data).

12.3 Natural Enemies

The larvae are parasitized by unknown tachinids and preyed by the carabid beetle *Macrocarabus lusitanicus* (Pino, unpublished data from north-western Spain).

12.4 Population Dynamics

No information is available.

12.5 Relationships with Climate Change

No information is available.

13 Pheromones Within Processionary Moths, *Thaumetopoea spp.*

Brigitte Frérot

13.1 Introduction

The field of chemical ecology and the identification of chemical signals open the opportunity to manipulate the insect behaviour in order to decrease the impact of the pest on crop or forest. Sex pheromones in Lepidoptera are female-produced chemicals that attract the conspecific males, induce courtship behaviour and mediate reproduction (Fig. 2.13). A significant number of the sex pheromones in Lepidopteran pests were identified and are compiled on the website “The

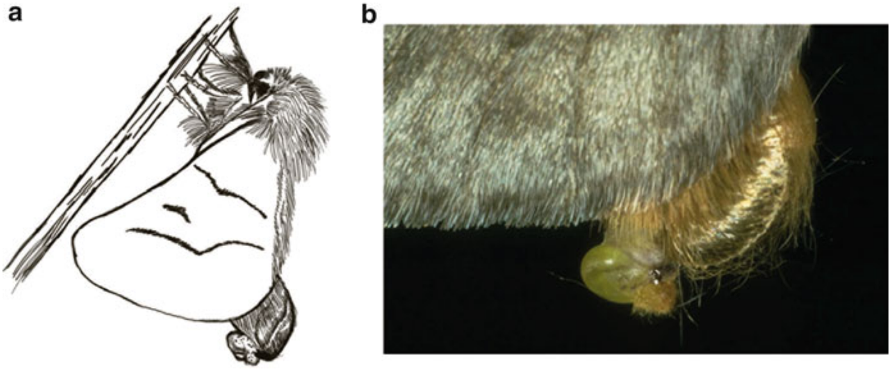

Fig. 2.13 Calling behavior in females of *Thaumetopoea* spp.; (**a**) calling posture; (**b**) Detail of eversion of the pheromone gland during calling behavior (Photo and drawing Guy Démolin)

Pherobase" (http://www.pherobase.com). In some social lepidopteran species chemical communication was also evidenced to contribute to maintain the cohesion of larvae colony through the deposit of a trail pheromone (Fitzgerald 1995, 2008; Ruf et al. 2000). The development of new control methods like larval disruption could be of interest.

13.2 Sex Pheromones in Thaumetopoea spp.

13.2.1 Winter Processionary Moths

Sex pheromone study in processionary moths started in 1980 with the identification of an unique and original pheromone structure in *Thaumetopoea pityocampa*, (Z)-13-hexadecen-11-ynyl acetate (Yne 11, Z13-16: Ac) (Guerrero et al. 1981) (Fig. 2.14a). It was the first time that such a chemical with an enyne bond was identified as a sex pheromone. This compound was then synthetized using different routes (Camps et al. 1983; Gardette et al. 1983; Shani et al. 1983). It displayed a high attraction for conspecific males when formulated as a bait in traps, leading to the development of new tools for monitoring populations of pine processionary moth (see Martin et al. 2014, Chap. 9, this volume). The synthesis did not provide a pure component and a limited proportion of the E11 isomer is present in the synthetic chemical. Different behavioural and trapping experiments showed that this isomer did not act as a synergist neither as a negative signal especially when in little amount (Quero et al. 1995).

Because the lepidopteran species producing a single component in a sex pheromone are rare (http://www.pherobase.com), the search for possible minor components was actively carried out using all the improvements in pheromone research technologies (Quero et al. 1997). The conclusion was that this pheromone is really characterized by a single component.

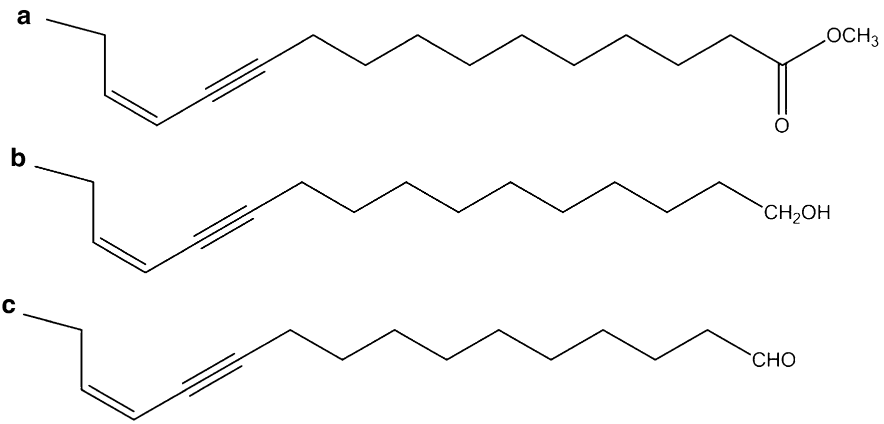

Fig. 2.14 Pheromone structure in *Thaumetopoea* spp. (**a**) *T. pityocampa* and *T. wilkinsoni*; (*a*, *b*, *c*) *T. jordana*

The sister species of *Thaumetopoea pityocampa*, *T. wilkinsoni* from Asia Minor, was shown to share the same sex pheromone, thus also including a single component (Frérot and Démolin 1993). Field experiments confirmed that *T. wilkinsoni* and *T. pityocampa* were attracted by the same compound. These two processionary moths shared also the same behavioural traits concerning female calling behaviour and mating period, which were observed during the first part of the night, some hours after imago moulting. Actually, individuals of *T. wilkinsoni* collected in Israel were shown to be capable of interbreeding with *T. pityocampa* when artificially kept together (Démolin, unpublished data).

An enyne pheromone pattern was also found in *Thaumetopoea jordana*. In this species the sex pheromone was identified as a complex blend of Yne 11, Z13-16: Ac 10 %, (Z)-13-hexadecen-11-yn-1-ol (Yne 11, Z13-16: OH) 50 %, (Z)-13-hexadecen-11-yn-1-al (Yne 11, Z13-16: Al) 40 % (Frérot and Démolin 1993) (Fig. 2.14a, b, c). Unlike *T. pityocampa* and *T. wilkinsoni,* this species does not develop on conifers but on Anacardiaceae, and, phylogenetically, it likely belongs to a different clade within the genus *Thaumetopoea* (see Kerdelhué et al. 2014, Chap. 4, this volume, part 2).

13.2.2 Summer Processionary Moths

All the summer processionary moths were subject to pheromone identification, except *T. libanotica* still under investigation and for which results are not yet been published.

In the oak tree processionary moth, *T. processionea*, the sex pheromone was investigated from a gland extract obtained from a French population. The analyses by GC-MS lead to the identification of a mixture of (Z,Z)-11,13-hexadecadienyl

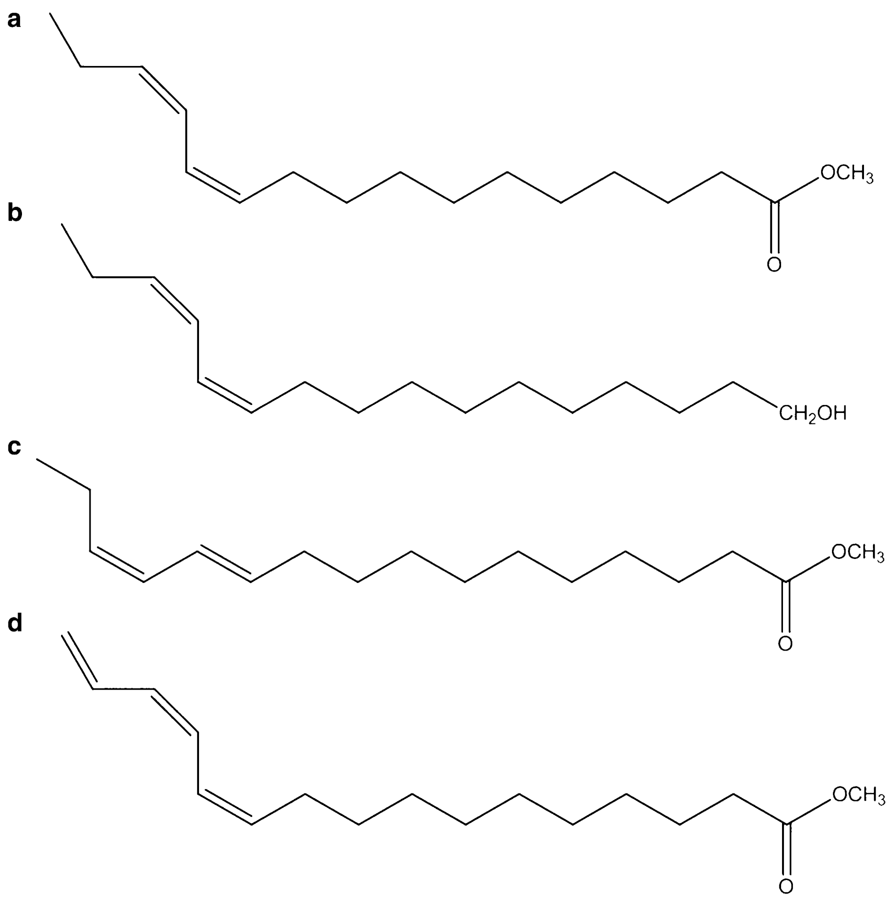

Fig. 2.15 Pheromone structure in *Thaumetopea processionea*

acetate 95 % (Z11, Z13-16: Ac) and (Z,Z)-11,13-hexadecadienol 5 % (Z11, Z13-16: OH) (Frérot and Démolin 1993) (Fig. 2.15a, b). Field experiments confirmed the attractiveness of this mixture but in Spain the females were significantly more attractive than the synthetic blend. Reinvestigation of the pheromone composition in a Spanish population evidenced an additional minor component, corresponding to an isomer of the previously identified diene acetate, (E,Z)-11,13-hexadecadienyl acetate (E11, Z13-16: Ac) (Fig. 2.15c) (Quero et al. 2003). The E,E isomer was shown to inhibit male attraction, pointing out that the purity of the main component is a crucial point to be kept in mind for trapping success (Breuer et al. 2003). Indeed, dienic compounds are hardly obtained free of geometric isomer by synthesis. They do not remain stable when formulated in caps and left under outdoor conditions. However 0.1 % of the E,E isomer can be tolerated. The E,Z isomer present in the extract was not proven to increase the level of attraction and should be as the other

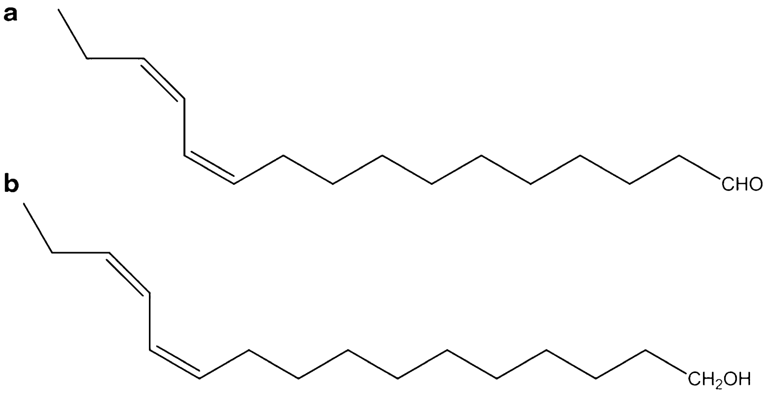

Fig. 2.16 Pheromone structure in *Thaumetopoea pinivora* and *T. bonjeani*

isomers present in the synthetic chemical. Therefore, the described formulation is as follows: Z11, Z13-16: Ac 88 %, E11, Z13-16: Ac 7 % and Z11, Z13-16: OH 5 %.

Later, Gries et al. (2004) also reinvestigated the sex pheromone composition in a German population of oak processionary moth. The presence of Z11, Z13-16: Ac was confirmed but a second additional compound was identified, (Z,Z)-11,13, 15-hexadecatrienyl acetate (Fig. 2.15d). The blend of 50/50 of both components was further reported as attractant in field trappings. These contrasted results depending on the population origin point out the need for further behavioural and/or field experiments on sex pheromones produced by the different populations all over the range of oak processionary moth.

Two other summer processionary moths, but conifer-feeding, *Thaumetopoea pinivora* and *T. bonjeani*, were described as closely related species based on systematics and biology. Male genitalia of both species bear the same pattern such as female abdominal scales do. Larvae of both species have a gregarious behaviour but without building a conspicuous tent. Sex pheromone identifications corroborated the similarities between both species which appeared to share the same blend, (Z,Z)-11,13-hexadecadienal 80 % (Z11, Z13-16: Al, Fig. 2.16a) and (Z,Z)-11,13-hexadecadienol 20 % (Z11, Z13-16: OH) (Fig. 2.16 a, b) (Frérot et al. 1990). The sex pheromone of a related conifer-feeding moth, *Thaumetopoea libanotica*, was investigated by Nemer and Frérot (unpublished data) by GC-MS analyses of pheromone glands and field trappings. The work confirmed that this species is very closely related to *T. bonjeani*.

Sex pheromones were also tentatively identified in another summer processionary moth but developing on *Pistacia* spp. under desert conditions, *Thaumetopoea solitaria*. Analysis of a few female gland samples evidenced a single compound characterized by 18 carbons and 2 double bonds at the putative positions 13 and 15 on the carbon chain. These results obtained around 1990 should be reinvestigated once the reproductive behaviour, i.e. timing of calling behaviour or mating, will be better known.

13.2.3 Concluding Remarks

Pheromone compounds identified in *Thaumetopoea* spp. shared the same pattern: a long chain with 16 atoms of carbons and bonds located at positions 11 and 13. The systematics of the group appeared homogeneous on the base of the pheromone chemistry, characterised by the enyne bond which is original within Lepidoptera. There is a correlation between the biological group to which the processionary moth belongs, winter versus summer, and sex pheromone chemistry.

Most of the identified pheromones are efficient for male trapping except in some populations of *T. processionea* that should be re-investigated. The sex pheromone of *Thaumetopoea herculeana* a processionary moth developing on Cistaceae and Geraniacae (Gomez Aizpurùa 1986), remains to be studied.

13.3 Trail Pheromones in Pine Processionary Larvae

Thaumetopoea pityocampa accomplishes as a larva different types of displacements called “processions”. The first type of procession is related to food consumption and concerns larvae of all instars developing together into a silky tent but feeding outside on pine needles. Larvae leave the tent together, following each other to forage on needles and once the feeding achieved crawl back to the protective tent by following the same path.

A second type of procession is exhibited by the last-instar, mature larvae searching for pupation into the soil. This behaviour was minutely described since a long time by Fabre (1899). The gregarious behaviour was associated by a head-to-tail displacement with tight links between all individuals forming the procession subject to tactile stimuli produced by movement of cuticular setae located at the end of the forehead larva abdomen. The stimulus acting on the head of the following larva were evidenced as an important cue for the procession (Démolin 1962, 1969a, 1969b). More broadly, tactile contacts were considered by Démolin (1969a, 1969b, 1971) as the basis of a “social memory” steering the initiation of the procession behaviour, and then reinforcing it along the way.

13.3.1 Trail Pheromones During Foraging Processions of Early-Instar Larvae

Early-instar larvae of *T. pityocampa* were known for a long time to maintain a social link via a silky pathway, a kind of “Ariadne” strand that can contribute to guide the larvae back to the tent during the feeding procession. However, the evidence of a trail pheromone was obtained only rather recently (Fitzgerald 2003). The second-instar larvae were experimentally showed to leave a marking trail during a foraging procession, and it was proved that this trail is acting on the behaviour of conspecific larvae, maintaining the procession cohesion. As the role of the silk produced by the larvae was investigated in this process, it appeared that no left silk seems necessary to mark trails nor to maintain processions. However, silk may play a subordinate role to trail pheromone, its function having being hypothesized to enhance steadfastness (Fitzgerald 2003). Despite their essential role in allowing larvae to move efficiently to and from the tent, chemical cues appear of less importance than tactile ones. Fitzgerald (2003) indeed noticed that the larvae unable to spin silk or to mark the substrate with the trail pheromone are still able to form processions suggesting that tactile cues alone may be adequate to allow larvae to form and maintain processions.

The trail pheromone is likely to be deposited by the ventral part of the larva body, with the ventral tip of the abdomen as the primary source. Fitzgerald (2003) also demonstrated that an acetone extract of both larvae and silk induces an attractive response on second-instar larvae. However, choice tests revealed that the effectiveness of the extracts largely varies over time, early-instar larvae preferring fresh trials. Moreover, recent, yet unpublished experiments additionally suggested that the pheromone trail is not specific to the larval colony. The trail left by a colony induces similar positive reactions on larvae randomly selected from other colonies (Yart et al., unpublished data).

13.3.2 Trail Pheromones During Pupation Processions of Mature Larvae

According to Fitzgerald (2003), the role/importance of chemical cues might have declined when prepupal larvae are leaving the tent in search of pupation sites. Neither silk nor the deposit of a trail signal seems to be required. The same observation was previously reported by Démolin (1971), who also quoted that lost or isolated larvae were seeking for conspecific. During this step, thigmotactic cues could take the priority, with a crucial role of stimuli associated with setae found on the tip of the abdomen of the preceding larva in the procession (Démolin 1969a, 1969b, 1971; Fitzgerald 2003). In contrast, Fabre (1899) reported that mature larvae are following silky strands during pupation processions. Our own, recent results (Yart et al., unpublished data) were also contrasting with those of Fitzgerald and Démolin cited above. A large production of silk was observed at all instar larvae, even the last one. Prepupal larvae were also found to be able to deposit and to discern a chemical trail since they preferentially use in a Y maze (glass Y-shape tube) the branch where conspecific larvae passed through (64 % against 36 %; $n = 546$, binomial test, $p < 0.001$). Unfortunately, the GC-MS analyses of larvae extracts did not lead to identification of any chemicals responsible for this behaviour.

13.3.3 Conclusions

Candidate compounds as trail markers were identified in other gregarious lepidopteran species. Fitzgerald (1995) and Fitzgerald and Webster (1993) showed 5β-cholestane-3-one to be a component of the trail marker for the foraging larvae of the eastern tent caterpillar, *Malacosoma americanum* (Lepidoptera: Lasiocampidae). Ruf et al. (2000) observed that the larvae of another lasiocampid moth, *Eriogaster lanestris*, readily followed trails prepared with the same compound. However, the identity of possible trail markers remains still unknown in pine processionary moth despite efforts (Fitzgerald 2003). Such an identification is a challenge for the future, and could be promising for the development of larval disruption techniques.

14 General Conclusions

The life history traits of the processionary moths of the genus *Thaumetopoea* can be generally divided into three groups (see also Kerdelhué et al. 2014, Chap. 4, this volume). The first two, i.e. the summer and winter pine processionary moths, are associated with coniferous host plants while the third is associated with broadleaf trees and shrubs. The switch to coniferous host can be seen as one of the amazing traits of the genus, also because it has been shown to be successful in terms of speciation and performance. It has coincided with the switch from the summer feeding to the winter feeding, and consequently with the change of the pupal diapause from winter to summer. These dramatic changes in the life history seem to be justified by the possibility to feed for a longer period of time, and mainly when competition with other herbivores is almost absent. The best example of such an adaptation is the group of the winter pine processionary moths (*T. pityocampa* and *T. wilkinsoni*), which are by far the most widely distributed and abundant species in the genus. Because of this special adaptation to winter feeding, based on a precise physiological reaction to temperature, they also result to respond directly to climate change by expanding the range into previously unsuitable regions. Although similar responses have been claimed for species of the other groups, both conifer and broadleaf feeding, there is no clear indication that climate change is driving the range expansion or any other type of recent shift, such as pestilence level. This is, however, an open question and must be addressed in the future. In addition, there are many other aspects of the life histories which are still poorly known and would contribute to a better comprehension of the ecology of the species. The availability of data about the species of Central Africa, Arabic peninsula, and south-western Asia is also essential for the definition of the evolutionary history of the genus and to predict the effects of the global change.

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Chapter 3
Climate Warming and Past and Present Distribution of the Processionary Moths (*Thaumetopoea* spp.) in Europe, Asia Minor and North Africa

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1 Introduction

The pine processionary moth, *Thaumetopoea pityocampa*, has been retained by the Intergovernmental Panel on Climate Change (IPCC) as one of the few model insect used as indicator of global warming (Rosenzweig et al. 2007). Indeed, the most striking feature consists of an expansion of the geographical range of this Mediterranean species, which is acknowledged to be directly associated with the

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recent climate warming up (Battisti et al. 2005). The understanding of the factors possibly governing moth natural expansion has largely progressed during these recent years. Thus, this chapter will first present a synthesis of the current knowledge about the drivers of moth expansion.

Although the range expansion has been precised in France (Robinet et al. 2012, 2014), it remained to be assessed all over Southern Europe in order to understand

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whether the moth response to climate change is identical in the different regions of the continent. Therefore, a first map of the current northern edge of moth expansion, from Western Europe to Turkey, will be presented. Then, the corresponding data will be detailed per country in a quite standardized format

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allowing to compare the moth situation among the different parts of the range. The major part of the moth range will be covered, with a total of 20 countries specifically addressed. Data will concern the present biogeographical range, the population dynamics and the past outbreaks, the particular biological features observed in the country, the host range, the current expansion and the trends expected for the future.

By contrast, the response of the other species of *Thaumetopoea* to climate change remains little known or a matter of debate, and in some cases even their present geographical distribution is still imprecise. The chapter will present a synthesis of the knowledge regarding these species.

Finally, it appeared that moth expansion could combine natural insect dispersal with man-mediated translocations. It is likely that such translocations existed since long ago but climate change may allow at present insect establishment in areas located far beyond the natural range of the insect (Robinet et al. 2012). The last section of the chapter will point out the importance of these man-mediated introductions in the expansion process.

2 What Are the Drivers of the Pine Processionary Moth's Expansion?

Mathieu Laparie and Alain Roques

2.1 Introduction

Climate warming is assumed as the main factor responsible for the aforementioned range expansion of the pine processionary moth in Europe (Battisti et al. 2005). While changes in the distribution of ectothermic organisms as a result of climate change have now been widely acknowledged and often associated with physiological limits of organisms (Walther et al. 2002; Root et al. 2003; Chown et al. 2010), the causal relationship with range edges have rarely been determined. In the pine processionary moth, however, supportive data from a number of experimental and modelling approaches show how climate warming has lowered – or removed – climatic barriers to its expansion towards higher latitudes and elevations. Although the comprehensive response of this species to climate change has not been untangled yet, its developmental limits are being delineated and have revealed the crucial importance of warming on the ongoing expansion.

2.2 Thermal Biology and Susceptibility of Larvae to Climate Change

Battisti et al. (2005) reemphasized that species active during winter are comparatively more impacted by climate warming, as average minimum temperatures have been increasing at a higher pace than average maximum temperatures (Easterling et al. 1997). In winter-developing species such as the pine processionary moth, the expected outcomes of warming winter temperatures are both higher survival rate and higher larval growth rate. While such changes may elicit dynamics in core populations, they become critical at range edges when species are constrained by their developmental thresholds. Provided that host trees are present, progressive warming will push the geographical limits of suitable habitats and enable the colonization of previously inappropriate pristine areas. First, global warming should on average reduce the likeliness of encountering lower lethal temperatures (LLT) in the coldest areas (Gaston 2003), thereby directly enhancing immediate survival. The process may be more complex in nature though, as even with increasing average temperature, lower lethal temperatures mostly occur stochastically for short durations, and climatic models predict increased likeliness of extreme events (Parmesan et al. 2000). Second, increased growth rate allows faster development and improves the ability to complete full development in previously unsuitable areas.

2.2.1 Thermal Changes Directly Alter Larval Survival in the Natural Range and Surrounding Areas

The pine processionary moth was classified as a moderately freezing tolerant insect, with an average supercooling point of −7 °C but a capability to survive cooler temperatures down to a LLT of −16 °C (Battisti et al. 2005; Hoch et al. 2009). Hoch et al. (2009) further demonstrated survival to cooler temperatures for short durations while in tents: they found more than 70 % of survivorship in larval colonies after gradual decrease to −17 °C, sustained exposure for one hour, and gradual return to 5 °C. However, the study revealed cumulative chill injury in larvae: despite the ability to survive short freezing events, larval survival decreases as larvae accumulate exposure to sub-zero temperatures (Fig. 3.1), which are rather frequent during winter in the actual range in nature. This finding further supports the beneficial effects of climate warming in edge populations, as it consolidates fitness and recruitment in colonized areas while broadening past bioclimatic envelope. Of note, Hoch et al. (2009) found rather large variance in individual supercooling points and a significant converse relationship with survival to cold exposure. Such variance may provide fuel for adaptive selection across the range of the pine processionary moth, and further studies should therefore investigate the heterogeneity of the response to temperature. Differentiation among populations may significantly alter pine processionary moth's future expansion.

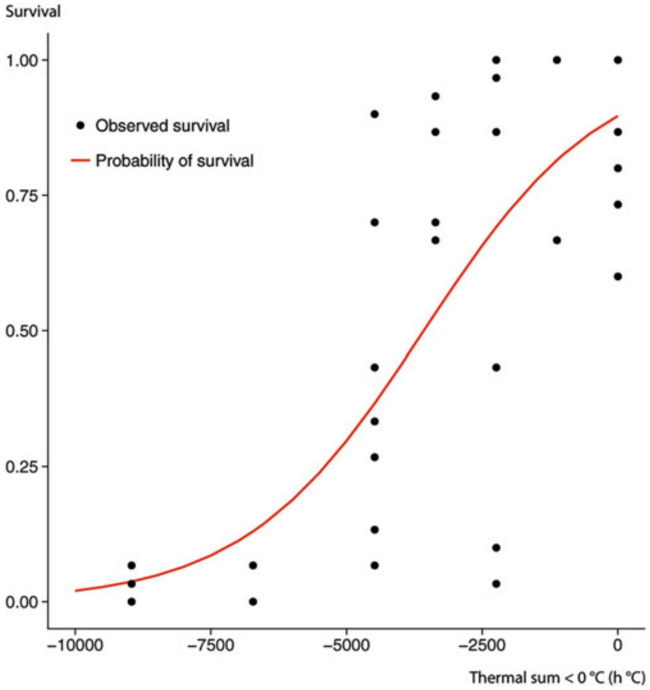

Fig. 3.1 Probability of survival and observed survival of *Thaumetopoea pityocampa* larvae depending on accumulating negative temperatures (sum of h°C below 0 °C) in a laboratory experiment (Modified from Hoch et al. 2009)

2.2.2 Feeding Activity and Its Outcomes Depend on Thermal Thresholds

Using faeces production as a surrogate of feeding activity and an automatic measuring setup, Battisti et al. (2005) have outlined how temperature modulates feeding activity and indirectly impacts growth rate and long-term survival.[1] The authors demonstrated that feeding behaviour of the pine processionary moth is governed by the combination of thresholds during consecutive day and night, *i.e.*, an Activation Temperature (AT) during daytime and a Potential Feeding Temperature (PFT) during the following night. The Realized Feeding Threshold (RFT) is the duration for which both prerequisites are consecutively met, *i.e.*, the duration larvae can actually spend feeding on needles. Battisti et al. (2005) exposed colonies to a range of thermal regimes and determined that foraging is enabled when AT

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[1] Direct effects of temperature on physiological processes and metabolic kinetics are also to be expected in ectothermic organisms (Liu et al. 1995). Their impact on development may be assessed from degree-days summations.

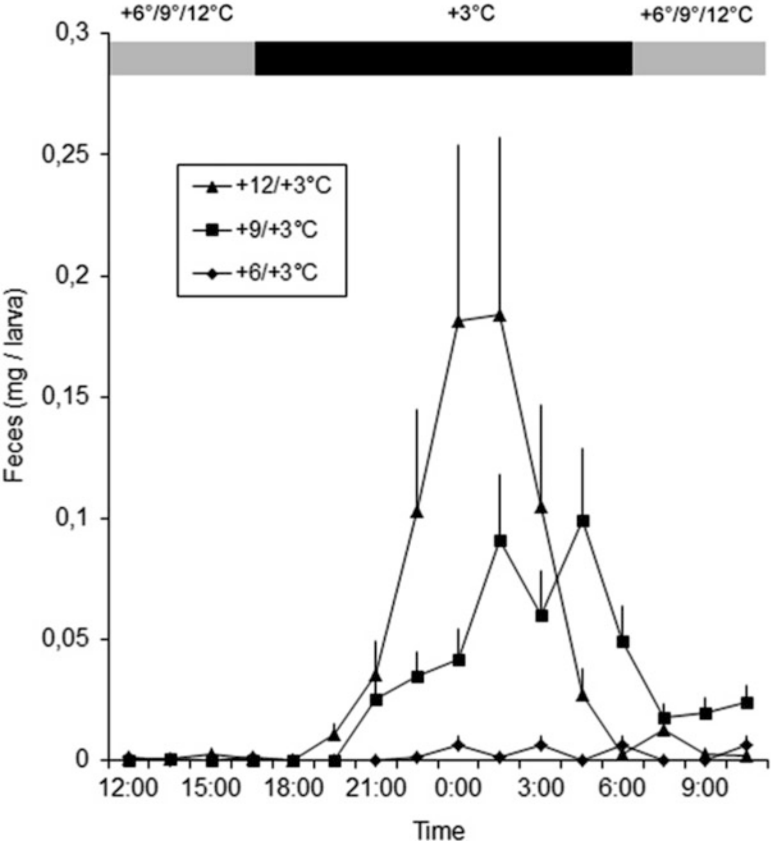

Fig. 3.2 Mean feeding activity of *Thaumetopoea pityocampa* colonies under different temperature regimes, measured as feces production (+SD). Temperature was changed through steps of 0.3 °C/min at the switch of the photoperiod (08:00 and 16:00, shown as *gray*/*black* changes in *horizontal top bar*). No feeding activity was recorded under a +3 °C/+3 °C treatment and +6 °C/0 °C (not shown) (Modified from Battisti et al. 2005)

exceeds 9 °C[2] and PFT exceeds 0 °C the following night (Fig. 3.2). As a consequence, larval feeding is strongly dependent on average winter temperatures, which are consistently rising with climate change. The resulting increased feeding activity may have manifold beneficial effects, such as accelerated development and ability to complete it in due time at high latitude or elevation, shorter fasting periods, and improved survival in areas with adverse conditions.

The feeding model and its role on survival were verified in a seminatural experiment of colony translocations along an expansion gradient from the historical areas to recently colonized areas and areas beyond the contemporary range in north-central France (Battisti et al. 2005). The experiment confirmed a significant decrease in

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[2] Actual feeding was observed starting from AT >6 °C, but 9 °C was chosen as a conservative value to ensure that larvae experienced induction for at least 1 h.

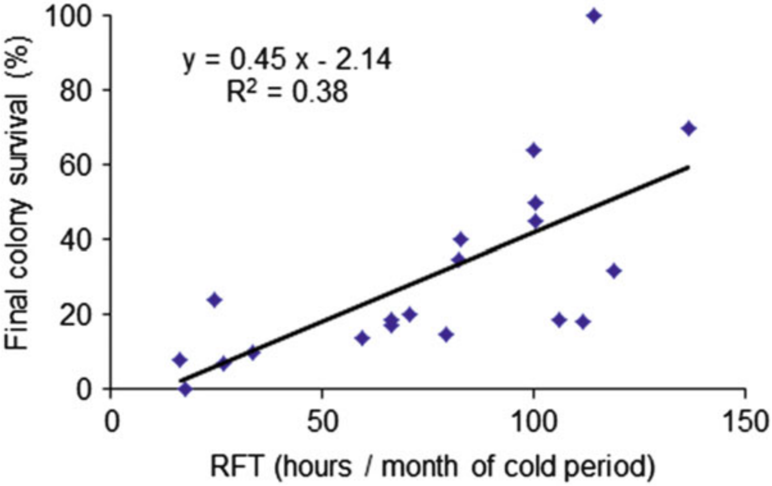


Fig. 3.3 Survival of pine processionary colonies measured at procession time as a function of the number of hours above the realized feeding threshold (RFT) during the winter cold period (October–March) (Modified from Battisti et al. 2005)

larval survival in the newly colonized areas and in those located beyond the front in relation with the harsher winter conditions occurring there. Moreover, the measured feeding activity during comparatively cold months was consistent with the predictions of the feeding model: it gradually decreased with reduced RFT at increasing elevation and latitude, ultimately resulting in lowered survival rates (Fig. 3.3).

2.3 *The Causal Influence of Winter Thermal Constraints on Pine Processionary Moth's Range*

Firmly demonstrating the not only facilitating but causal effect of climate warming on the ongoing expansion requires confirming that past range limits were determined by thermal constraints. Robinet et al. (2007) used a mechanistic model to reconstruct the temporal evolution of the bioclimatic envelope assumed from both the aforementioned thermo-biological parameters and the long-term climatic records, and observed a partial match with the expansion actually monitored in the Paris basin. The modelling highlighted that the number of feeding nights followed an intense latitudinal gradient, and considerably shifted northwards over time. Moreover, the moving range of habitat suitability confirmed that thermal barriers to the northward expansion existed in 1992–1996 but disappeared in 2001–2004 (Fig. 3.4), concomitantly with the progression of the pine processionary moth towards Paris. Noteworthy, the predictions suggest that the species is no longer limited by climatic constraints in the Paris basin.

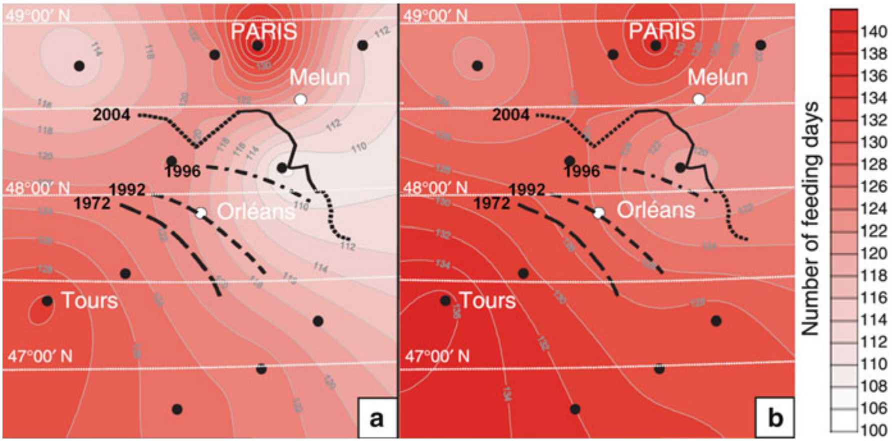


Fig. 3.4 Spatial changes in the feeding potential of processionary larvae in the Paris basin from 1992–1996 (**a**) to 2001–2004 (**b**). The number of nights with potential feeding increases from *white* (low) to *red* (high) according to the scale on the right. *Black lines* indicate the position of the front edge at different years (Modified from Robinet et al. 2007)

Although such a process remains to be verified in other parts of the range, especially in South-eastern Europe, it is likely that the future distribution of *T. pityocampa* rather depends on availability of host trees and dispersal of females (Robinet et al. 2007). Host trees being non-limiting in Europe (Battisti et al. 2005; Robinet et al. 2007), this finding triggers a warning signal as the expansion dynamics could increase dramatically in a near future; they may namely be greatly facilitated by accidental human-mediated long distance dispersal events (Robinet et al. 2012, 2014).

2.4 *Increased Summer Temperature and Extreme Summer Climatic Events Have Mixed Effects on the Pine Processionary Moth's Distribution*

Long-term monitoring of the pine processionary moth provides further support to the tight relationship between its expansion and climate warming (Hill et al. 2002; Crozier 2004; Hickling et al. 2005). Nonetheless, the effects of short-duration changes such as summer heat waves on short-lived adults have long been underestimated (Battisti et al. 2006). Flight activity of females was found to occur starting from 14 °C, and to be significantly correlated with mean night temperature (Battisti et al. 2006). The pine processionary moth can therefore benefit from increased summer temperature to colonize new areas, as long as the heat wave period covers the emergence peak and flight window of females. Consistent with this assumption, unprecedented expansion was observed in the Italian Alps following the historical 2003 heat wave (Battisti et al. 2006). This significant range leap

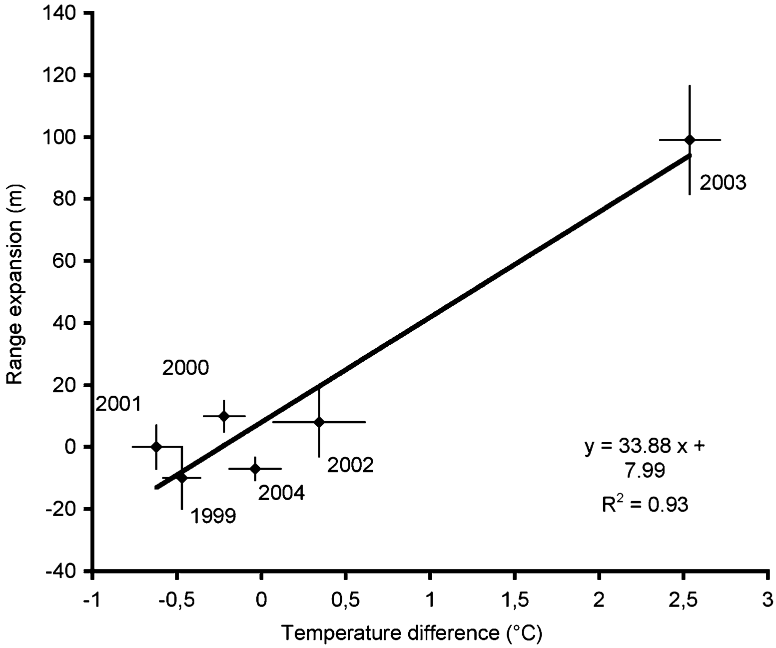


Fig. 3.5 Relationship between the annual expansion (±) of *Thaumetopoea pityo*campa in the Italian Alps and the temperatures conditions occurring during the female flight period. Temperature difference (±) is expressed as the difference between the mean night temperature of this period in each year and the corresponding average of the period 1951–2004 (Modified from Battisti et al. 2006)

was associated with a strong increase of 2.4–3.5 °C in the night temperature during female flight period compared to the mean temperature recorded in the other years of the period 2001–2004, resulting in an average of 5.3 times more nights above the take-off threshold (Fig. 3.5; Battisti et al. 2006),

Contrasting from the increase of winter temperatures which presumably promotes the pine processionary moth's dynamics all over its range, extreme heat events may have mixed effects depending on topography and regions. Although the 2003 summer heat wave dramatically accelerated the expansion in Italian Alps (and putatively other high elevation regions), it had detrimental effects on populations within the Paris basin where a temporary regional collapse occurred (Robinet et al. 2013). Likely explanations are multiple and encompass both direct and indirect factors. Among direct factors, reaching of upper lethal temperatures and disruption of mating behaviour appear as relevant candidates. Increased mortality of eggs – the expected dominant life stage during the 2003 heat wave – under the temperatures experienced during the abnormal summer was experimentally rejected, and no developmental penalties were found in individuals further monitored till third instar (Robinet et al. 2013). Indeed, eggs masses could survive temperatures of 40 °C for several days (also observed in Portugal by

Santos et al. 2011b) and their upper lethal temperature threshold is undoubtedly much higher than the 32 °C previously reported by Huchon and Démolin (1970). Whether the value was underestimated or the discrepancy highlights ongoing adaption to global warming in the expanding populations is not known yet. The susceptibility of first instar larvae should now be similarly investigated because eggs likely better resist heat and desiccation than newly-hatched larvae (Santos et al. 2011b). Moreover, given the expectation that the heat wave accelerated egg development and caused early hatching peak, a significant proportion of first-instar larvae may have experienced the heat anomaly and suffered desiccation and/or thermal stress. Finally, whether and how temperature above the flight threshold alters mating behaviour remains unknown. However, the catches of flying females in 2003 matched the expectations for regular summers, which shows that extreme temperature in the Paris basin did not cause the collapse by disrupting adult dispersal.

Warming during late summer and autumn presumably accelerates the development of early larval instars. The effect of such an acceleration on the overall development of pine processionary larvae is yet unknown but early, erratic processions are at present frequently recorded with the regard to the usual cycle reported in the past (Huchon and Démolin 1970).

Possible outbreaks following favourable years may have indirect detrimental effects on the longer term. Tamburini et al. (2013) reported a negative density-dependant feedback with a 1-year time lag in several alpine populations. Density-dependent factors possibly driving pine processionary moth’s dynamics include lowered host quality and increased risks of pathogen or virus epidemics (Tamburini et al. 2013). Food shortage associated with larval overcrowding may outweigh the beneficial effect of increased temperatures on development time. This may delay processions and result in insufficient time to complete metamorphosis before the emergence and mating peak (Démolin 1990). Completing metamorphosis while maintaining synchronous emergences may therefore rely on prolonged diapause, an adaptive mechanism that was also suggested as a way to dodge outbreak-induced adverse conditions (Tamburini et al. 2013), and contributes to the apparent drop in trapping rates following outbreaks. Prolonged diapause is also generally assumed as a bet-hedging strategy to deal with unpredictable events (Menu and Debouzie 1993), which suggest a density-independent component. This is consistent with comparatively high frequency of prolonged diapause found in pine processionary moth’s populations at high elevation (Géri 1983a, b). Overall, prolonged diapause may prove being fundamental in the sustained expansion of the pine processionary moth despite the mitigating effects the species may encounter at its range margins: it helps both (i) withstanding consequences of outbreaks in areas with few host trees, and (ii) rapidly overcoming the negative effects of stochastic extreme climatic events, as observed with the rapid recovery in the Paris basin after 2003.

3 Mapping the Past and Present Range of the Pine Processionary Moth in Europe and the Mediterranean Basin

Christelle Robinet and Jérôme Rousselet

The pine processionary moth, *Thaumetopea pityocampa*, is present in regions under the Atlantic and Mediterranean climates in Europe (Albania, Bosnia and Herzegovina, Bulgaria, Croatia, France, Greece, Italy, Macedonia, Montenegro, Portugal, Serbia, Slovenia, Spain and Switzerland), in a part of European Turkey and in North Africa (Algeria, Morocco, Tunisia and Lybia) (EPPO 2004; Kerdelhué et al. 2009). Its distribution was considered to be closely related to climatic constraints, especially winter and summer temperatures and annual sunshine duration (Huchon and Démolin 1970). The distribution range was relatively steady until the late 1990s but since then records revealed a significant expansion towards higher latitude and elevations in southwestern Europe, and this expansion was clearly associated to climate warming (Battisti et al. 2005; Rosenzweig et al. 2007).

Although this process has been precisely documented in some areas (see sections below), no global picture of the whole species' range from Europe to the Middle East and North Africa was available until now. Moreover, only partial and scattered maps of the past distribution were available to figure out the magnitude as well as the speed of the moth expansion over the last years. Therefore, it appeared essential to draw a reference map of the present distribution of *T. pityocampa* in Europe in order to allow an accurate measurement of the further moth expansion expected with global warming. Using a standardized method was required so that it can be applied exactly in the same way for comparison in the future.

The moth distribution, or more precisely its northern edge, was thus mapped all over Europe during winter 2011–2012, from Western France (Brittany) to the European part of Turkey (Eastern Thrace), over a regular grid of 16 km × 16 km (European projection Lambert Conformal Conic) (Fig. 3.6). The northern front edge was thus delimited over more than 3,000 km. The altitudinal edge was also precised in the Alps (France, Italy and Switzerland), in the Massif Central and the Pyrenees (France). Two pioneer colonies located far from the main species distribution (at approximately 90 and 160 km) were also clearly identified in France at this spatial resolution. In contrast, the 16 km resolution resulted in merging some other pioneer colonies located near Paris with the main distribution range (see section below; Robinet et al. 2012). In 2013, the most northern population of *T. pityocampa* corresponded to one of these pioneer colonies (N 49°30′; Chamouille).

However, it has not been yet possible to delimit the southern front edge of the species in North Africa due to missing information in this area. Assessing whether the southern edge of the species distribution is contracting or not with climate change thus remains challenging.

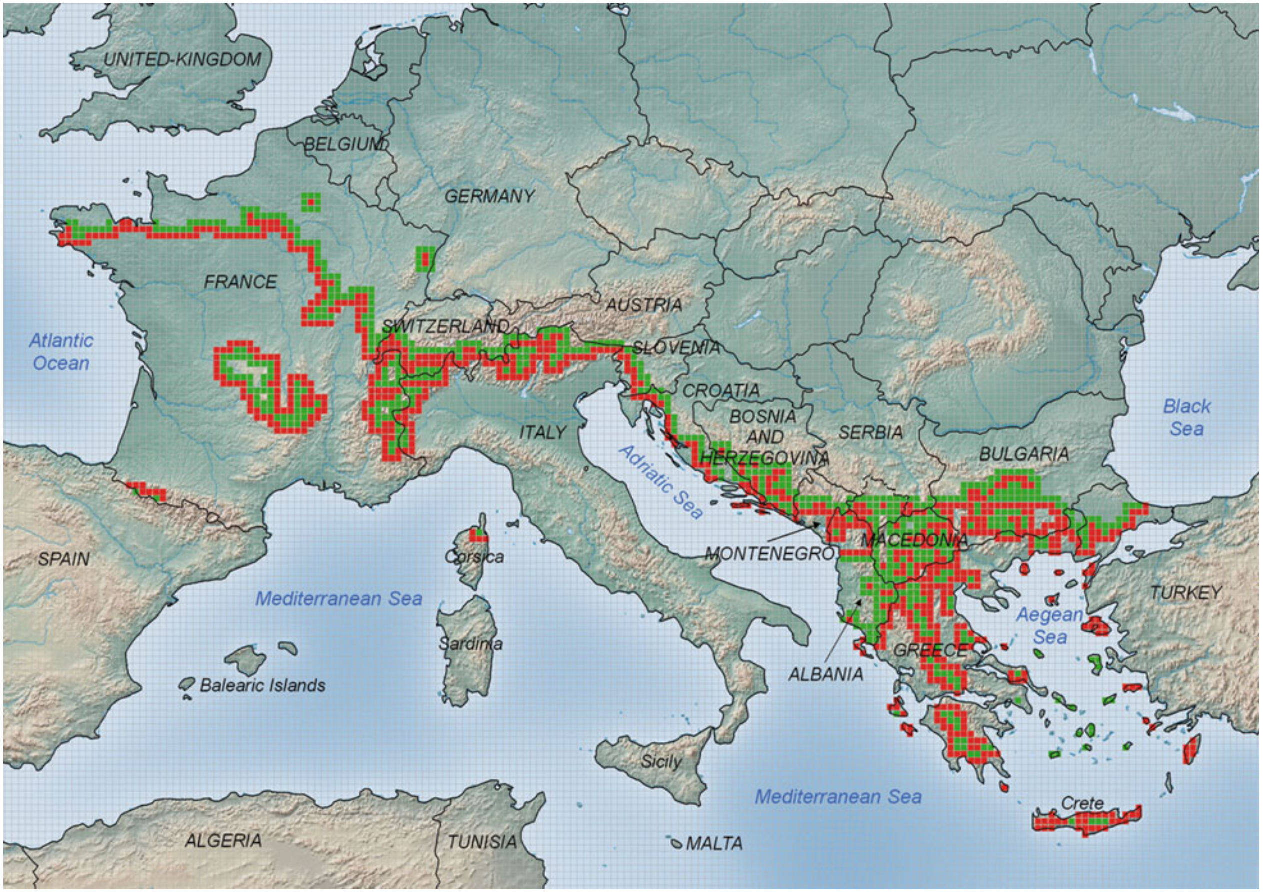


Fig. 3.6 The 2011–2012 front edge of the pine processionary moth throughout Europe figured over a 16 km × 16 km grid. Red squares represent the northern and altitudinal front, defined as the furthest squares where at least one processionary tent was found. *Green squares* indicate areas beyond the front where the absence of processionary moths has been clearly assessed

4 Past and Current Situation of the Pine Processionary Moth, *Thaumetopoea Pityocampa*, in Western and Central Europe

4.1 The Pine Processionary Moth in France

Christelle Robinet, Jacques Garcia, Francis Goussard, and Jérôme Rousselet

A northwards expansion of the pine processionary moth was first detected in the 1990s in the southern part of the Paris basin (Démolin et al. 1996; Goussard et al. 1999). In this region, the existence of historical maps of the species' past distribution allowed to draw accurately the movements of the front edge and assess the expansion patterns (Fig. 3.7). Moth spread rate reached up to ca. 5.6 km/year between 1992 and 2004 (Battisti et al. 2005) and is still reaching 4–5 km/year on average (Robinet et al. 2012).

The range expansion was particularly rapid in the South of the Paris basin (Fig. 3.7), but at country scale, there is also clear evidence of the northwards range expansion from Brittany to the Swiss border (Fig. 3.8) but also towards higher elevations in the Alps, in the Massif Central and in the Pyrenees.

Comparing maps drawn at different periods was anyway problematic because the survey methods differed along the years. Thus, since winter 2005–2006 the mapping of the distribution of the pine processionary moth in France has been standardized over a regular cell grid (e.g., at a spatial resolution of 8 km × 8 km for country scale mapping). It consists in assigning positively a cell as soon as a processionary larval tent is spotted within this cell. As soon as no tent is found when driving on all suitable roads, the moth is considered absent from the cell. However, the next cell beyond is surveyed in order to detect possible close-by satellite colonies, resulting for instance from a lack of host trees in the cell above. Finally, the front edge is drawn by connecting the adjacent positive cells where the species is present. Although time-consuming, this standardized method has to the advantage to be replicable in time and to provide both presence and absence data. It is very convenient to map species distribution at large scales and delimit the northern and southern edges but caution is needed in mountainous areas as the method is not suited to consider altitudinal limits as well as slope exposition which is largely affecting moth distribution.

4.1.1 Population Dynamics and Outbreaking Periods in the Past

Around 500 sites are currently surveyed in France every winter by the French Forest Health Department (DSF) on pine stands infested by the species for several years. This monitoring network allows reconstructing time series of the population dynamics since the early 1980s. Although the frequency and intensity of the

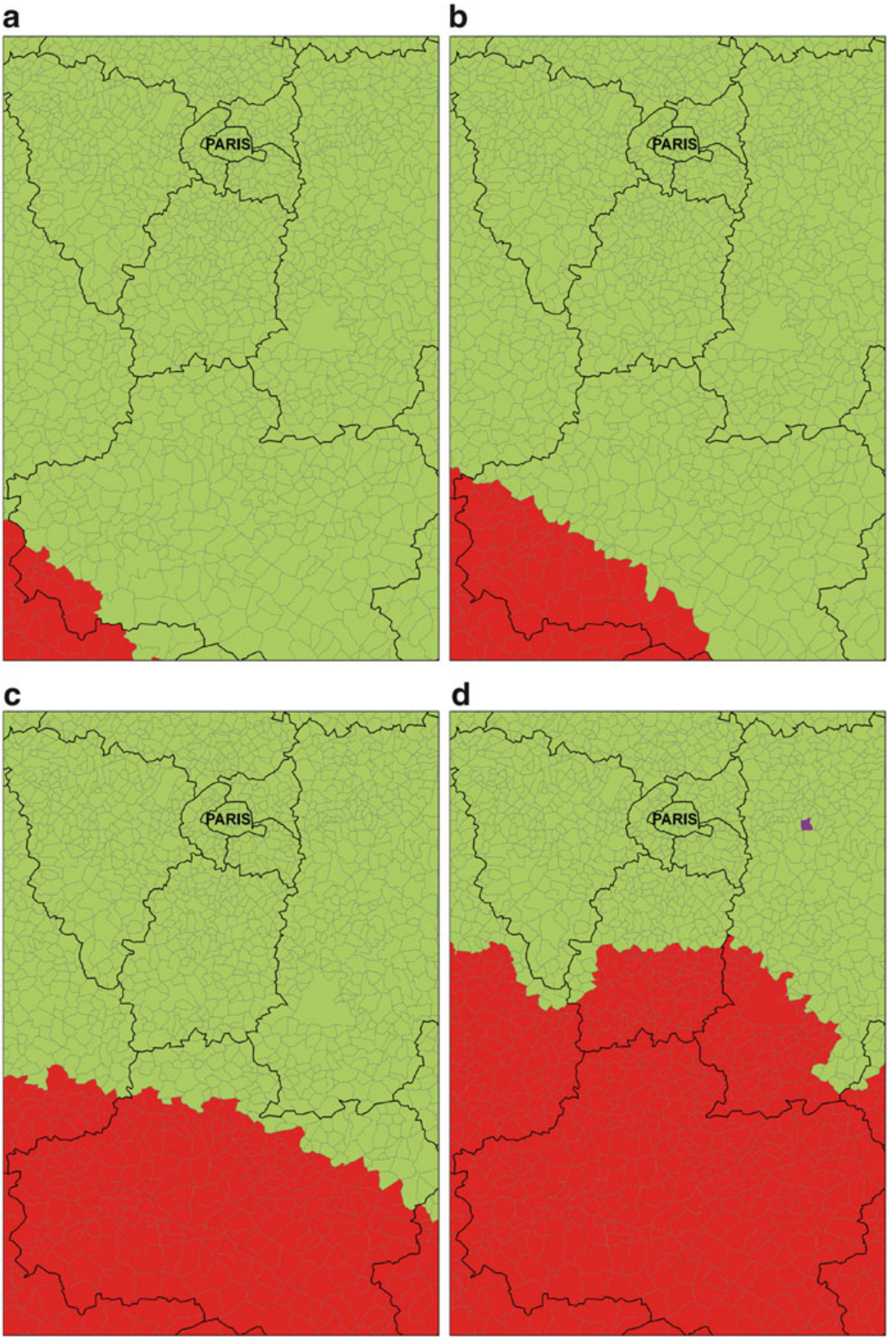


Fig. 3.7 Spatial expansion of the pine processionary moth in the South of the Paris basin from 1972 to winter 2010–2011. Areas with moth presence are figured in *red*. The pioneer colonies discovered near Paris since the 2000s are figured in *purple* (for more details, see Fig. 3.37). (**a**) 1972 (source: Abgrall 2001); (**b**) 1992 (source: Goussard et al. 1999); (**c**) 1996 (source: Goussard et al. 1999); (**d**) winter 2005–2006 (URZF INRA Orléans, unpublished); (**e**) winter 2010–2011 (URZF INRA Orléans, unpublished); (**f**) same as before but showing the new pioneer colonies having appeared or extended during winter 2011–2012. The spatial resolution is at town level, the *thin grey* features representing the administrative limits of the towns, and the *thick black* ones those of the departments

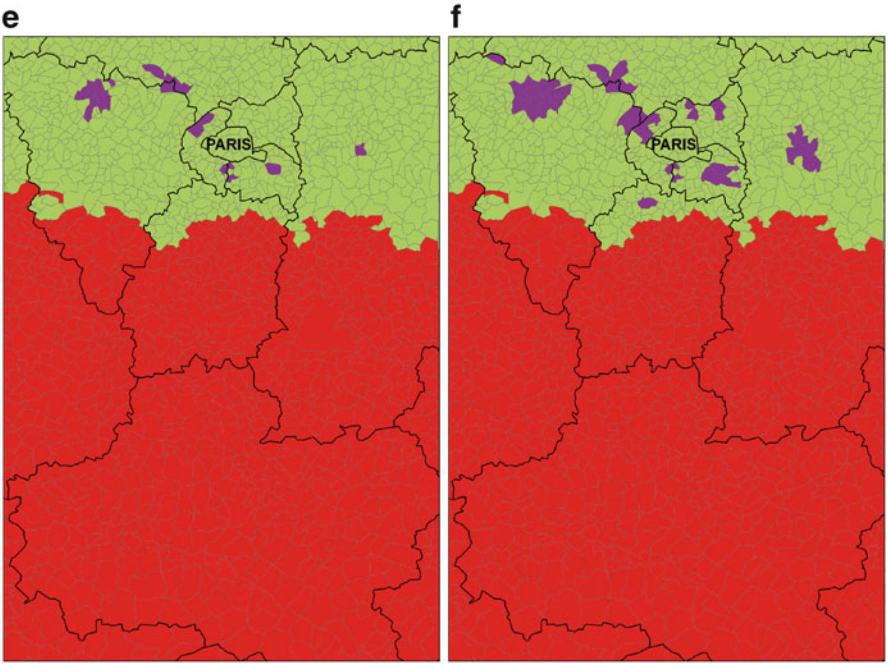


Fig. 3.7 (continued)

outbreaks are highly variable, a 6-year outbreak cycle can be observed in some pine stands colonized for a long time (before the 1980s) (Abgrall 2001; Robinet and Roques 2005). Despite a large geographical variability, the most important outbreaks occurred in 1985, 1992, 1997–1998, and 2003–2004 (Bouhot-Delduc 2005). Climatic anomalies can disturb the population dynamics (Huchon and Démolin 1970), especially in regions more recently colonized (Robinet and Roques 2005). On the expansion range, no outbreak cycle is generally observed (Francis Goussard, personal communication).

4.1.2 Particular Biological Features Observed in the Country

Like everywhere else in the species distribution, the population phenology strongly depends on latitude and elevation (Huchon and Démolin 1970). Several particular biological features occurred in some parts of France. (1) Despite high variability among the regions, larval development takes place in the cold season, generally between September and March. However on a small island, called Île de Ré, the larvae can generally complete their development before winter (i.e., before December) and make processions to burry in the soil before the coldest season. This island is located in the Atlantic Ocean very close to the continent and

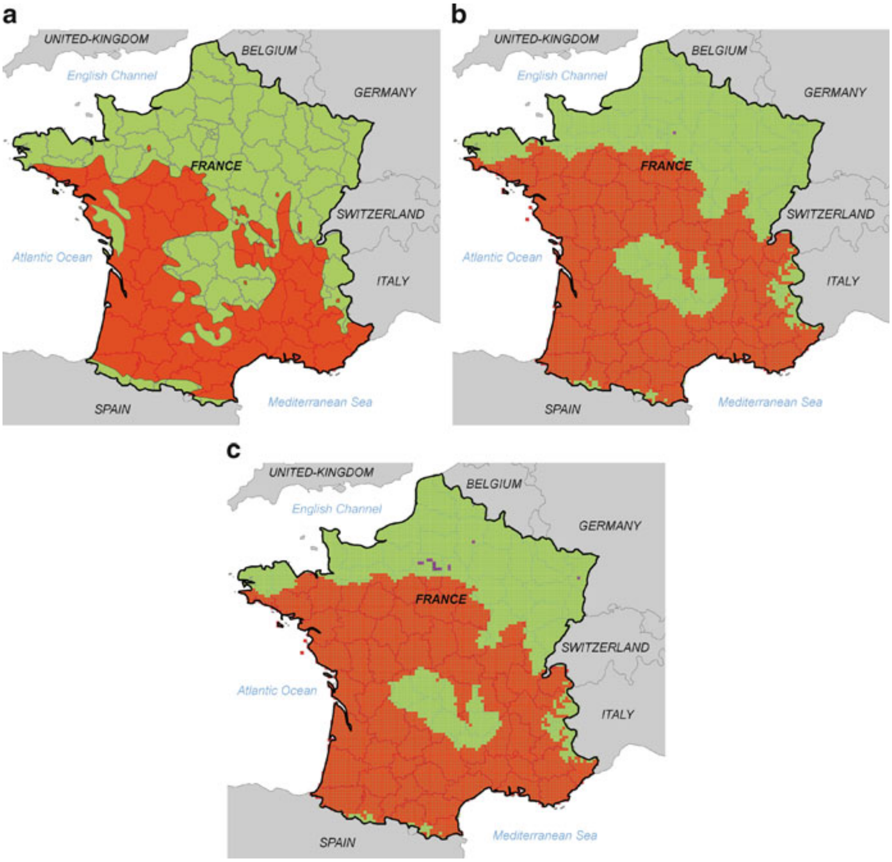


Fig. 3.8 Range expansion of the pine processionary moth in continental France (Corsica excluded) from 1969 to 2011. Areas with moth presence are figured in red. Isolated pioneer colonies discovered after 2000 are figured in *purple*. (**a**) moth presence during 1969–1979 (sources: CTGREF-INRA 1980); (**b**) moth presence during winter 2005–2006 on a 8 km per 8 km grid (Robinet et al. 2010a, b); (**c**) moth presence during winter 2010–2011 8 km per 8 km grid (URZF INRA Orléans, unpublished)

the temperature is mild throughout the year. (2) With increasing variability in temperatures, the species phenology is more and more disturbed. For instance, many processions were locally observed in the Paris basin in late September in 2011 (Jérôme Rousselet, personal communication). These processions were not due to the lack of food but probably due to early adult emergence and suitable climate conditions for a rapid larval development. This phenomenon is supposed to result from various climatic anomalies from the winter 2010–2011 until late summer 2011. (3) Regarding the diapause, a very unusual feature has been happening for many years on the Corsica Island. In these mountains, the diapause is always extended and the life cycle is completed within 2 years or more

(Huchon and Démolin 1970; Géri 1980). However, depending on the valleys, the year of emergence and larval development is not the same. In some valleys, most of the tents are observed in even years, and in other valleys, they are mostly observed in odd years.

4.1.3 Host Range

The pine processionary moth generally attacks pines (notably *Pinus sylvestris*, *P. nigra*, *P. pinaster*, *P. halepensis*), cedars (*Cedrus atlantica*, *C. libani*) and eventually other conifers such as Douglas-fir, *Pseudotsuga menziesii*, and white fir, *Abies concolor* (Martin 2005). These host trees are largely distributed in France, not only in forests but also in urban areas as ornamental trees. Therefore the pine processionary moth does not seem not limited by its host trees in France.

4.1.4 Expansion with Global Warming

One of the most important climate variables for the larval development and winter survival of the pine processionary moth is the mean of minimum temperature from October to March (TNOM, Robinet et al. 2007). This temperature has increased by around 1.1 °C between 1972–1981 and 1994–2003 in the South of the Paris basin (Battisti et al. 2005). Despite large fluctuations, the temperature has increased by around 0.02 °C per year between 1981 and 2011 in the South of the Paris basin, with very warm winters in 1994–1995, 2000–2001, and 2006–2007 (TNOM > 4.5°).

4.1.5 Trends for the Future

A preliminary model was developed to simulate the potential spread of the pine processionary moth in France based on the moth dispersal capability, human-mediated dispersal, potential growth, survival to cold temperatures, and distribution of host trees (Robinet 2006; Robinet et al. 2014). The spread is now mostly limited by the dispersal capabilities but human-mediated dispersal could create satellite colonies and artificially accelerate the spread. It is very likely that northwestern and northern France will be colonized in the coming years. However other factors should be considered in the future such as the sunshine and the possible limitation of the range expansion by unfavorable photoperiod during winter in northern territories. The model should also be improved to determine more precisely the trend in mountainous areas, and more generally, to account for the effects of climate warming on the insect phenology as this change could in turn affect the time-window individuals are exposed to critical weather conditions.

4.2 The Pine Processionary Moth in Italy

Andrea Battisti

4.2.1 Present Biogeographical Range

The pine processionary moth *Thaumetopoea pityocampa* has nowadays an almost continuous distribution in Italy, across both latitudinal and elevation gradients where the host plants (mainly *Pinus* spp.) occur (Fig. 3.9). The only spots that can still be considered free are certain northern-facing slopes in the Alps, where the climatic conditions during winter (especially solar radiation) do not allow the survival of the colonies (Battisti et al. 2005). All the Italian populations belong to the *pityocampa* clade, with the only exception of the small island of Pantelleria, south of Sicily, where a population of the North-African ENA clade is occurring on native *Pinus pinaster* stands (Kerdelhué et al. 2009). Major islands are colonised as

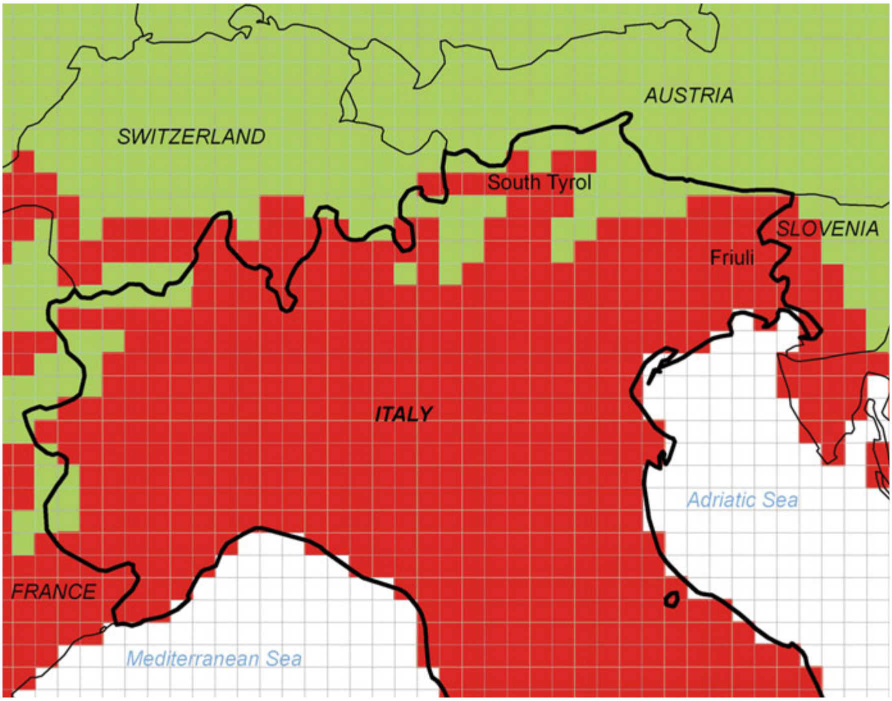


Fig. 3.9 The present distribution range of the pine processionary moth in northern Italy figured over a 16 km × 16 km grid. *Red squares* represent the northern and elevational front, defined as the furthest squares where at least one processionary tent was found. *Green squares* indicate areas beyond the front where the absence of processionary moths has been clearly assessed. South Tyrol and Friuli indicate the regions where most of the studied on the recent range expansion have been conducted

well, including Sardinia which was free of the insect until its discovery in 2006 (Luciano et al. 2007), likely introduced from mainland nurseries with large potted trees (Kerdelhué et al. 2009). An eradication programme based on large-scale *Btk* applications and monitoring has been set up in the island.

4.2.2 Population Dynamics and Outbreaking Periods in the Past

The pine processionary moth is the most destructive insect affecting the growth of some pine species throughout the Italian territory. Its presence in Italy has been well-known for a long time, but it was first recorded in an unequivocal way by Mattioli, who described the larvae and their webs briefly in the "*Commentarii in libros Dioscoridis de medica materia*" (cfr., e.g., Venetian edition of 1568) (Masutti and Battisti 1990). It can be assumed that also the Austrian entomologists Denis and Schiffermüller described their *Bombyx pityocampa* in 1775 on the basis of Italian material, specifically from south Tyrol. In spite of that, the insect had never become a threatening forest pest until several large afforestation programs started at the end of the nineteenth century. Since then, the outbreaks became frequent, although irregular, in various Italian regions.

4.2.3 Particular Biological Features Observed in the Country

The life history follows the pattern observed in northern rim of the Mediterranean basin, with earlier emergence of moths as long as latitude and elevation increase. Prolonged diapause is a typical feature of expanding populations at the northern edge, with individuals of the same cohort spreading the emergence up to 8 years.

4.2.4 Host Range

The pine processionary moth feeds on all native pines with the only exception of *Pinus cembra*, on which it does not grow beyond the third instar (the larvae grow so slowly that they are killed by winter frost in an early instar, Battisti unpublished data). *Pinus nigra*, widespread in afforested areas, is the most susceptible host plant. With the recent climate change effect, however, other hosts became equally susceptible of infestation (Stastny et al. 2006). In addition, the moth is also occurring in town and in agricultural landscapes, thriving on ornamental trees (*Pinus*, *Cedrus* and occasionally other conifers) in gardens and nurseries.

4.2.5 Expansion with Global Warming

The recent shift of the range all over the country is largely explained by climatic change observed in the last decades. The species has reached almost all the upper stands of pine and it is invading the stands of mountain pine as well. In a test carried on this host under extreme mountain conditions, larval mortality and relative growth rate did not differ between host trees grown in ambient or elevated CO_2 (Petrucco Toffolo and Battisti 2008). In relation to the link between global warming and population dynamics, long-term data from two provinces in the Southern Alps (Trento: 1990–2009, Bolzano/Bozen: 1975–2011) were used to evaluate the relative importance of climate and density-dependent factors as regional drivers. Both summer temperatures and rainfall significantly affected population growth rate, with different outcomes depending on the local conditions. Although previous studies indicated that low winter temperatures have negative effects on insect performance, our analyses did not show any negative effect on the population dynamics (Tamburini et al. 2013).

4.2.6 Trends for the Future

As extended snow cover may be an important mortality factor of larval colonies on the dwarf trees of mountain pine, the survival of colonies transplanted at two extreme sites of Eastern Alps was tested. The snow cover extended over more than 1 month proved to be an important mortality factor of larval colonies on mountain pine. We concluded that the first instar larvae of the pine processionary moth are not concerned by unusually low temperature and CO_2 increase whereas they can be later strongly affected by snow accumulation. The decrease of snow cover observed in the last decades, however, may reduce such a risk (Petrucco Toffolo and Battisti 2008).

4.3 The Pine Processionary Moth in Spain

José A. Hódar, Rodolfo Hernańdez, Gerardo Sańchez Peña, and Regino Zamora

4.3.1 Present Biogeographical Range

The pine processionary moth is present almost everywhere in Spain, being limited only where pines are lacking (Fig. 3.10). This happens at the top of the high mountains (The Pyrenees, Central Mountains, Sierra Nevada), in SE Iberian Peninsula due to aridity (Cabo de Gata), and extensive cultivation areas, as the basins of the main rivers (Duero, Tajo, Guadiana, Guadalquivir). Commonly found in urban areas due to use of *Pinus* spp. as ornamental trees in gardens and urbanizations.

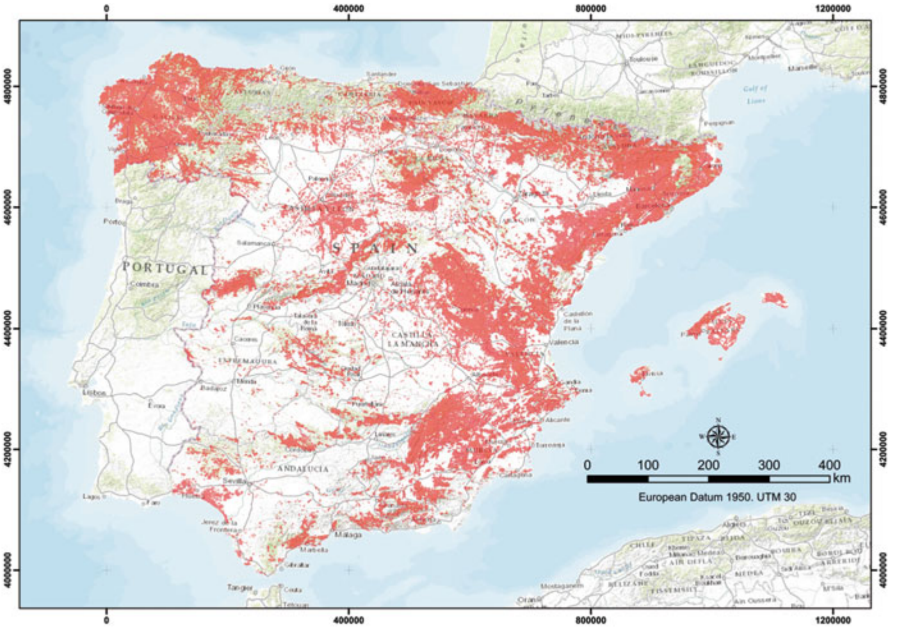


Fig. 3.10 Area covered by pine woodlands in Spain figured in *red*. This area represents the main distribution range of the pine processionary moth in Spain. Moth colonies can also be found in lowlands on isolated trees elsewhere. Only the top of the high mountains and the arid SE Iberian Peninsula are completely free of pine processionary moth (Data from SIG laboratory, Databases and Territory Analysis, INIA-CIFOR)

Absent in Canary Islands, introduced into the Balearic Islands (recently recorded in Formentera). No detailed distribution mapping at the country level, some detailed mapping and monitoring at a regional level.

4.3.2 Population Dynamics and Outbreaking Periods in the Past

No clear trends can be figured out due to the lack of systematic monitoring until last ca. 20 years (except some noteworthy cases as Mora de Rubielos, with systematic records from 1971). However, there is a general agreement in researchers and policymakers that pine processionary moth has increased in abundance and virulence during last decades, noteworthy in pine plantations. It is matter of discussion to what extent this is the result of climatic change, the consequence of massive afforestations during the second half of twentieth century (3.4×10^6 ha afforested, 90 % with conifers, by public administrations between 1940 and 1984), or both. At least in some parts of the country, the incidence of outbreaking levels generally shows a 6-year cycle (excepting diapause disruptions), mainly in planted areas and young stands, while in natural stands cycles are longer or absent.

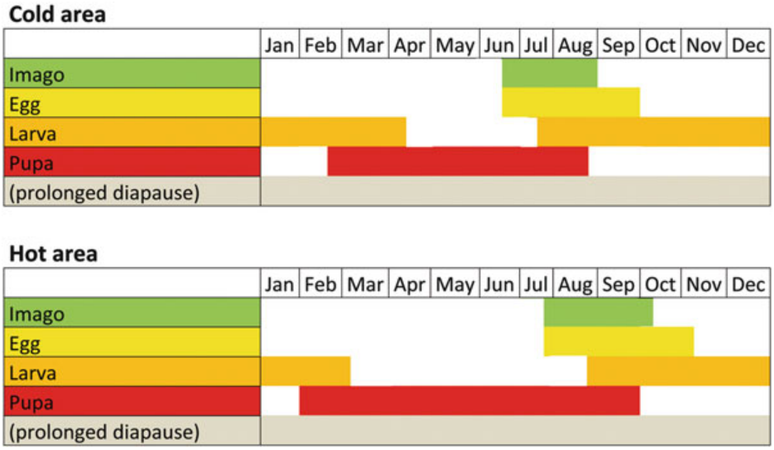


Fig. 3.11 Pine processionary moth phenological differences between cold and warm localities in Spain

4.3.3 Particular Biological Features Observed in the Country

No particular features were observed. A general description of phenology and life history of pine processionary moth in Spain can be found in Montoya and Hernández (2003) and Muñoz López et al. (2007). Cold and mild localities show sharp phenological contrasts due to differences in thermal environment (Fig. 3.11) but, taking apart diapause, the species behaves always as univoltine.

4.3.4 Host Range

Almost every pine present in Spain is attacked by pine processionary moth, but susceptibility depends of the pine species and the mixture of species at the stand level. Thus, *Pinus nigra* and the exotic species are always preferred, and their presence greatly determines the degree of attack to other less palatable species as *P. pinaster* or *P. halepensis*. For instance, *P. pinaster* is in general not very attacked in high mountains of SE Spain when mixed with *P. nigra* and *P. sylvestris*, but it is the staple food in the mild coastal areas of NW Spain in absence of other more palatable pines. *Pinus pinea*, the less susceptible species, suffer nevertheless important defoliations leading to health problems to pine cone collectors. Most of the introduced pines (*P. canariensis*, *P. radiata*, *P. ponderosa*) are heavily attacked by pine processionary moth, being especially problematic the situation of extensive plantations of *P. radiata* in Basque Country. At this area plantations are set at low elevations with mild climate, thus favoring the pine processionary. Occasional attacks to introduced *Cedrus* spp. have also been reported.

4.3.5 Expansion with Global Warming

Expansion in Spain is possible just in elevation, since every lowland area bearing pines also bears pine processionary moth. Recent monitoring suggests moth movements uphill in mountain ranges due to rising temperatures, but also due to conifer afforestations in mountainous areas previously covered by shrublands or pasturelands and devoted to livestock. An increase of 0.48 °C per decade has been reported for the average temperature in the Iberian Peninsula for the period 1973–2005, and a higher increment in future is predicted (AEMET 2009). As a consequence, pine processionary moth has recently been recorded in completely unusual elevations for the species just 20 years ago (2,250 m in Sierra Nevada, 2,200 in Sierra de Baza, 1,800 m in Sierra de Gúdar, 2,000 m in southern slopes of Pyrenees range), but again systematic data are lacking. During last years some programs of detailed population monitoring have been implemented (e.g. in Sierra Nevada, SE Spain), but still is too early for concluding results.

4.3.6 Trends for the Future

The advisable tendency is a progression in elevation and perhaps an increase in virulence in zones with chronic affection until now. Also, a retraction in the arid limit of SE Spain cannot be completely ruled out, depending on the distribution of pine woodlands in future climatic scenarios. There are also some tests for modelling the population dynamics (in Sierra Nevada).

4.4 The Pine Processionary Moth in Portugal

Manuela Branco, Helena Santos, and Maria-Rosa Paiva

4.4.1 Present Biogeographical Range

Pine processionary moth is widespread throughout the territory of continental Portugal, colonizing pure and mixed plantations, as well as dispersed trees. As from the first half of twentieth century, intense forestation campaigns were conducted in Portugal mostly with maritime pine, *Pinus pinaster*. Although the cultivated area decreased from 1,288,000 ha in the 1960s, to 710,600 ha in 2006, *P. pinaster* is still one of the three most representative forest species in Portugal (AFN 2010). Intense outbreaks of pine processionary moth, with average larval densities of over one tent per tree and defoliation above 50 % have been observed, mainly in young stands all over the country (Arnaldo et al. 2010; Barrento et al. 2008; Branco et al. 2008).

In spite of its importance, little or no information on the population dynamics and outbreak periods of pine processionary moth was available until the twenty-first century, mostly due to the lack of long-term systematic monitoring. Similarly, the occurrence of outbreak cycles has not been reported. Still, in urban and peri-urban areas, pine processionary moth often occurs at high densities raising public concern, particularly in schools and public gardens.

4.4.2 Particular Biological Features Observed in the Country

The phenology and life history of pine processionary moth in Portugal follows a pattern similar to those observed for other Mediterranean populations. Thus, egg laying takes place from the end of July to September, larval development from September to February-March and pupation thereafter, until the following summer. In Northern regions of Portugal, the peak of adult emergence occurs between June and August, that is earlier than in southern areas, where it occurs in August–September (Arnaldo and Torres 2006).

In 1997 a pine processionary moth population having an atypical cycle, was discovered in a pine stand, with about 37,000 ha, located in Leiria region, which has been continuously managed since the thirteenth century. The distinctive phenology of this population is characterized by spring adult emergence (May/June), summer larval development (June/October) and pupation in the fall and winter (see Battisti et al. 2014; Chap. 2, this volume).

4.4.3 Host Range

The main host of pine processionary moth in Portugal is the maritime pine, since it represents about one third of the total forested area of the country. *Pinus pinea* comes second, being cultivated for pinion seeds, mainly in regions south from the river Tagus. Still, over the last decade, in consequence of serious damage caused by the pinewood nematode to *P. pinaster*, part of the area occupied by this species has been converted to *P. pinea.*

Although references to pine processionary moth outbreaks in *P. pinea* were not found for Portugal, the authors observed some cases in young plantations such as reported by Paiva et al. (2010). Other pine species are also prone to intense defoliation, namely the exotic *P. nigra* and *P. radiata*. An attack on the ornamental species *Cedrus deodara*. has been observed in Setúbal Peninsula, in December 2012 (Paiva, personal observation).

In a study conducted by Mateus et al. (1998) in an arboretum near Abrantes, central Portugal, the host range of the local pine processionary moth population was found to be wide, although significant differences occurred regarding tent density per tree, *P. pinaster* being one of the most intensively attacked species.

4.4.4 Expansion with Global Warming

Expansion in Portugal is not applicable, as the species is present all over the country from sea level to the highest mountains, provided pine plantations are present. A significant warming of about +2 ° C was reported for the period 1976–2000, which was preceded by a period of global cooling of circa −1 °C, on a previous period from 1946–1975 (Miranda et al. 2002). Furthermore, the increase of the maximum temperatures observed was higher than for the minimum temperatures, thus resulting in a wider range of diurnal temperatures. Possible consequences of these changes for the distribution of pine processionary moth are unknown.

Yet, the atypical population with asynchronous phenology has been observed to expand both northwards and southwards from its original outbreak point, along the coast (Fig. 3.12). Summer “hot days”, with maximum temperatures ≥ 35 °C that can be observed in inner regions (Fig. 3.13), might limit the distribution of the summer population. However, an adaptation of this population to hot summers is also plausible (Santos et al. 2011a), thus increasing its potential ecological range of distribution.

4.4.5 Trends for the Future

The present status of the typical winter population is expected to remain stable and severe outbreaks on young pine plantations, of increased severity, particularly on *P. pinea* are predictable. An expansion of the summer population is expected along the coast, with high impact on touristic activities concentrated on this area, such as camping parks, golf facilities and seaside touristic villages. A rate of spread of about 3 km per year was observed over the past 15 years and it is predictable that a similar trend will continue in the future.

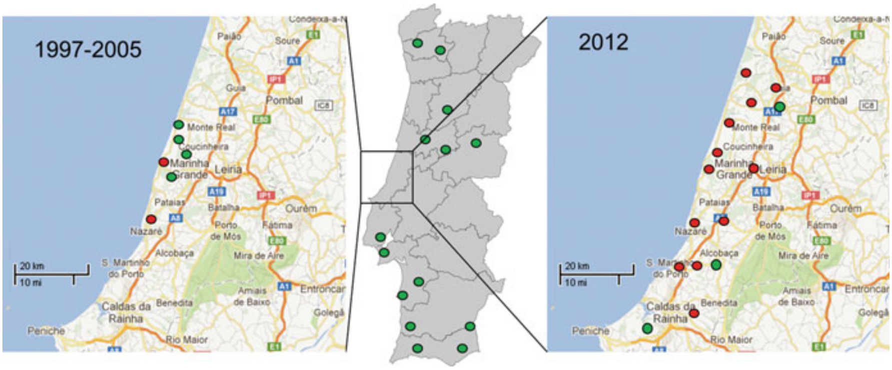


Fig. 3.12 Expansion of an atypical summer population of pine processionary moth in Leiria, from observation of male traps conducted from 1997 until 2005 and in 2012, *red dots* represent presence, *green dots* represent absence

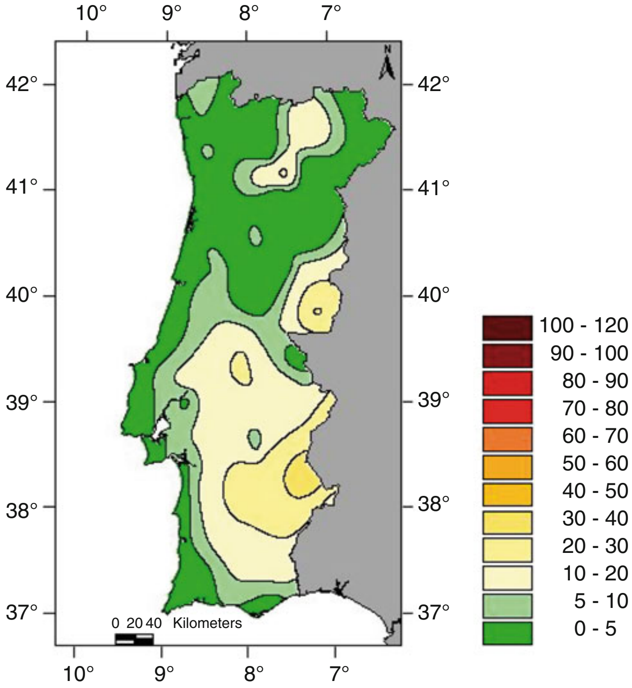


Fig. 3.13 Average annual number of days with maximum temperature ≥35 °C ("hot days"). Data from 1961–1990 observations (Adapted from Miranda et al. 2002)

4.5 The Pine Processionary Moth in Switzerland

Beat Forster, Cynthia Nussbaumer, and Franz Meier

4.5.1 Range of the Moth and Host Trees

The pine processionary moth (*Thaumetopoea pityocampa*) only occurs in southern Switzerland on the south slope of the Alps, in the Valais, an inner alpine valley, and in the basin of Lake Geneva. The range is very stable and did not change in the last 120 years. Only in 1908, a single spot is documented in the region of Erstfeld, in a main valley in the northern Prealps (Fig. 3.14). Probably *T. pityocampa* was introduced there accidentally, maybe along the main transit railroad. Also a flight of adults across the Alps with strong winds is possible. But this Erstfeld occurrence quickly disappeared because of unfavourable climate conditions.

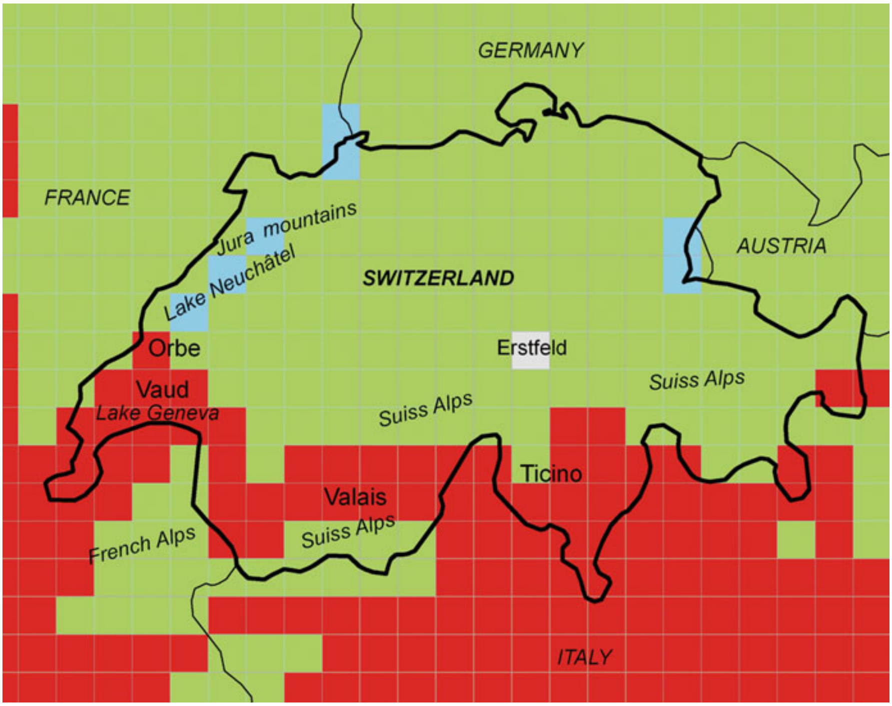


Fig. 3.14 Range of *Thaumetopoea pityocampa* in Switzerland and neighboring countries on a 16 km-cell grid (*red*: presence of one moth colony at least, *green*: absence; *grey*: temporary occurrence in 1908; *blue*: potential range that could be colonised)

Observed host trees are mainly pines (*Pinus sylvestris* and *P. nigra*), rarely larva tents can be found on *Cedrus* spp. and on Douglas fir (*Pseudotsuga menziesii*).

4.5.2 Population Dynamics and Outbreaks

The Swiss population is quite stable in time and range. After warmer years, more tents can be observed in the crowns but there are no real outbreaks. In Southern Switzerland the moth's density was queried in the 1990s and again since 2008 (Fig. 3.15). Stronger defoliations of pines only occur very locally. Attacked trees rarely die. In Valais, a strong population density can often be observed between 900 and 1,000 m a.s.l. (Keller 1903).

Until about 1980 tents occurred in the Alps below 1,100 m a.s.l. Along the Jura mountains in canton Vaud, the moth only reached about 600 m a.s.l. (Barbey 1925). After years with unfavourable weather conditions, attacks sometimes dropped in elevation by 100 m or even more. On the other hand, in the last decades, in Valais

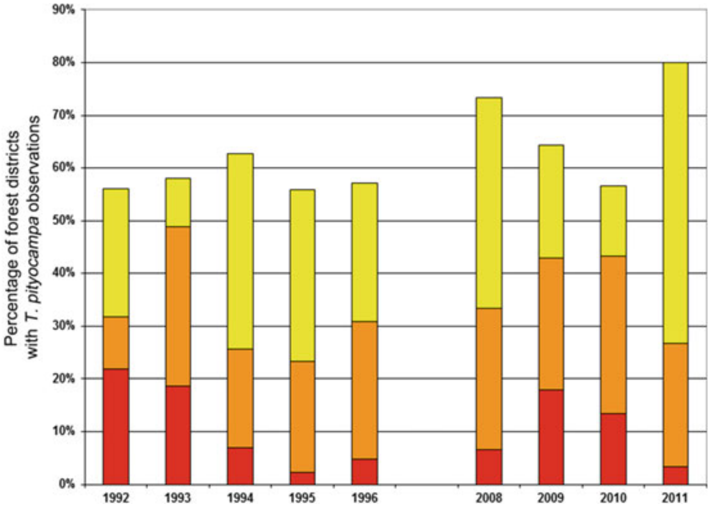


Fig. 3.15 Observed damage intensities of *T. pityocampa* in the forest districts of Southern Switzerland. Fluctuations of damage are well visible, but no real mass attacks. *Red*: strong attack; *orange*: medium attack; *yellow*: slight attack

some single observations could be made up to 1,400 m a.s.l. (Bryner 2000). In Ticino the highest occurrence was even described at 1,600 m (Rezbanyai in Bryner 2000), but in this study only trap catches of adults are concerned.

After Barbey (1925) and Bryner (2000) larvae are consuming needles from September to November and again in March and April. Processions can be observed in April and May. Adults fly from mid of July, in Valais earlier than in Ticino.

4.5.3 Influence of Global Warming

As described above, *T. pityocampa* populations gained new habitats by moving upwards slopes and valleys. But compared with other countries, no dispersions to the north could be registered. One reason may be the barrier of the Alps that cannot be crossed easily. But along the southernmost chain of the Jura mountains, no barrier would prevent the moth's expansion. Along Lake Neuchâtel, habitats seem to be favourable and some lower parts of the Swiss Plateau could be colonized by the moth (Fig. 3.14). But for decades, its northernmost occurrence remains stable near the city of Orbe. Therefore the local climate was analysed (Nussbaumer, unpublished) and compared with the moth's exigencies to habitats after Huchon and Démolin (1970). It was demonstrated that a further expansion of the moth in Switzerland could be possible, but it did not occur, probably because the local climate did not change enough. Despite a distinctive global warming for whole Switzerland, the region of Orbe to Lake Neuchâtel does not show exactly the same trend. The mean temperature of January, for example, was even slightly dropping during the last decade.

4.6 The Pine Processionary Moth in the Upper Rhine Valley: Climatic Resistance and Development of an Isolated Occurrence

Paula Halbig, Lars Henke, Jean Poirot, Eiko Wagenhoff, Horst Delb, and Dietrich Klimetzek

4.6.1 Development of a Pine Processionary Moth Population in Obernai, Alsace

Immediately after its accidental introduction with plant material in 2007, the Mediterranean pine processionary moth settled successfully in Obernai, Alsace, France. A pheromone trap-based monitoring resulted in more than 600 and appr. 400 moths caught in 2008 and 2009 respectively. Furthermore, expansions to ambient villages within distances up to 5 km were recorded in 2009; these pine processionary moth tents, however, were instantly destroyed. Although the population declined in subsequent years, pine processionary moth is still active: Traps caught a dozen moths each in 2010 and 2011 and more than 30 tents were found both years. In 2012, despite an exceptional cold period in February with night temperatures of -19 to -15 °C and of only -8 °C at maximum during the day for more than two weeks, appr. 20 tents were counted and check of tents in April resulted in vigorous larvae. No mortality was detected in the centre of Obernai, but half of the larvae died at the edge of the town (F. Bronner, Greenspace Service Obernai, written communication 25.09.2012). Thus the population suffered from cold temperatures, but pine processionary moth larvae mainly resisted, confirming their classification as moderate freezing tolerant (Hoch et al. 2009).

4.6.2 Monitoring of Potential Expansion of Pine Processionary Moth to Germany

Triggered by the eastwards spread of pine processionary moth in Obernai, situated in a distance of appr. 21 km to the German frontier, a monitoring in the German Upper Rhine Valley was initiated in July 2009. 10 pheromone traps were placed in largely pine dominated stands along the German-French border from Bad Krozingen to Karlsruhe, which, however, did not confirm any expansion of pine processionary moth. Due to the continuing risk of introduction or spreading, pine processionary moth monitoring in Baden-Württemberg was intensified in the summer 2010, employing 15 delta traps with commercial lures mainly installed in pine stands of the most endangered region between Rheinhausen and Neuried during the whole flight period from June to August. Just as in 2010 no spread of pine processionary moth to Germany was ascertained.

4.6.3 Climate and Habitat Analysis

To assess the potential risk of pine processionary moth establishment in Baden-Württemberg, climatic and stand data were analysed in context of the so far known habitat requirements of pine processionary moth. A state-wide climate analysis from 2000 to 2009 was conducted using GIS-Software SAGA and ArcGIS. For a potential distribution, absolute mortality limits of ≥1,800 h annual insolation and a mean minimum of −4 °C in January must be reached (Battisti et al. 2005). That way two-thirds of Baden-Württemberg's territory were classified as a potential range. A long-term permanent distribution requires >0 °C as minimal January air temperature plus 1,800 h insolation per year. Each degree colder in January can be compensated by 100 h additional annual insolation, leading to a combination of −4 °C with 2,200 h (Huchon and Démolin 1970). These conditions were only partly fulfilled in Baden-Württemberg. However, areas in red mark the highest and light shading mark the lowest risk of becoming long-term distribution regions (Fig. 3.16).

In the monitoring area Lahr, winter temperatures for larval feeding were examined in some detail. Air temperatures >0 °C at night as potential feeding temperatures are required from December to February; moreover an activation temperature >9 °C must be reached during the day (Battisti et al. 2005). Lethal temperature values for larvae were checked, using −13.7 °C for L2 from October to November as well as −16 °C for L3/L4 in November and December (Buffo et al. 2007). Both, temperature values for larval feeding and lethal temperatures were rarely attained from 1995 to 2010 and 1961 to 2010 respectively at Lahr. The presence of suitable host trees was analysed in the Upper Rhine Valley, applying FoGIS (Forest GIS of Baden-Württemberg) and ArcGIS to locate pine stands with ≥50 % pine (*Pinus sylvestris*) proportion, resulting in 25 % of the forest area as potentially endangered by pine processionary moth.

4.6.4 Conclusion

Although the abundance of the pine processionary moth population in Obernai has been decreasing since 2010, an expansion or introduction to Germany is still possible. Increasing temperatures could lead to a doubling of expansion rate (Robinet et al. 2012). Based on the climatic analysis, the monitoring areas appear neither currently nor in the near future endangered by pine processionary moth. However, annual insolation and January air temperature undergo an increase leading to more favourable conditions. Additionally its plastic lifestyle increasingly

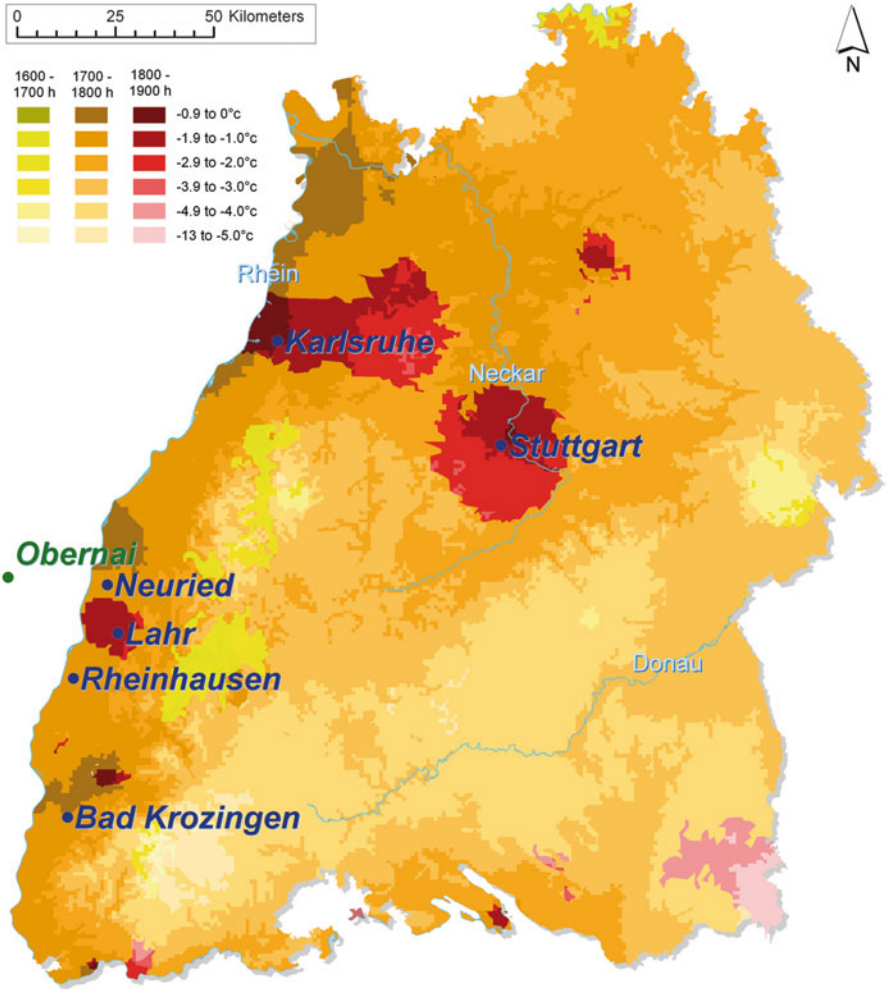


Fig. 3.16 Potential long-term permanent distribution areas of pine processionary moth (*red*/*dark*) and areas at medium (*orange*) and small (*yellow*/*light shading*) risk of settlement in Baden-Württemberg according to annual insolation and average minimum January air temperature (cf. text)

enables pine processionary moth to survive extreme climatic conditions. It is able to shift critical instars in course of the year as well as extending its diapause (Pimentel et al. 2006; Seixas Arnaldo et al. 2011). Taking continuous trends of global warming and pine processionary moth's lifestyle into account it must be assumed that sooner or later pine processionary moth will establish steadily in the Upper Rhine Valley.

5 Past and Current Situation of the Pine Processionary Moth, *Thaumetopoea Pityocampa*, in the Balkans

5.1 The Pine Processionary Moth in Slovenia

Jan Podlesnik and Maja Jurc

5.1.1 Present Biogeographical Range

The first record of *Thaumetopoea pityocampa* in Slovenia dates to 1903 (location: Sela on Karst). It spread from Friuli in Italy, where it was recorded since 1898 (Kafol 1951). Nowadays *T. pityocampa* is present all across the western part of Slovenia; i.e., the regions of Istria, Karst, Primorska and Tolmin (Jurc et al. 2003). In the last 10 years individual sightings were made in the upper Primorska region around Bovec and above Log pod Mangartom at 1,200 m.a.s.l., which is one of the northernmost locations of pine processionary moth in Slovenia. In 2011 it was recorded in an alpine valley in northern Slovenia near Bohinjska Bistrica (Notranji Bohinj), in the heart of the Julian Alps. In 2010/2011 it spread across a wider area in the southern part of Slovenia near Ilirska Bistrica (Slovenian Forestry Service 2011; Fig. 3.17).

5.1.2 Population Dynamics and Outbreaking Periods in the Past

The outbreaks of *T. pityocampa* mostly occurred during years with higher average temperatures and lasted only for short periods of time. Gradations were recorded in years 1928–1929, 1937–1938, 1944–1945, 1948–1950, 1953–1954, 1958–1959, 1965–1966, 1969–1970, 1972–1973, 1976–1979, 1982–1983, 1992–1993, mostly in the Karst region around Črni Kal, Osp, Socerb, Sočerga, Kubed, Dekani and Škofije. Particularly pronounced gradations were reported between 1944 and 1950, when only in 1949 there was a 25–100 % defoliation rate on 259 ha of *Pinus nigra* stands. In 1950 in the Karst region larvae were suppressed by removing their tents and using insecticides – more than 1,502 ha of pine plantations were treated with 16.5 % DDT emulsion (Titovšek 1994; Jurc 2001).

5.1.3 Particular Biological Features Observed in the Country

In Slovenia *T. pityocampa* develops one generation a year. The flight period begins in the beginning of July and lasts until August; during these months it also disposes eggs. Larvae overwinter in fourth instar inside their tents. In late winter or early spring the larvae become active again and start feeding until they reach the fifth larval instar. From 15th of March to 1st of May the larvae move to the ground where

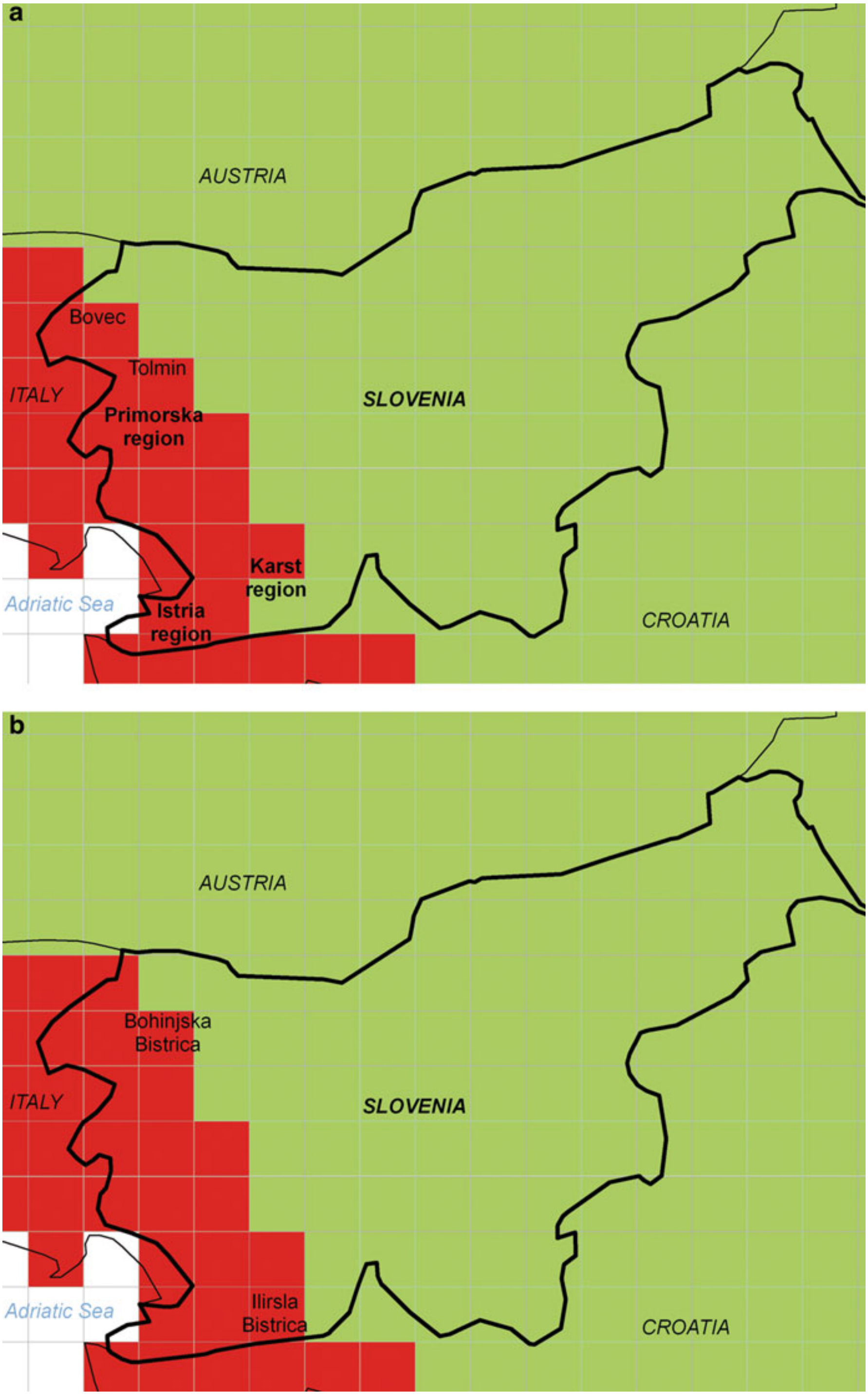


Fig. 3.17 Distribution of *Thaumetopoea pityocampa* in Slovenia and neighboring countries on a 16 km-cell grid. *Top*: before 2000; *bottom*: during winter 2011–2012. *Red squares* show the presence of *T*. *pityocampa* whereas the moth is absent in areas figured in *green*

they pupate buried in the ground. A severe winter (−25 to −29 °C) does not harm the larvae, but humid winters can cause high larval mortality (Kafol 1951). In Slovenia *T. pityocampa* appears on *Pinus nigra*

5.1.4 Expansion with Global Warming

The past and present distribution of *T. pityocampa* is shown in Fig. 3.17 (Slovenian Forestry Service 2011). Average 10 year temperatures around year 1970 were from 0.5 to 1.5 °C lower than the average temperatures of last 10 years, measured by 6 weather stations in the relevant areas (ARSO 2012). This is probably one of the reasons why *T. pityocampa* spread and started to appear at higher elevations in the northern Tolminska region, around Log pod Mangartom. In 2010/2011 it spread to an alpine valley near Bohinjska Bistrica. In the last 2 years it also spread to new locations in southern Slovenia around Ilirska Bistrica.

5.2 The Pine Processionary Moth in Croatia

Dinka Matošević

5.2.1 Present Biogeographical Range

The first record of moth infestation in Croatia was from island of Mljet in 1889. Then, severe infestations in pine forests were noticed on the northern coast of Croatia during the period 1902–1926. At that time, Knin was the farthest location from the coast where pine processionary moth was observed (Langhoffer 1927). Observing severe outbreaks on pines in the coastal region of Croatia, Radčenko (1927) concluded that pine processionary moth is distributed in the area up to 1,000 m a.s.l. although rarely found at such elevation. He also concluded that the moth prefers dry and warm years. Later, Beltram (1947) noticed that the moth is not found above 800 m a.s.l. because of the too cold climate there.

Androić (1957) supplied a distribution map of pine processionary moth in Croatia, showing that it is present on all Croatian islands and on the coast, and Harapin (1984) precised the range limits in the early 1980s (Fig. 3.18). Moth range is not completely overlapping with pine distribution in Croatia because temperature limits its presence to the coastal belt only. Thus, the distribution of pine processionary moth is coinciding with the July isotherm of 22 °C (precisely between 22 and 23 °C) which corresponds to the yearly isotherm between 13 and 14 °C (Androić 1957). Actually, the moth range is overlapping with the northern border of the optimal growing zone for pubescent oak (*Quercus pubescens*), which is also the southern border of the natural range of silver fir (*Abies alba*) and common beech (*Fagus sylvatica*) in Croatia (Androić 1957). Topographically, this area corresponds to the mountain

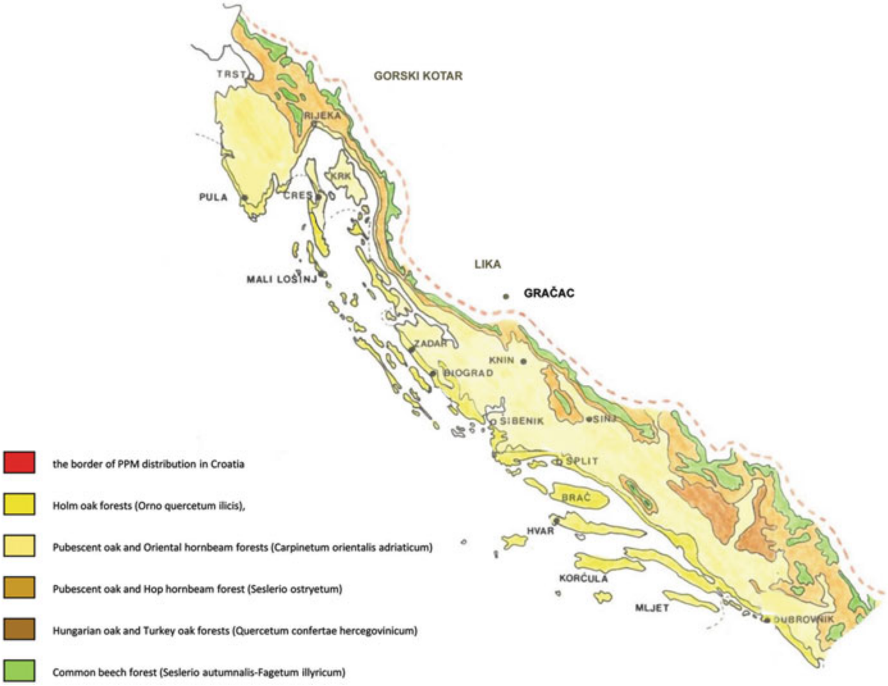


Fig. 3.18 Distribution of pine processionary moth in Croatia in 1984 (Modified from Harapin 1984)

border between the Mediterranean zone (coast and in its immediate hinterland) and the Alpine or Dinaric (Lika and Gorski Kotar) regions of Croatia.

Moth spread into the mainland thus depends on climate which is mediated by topography. Indeed, the pine processionary moth is present in the areas where the topography allows warm air currents to penetrate, giving the characteristics of Mediterranean or Sub-Mediterranean climates (eg. Gračac, Knin).

Minimal temperatures in the months when pine processionary moth is in egg or larval stages are the limiting factors for its further spread into the mountains. Laboratory trials carried out in Croatia showed that 12 °C is a limiting temperature for embryonic development, and 11 °C for the development of the first larval instar (Androić 1957).

5.2.2 Host Range

The main host plants of pine processionary moth in Croatia are *Pinus nigra*, *P. halepensis*, *P. pinea*, *P. sylvestris* and *P. pinaster*. *Cedrus* spp. are also mentioned as host plants (Beltram 1947; Harapin 1984).

5.2.3 Expansion with Global Warming

The present distribution of pine processionary moth in Croatia, shown in Fig. 3.19, is quite similar to the one previously detailed by Beltram (1947), Androić (1957) and Harapin (1984). Recent data showed that 2,000–3,000 ha of pine forests were damaged in the coastal region each year since 2001. However, the moth has not yet been found in the pine forests or plantations of the continental part of Croatia. The front edge has not moved to mainland Croatia and has not jumped across the mountain range which is the main obstacle for its moving up north. Egg masses and larval colonies are still not found in these mountains as well. Both alpine climate and the climate corresponding to the vegetation zone of silver fir and common beech forests are major limiting factors for moth expansion.

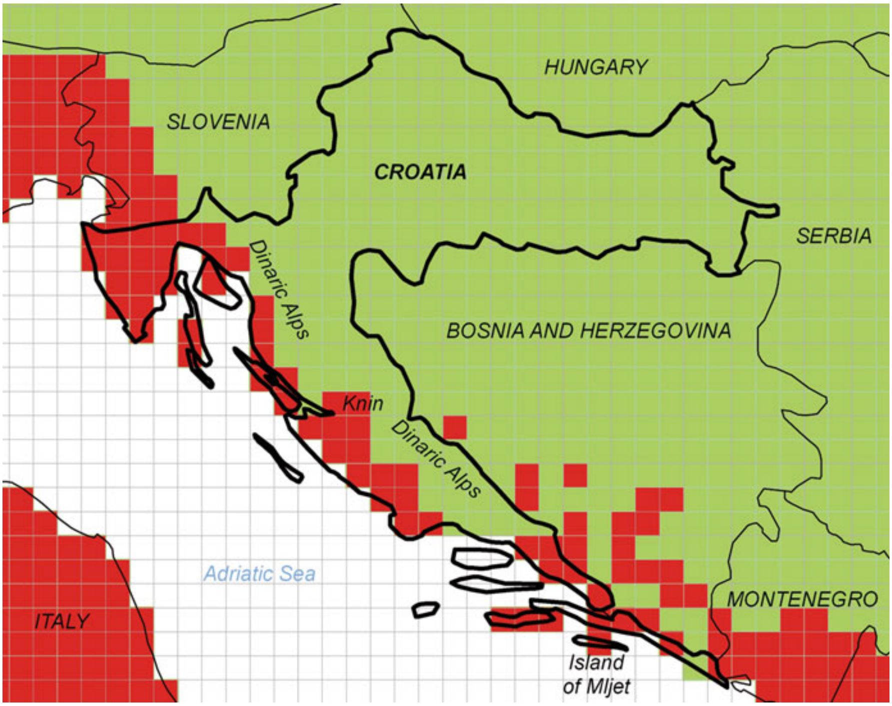


Fig. 3.19 Distribution of pine processionary moth in Croatia and neighboring countries during winter 2010–2011 on a 16 km-cell grid. *Red squares* show the presence of *T. pityocampa* whereas the moth is absent in areas figured in *green*

5.3 *The Pine Processionary Moth in Bosnia and Herzegovina*

Mirza Dautbašić

5.3.1 Present Biogeographical Range

From both an economic and ecological point of view, the pine processionary moth, *Thaumetopoea pityocampa*, is a very important pest of Austrian black pine (*Pinus nigra*) in the sub-Mediterranean range of Bosnia and Herzegovina. Unfortunately, moth impact was largely underestimated in the country's forestry practices during the past. The species was first mentioned in Bosnia and Herzegovina during the late 1970s where it was only recorded only in canyons of the Neretva River (Konjic, Prozor) (Androić 1978).

The occurrence of a serious moth outbreak in Herzegovina Region, near Mostar City, in 2007, led to start investigations on its distribution and infestation level in the whole country. So far, pine processionary moth was recorded in the following locations: Borci, Bosansko Grahovo, Buško jezero, Čapljina, Čitluk, Glavatičevo, Grude, Konjic, Livno, Mostar, Posušje, Prozor, Rujišta, Široki Brijeg, and Trebinje (Fig. 3.20). The high Bosnian Mountains are natural barriers for the further spreading of the moth into the central part of the country. Rather low at high elevations such as Ruište (840 m) and Borci (850 m), the infestation was very high at Mostar and Trebinje.

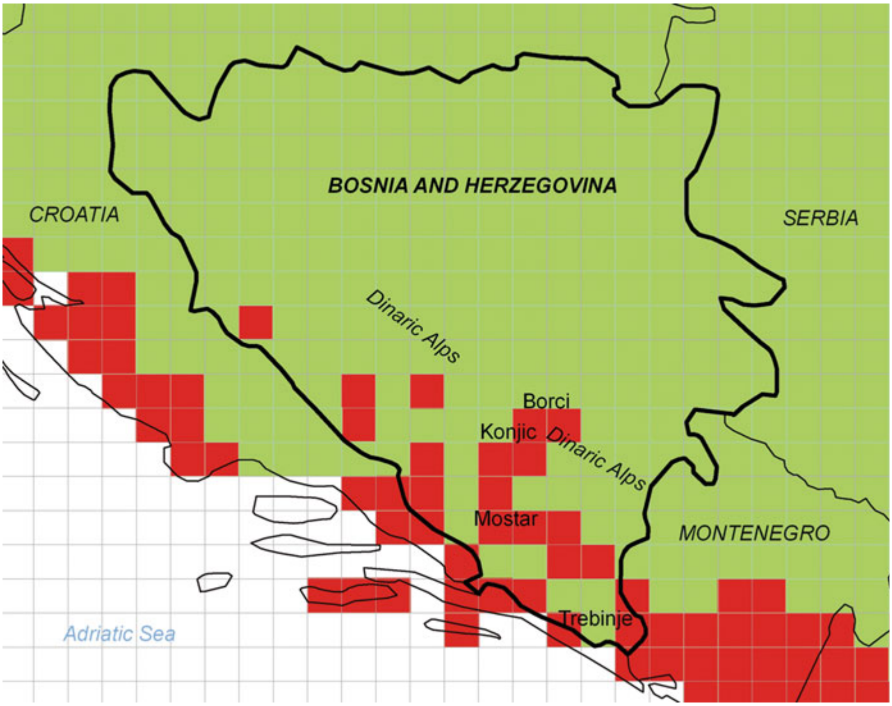


Fig. 3.20 Distribution of *Thaumetopoea pityocampa* in Bosnia and Herzegovina and neighboring countries during winter 2010–2011 on a 16 km-cell grid. *Red squares* show the presence of *T. pityocampa* whereas the moth is absent in areas figured in *green*

5.3.2 Host Range

In Bosnia and Herzegovina, pine processionary moth exclusively attacks Austrian black pine but does not infest the other pine species growing in the country (*P. sylvestris*, *P. halepensis*, *P. mugo* and the endemic species, *P. heldreichii*).

Three major egg parasitoid species have been identified: *Baryscapus servadeii, Ooencyrtus pityocampae* and *Anastatus bifasciatus*. No control methods have been applied against this pest in Bosnia and Herzegovina.

5.4 The Pine Processionary Moth in Serbia and Kosovo

Milka M. Glavendekić and Ljubodrag Mihajlović

5.4.1 Present Biogeographical Range

In the former Yugoslavia, the pine processionary moth was commonly reported from the Mediterranean and Sub-Mediterranean regions. In Serbia, it regularly occurred in the vicinity of Peć (AP Kosovo), and during the late 1970s the moth was observed at Mt. Prokletije, in the locality of Žare, at an elevation of 1,100 m. A further outbreak occurred at the same locality during 1996–1997 but was suppressed by high egg parasitism (app. 70 %) caused by the specialist eulophid parasitoid *Baryscapus servadeii* (Mihajlović and Roganović 1997).

Sex pheromone monitoring carried out during 2009–2012 revealed moth movements eastwards from Peć to Rabovce (Orahovac). In addition, moths were recorded for the first time in South-Eastern Serbia in the forest monocultures of *Pinus nigra,* which were afforested in 1988 by the Public Enterprise “Srbijašume” of the Forest Department of Bujanovac, in the localities of Trnovačka Reka, Rajince, Crnotince (near Preševo) and Rujan (near Bujanovac). Monitoring was performed in pine plantations located between 482 and 646 m (Glavendekić and Mihajlović 2012). Pheromone monitoring in 2012 confirmed these results (Table 3.1). Additional records

Table 3.1 Pheromone monitoring in Serbia in 2012

Forest unit and compartment	Coordinates	Captures
Preševo, 150a	N 42°22,866 E 21°40,944	9
Preševo, 148a	N 42°22,996 E 21°40,175	30
Preševo, 129a	N 42°21,713 E 21°42,198	8
Trnovačka reka, 19	N 42°28,631 E 21°43,224	15
Rujan, comp. 22j	N 42°25,867 E 21°47,938	11
Rujan, comp. 5a	N 42°21,671 E 21°48,070	41
Rujan, comp. 4b	N 42°21,665 E 21°48,437	22
Rujan, comp. 5a	N 42°21,584 E 21°47,825	103

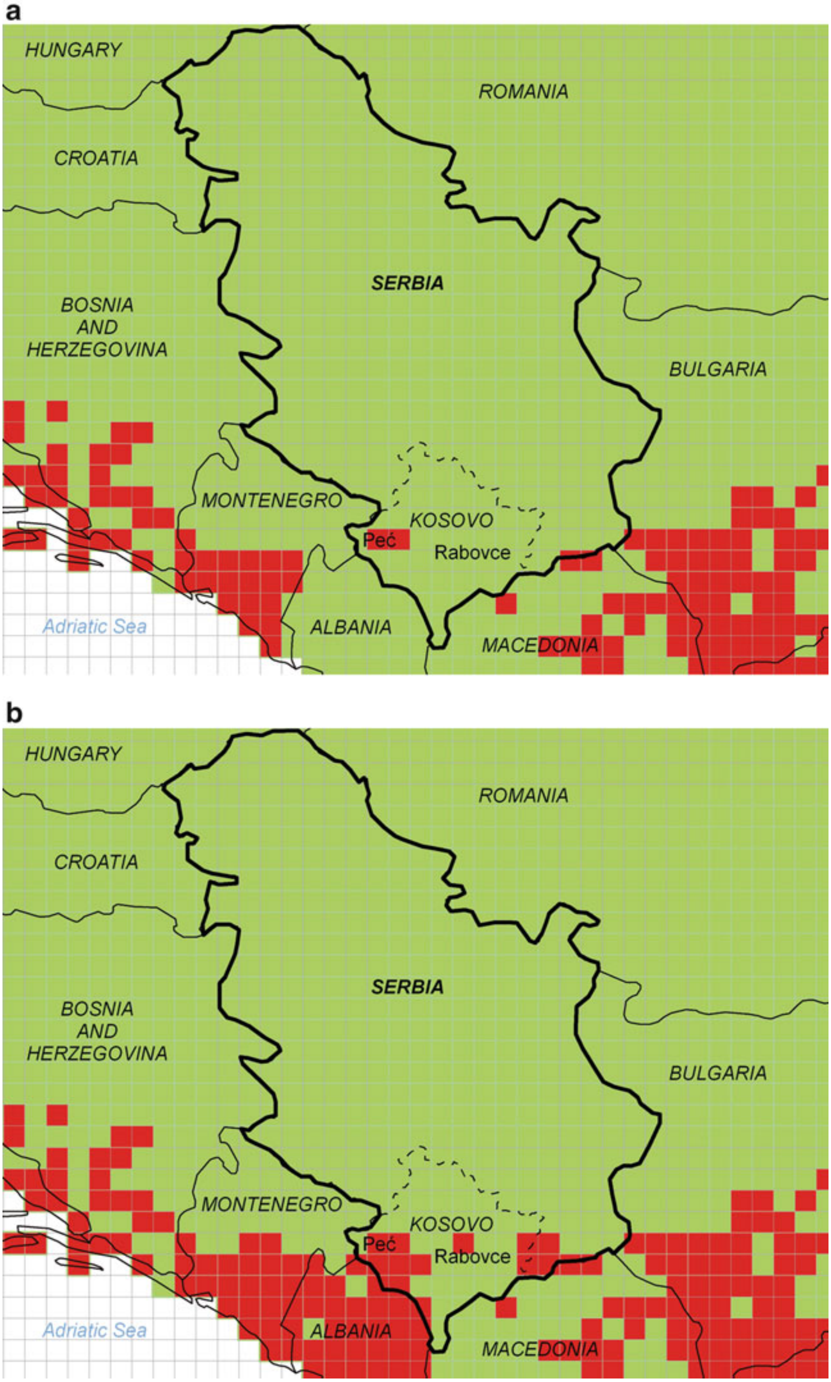


Fig. 3.21 Distribution of pine processionary moth in Serbia and Kosovo and neighboring countries on a 16 km-cell grid. *Top*: before 2008; *bottom*: winter 2010–2011. *Red squares* show the presence of *T. pityocampa* whereas the moth is absent in areas figured in *green*

from the Republic of Macedonia (see 5.7, this chapter) indicated that moth presence in the locality Rujan (forest compartment 5a) is likely to result from a northwards expansion along the valley to Serbia. In this place, larval tents were observed for the first time in December 2011 on black pine. Moth range is thus expanding eastwards from its previous distribution in Peć and northwards from Macedonia (Fig. 3.21.).

5.4.2 Particular Biological Features Observed in the Country

Adult flight period in Serbia starts in August and males are captured in pheromone traps until late September. In the expansion area at Rujan, larvae were still feeding on the top of pine crowns by late December after an extremely mild autumn. The first frosts occurred in January where some larvae proved to be capable of surviving few days with temperature below −20 °C and to resume development when then reared in insectarium in Belgrade. The encyrtid egg parasitoid *Ooencyrtus pityocampae* was found during autumn 2012 in the same locality, thus following pine processionary moth in the newly occupied pine stands

5.4.3 Expansion with Global Warming

Data covering from the period 1951–2005 revealed significant changes in temperature in Serbia. Average summer air temperature has been rising for more than 1 °C during 100 years on more than two-thirds of the Serbian territory but a slight negative trend in summer temperature is recorded in the South-East of Serbia (Popović 2007).

5.5 *The Pine Processionary Moth in Montenegro*

Milka M. Glavendekić

5.5.1 Present Biogeographical Range

Pine processionary moth is common along the coast of Montenegro, being observed in Bar, Petrovac, Miločer, Črvanj and Budva. In the continental part of Montenegro it has been recorded in the vicinity of the cities of Cetinje, Podgorica, Nikšić and Danilovgrad. The first outbreak of pine processionary moth in Montenegro was recorded in 1924–1925 in pine forests of Nikšić County. Then, local outbreaks were noticed after the Second World War on the Adriatic coast and in the vicinity of Cetinje, Podgorica and Nikšić. Large outbreaks were observed in pine plantations during 1957–1961, covering areas from 145 to 1,234 ha (Stamatović 1961). During winter 1959–1960, an outbreak occurred in a ca. 70 years-old pine forest with 200–300 trees in the vicinity of the capital Podgorica, where all pine trees and also planted *Cedrus atlantica* were infested (Mijušković 1961). A further outbreak occurred there during 1968–1970, and pine forests suffered a severe defoliation (Mijušković 2002). The last outbreak occurred in 2005–2006 in the Forest Enterprise of Danilovgrad, at the localities Bzo (1,024 m) and Topolovo (1,080 m). During our research, carried out from 2003 to 2012, a continuous increase in population levels of pine processionary moth has only been observed at the locality Ćemovsko Polje in plantations of *Pinus nigra* and *P. halepensis* in the suburbs of Podgorica.

5.5.2 Particular Biological Features Observed in the Country

The flight period starts from early August in the coastal area and at low elevation. At higher elevation, from 1,000 to 1,540 m, the first adults were captured in pheromone traps from the middle of July until the last decade of September. Mijušković (1961) noted that egg masses include 148–279 eggs, mainly laid in seven rows. In our observations, larvae hatched after 30–35 days. Hatching started from September 5th but extended to October 10th. On September 23rd, both first and second-instar larvae were observed. Due to mild winter temperatures, the larvae feed continuously during winter (Mijušković 2002).

The encyrtid egg parasitoid *Ooencyrtus pityocampae* has already been observed since 1959 in forests near Podgorica where it parasitized 16.9 % of the moth eggs (Mijušković 2002). *O. pityocampae* is the only egg parasitoid recorded so far in Montenegro at low elevation (Ćemovsko Polje, suburbs of Podgorica) but no egg parasitoids were observed at elevations above 1,000 m (Glavendekić 2010).

5.5.3 Host Range

Pine processionary moth attacks *Pinus nigra, P. halepensis, P. heldreichii* and *P. pinaster* in Montenegro.

5.5.4 Expansion with Global Warming

There is an evidence of climate change in Montenegro. As far as the temperature is concerned, almost all measuring places showed that the last observed decade (1999–2008) is, in average, the warmest one during the instrumental period from 1949 on (Burić 2011). Thus, during the 1951–2008 period, the number of summer days, i.e.; showing a maximum daily temperature above 25 °C, increased by 3.6 days per decade in Podgorica whilst the annual amounts of precipitation showed a growth tendency in the last two decades in Podgorica as well as in the other parts of Montenegro. Thus, it could be considered that climate change in Montenegro is favorable to the expansion of pine processionary moth, and its range effectively expanded towards higher elevation, the insect being observed at 1,024–1,540 m (Fig. 3.22). In 2005, a first outbreak of pine processionary moth was even observed

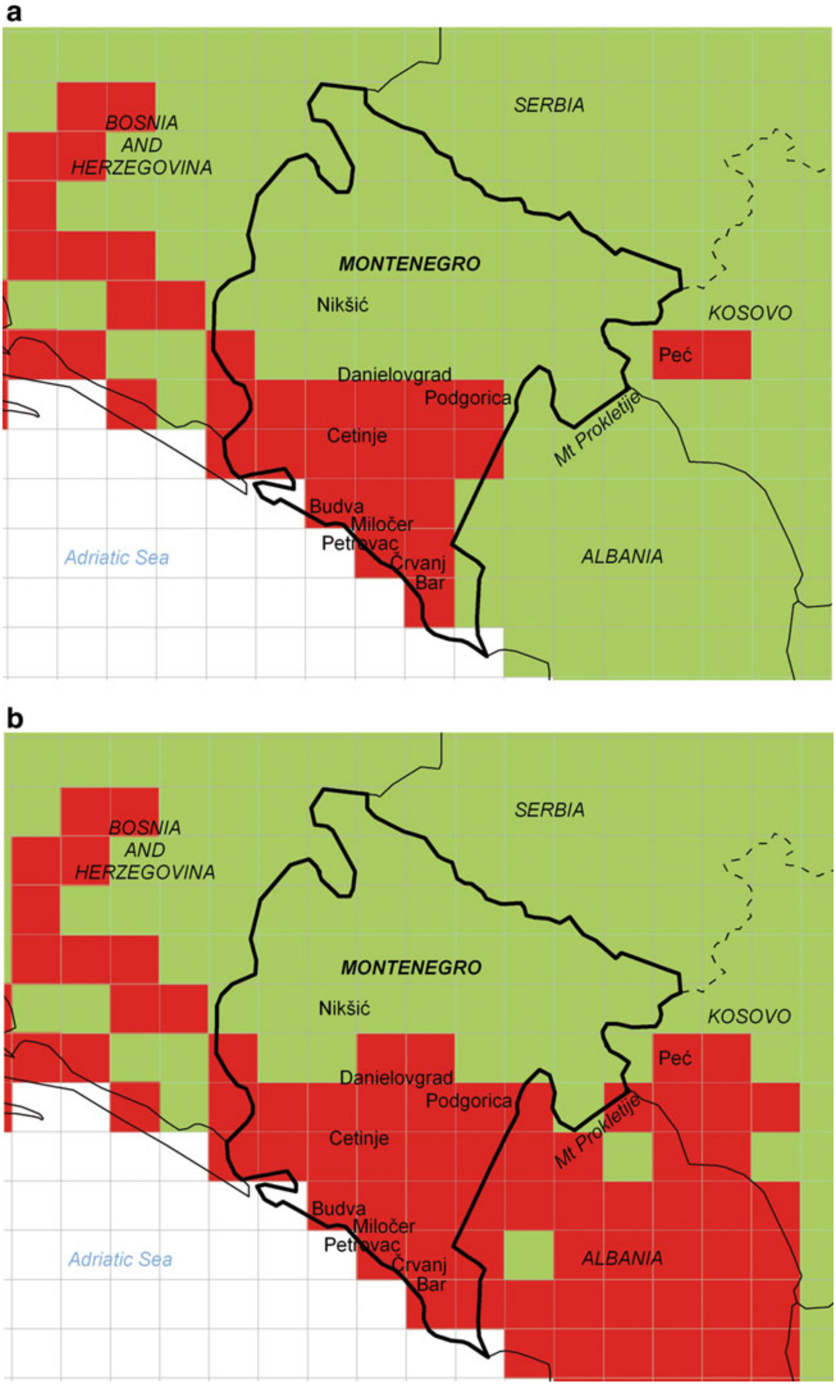


Fig. 3.22 Distribution of pine processionary moth in Montenegro and neighboring countries (**a**) before 2008; (**b**) during winter 2010–2011 on a 16 km-cell grid. *Red squares* show the presence of *T*. *pityocampa* whereas the moth is absent in areas figured in *green*

at an elevation of 1,024–1,080 m. Moreover, up to now there is no evidence that the natural enemies followed moth colonies in the newly occupied pine stands.

5.6 The Pine Processionary Moth in Albania

Ejup Çota

5.6.1 Present Biogeographical Range

Albanian forests presently cover 1,026,410 ha, i.e., 51 % of the country surface whilst agricultural lands only cover 24 %, the remaining 25 % corresponding to rocky areas, water bodies and settlements. Forests are either pure or mixed and mainly consist of beech, black pine, oak, maritime pine, fir and other broadleaves and conifers. Black pine, *Pinus nigra,* the main host of the pine processionary moth is present in the counties of Lure (Diber), Balgjaj (Mat), Llogara (Vlore), Voskopoje (Korce), Terbune (Puke), Gramsh, Erseke (Dida et al. 2001). Mountain pines occur above the beech and fir forests under conditions of hard climate and poor soils, at elevations of 1,600–2,100 m in the north and from 1,700 to 2,300 m in the south. They are represented by *Pinus leucodermis, P. peuce* and *P. heldreichii* (Dida et al. 2001).

It is likely that two periods of expansion of pine processionary moth occurred in Albania (Fig. 3.23). The first one took place before 1994. Actually, there was no relevant information about the distribution and the bioecology of the moth before the late 1980s (Llubani and Zadrima 1989). Nevertheless, it was known that the pest was present since many years ago in the country, with infestation rates ranging 25–30 % in black pine stands (Çota, unpublished data). Then, a large outbreak was observed in 1994, where about 16 % of the pine forests were heavily infested. The infested area reached about 70 000 ha (personal information of M. Dida, F. Ducci and G. Zeneli). The infestation rate ranged from 5 to 95 %.

More recently, pine processionary moth was monitored from 2009 to 2012 at the northern border of Albania, mainly in Puka and Kukës, in a region mainly dominated by black pine, which could have favored the expansion and damage caused by this species. Indeed, while the winter temperature was increasing, the moth expanded towards the northern mountainous areas of Albania. In 2009, the infestation rate in Puka region (northern frontier) was 2–4 tents/pine trees over 100 examined trees. This high infestation rate was rather stable with 2–3 tents/tree in 2010 and 3–4 in 2011.

5.6.2 Particular Biological Features Observed in the Country

At lower elevation/latitude, larval feeding ends by late winter or early spring, diapause is facultative, and moths emerge in late summer. The larvae can tolerate

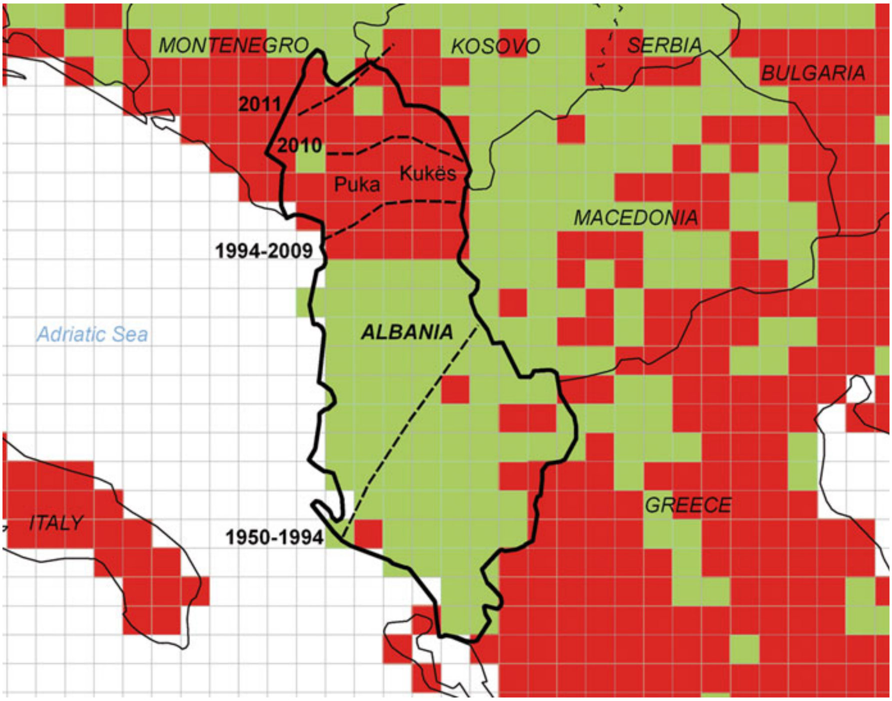


Fig. 3.23 Past and present distribution of pine processionary moth in Albania and neighboring countries on a 16 km-cell grid. *Red squares* show the presence of *T. pityocampa* whereas the moth is absent in areas figured in *green*. The lines 1950–1994, 1994–2009, 2010, 2011 show the front edge of the moth distribution at these different periods

temperatures as low as −15 °C for several days provided that the colony is numerous and the tent is well built. We observed that winter temperatures increased, reducing the number of days with frost. This is a key factor determining the outbreak capacity of pine processionary moth, as low winter temperature strongly determines the larval survival of this insect (e.g. Breuer et al. 1989; Halperin 1990).

5.7 *The Pine Processionary Moth in the Republic of Macedonia*

Sterja Nasceski and Irena Papazova

5.7.1 Present Biogeographical Range

Pine processionary moth was already recorded 50 years ago in nearly all the natural black pine stands of the Republic of Macedonia (Serafimovski 1959; Kusevska et al. 1978). It was observed in the southern part of the country

(Gevgelija at an elevation of 535 m a.s.l. to Visoka Čuka at 1,200 m.; Mariovski basen, where is the main focus of infestation, to Ligurasa – Tribot – Karavastina at 1,200 m a.s.l.), as well in the north (from Pusta Breznica to Skopje), the Central part (it can occasionally be found near Krusevo on 1,300 m.a.s.l), the east along the border (Malesevki Mountains, Golak, Plačkovica, Ograzden), and the west to Bitola, Resen and Ohrid Region. In these natural stands, the processionary moth did not constitute particular threat because of the natural regulation of its populations, and the resulting damage is thus reduced to a minimum.

But the pine processionary moth has extended to the man-made pine plantations which cover 160,000 ha, 95 % from them being black pine monocultures. At present it can be found nearly everywhere, from Gevgelija on south through the whole flow of Vardar River to Skopje; in the east at Kriva Palanka, Kratovo, Golak, Malesevski Mountains, Plackovica, and Sveti Nikole; in the west at Prilep, Resen, Ohrid, Struga occasionally in Krusevo and Brod; and a single presence is registered in Demir Hisar and Kičevo Region. Presently, the most jeopardized black pine cultures are those in the regions near Vinica, Delcevo, Radoviš, Kočani, Štip, Veles, Negotino, Sveti Nikole, Bitola and Prilep. (Fig. 3.24).

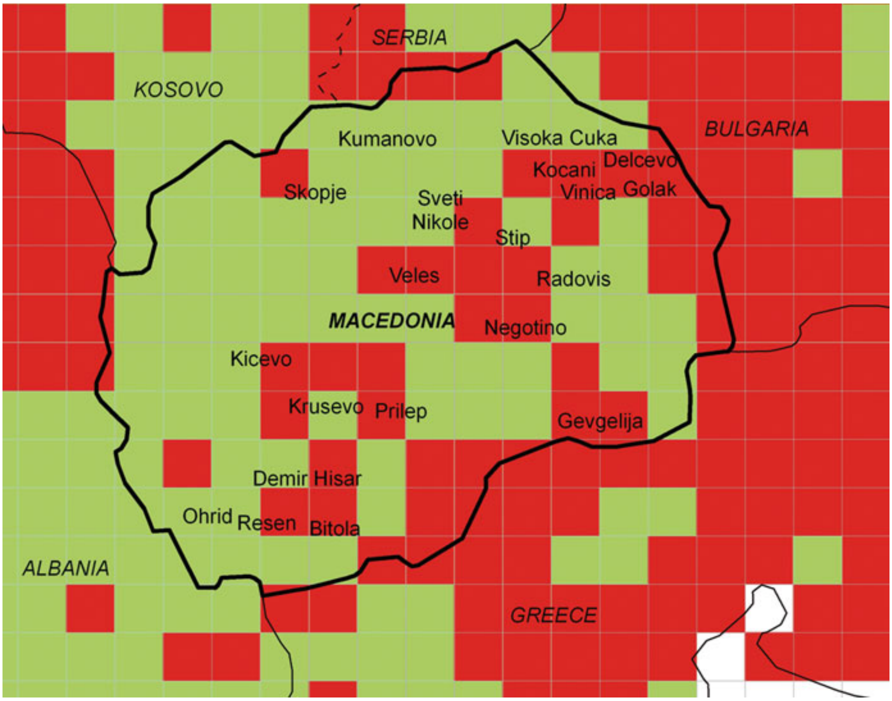


Fig. 3.24 Distribution of pine processionary moth in the Republic of Macedonia and neighboring countries during winter 2010–2011 on a 16 km-cell grid. *Red squares* show the presence of *T. pityocampa* whereas the moth is absent in areas figured in *green*

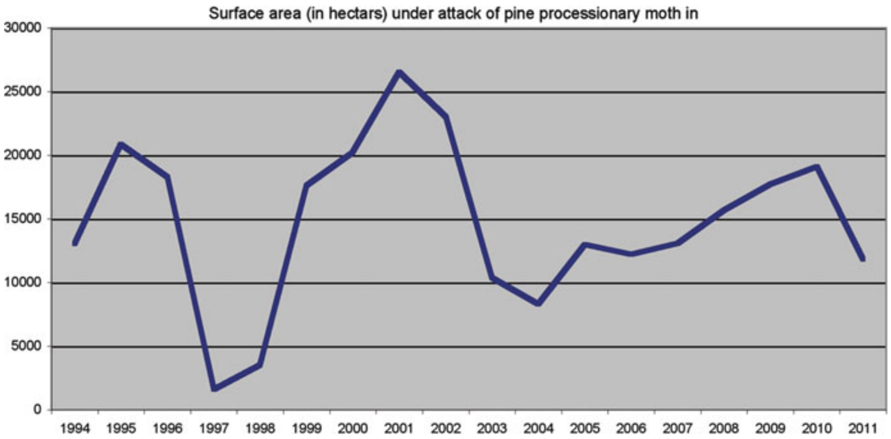


Fig. 3.25 Annual variations in the size of forest surfaces attacked by processionary moth from 1994 to 2011 in the Republic of Macedonia

5.7.2 Population Dynamics and Outbreaking Periods in the Past

Pine processionary moth showed gradations in the pine stands of the Republic of Macedonia at regular intervals of 4–5 years. Thus, moth outbreaks were registered in 1990, 1995 and 1996, when more than 20,000 ha of pine stands were attacked.

The first outbreak on the large area was noticed in 1986, when 3,000 ha of pine forests were damaged in the region of Bitola. Since then, cyclical heavy infestations occurred, increasing in intensity with changes in climatic conditions. In 1992, 4,500 ha became infested whilst the damaged area reached 20,000 ha in 1995. Control measures resulted in population collapse in the following years. However, in 1999, the level of infestation increased, and 26,500 ha subsequently became infested (Fig. 3.25).

In 2009, there was another outbreak and by May 2010 significant damage was reported. Moth monitoring using the number of larval tents revealed a critical population density in the country although annual and regional fluctuations were noticed. Moth presence was ascertained in 27 regions. During 2003–2010, the number of larval tents ranged 400–20,400 in Bitola region whilst these values varied between 460 and 19,000 in Kočani region. In 2011, nearly 8,000 ha showed very high population density, with serious threats for total defoliation, and possibly destruction. In this year, the number of larval tents varied from 3,400 per ha at Mirjanina crkva-Štip to 8,600 at Gočeva Gora – near Negotino.

5.7.3 Particular Biological Features Observed in the Country

Swarming and egg-laying of pine processionary moth starts by late July and lasts until the beginning of August in sites located at high elevation (700–900 m), in the Republic of Macedonia. However, these processes start 7–10 days later in sites at lower elevation (200–500 m). Larva development depends on the climatic conditions. In a year with mild winter (such as years 2001/2002), larval development is completed by mid-February when the larvae begin to process. By contrast, in years with cold and long winters (such as years 2011/2012), the development is delayed and only completed by mid- or late May.

Several species of egg parasitoids have been identified in Macedonia: *Ooencyrtus pityocampae*, *Tetrastichus tibialis*, *Trichogramma semblidis* and *Trichogramma embryophagum*. Natural parasitization by these egg parasitoids only reached 13.5 %, which is not enough to induce a natural regulation of moth populations in the pine plantations.

5.7.4 Hosts

Predominantly on *Pinus nigra*, but occasionally on *P. sylvestris, P. peuce, P. brutia*, *P. pinaster*, and *Pseudotsuga menziensii*.

5.7.5 Expansion with Global Warming

As a likely result of global warming, larval colonies were registered in 2009 for the first time at Zmiski Rid near Kumanovo as the most northern location in the country (Fig. 3.24). High densities of larval tents were also observed on the 500 ha of this area in 2010.

5.8 The Pine Processionary Moth in Greece

Dimitrios N. Avtzis

Conifer forests of Greece are mainly composed of pine species, with *Pinus halepensis, P. brutia, P. nigra*, *P. pinea* and *P. sylvestris* being the most abundant ones (Arabatzis 1998). The dominating needle-feeding pest of these forests, and one of the most dangerous pests in Greece in general is the Pine processionary moth, *Thaumetopoea pityocampa* (Avtzis and Avtzis 2001). This species infests each and every one of the endemic and exotic pine species in Greece; yet the larvae shows a clear preference for some specific host species (*Pinus halepensis, P. nigra* and *P. radiata*) over others (*Pinus pinea, P. pinaster*), something that has been attributed to differences in the chemical composition and ingredients of needles (Avtzis 1986; Breuer et al. 1989; Schmidt 1989). In particular, larval mortality was positively correlated with the concentration of silica in the needles and the metabolization of phenols (Schopf and Avtzis 1987). It was thus suggested that the combined effect of hardness and resin composition of

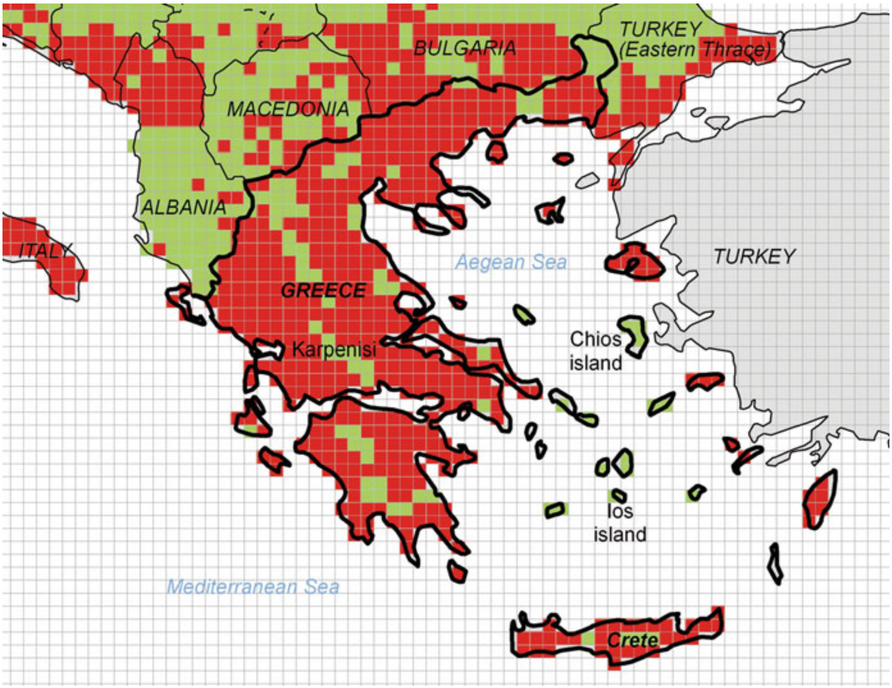


Fig. 3.26 Distribution of pine processionary moth in Greece and neighboring countries during winter 2010–2011 on a 16 km-cell grid. *Red squares* show the presence of *T. pityocampa* whereas the moth is absent in areas figured in *green*

needles determines host selection by pine processionary moth (Devkota and Schmidt 1990).

A direct consequence of the wide spectrum of host species is that pine processionary moth occurs wherever pine grows in Greece from sea level up to 1,800 m (Avtzis 1983). The occurrence of pine processionary moth in Greece (Fig. 3.26) is inhibited only either by unsuitable weather conditions (Karpenisi) or mainly due geographic isolation of the areas (e.g., some islands such as Hios where the moth has not yet been introduced or areas with an elevation higher than 1,800 m) (Avtzis 1983; Buxton 1983). However, even in the areas where it occurs, the population density of the pest in Greece varies over different areas (Avtzis 1986). As possible reasons that could account for the fluctuating population density of the moth in Greece, Kailidis (1991) suggested the exposition of the stand (associated with the general preference of the pest for warm, dry and sunny places on trees) as well as the occurrence of *Quercus coccifera* at the lower levels of vegetation (that poses an impediment during the procession of pine processionary moth).

The importance and significance of pine processionary moth in Greece is reflected on the amount of studies conducted that investigated the most effective methods to control this pest. From chemical insecticides and pyrethrinoids to the currently and most commonly used biological approach of *Bacillus thuringiensis*, Greek researchers have struggled to put pine processionary moth under control (Kailidis 1965; Georgevits 1979; Avtzis 1984). However, as pine processionary moth is a pest that constantly concerns the Greek forest services and authorities, research on control strategies is still being conducted. To that, recent advances in the science technology of pest management have facilitated the combination of different approaches (e.g. mating disruption with a mixture of pheromones and then subsequent application of *B. thuringiensis*-containing insecticides) increasing the efficacy of the methods (Michaelakis et al. 2011).

5.9 The Pine Processionary Moth in Bulgaria

Plamen Mirchev, Georgi Tsankov, and Georgi Georgiev

Pine processionary moth, *Thaumetopoea pityocampa*, was reported for the first time in Bulgaria in 1906 (Drenovsky 1923). During the first half of twentieth century, mainly faunistical studies were conducted in order to establish the species habitats and to outline its distribution. Several outbreaks were reported during this period, predominately in the Rhodopes Mountains, causing significant damage in the attacked stands. Since 1950, the areas infested by the pest were annually surveyed, providing statistics on its fluctuations in Bulgaria (Fig. 3.27).

During the period 1951–2012, a total of 1,070,246 ha of pine forests were infested, with an average of 17,262 ha per year. The changes in *T. pityocampa* damage could be separated into three steps: (a) 1951 to 1971 with the infested areas amounting 5,133 ha on the average; (b) 1972 to 1976 with an increase in moth population density and the infested areas reached up an average of 8,650 ha; and (c) 1977–2012 with the average infested areas increasing to 25,627 ha, i.e., ca. five times larger than during the 1950–1970s.

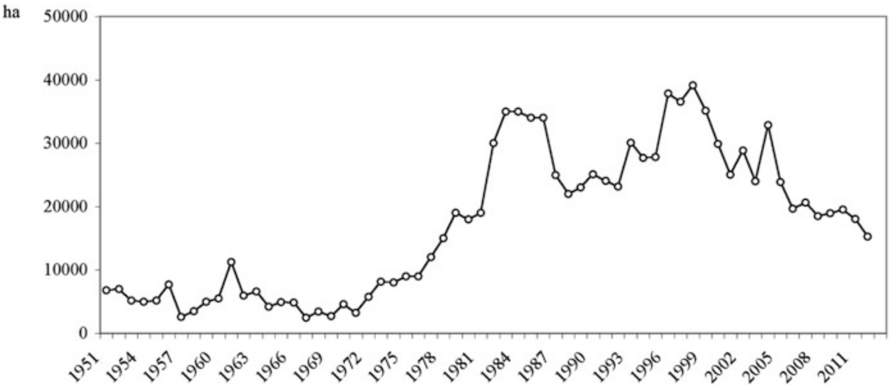


Fig. 3.27 Annual variations in the size of forest surfaces attacked by the pine processionary moth in Bulgaria from 1950 until 2011

The significant increase in the areas infested by moth since 1970 was primarily due to the massive afforestations carried out after 1960 in Bulgaria. In 25 years the plantations of *Pinus sylvestris* have increased by more than two times, and those of *P. nigra* by almost three times. These changes were particularly significant in the natural range of *T. pityocampa*. For example, in the region of Kardzhali, the areas of Scots pine increased by nearly nine times, and those with Austrian Black pine by nearly three times (Mirchev et al. 2000).

Historically, pine processionary moth is distributed in mountainous areas of South Bulgaria – Rila, Pirin, the Rhodopes, Osogovo, the Central Balkan Range and Sredna gora. Within these limits it occurs in pine stands on northern slopes at up to 1,200 m a. s. l., and on southern slopes up to 1,350 m (Fig. 3.28). However since 1999, the species extended into new areas of the country

In 1999, the moth overpassed Kalofer Hills which was the natural eastern border of its distribution in Bulgaria. With an annual velocity of 3–5 km it further colonized new habitats on the slopes of the artificial pine plantations in the Balkan Range and Sredna Gora mountains. Mirchev et al. (2011) detailed some factors which may help predicting the spread of *T. pityocampa* in Bulgaria. First, there is an available food basis, consisting in a huge reserve of untouched Scots and Austrian pine stands. Thus, in 1998, a year showing a maximum infestation, less than 5 % of

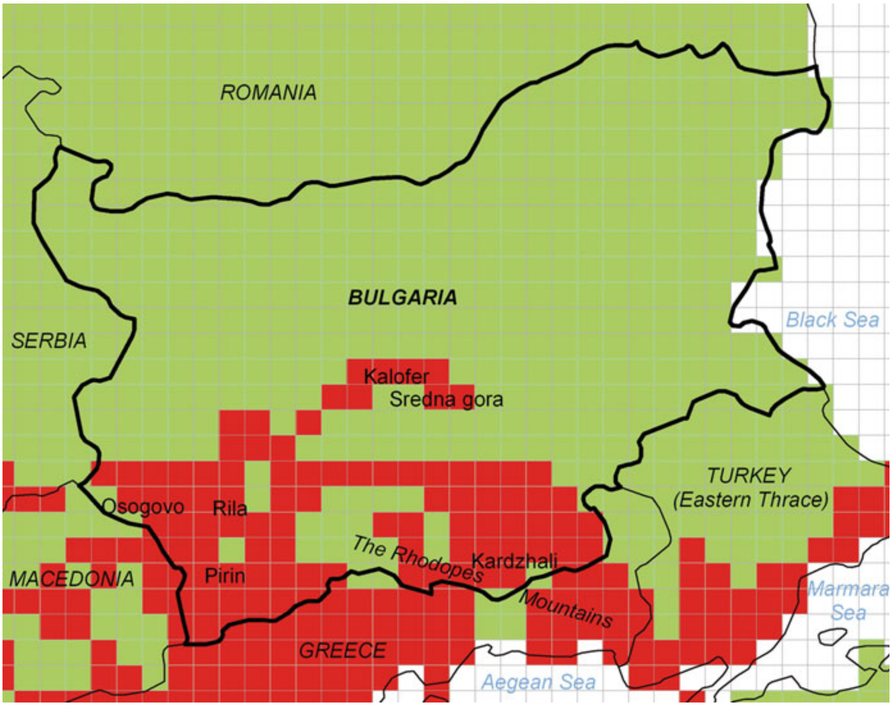


Fig. 3.28 Distribution of *Thaumetopoea pityocampa* in Bulgaria and neighboring countries during winter 2010–2011 on a 16 km-cell grid. *Red squares* show the presence of *T. pityocampa* whereas the moth is absent in areas figured in *green*

the pine forests in Bulgaria were attacked by pine processionary moth. Second, the analysis of the climatic parameters proposed by Battisti et al. (2005) to regulate moth survival and feeding during winter, i.e., survival temperature of –16 °C and day activation temperature of +9 °C in the larval tent, revealed that only the region of Central Northern Bulgaria is unsuitable for pest development due to a pronounced continental climate and critically low winter temperatures.

Actually, the expansion of *T. pityocampa* is realized mainly by an ecological form of the species that completes its larval development before cold weather and overwinters in the soil. Another biological feature also favours the expansion – pupal diapause, where a part of population can emerge up to 6 years after pupation (Démolin 1969a). Additional arguments rely on the ecological plasticity of the species, which helps it to overcome the extreme temperatures and provides an opportunity to expand its range. The third factor influencing *T. pityocampa* distribution is the topography of Bulgaria. The ridge of Western and Central Balkan Range is an insuperable barrier for pine processionary moth to north due to both its high elevation and the predominance of non-host beech forests. However, *T. pityocampa* expands its range to east and could penetrate in Northern Bulgaria through low elevation passes in the Eastern Balkan Range. *T. pityocampa* could also penetrate to the north using the corridor along the Black sea coast where many pine plantations have been settled (Mirchev et al. 2011).

6 Detail of the Past and Situation of the Pine Processionary Moths, *Thaumetopoea pityocampa* and *T. wilkinsoni*, in North Africa and Asia Minor

6.1 The Pine Processionary Moth, Thaumetopoea pityocampa, *in Algeria*

Mhamed El Mokhefi, Gahdab Chakali, Mohamed Zamoum, Atia Bensidi, and Andrea Battisti

The pine processionary moth *Thaumetopoea pityocampa* occurs everywhere there are pine (*Pinus* spp.) and cedar (*Cedrus atlantica*) forests and trees in Algeria (Fig. 3.29). Present elevation range extends to upper timberline, notably on cedar, although it is not clear whether timberline has been reached recently because of global warming or the moth was already present at low density. Certainly the outbreaks observed at high elevation are recent (Sbabdji and Kadik 2011). Definitely its expansion to the south has been facilitated by the large afforestation effort made during the twentieth century and called ‘barrage vert’, i.e. the planting of millions of hectares with Aleppo pine (*Pinus halepensis*) along the Saharian Atlas, a mountain chain dividing the Sahara desert from the coastal area (Zamoum 1998). This expansion has been associated with large-scale pest management, mainly based on *Btk* applications over hundreds thousand hectares every year in the last decades.

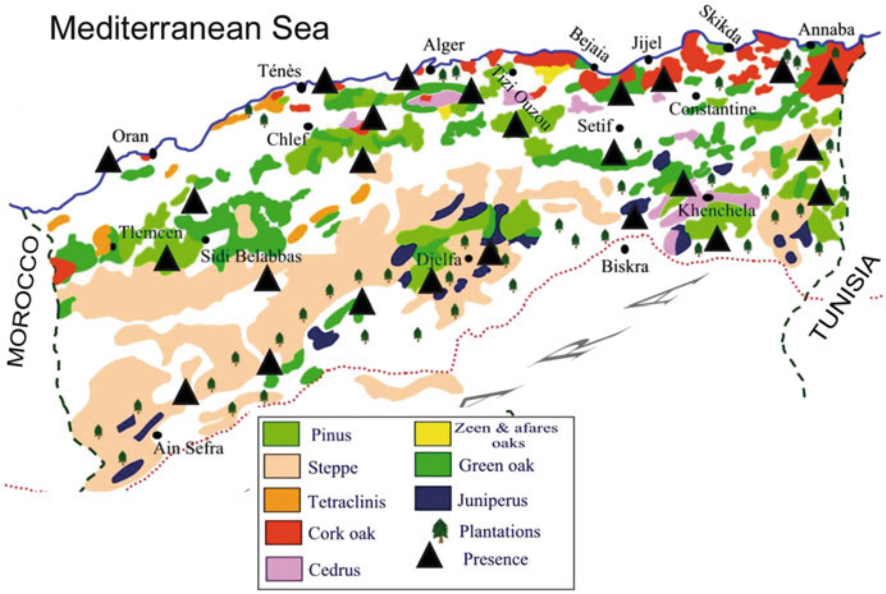


Fig. 3.29 Present distribution of *Thaumetopoea pityocampa* in Algeria in relation to the range of conifer species

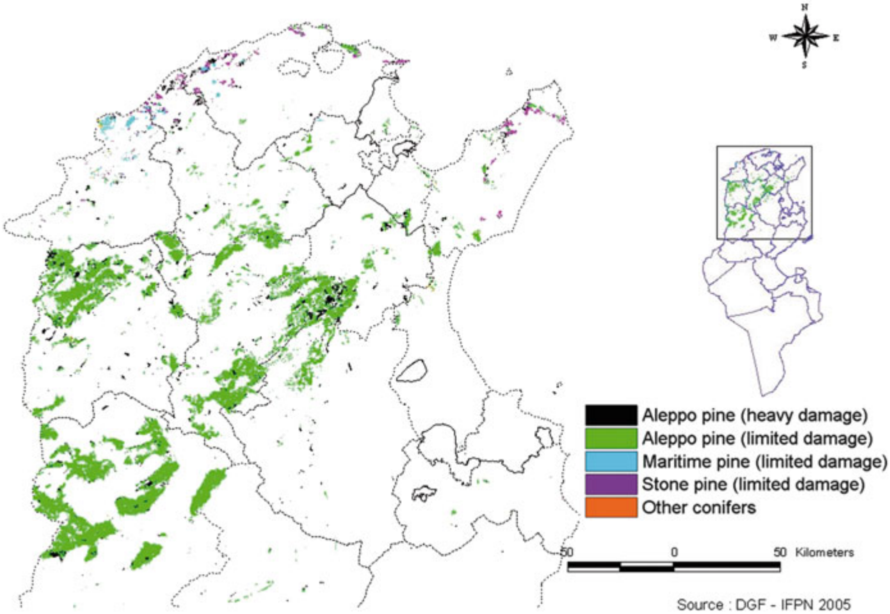
A recent genetic survey has shown that a population from this southern area belongs to the *pityocampa* clade, i.e. to the populations extending from the Balkan peninsula to the west, including the Iberian peninsula and the north-western Africa, whereas another population located closer to the coast belongs to the ENA clade of *T. pityocampa*, which is centered in Tunisia and extends to north-eastern Africa as well (Cyrenaica) (Kerdelhué et al. 2009, 2014, chapter 4 in this book). It appears likely that the contact area between the two clades is located in Algeria and a project has been started to better clarify the situation. Populations have been sampled all over the country and the results will reveal where the contact area is and the possible consequences of the occurrence of the two clades on the insect pest management.

6.2 The Pine Processionary Moth, Thaumetopoea pityocampa, *in Tunisia*

Mohamed Lahbib Ben Jamaa

6.2.1 Distribution Area and Preference of Pine Processionary Moth

The pine processionary moth, *Thaumetopoea pityocampa*, is one of the most important forest pests in Tunisia, present everywhere in all the Tunisian pine



Source : DGF - IFPN 2005

Fig. 3.30 Present distribution of Thaumetopoea pityocampa in Tunisia in relation to the range of conifer species

forests (Rivé 1966) (Fig. 3.30). The moth larvae feed on coniferous species, mainly *Pinus halepensis* (Aleppo pine) which covers about 360,000 ha (Selmi 2006). It may show different preferences for pine host species in the different regions of the Mediterranean basin, but in Tunisia *P. halepensis* and *P. canariensis* are more attacked than *P. pinea* and *P. pinaster* when they are growing in the same stand (Rivé 1966).

The tolerance of Aleppo pine provenances to the attack of the pine processionary moth was compared by counting the number of tents on 30 Tunisian and exotic provenances (Sghaier et al. 1999). This work was carried out between 1993 and 1995 in Arboretum of Korbous (10°35′E, 36°50′N, elevation 180 m) created in 1963 in the North-East of Tunisia. Covariance analysis was applied to compare the number of tents per tree in relation to total tree height at the age of 30 years. It appeared that, for an equal tree height, the rate of attack did not differ significantly between the provenances, suggesting that the previously observed differences in attack could not be attributed to the intrinsic genetic resistance of the provenances but to the difference in height among the surveyed trees (Sghaier et al. 1999). This result confirm those of Démolin and Rivé (1968), for whom there is a difference in preference of pine processionary moth for pines species but this difference is disappearing when the stand is nonspecific. Mendel (1988) found no relationship between the needle morphology and the host preference in *T. wilkinsoni*.

6.2.2 Natural History

In Tunisia, the life cycle of *T. pityocampa* is normally annual but may extend over 2 years at high elevation (Jebel Chaâmbi, Jebel Selloum) for a part of the population. The emergence of adults depends on elevation and climatic conditions. Early emergences are observed at high elevation (Jebel Chaâmbi, 1,544 m; Jebel Selloum, 1,373 m), from 15th July to 1st August at the southern edge of their range. At mid-elevation in Jebel Chaâmbi, Jebel Selloum and Le Kef, belonging to the upper semi-arid bioclimatic range with mild winter, the emergence of adults occurs from the 1st to 15th August (Rivé 1966; Démolin and Rivé 1968). In the mild winter zone, adult emergence is earlier but larval development is longer (6–7 months Démolin 1969a, b) whereas in other parts of Tunisia, larval development lasts 3–5 months. The first instar lasts 12 days, the 2nd 14 days and the 3rd one 30 days. However, the fourth and fifth instars duration varies from 30 days to 90 days according to the severity of the winter (Dissescu and Ceianu 1968). In the mountains, pupation takes place on February whereas it occurs in September and January-February on the littoral.

6.2.3 Effect of the Climate

Colonies of pine processionary moth can survive and resist to low temperatures (-10 °C) as well as tolerate high temperatures (<25 °C), but during the aerial phase they cannot support very high temperature (more than 25 °C) for a long time without physiological effect (weakness) (Démolin 1969a, b). The vital optimum would correspond to an average monthly temperature between 18 and 20 °C; mass effect, tent, and larval movements being susceptible to compass (or restore) variations around this average (Démolin 1969a, b).

In mild winter, tents will be well architected and the epizooties risks will be less frequent. The population is more stable (lack of prolonged fluctuations). The natural enemies (predators and parasitoids) are able to maintain large populations. The winter tents are in general, situated at the branch tips in the upper part of the crown (Démolin and Rivé 1968). In the South, where the temperature is high, the sun does not play any role for the pine processionary moth and the winter tents are less architected. The development of larvae must be at post-summer, allowing the population to avoid temperatures higher than 25 °C (Démolin 1969a, b).

6.2.4 Effect of Defoliation

The larvae feed on pine needles, though even complete defoliation of a pine does not necessarily result in death of the tree but it may dramatically delay development. Repeated defoliation causes loss of increment and may result in tree death. The effect of the defoliation on tree growth is evaluated in Tunisia since the 196 s

(Rivé 1967). This study was carried out on young Aleppo pine trees (3–4 years old) in December of 1965 in the arboretum of Mejez Elbab. In total, 54 infested trees were compared with 54 non-infested trees divided on 6 repetitions. Trees defoliated twice loose about 30–40 % on their growth in height and from 12 to 65 % on their growth in diameter (Rivé 1967).

6.3 The Pine Processionary Moth, **Thaumetopoea pityocampa,** *in Morocco*

Moulay Ahmed El Alaoui El Fels and Saïd El Mercht

Pines and cedar are the dominant species in the conifer forests in Morocco. Native pines include Aleppo pine (*Pinus halepensis*), maritime pine with two subspecies (*P. pinaster* subsp. *hamiltonii* var. *maghrebiana* and var. *iberica*), and north African black pine (*P. nigra* var. *mauretanica)*, with a total surface of ca. 82,115 ha. In addition, conifer afforestations using pines cover approximately 200,000 ha. Morocco is also sheltering the largest surface of Atlas Cedar (*Cedrus atlantica*) within the Mediterranean basin, with approximately 133,600 ha.

The pine processionary moth, *Thaumetopoea pityocampa*, has been recorded since a long time in Morocco (Delepiney 1939) because it constitutes a major forest defoliator capable of damaging all pine species but also Altas cedar. Thus, this species aroused much more interest from scientists than the congeneric *T. bonjeani*, which specifically attacks Atlas cedar (see Battisti et al. 2014, this volume). A number of papers detail its biological cycle, population dynamics, natural enemies, impact on productivity of host trees (among others, Benazoun 1976; Questienne and Miermont 1979; El Yousfi 1982, 1983; Messaoudi 1982; Mzibri 1991; Rattal 1991; Ben Jamâa 1992; El Hassani et al. 1994). Large outbreaks of pine processionary moth have been recorded since the beginning of the last century (1926–1932, 1937–1939, 1947–1952, 1960–1965, 1974–1979) and have not ceased until now.

From 1960 on, pine processionary moth expanded its range in new areas in relation to the large afforestations carried out in Morocco (El Hassani et al. 1994; Ghaioule et al. 1998). Moreover, the introduction in the country of exotic pine species such as Canarian pine (*Pinus canariensis*) and Monterey pine (*P. radiata*), probably contributed to its fast propagation (El Hassani et al. 1994). However, its global distribution was still limited in the late 1970s as it appeared from the map by Questienne and Miermont (1979) (Fig. 3.31). Considering the duration of annual insolation and the minimal temperatures, these authors also defined zones where the moth can further establish. Actually, most of the zones were effectively colonized in 1992, except the central part of the country (Ben Jamâa 1992).

The definition of a control program did not allow to stop moth expansion and damage and large pesticide treatments had to be carried out every year since 1980 (Fig. 3.32), with an average treated surface of approximately 20,000 ha per year (Ben Jamâa and Jerraya 1999).

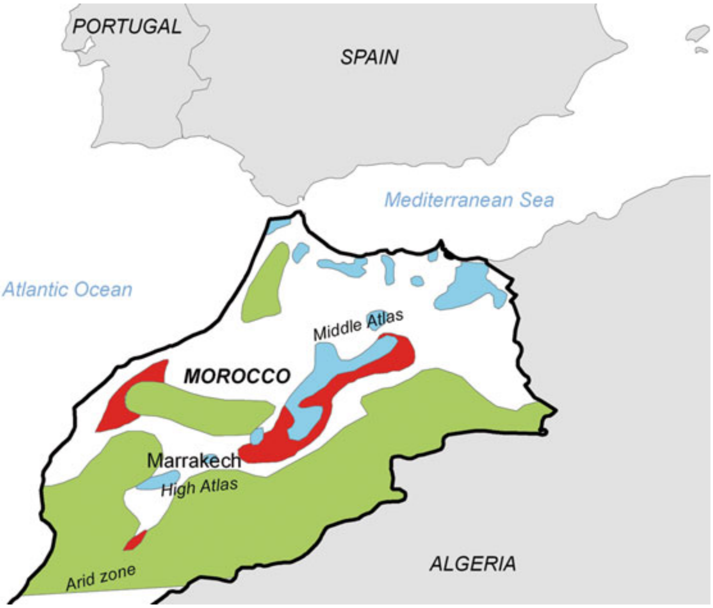


Fig. 3.31 Distribution range of the pine processionary moth in Morocco in 1979, and areas of potential moth establishment considered at that time by Questienne and Miermont (1979). Moth presence figured in *red*; moth potential presence figured in *blue*; adverse areas where moth cannot establish fig. in *green*

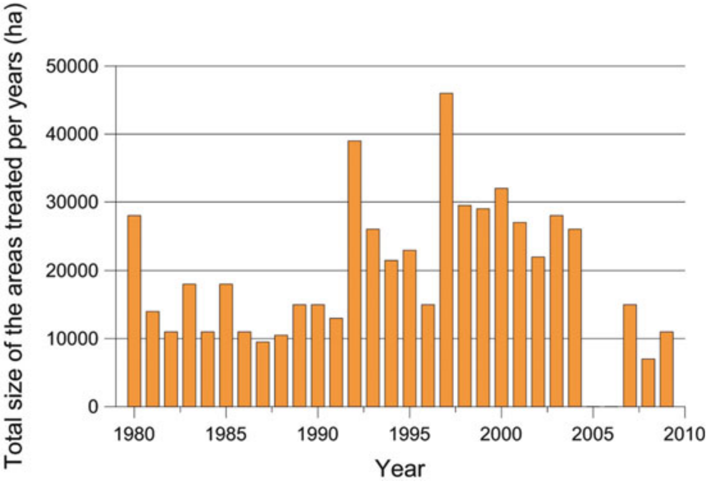


Fig. 3.32 Annual variations in the total area treated against pine processionary moth from 1980 to 2009 in Morocco

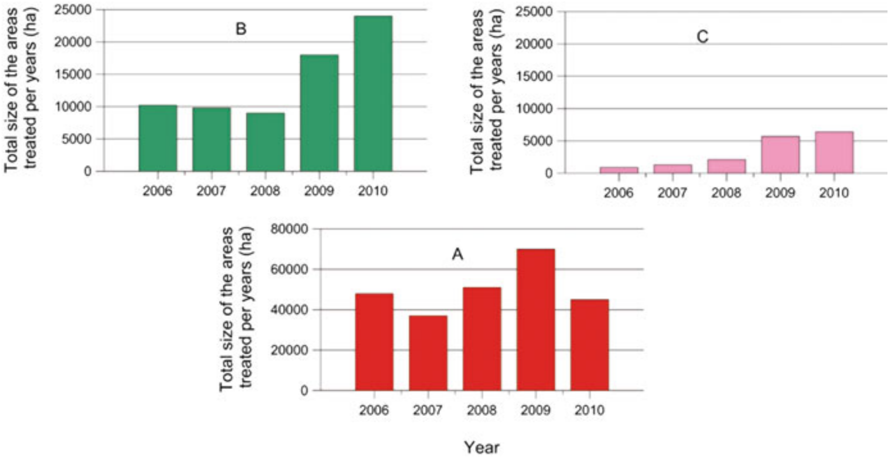


Fig. 3.33 Annual variation in forest surfaces infested by pine processionary moth in Morocco during 2006–2010. (**a**) Global damage (*data missing for 3 regions over 9 in 2010); (**b**) Middle Atlas; (**c**) North-West region

The infestation data worked out by the regional forest managers between 2006 and 2010 suggest that damage increased during the last years (Fig. 3.33a). Indeed, damage is observed in nine regions of Morocco but it especially increased in the Middle Atlas (Fig. 3.33b) and Northwestern regions (Fig. 3.33c).

No detailed, updated map of the pine processionary distribution is presently available but it can be told that the moth is probably present everywhere in Morocco except in the Saharan areas (Fig. 3.34). This expansion seems primarily due to the introduction of exotic pine species as ornamentals, especially in the urban areas, and to the continuous afforestation projects using conifers. At present, processionary colonies are observed even at high elevation in recent afforestations in the high Atlas mountains close to Oukaïmeden such as the plantations of cedar and maritime pine at Aït Lqaq (2,300 m) and those of Aleppo pine at Tachdert (2,400 m).

The great adaptive potential of the species allows to cope with the large variations in climatic conditions between regions. The lifecycle is known to depend on the climatic conditions, in particular the temperature (El Hassani et al. 1994). Thus, adult flight begins earlier at high elevations, which makes it possible the larvae to escape low temperatures during winter, while it starts later at plain areas like Marrakech in order to avoid hatching during the hot summer days (Fig. 3.35).

In addition, the duration of each larval stage is variable according to the areas. In areas with mild winter, the duration of the fourth and fifth larval instars lasts approximately 30–45 days whilst it can reach 90 days in the areas with cold winter. Processions start in February–March in cedar forests of the continental areas but can occur until the end of April in other cedar forests and on Aleppo pine in the Eastern high plateau (El Hassani et al. 1994). Finally, one should not forget the diapause, an important biological mechanism, which can be prolonged up to 6 years (Démolin 1969b).

Fig. 3.34 Present distribution range of the pine processionary moth in Morocco: area in *red*

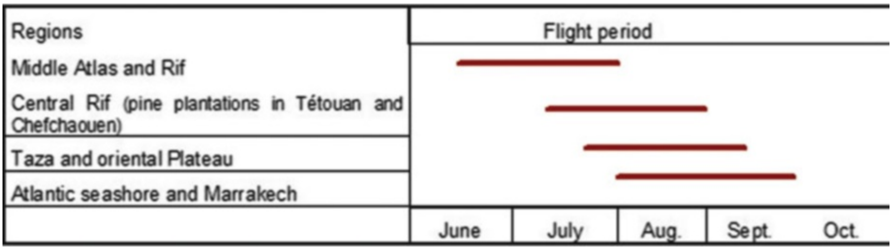


Fig. 3.35 Adult flight periods of pine processionary moth in different regions of Morocco

6.4 *The Pine Processionary Moths,* Thaumetopoea pityocampa *and* wilkinsoni*, in Turkey*

Mustafa Avcı and Kahraman İpekdal

Forests in Turkey cover 21.2 million ha. Red pine (*Pinus brutia*) is one of the most preferred host species of the pine processionary moth and it has a range of 5.4 million ha. Distribution rate of red pine is 47 % in the Mediterranean Region, 40 % in the Aegean Region, and 10 % in the Marmara Region (Taşolar 2002). Anatolian black pine (*Pinus nigra* ssp. *pallasiana*), Scots pine (*P. sylvestris*), stone pine

(*Pinus pinea*), and cedar (*Cedrus libani*) cover 4.2 million ha, 1.2 million ha, 42,000 ha, and 417,000 ha, respectively (Turkish General Directorate of Forestry 2006). The pine processionary moth distributes in 1/7 of the forests in Turkey (Mol and Küçükosmanoğlu 2002) with a higher density in regions under the Mediterranean climate. It exits totally in a region of 1,800 km long and 160 km wide on the Turkish coast line. This region includes the Mediterranean, Aegean, Marmara, and Black Sea Regions. Pine processionary moth currently affects a forested area of about 1.5 million ha in Turkey (Turkish General Directorate of Forestry 2003).

The pine processionary moth has different names in Turkish, such as "ağu böceği, çam büyüsü, gürdük, keseli tırtıl, keseli kelebek"; but its common name is "çam kese böceği" which means pine tent insect.

The oldest record that we could find about existence of pine processionary moth in Turkey goes back to 1885 when an article was published by Julius Lederer. According to this paper, Albert Kindermann, a German lepidopterist, who organized an expedition to collect butterfly in Samsun, Amasya, Tokat, Sivas, and Diyarbakır, reports that he observed many tents on the pines between Samsun and Amasya in May. This short note proves that the pine processionary moth existed in the Black Sea Region back in the nineteenth century.

Another old record was found in the Ottoman Section of the Turkish State Archives. Two Ottoman documents dated to 2 April 1904 summarize methods to control pine processionary moth populations in Istanbul. Thus we can easily say that the pine processionary moth existed in the Marmara Region back in the twentieth century. In the 1940s, serious pine processionary moth damage was reported in some of the mansion yards in Bursa (Sekendiz and Varlı 2002). A passenger train heading from Ankara to Izmir skidded due to larva processions on the railway in Çamlık station (İzmir) in 10 May 1949 (Acatay 1953). Due to an increase in afforestation actions, the pine processionary moth has become more important especially after 1960s in Turkey (Sekendiz and Varlı 2002). Figure 3.36 is showing the present distribution of pine processionary moth in Turkey and its relative importance in the different provinces.

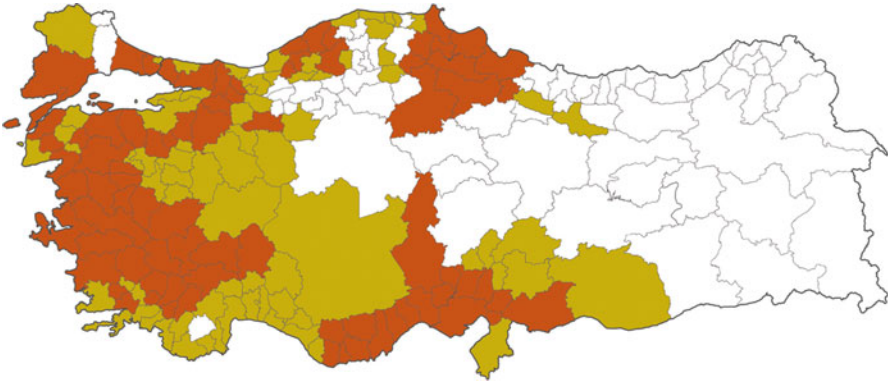


Fig. 3.36 Distribution and density of pine processionary moth in Turkey. In *red*: high density; in *orange*: low density

All these records showed that the pine processionary moth had continuous populations big enough to be recognized in the Aegean, Marmara, and Black Sea Regions at least for the last 200 years. Thus it is obvious that pine processionary moth did not invade these regions a very short time ago. However, there is a significant decrease in pine processionary moth haplotype diversity in Turkey from south to north (İpekdal 2012) which suggests a later invasion into the north.

Until recently, the common pine processionary moth species in Turkey had been thought as *T. pityocampa*. However, current studies (Simonato et al. 2007; İpekdal 2012) showed that the common species in Turkey is *T. wilkinsoni* with a smaller *T. pityocampa* range in the European Turkey (See Fig. 4.7 in Kerdelhué et al. 2014, Chap. 4, this volume).

Phenology differs significantly either latitudinally or longitudinally in Turkey (Akbulut et al. 2002; Çanakçıoğlu and Mol 1998; Schmidt 1990; Özkazanç 2002; Avcı 2011). Adults emerge between July and September, depending on the latitude and elevation. Female moths lay their eggs generally at the end of summer and larvae hatch in early fall; yet, there can be 1 month delay at lower latitudes (Özkazanç 2002).

Pine processionary moth populations in Turkey live on a land that had been used as a refugium during the ice ages. Additionally, north-western Turkey includes a contact zone for the two *Thaumetopoea* species, *T. wilkinsoni* and *T. pityocampa* (see Kerdelhué et al. 2014, Chap. 4, this volume). Therefore it is not only interesting to conduct morphology, phenology and genetic studies on Turkish populations of pine processionary moth, but also crucial to understand nature of these populations and to plan better management strategies on the region.

6.5 *The Pine Processionary Moth,* Thaumetopoea wilkinsoni, *in Israel*

Zvi Mendel

The overall geographic distribution of *T. wilkinsoni* overlaps the area of occurrence of its major pine host, *P. brutia* ssp. *brutia* (known as Brutia pine, Calabrian pine, Turkish red pine, or East Mediterranean pine). The moth colonized the *P. halepensis* forests in Transjordan and in the area of *P. brutia* ssp. *brutia* in Kurdistan (the border areas between Turkey and Iraq) during the last decade (Marwan Abdelwali, personal communication), and, it was absent until the last decade from the eastern *P. brutia* ssp. *brutia* area of the Black Sea. The moth population in the Brutia pine forests of Crete is genetically intermediate between *T. wilkinsoni* and *T. pityocampa* (Simonato et al. 2007). The moth is absent from areas of the other subspecies of Brutia pine, e.g., *eldarica, pityusa* and *stankewiczii*, and Quetta (Afghan) pine, which ranges from the Crimea to Afghanistan. In Israel it was first recorded in 1936 in the 40-ha Umm Safa forest in Samaria (25 km NNW of Jerusalem), on 10-year-old Aleppo and Brutia pines, planted near old, autochthonous Aleppo pine. This may suggest that *T. wilkinsoni* is indigenous here, and that it was found because it became conspicuous in young plantations, next to old, already infested trees. However, the absence of the moth from native *P. halepensis* forests in the Carmel and the Galilee in Israel, in the plantations on the Golan, and in native pine forests in Jordan until the twenty-first century, and also the small genetic differences between the Israeli population and those of eastern Turkey or southern Lebanon (Simonato et al. 2007) may suggest that the population in Israel is a recent introduction (Mendel 1990). It is interesting to note that *P. halepensis* in East Mediterranean is probably an outlier of the pine population in North Africa (Schiller et al. 2004) and we guess that while spreading the tree was not accompanied by the moth. Since the late 1940s of the nineteenth century, the spread of the moth at various rates paralleled the afforestation projects that covered the hilly regions with *P. halepensis* (Halperin 1968, 1990). In the late 1960s a population extending from southern Lebanon was established in the Upper Galilee. The complete coverage of the Israeli pine area was completed in 2009–2010, when the two populations (from Umm Safa and southern Lebanon) intermingled.

7 Past and Present Range of the Other Processionary Moths

7.1 *The Oak Processionary Moth,* Thaumetopoea processionea

Nicolas Meurisse, Axel Schopf, and Andrea Battisti

Established populations of *T. processionea* are known from almost all European countries with the noticeable exception of the northernmost ones (Fig. 3.37). There are no reports from Iceland, Ireland, Denmark, Norway, Sweden, Finland, Latvia, Estonia and Lithuania. In the Mediterranean islands, *T. processionea* is established in Cyprus, but absent from Corsica, Sardinia and Malta. Records exist from Turkey, including Anatolia (Kanat and Aknulut 2005), and the Near East. More details are provided in Groenen and Meurisse (2012).

In 2006 *T. processionea* was found in west London which was the first recorded breeding population in Great Britain (Townsend 2007; Townsend 2009). Human activity, including the commercial movements of infested nursery trees, was thus shown to be a possible source of spread over geographical barriers (Baker et al. 2009; Townsend 2013).

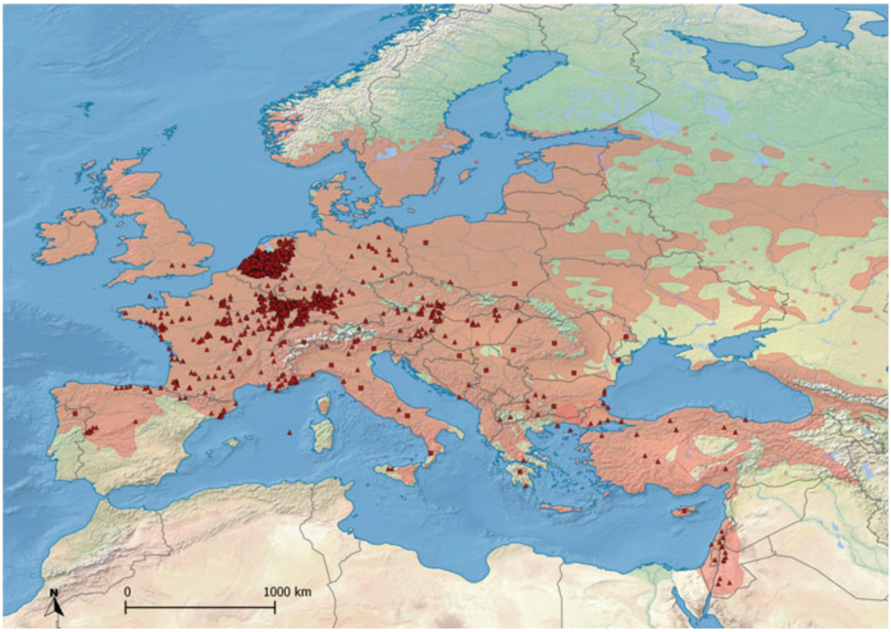


Fig. 3.37 Present and potential distribution of *Thaumetopoea processionea*. *Red triangles* indicate populations records (i.e. records that were properly dated and mapped, all during the 1750–2010 period). *Red squares* indicate records at the regional level (i.e. records that were only partially dated and mapped). The *red-shaded* area indicates the actual cumulative distribution of the host trees *Quercus boissieri, Q. calliprinos, Q. cerris, Q. frainetto, Q. petraea, Q. pubescens, Q. pyrenaica and Q. robur* (Adapted from Groenen and Meurisse 2012)

7.2 The 'Summer' Processionary Moths Associated with Conifers, **Thaumetopoea bonjeani, T. ispartensis, T. libanotica,** *and* **T. pinivora**

Andrea Basso, Andrea Battisti, and Stig Larsson

In this group there are a few species with scattered distribution in Europe, Africa, and Asia (Fig. 3.38). They are all associated with *Cedrus* spp. with the only exception of *T. pinivora* which feeds on *Pinus* (see below). As a consequence, their ranges are highly fragmented and largely overlap with those of the host plant species. *T. bonjeani* is associated with *Cedrus atlantica* in the mountains of Morocco and Algeria, while *T. ispartaensis* and *T. libanotica* occur on *Cedrus libani* in the mountains of Turkey and Lebanon, respectively. Another recently described species, *T. sedirica*, occurs in Turkey close to the site of *T. ispartaensis* and its identity needs confirmation. A further species morphologically belonging to

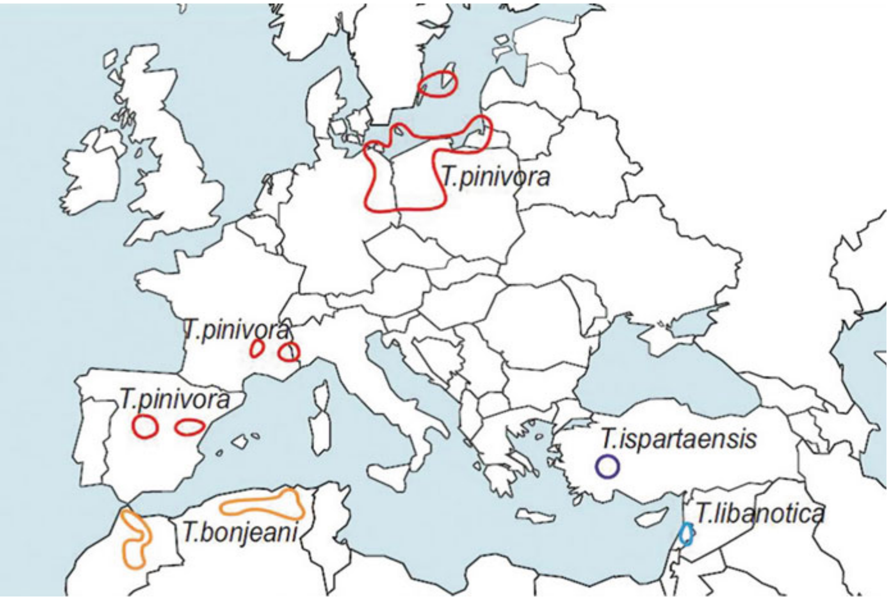


Fig. 3.38 Schematic distribution of the ‘summer’ processionary moths. *Thaumetopoea bonjeani*, *T. ispartensis*, *T. libanotica*, and *T. pinivora*

this group is *T. cheela* from India/Pakistan, where it could live on *Cedrus deodara*, although this needs to be confirmed.

The northern pine processionary moth *Thaumetopoea pinivora* has a scattered distribution with fragmented populations in two separate regions; northern and south-western Europe (Cassel-Lundhagen et al. 2013; Fig. 3.39). In the north the distribution seems to be concentrated around the Baltic Sea in Germany, Lithuania, Poland, and Russia (Kaliningrad). *T. pinivora* is established at least since the 1930s on the Danish island Bornholm (Per Stadel Nielsen, personal communication). In Sweden, the population on Gotland is by far the biggest. A small population is established on the island of Öland, also in the Baltic Sea. There is no reliable information on how long the populations have been on Gotland and Öland, but at least on Gotland there are reports from local residents that larvae were present at least in the 1930s. Lepidopterologists have caught flying individuals also along the Swedish east coast for at least 20 years (Palmqvist 1984; Franzen 2004); in these cases it is likely that it was males originating from the populations at Gotland, Öland or Bornholm. No established populations are known from the Swedish mainland. In south-western Europe, the species in known from several sites in Spain and from a few in France.

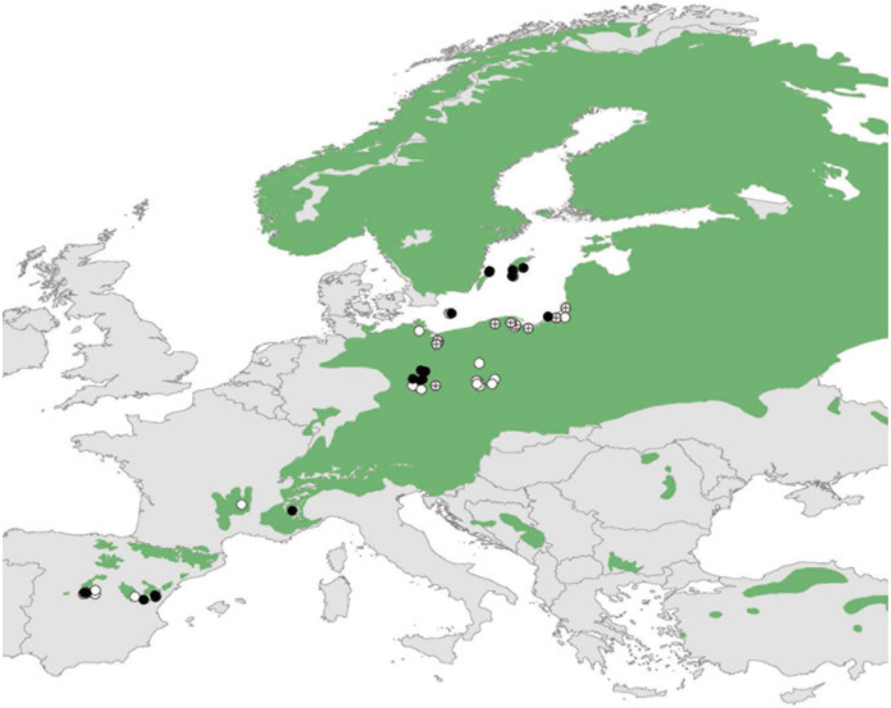


Fig. 3.39 Known records of *Thaumetopoea pinivora*. *Black circles* figure populations sampled in Cassel-Lundhagen et al. (2013); *open circles* correspond to records in literature; *crossed circles* to outbreaks noticed in literature. The range of *Pinus sylvestris* is figured in *green*

7.3 The Pistachio Processionary Moth, Thaumetopoea solitaria

Zvi Mendel and Alex Protasov

Figure 3.40 displays the natural range of *T. solitaria*, based on several sources cited in the chapter on the natural history of the pistachio processionary moth (see Battisti et al. 2014, Chap. 2, this volume); the displayed borders of the natural range of the main hosts of the moth are based on various sources, but mainly Schmuker (1942). The moth is distributed from Macedonia and the eastern Mediterranean region to Afghanistan.

The common host trees of *T. solitaria* are *Pistacia* spp., belonging to the *Pistacia* group, and comprise *P. palaestina, P. terebinthus, P. atlantica* and *P. vera.* All are deciduous, growing in rather harsh sites or semidesert areas. *Pistacia paleastina* is probably a twin species of *P. terebinthus* that occurs in the eastern areas, including Greece and the Near East, usually at lower elevations. *Pistacia atlantica* occurs from the Atlantic coast of North Africa to Central Asia; the eastern population is

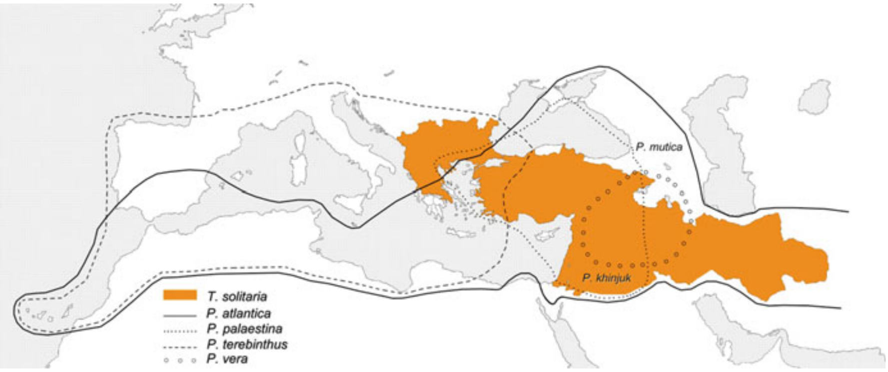


Fig. 3.40 Natural range of *Thaumetopoea solitaria* and the borders of the natural range of *Pistacia* spp., its main host trees

known as *P. mutica* or as *P. atlantica* subsp. *mutica* and occurs mainly between the Black Sea and the Caspian Sea; the natural range of *P. vera* is in western Central Asia (Zohary 1973). Another tree species that falls in the same groups and occurs within the range of *T. solitaria* is *P. khinjuk*. These six tree species belong to a monophyletic group that comprises three pairs of species: *palaestina* – *terebinthus*, *atlantica* – *mutica*, and *vera* – *khinjuk*. The species of each pair are genetically similar (e.g., Kafkas and Perl-Treves 2002; Al-Saghir and Porter 2012), therefore we assume that *T. solitaria* may be found also on *P. mutica* and *P. khinjuk*. The absence of *T. solitaria* from large areas of *P. terebinthus* and *P. atlantica* in the central and western Mediterranean regions suggests that, similarly to other *Thaumetopoea* species, *T. solitaria* colonized the present-day landscapes much later than its principal hosts.

7.4 Thaumetopoea herculeana

Mauro Simonato, Laura Berardi, Juan Pino, and Andrea Battisti

The moth has an almost continuous distribution in the Iberian peninsula, Spain and Canary Islands and Portugal (Agenjo 1941; Gómez-Bustillo 1979; Gomez de Aizpurua 1986; Bacallado Aránega and Hernández Pacheco 1990) (Fig. 3.41). Isolated findings exist from Morocco, Algeria, Tunisia, Libya Cyrenaica, and Palestine, although most of the material is old (Agenjo 1941) and would need reconfirmation.

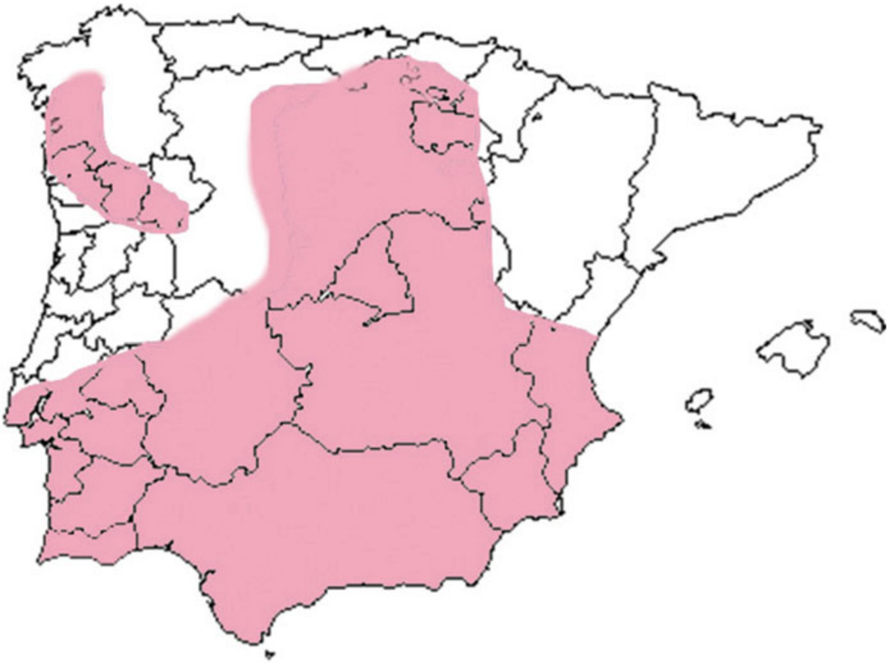


Fig. 3.41 Distribution map of *Thaumetopoea herculeana* in the Iberian Peninsula according to Gómez-Bustillo (1979)

7.5 *Thaumetopoea jordana*

Andrea Battisti and Zvi Mendel

The moth is known from a small area situated in the lower part of the Jordan valley river, between Jordan and Israel (Trougth 1954; Furth and Halperin 1979; Halperin 1990). It has been also recorded from Asir mountains in Saudi Arabia (one male and one female collected by Abdul Mun'im S. Talhouk on 20.XI.1981, in Wiltshire 1982). *R. tripartita* is a semi-deciduous shrub; it is the only known host of *T. jordana*. The plant is distributed in rather isolated populations across North Africa into the Middle East in relict desert or refuge Mediterranean habitats (Furth 1985). *R. tripartita* is related to Afro-tropical *Rhus sensu lato* (Quezel 1979).

7.6 Thaumetopoea apologetica, T. cheela *and* T. dhofarensis

Andrea Battisti

These species are known only as adults from Lepidoptera collections. *T. apologetica* is known from the Eastern African region (Ethiopia) (Seitz 1930) and there is no information about precise occurrence and host plants. *T. cheela* is a species living in the Indian region (Seitz 1933), present between Pakistan and India, and feeding on *Rhus cotinus*, a species of the Anacardiaceae family (Furth and Halperin 1979). Precise data about the geographical occurrence are missing. *T. dhofarensis* is known from Arabic region (Dhofar Oman) and the host plant is unknown (Wiltshire 1980).

8 The Unexpected Importance of Man-Mediated Introductions of Processionary Moths Outside the Natural Range

Alain Roques, Christelle Robinet, and Jérôme Rousselet

Until recently, the expansion of the pine processionary moth, *Thaumetopoea pityocampa*, from its Mediterranean original range, was considered to correspond simply to a natural dispersal process jointly mediated by the positive insect response to winter warming up and by the plantations of susceptible pine hosts in previously non-forested or deforested areas (Battisti et al. 2005). For example, the moth naturally progressed by more than 100 km in the Paris basin between 1972 and 2012, with a significant acceleration during the last 10 years when increasing temperatures allowed it to cross previously unfavorable areas in the south of the Paris basin (Robinet et al. 2007; this chapter). Up to recently, man-mediated movements seemed completely incongruous because of the urticating characteristics of the larvae (Battisti et al. 2011; Moneo et al. 2014, Chap. 8, this volume).

However, the survey of the northern front edge of the moth in France revealed the occurrence of an unexpectedly large number of isolated larval colonies located far beyond the limits of the main range of the species (Robinet et al. 2012; Figs. 3.7 d, e, f; 3.8 b, c). A total of 12 colonies were thus detected since 2003, 10 of which around downtown Paris (Fig. 3.42), one in Alsace, near the German border (Obernai, detected in 2008; cf. Sect. 4.6 above and Figs. 3.6 and 3.8c), and one in northern France (Chamouille, detected in 2011; cf. Figs. 3.6 and 3.8c). At the time of their detection, the colonies in the vicinity of Paris were located between 30 and 55 km to the nearest point of the front edge (except the colonies at Palaiseau) whereas those in northern France and Alsace were 120 and 190 km far from the front, respectively. It is likely that these colonies remained undetected for several years before they were recorded.

The combined use of genetic markers, measurement of female flight capabilities, and comparative analyses of the natural enemy complexes revealed that most of the pioneer colonies located near Paris likely resulted from long-distance translocations as a result of human activities rather than from a natural expansion of the moth (Robinet et al. 2012). Indeed, flight mill experiments confirmed that the limited flight capabilities of the female moths, even if larger than previously considered (see Battisti et al. 2014; Chap. 2, this volume) would not have allowed the insects to

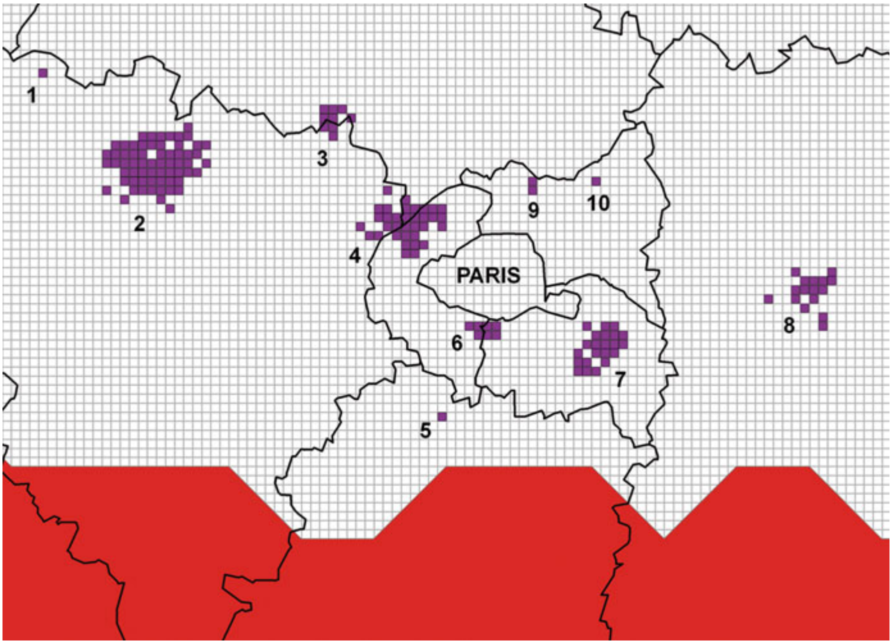


Fig. 3.42 Areas colonized during winter 2011–2012 by the pioneer colonies of pine processionary moth observed in the vicinity of downtown Paris. The grid corresponds to 1 km × 1 km cells. Each *purple* square indicates the presence of one colony at least in the cell. The natural front edge in 2010–2011 over the 8 km resolution grid is figured in *red*. Locations of the colonies and date of first detection: *1* – Moisson/Mousseaux sur Seine (2012); *2* – Flins-Aubergenville (2008); *3* – Eragny-Conflans Sainte Honorine (2008); *4* – Nanterre (2007); *5* – Palaiseau (2012); *6* – Bagneux-Arcueil (2010); *7* – Saint-Maur-des-Fossés (2008); *8* – Disneyland-Bailly-Romainvilliers (2003); *9* – La Courneuve (2012); *10* – Aulnay-sous-bois (2012)

fly over the distance to the nearest established colonies at more than 25 km. It is even more obvious for the colonies located in northern France and Alsace, at more than 100 km from the front of natural expansion. In addition, congruent mitochondrial and DNA microsatellite analyses excluded that most colonies originated from closeby populations. Five over the 7 pioneer colonies of the Paris basin submitted to genetic analyses were assigned either to Italy and south-eastern France or to Spain and south-western France, the two others being possibly related to the nearby populations of north-western France (see Fig. 4.10, Kerdelhué et al. 2014; Chap. 4, this volume). Looking at the parasitoid complexes of pine processionary moth in the same pioneer colonies, Robinet et al. (2012) did not notice the presence of any egg parasitoids but observed that 15–30 % of the tents hosted a specific larval-pupal parasitoid, *Phryxe caudata*. This tachinid fly presents two generations, the first one developing inside the processionary larvae from second to fourth instar while the second one parasitizes the last instar larvae, and emerges from the pupae developing in the soil (Biliotti 1956; Géri 1980; Buxton 1990). Taking into account that the white silk tents are easy to spot on small pines and that pine trees are usually not planted in summer during the egg stage, Robinet et al. (2012) suggested that the likely pathway for these long-distance jumps is the trade of mature pine trees transplanted for ornament from nurseries located in the southern area, the moth being moved as pupae with the accompanying soil. A similar pathway has been hypothesized for the introduction of oak processionary moth in England (Evans 2008). The capacity of the moth pupae to enter prolonged diapause, and to stay inactive for several years in the soil, also increases the probability of accidental translocations of the insect at this stage (Géri 1980).

The location of all of the pioneer colonies in man-made habitats constituted of recent plantations of large pine trees near human dwellings supports this hypothesis. Thus, these colonies were first detected in such plantations along highways (Arcueil), in runabouts (Obernai), around urban buildings (Bagneux, Saint-Maur-des-Fossés), around swimming pools (Eragny), in parks of university (Nanterre) and factory (Flins-Aubergenville), and in recreative parks (Disneyland Paris at Bailly-Romainvilliers; Parc de La Courneuve; Chamouille). Moreover, once the moth is introduced with plantations in urban and semi-urban areas, the combination of global warming and urban microclimate is favoring its survival and establishment. A comparative survey of the colony survival during two recent, severe cold periods having occurred during winter 2009 and 2010 in the Paris basin revealed that the larvae survived significantly better in urban areas, which behave like heated islands, than in the main range (Robinet et al. 2012). These processes also led the moths to establish in highly-populated areas, thus constituting a serious threat for human health.

Such transportations may have existed for a long time although they probably increased recently with the ‘green’ fashion. However, if pupae were transported before the late 1990s, it is likely that the moth offspring did survive the harsh winter conditions in northern areas. A random simulation of translocations over France clearly revealed an increase in the probability of establishment since 1995 (see Figs. 5.8 and 5.9; Roques et al. 2014, Chap. 5, this volume; Robinet et al. 2014), which is the congruent with the discovery of an increasing number of pioneer colonies after the 2000s.

Indeed, climate models based on the survival constraints of the moth (see Sect, 2; this chapter) show that a large part of Western, Central and Eastern Europe is becoming increasing favourable to the establishment of larval colonies if the moth is accidentally introduced (see Fig. 5.2, Roques et al. 2014, Chap. 5, this volume). Thus, human-mediated dispersal creating satellite populations is likely to accelerate significantly the spread of the pine processionary moth in the future (Robinet et al. 2014).

Actually, there is no reason that such man-mediated translocations of moth populations with the trade of large trees would be restricted to areas beyond the front edge and do not occur from one region to another of the main natural range. This would explain, at least partly, some genetic admixtures observed in some part of the natural range (see Kerdelhué et al. 2014; Chap. 4, this volume). Roques et al. (2011) also hypothesized that long-distance jumps may be involved in the relatively high rate of spread of the moth in the Paris basin between 2007 and 2009.

9 Conclusion

In conclusion, although a large part of western and central Europe is at present climatically favorable to establishment, pine processionary moth is colonizing it slowly, at ca. 5 km per year in the western part, due to the limited flight capabilities of females. However, the expansion appears at present to result from a combination of natural spread and long-distance jumps mediated by the human trade of large trees. Accidentally-introduced colonies are thus likely to establish and create satellite populations in a large part of the yet non-infested regions of Europe, especially near urban areas, and to accelerate the colonization of Europe by the moth (Robinet et al. 2014). For this reason, it would be important to quantify this chance of accidental transportation in order to be capable of predicting these long-distance jumps and the expansion of the species' distribution. However, the genetic admixture resulting from the combination of naturally-expanding and introduced populations would become increasingly difficult to be disentangled with continued climate change (Walther et al. 2009).

If the moth expansion has been deeply studied in the western part of the range, it remains to be characterized in the eastern part in order to appreciate whether the processes are similar, and especially if the man-mediated movements play the same role there. Another great challenge is the precise delimitation and the survey of the southern front edge in northern Africa in order to understand whether climate change may led to a retraction of this southern range as it has been observed in other lepidopteran species (Parmesan et al. 1999).

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Chapter 4
Genetic Diversity and Structure at Different Spatial Scales in the Processionary Moths

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1 Introduction

This chapter presents the evolutionary history of *Thaumetopoea* species associated with pines, as revealed by molecular markers at different temporal and spatial scales. This field of research has remained unexplored in this genus until the beginning of the 2000s, and all the data and results presented here correspond to

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relatively recent discoveries and ongoing works using both sequencing technologies and population genetics tools. Most of the subchapters focus on the winter pine processionary moths, known as the *T. pityocampa*/*T. wilkinsoni* species complex. We will first present a phylogenetic perspective of the evolution of the genus (including *Thaumetopoea* species associated with pines, cedars and broad-leaved plants), which allows to build hypotheses about the evolutionary pathways of main biogeographical and ecological traits. The second subchapter is restricted to the phylogeographical patterns of the winter pine processionary moth over the Mediterranean basin, and shows where the populations survived past climate changes, and how they managed to recolonize northern and altitudinal biotas during interglacials, eventually forming contact zones of divergent lineages.

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The third subchapter specifically addresses the question of the most recent geographical expansions, from the last glacial maximum to the fairly recent expansion that is being observed for the last decades. It opens perspectives of genetic studies developed at a local spatial scale (landscape genetics). Then the fourth subchapter gives an overview of the evolutionary history of the northern pine processionary moth, *T. pinivora*, which occurs in Europe as scattered populations and has experienced a recent outbreak on the Swedish island of Gotland. Both global and local genetic structures are studied for this species to elucidate its evolutionary history as well as its contemporary distribution dynamics. Last, we present the genetic and ecological characteristics of a very peculiar population of *T. pityocampa*, discovered in Portugal in 1997, which has a shifted phenology compared to all other populations of this species, including a sympatric one. The results suggest that this population diverged recently, and already shows signs of adaptive ecological differentiations. In brief, this chapter presents results obtained through molecular approaches that give insights about the effects of past (Quaternary) climate changes on the populations of winter and northern pine processionary moths in different regions, and allow to study the contemporary changes affecting present-day populations in front of the present climate warming.

2 Evolutionary History of the Genus *Thaumetopoea*

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2.1 Introduction

The evolutionary history of insects largely depends on a number of abiotic and biotic factors, and from their interactions. Climate changes for example can cause expansion, contraction, or fragmentation in the geographical distribution of many insect species (Hewitt 2000) determining isolation of interbreeding populations and possibly leading to allopatric speciation. Among biotic factors, host plant is probably the main source of diversification in herbivorous insects (Mitter et al. 1988). Lepidoptera developed a variety of methods to circumvent plant defences that include both behavioural and biochemical/physiological adaptations (Dussourd 1993). These adaptations in turn limit host shifts of phytophagous insects only between closely related host plants (same genus/ family) (Lopez-Vaamonde et al. 2003) or between unrelated plants with similar secondary metabolic compounds (Ehrlich and Raven 1964; Strong et al. 1984).

Another biotic factor favouring species diversification is represented by natural enemies that can promote diverse evolutionary paths toward the acquisition of enemy-free space (Singer and Stireman 2003). In particular defensive mechanisms could play an important role in the niche definition and in speciation of herbivorous insects.

Processionary moths are an interesting case to better assess the role of these main evolutionary forces in the speciation process. They are all included in the genus *Thaumetopoea* Hubner, (described in Chap. 2) (Lepidoptera Notodontidae), even though a recent revision suggested to split it into three genera (namely *Traumatocampa*, *Thaumetopoea* and *Heliantocampa*, de Freina and Witt 1982, 1987). They occur mainly in the Mediterranean and Iranoturanic regions (Agenjo 1941; Kiriakoff 1970). Larvae attack trees and shrubs of very different families (Anacardiaceae, Cistaceae, Fagaceae, and Pinaceae). They are protected against vertebrate predators attacks by urticating setae, and thereby represent a sanitary risk for humans and domestic animals (Battisti et al. 2011).

In this subchapter, we present the main results of a phylogenetic study we carried on the genus *Thaumetopoea* (Simonato et al. 2013) in order to clarify the evolution of some morphological and phenological traits. This approach is useful to address some taxonomic problems, evaluating whether the morphological characters used to define taxa agree with the phylogenetic relationships found or are rather convergent. The study covered the most common species of the genus *Thaumetopoea*, while a few rare species were not available (*T. apologetica* (Africa), *T. cheela* (India), *T. jordana* (Jordan) and *T. dhofarensis* (Oman)).

2.2 Approach

The list of the *Thaumetopoea* species considered as well as the moth species used as outgroups is provided in Table 4.1, together with information on biogeography, host plant, ecology, and morphology.

One individual per species was used in the genetic analysis. Three portions of mitochondrial DNA and three nuclear genes were sequenced for each species of the *Thaumetopoea* genus. For the outgroup taxa *Ochrogaster lunifer* (Notodontidae), *Lymantria dispar* (Lymantriidae) and *Hyphantria cunea* (Arctiidae), information was obtained from both GenBank and *de novo* sequencing. Phylogenetic trees were inferred using both a Bayesian inference (BI) and maximum likelihood (ML) methods (Felsenstein 2004; Ronquist and Huelsenbeck 2003). Posterior probabilities were calculated for each node of the BI trees. Nonparametric bootstrap tests (Felsenstein 1985) were performed to assess the robustness of ML tree topologies. All further details about sequencing and data analysis can be retrieved in Simonato et al. (2013).

Several traits listed in Table 4.1 and based on literature were used to discuss the molecular phylogeny. Biogeographic traits were based on classical zoogeographic categories and on specific areas of occurrence. Individual reports of species occurrence were checked for consistency with the most recent taxonomic position of taxa, and doubtful cases were excluded. The knowledge about host plants range, in particular for those species with a widespread and continuous distribution over large areas, was useful to define the general distribution of taxa. For each host-plant genus we assessed the presence/absence of resins, defined as hydrocarbon secretions produced and transported in specific resin ducts of plants (Kramer and Kozlowski 1979). As one prominent characteristic of the processionary moth is sociality at larval stage, four traits associated with this behaviour were identified and used in the analysis. First, foraging type was classified into three levels according to Fitzgerald (1993), i.e. nomadic (larvae moving from one patch of food to another), patch-restricted (larvae living directly on their food source), and central place (fixed nesting site from which larvae move to get food). Second, the presence/absence of a conspicuous silk tent where the larvae rest when they are not feeding was recorded. Third, gregariousness of larvae was classified as present throughout the whole stage or only in the early instars. Fourth, the procession behaviour, consisting of head-to-tail line of larvae moving in the host plant to feed or to the pupation site, was recorded as presence/absence. Two more traits associated with life history and relevant for ecological adaptation were used. They are pupation site (silk tent, litter, soil) and overwintering stage (egg, larva, prepupa/pupa) of the typical univoltine cycle of all species of *Thaumetopoea*. The frequent possibility to enter prolonged diapause over 1 or more years was not considered because of lack of precise information in several species.

The morphological traits of eggs, larvae and adults, used for taxa identification were also classified for their presence/absence or status in the different species. This was the case for the front of the adults (crested or smooth) and for the occurrence of a prominent spine on the foreleg tibia (present/absent) (Agenjo 1941; de Freina and Witt 1982, 1987). The presence/absence of scales covering the egg clusters was evaluated as well as their shape, classified into combined categories of length (short: 0.7–0.8, medium: 1.4–1.9, long: 2.3–3 mm) and width (narrow: 0.2–0.5, medium: 0.7–0.9, wide 1.6–1.7 mm) (Agenjo 1941). The colour of the scale was also considered in previous taxonomic work but could not be used in the analysis because of lack of precise information in several species. The presence/absence of urticating setae on the larvae was evaluated based on the numerous reports summarised by Kiriakoff (1970) and de Freina and Witt (1987). For the case of *T. herculeana*, reported to be non-urticating (Agenjo 1941), the larvae used for the genetic analysis were inspected. The traits were mapped on the molecular phylogeny to trace their evolution within the *Thaumetopoea* genus. The ancestral character states were reconstructed by applying the parsimony algorithms implemented in MacClade 4.08 (Maddison and Maddison 2005). The analysed characters were treated as binary or multistate and as unordered.

Table 4.1 List of *Thaumetopoea* species and traits used in the analysis

Trait	*T. bonjeani*	*T. herculeana*	*T. ispartaensis*	*T. libanotica*	*T. pinivora*	*T. pityocampa*
Biogeography						
Distribution	Localized	Localized	Localized	Localized	Localized	Widespread
Region	NW Africa	W Mediterranean	E Mediterranean	E Mediterranean	N Europe, W Europe	S Europe, NW Africa, W Asia
Zoogeography	Mediterr anean	Mediterranean	Mediterranean, Iranoturanic	Mediterranean, Iranoturanic	Eurosibiric	Mediterranean, Eurosibiric
Temperature	Meso	High	Meso	Meso	Meso, low	High, meso
Humidity	Low	Low	Low	Low	Low	Low, meso
Host plant						
Host group	Gymnosperm	Angiosperm	Gymnosperm	Gymnosperm	Gymnosperm	Gymnosperm
Host family	Pinaceae	Cistaceae	Pinaceae	Pinaceae	Pinaceae	Pinaceae
Host genus	*Cedrus*	*Helianthemum*, *Cistus*	*Cedrus*	*Cedrus*	*Pinus*	*Pinus*, *Cedrus*
Anti-herbivore chemicals	Present	Present	Present	Present	Present	Present
Eaten foliage	Mature	Young	Mature	Mature	Mature	Mature
Ecology						
Foraging	Patch-restricted	Nomadic	Patch-restricted	Patch-restricted	Patch-restricted	Central place
Silk tent	Scarce	Scarce	Scarce	Scarce	Scarce	Abundant
Gregariousness as larva	Present	Present	Present	Present	Present	Present
Procession	Present	Present	Present	Present	Present	Present
Pupation	Soil	Soil	Soil	Soil	Soil	Soil
Overwintering	Egg	Egg	Egg	Egg	Egg	Larva
Diapause	Present	Present	Present	Present	Present	Present
Morphology						
Front of adult	Crested	Crested	Crested	Crested	Crested	Crested
Fore tibia	With spine	With spine	With spine	With spine	With spine	With spine
Egg scales	Present	Present	Present	Present	Present	Present
Scale length mm	1.91	1.5	1.7	1.74	1.62	2.94
Scale width mm	0.72	0.34	0.94	0.85	0.81	1.63
Scale type	Medium/medium	Medium/narrow	Medium/medium	Medium/medium	Medium/medium	Long/wide
Urticating setae on larvae	Present	Present	Present	Present	Present	Present
Urticating setae on moth	Absent	Absent	Absent	Absent	Absent	Absent

T. pityocampa ENA	*T. processionea*	*T. solitaria*	*T. wilkinsoni*	*O. lunifer*	*H. cunea*	*L. dispar*
Widespread	Widespread	Localized	Widespread	Localized	Widespread	Widespread
NE Africa	Europe	E Mediterranean	E Mediterranean	Australia	N America	Europe, Asia
Mediterranean	Mediterranean, Eurosibiric	Mediterranean, Iranoturanic	Mediterranean	Australian	Nearctic	Eurosibiric
High	Meso	High	High	High	Meso	Meso, low
Low	Meso	Low	Low	Low	Meso	Meso, high
Gymnosperm	Angiosperm	Angiosperm	Gymnosperm	Angiosperm	Angiosperm	Angiosperm, Gymnosperm
Pinaceae	Fagaceae	Anacardiaceae	Pinaceae	Leguminosae	Polyphagous	Very polyphagous
Pinus, *Cedrus*	*Quercus*	*Pistacia*	*Pinus, Cedrus*	*Acacia*	Polyphagous	Very polyphagous
Present	Absent	Present	Present	Present	Absent	Absent
Mature	Young	Young	Mature	Young	Young	Young
Central place	Central place	Patch-restricted	Central place	Central place	Nomadic	Nomadic
Abundant	Abundant	Scarce	Abundant	Abundant	Abundant	Absent
Present	Present	Present	Present	Present	Absent	Absent
Present	Present	Present	Present	Present	Absent	Absent
Soil	Nest	Litter	Soil	Litter	Litter	Litter
Larva	Egg	Egg	Larva	Prepupa	Pupa	Egg
Present	Present	Present	Present	Absent	Absent	Absent
Crested	Smooth	Smooth	Crested	Smooth	Smooth	Smooth
With spine	Without spine	Without spine	With spine	Without spine	Without spine	Without spine
Present	Present	Present	Present	Present, diverse	Absent, hairs	Absent, hairs
2.88	0.73	1.5	2.38	1.4	Not applicable	Not applicable
1.67	0.15	0.47	1.59	0.2	Not applicable	Not applicable
Long/wide	Short/narrow	Medium/narrow	Long/wide	Medium/narrow	Not applicable	Not applicable
Present	Present	Present	Present	Absent	Absent	Absent
Absent	Absent	Absent	Absent	Present	Absent	Absent

2.3 *Phylogeny of the* Thaumetopoea *Genus and Evolution of the Main Traits*

The phylogenetic tree obtained from the molecular data showed that *Thaumetopoea* species were split in three well supported clades named A, B, and C (Fig. 4.1).

Clade A included *T. herculeana*, *T. processionea* and *T. solitaria*. Clade B contained *T. pityocampa* ENA, *T. pityocampa* and *T. wilkinsoni*. Clade C encompassed *T. bonjeani*, *T. ispartaensis*, *T. libanotica* and *T. pinivora*. Clades B and C were grouped as sister taxa with very high BI/BT support, while clade A represented an earlier branching off within the *Thaumetopoea* genus. The evolution of several traits, ranging from biogeography, host plants, ecology, and morphology

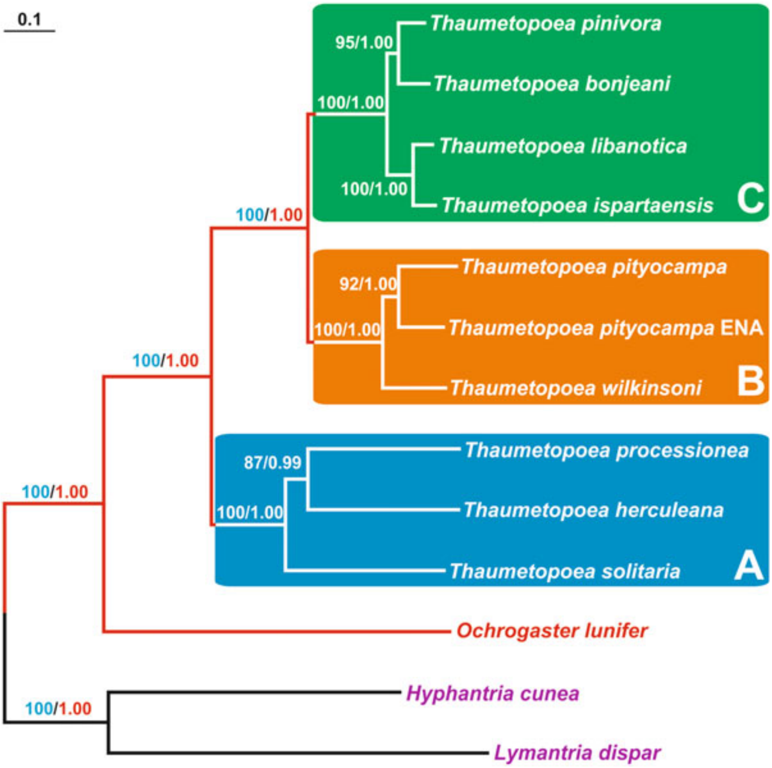

Fig. 4.1 Maximum likelihood tree inferred from all the available genes (10,357 bp) for the 13 species considered in this study. The analysis was performed by applying the evolutionary model and the partitioning scheme described in Simonato et al. (2013). The statistical support of the clustering is indicated by bootstrap/posterior probabilities figures. The bootstrap values are expressed as percentage while the posterior probabilities, computed through Bayesian inference, are presented as fraction of 1. The maximum support to the clustering is represented respectively by 100 and 1. The scale bar represents 0.1 substitutions per nucleotide site (Figure modified from Simonato et al. 2013)

was traced on the reference tree. This approach allowed to identify some of the features that characterized the common ancestor of *Thaumetopoea* moths or represented novelties restricted to some species of this genus (Fig. 4.2).

2.3.1 Biogeography

The analysis of the biogeographic traits (Fig. 4.2a) indicated that the ancestor of the genus had a Mediterranean distribution, with at least one species with such a distribution in each of the three clades of *Thaumetopoea*. The ancestor of *Thaumetopoea* had a biogeographic distribution centred in the Mediterranean basin, and it very likely derived from a stock of taxa living in the African continent where several Thaumetopoeinae genera occur, including one species of *Thaumetopoea* (*T. apologetica*) (Kiriakoff 1970). Successively, a shift to regions with continental climate (higher latitudes in Europe) occurred independently in each clade for *T. pinivora*, *T. processionea* and *T. pityocampa*, respectively. The occurrence of species with similar distribution in each of the clades excludes the possibility that geography has driven the split of the main clades within the genus. The spread outside the Mediterranean basin for *T. processionea, T. pityocampa* and *T. pinivora* was probably linked to the range expansion of their respective host plants after the last Quaternary glaciation, and occurred independently in each clade.

The confinement to separated areas is a very likely factor speeding up the speciation process, through geographic isolation, inside two clades: range fragmentation due to biogeographical events and climatic changes during the late Tertiary, influencing host availability, has been invoked to explain allopatric speciation in clade B (Kerdelhué et al. 2009) and may also explain speciation in clade C. In addition, the species of clade B have responded to the recent climate change by a rapid expansion to higher elevation and latitude (Battisti et al. 2005; Kerdelhué et al. 2009; Rousselet et al. 2010), while potential climate-driven range shifts expected in clades A and C have been hypothesized (Aimi et al. 2008; Groenen and Meurisse 2012).

2.3.2 Host Plants

Shifts in host plant use seem indeed to be the main factor that determined speciation within the genus. The analysis of the host plants shows that the genus *Thaumetopoea* is associated with four plant families, one in the Gymnosperms (Pinaceae) and three in the Angiosperms (Anacardiaceae, Cistaceae, Fagaceae) (Fig. 4.2b). All species feeding on Pinaceae belongs to clades B and C, while all species feeding on Angiosperms are grouped in clade A. Species in clades A and B appear to be oligophagous, being able to feed on more than one genus in each host plant family, while specialization toward monophagy is observed in clade C, with species associated with *Pinus* (*T. pinivora*) or *Cedrus* (*T. bonjeani*, *T. ispartaensis*, *T. libanotica*). The last common ancestor of *Thaumetopoea* moths exploited

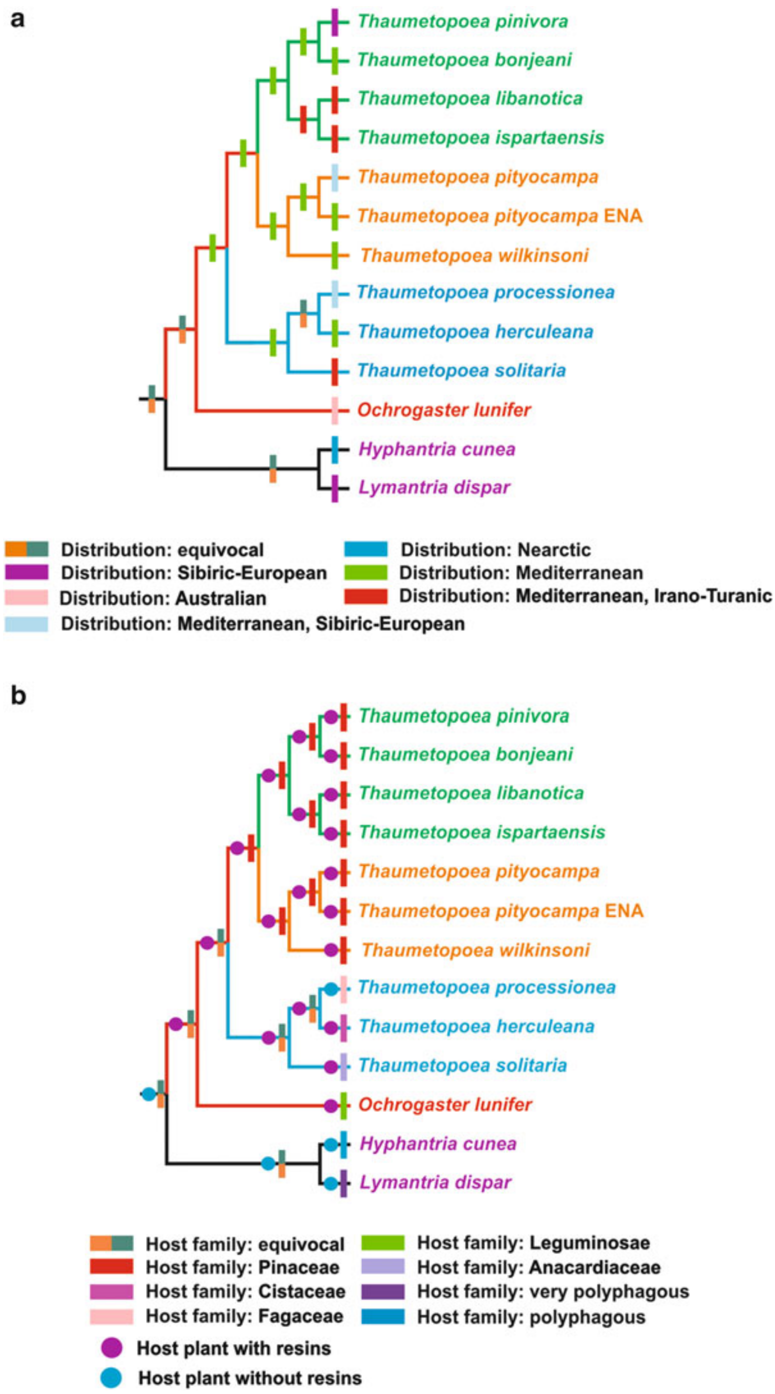

Fig. 4.2 Evolution of some characters in the *Thaumetopoea* genus. The evolutionary pathways of the investigated traits (indicated as *coloured bars* and *circles*) were reconstructed on the reference tree by applying a parsimony algorithm as reported in Simonato et al. (2013). (**a**) Evolution of biogeographic distribution; (**b**) Distribution of resins in plants and host plant family; (**c**) Foraging strategy and type of foliage eaten; (**d**) Life stage and location of overwintering; (**e**) Evolution of adult and eggs morphological features (Figure modified from Simonato et al. 2013)

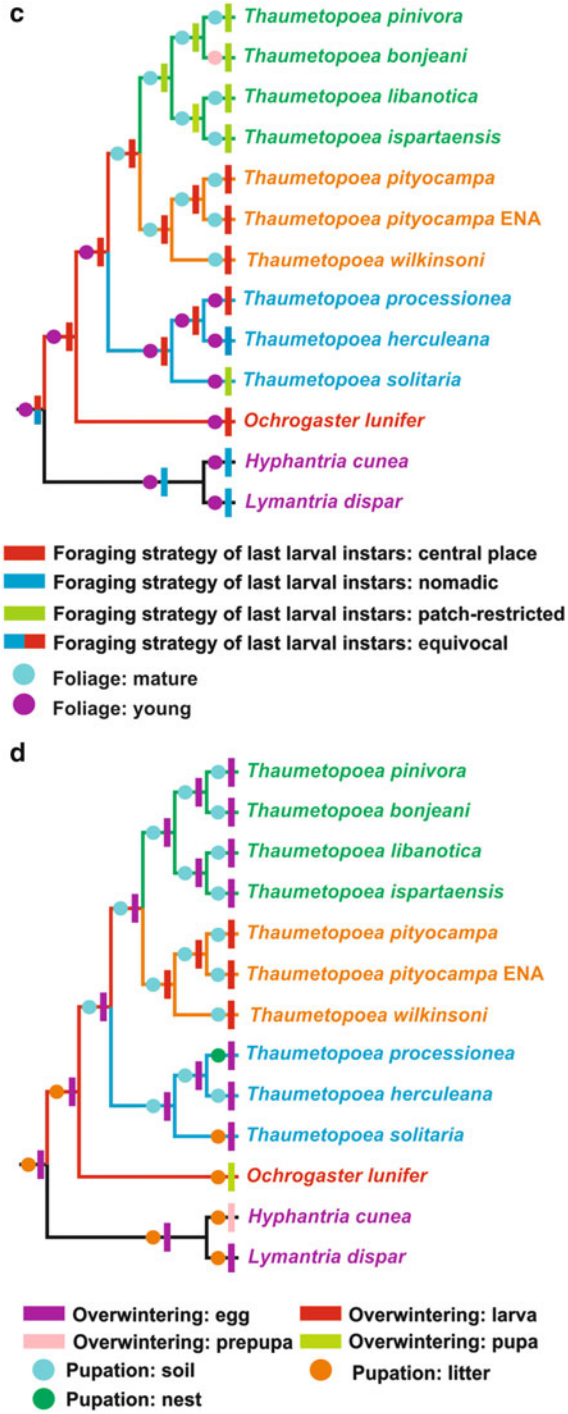

Fig. 4.2 (continued)

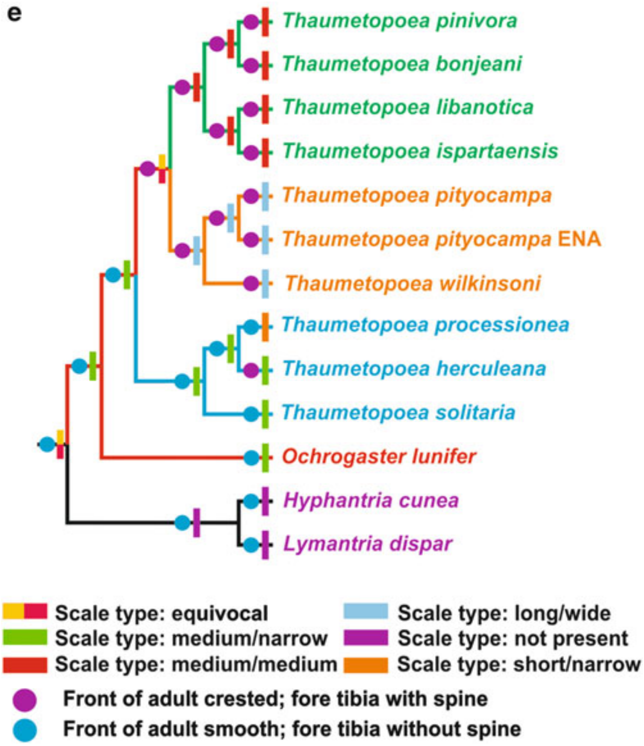

Fig. 4.2 (continued)

Angiosperm plants as larval food, but current evidence does not allow to unambiguously identify the exact family. Presence of resin canals is common to all host plants of *Thaumetopoea*, with the only exception of *T*. *processionea*, which feeds on Fagaceae (mainly *Quercus* spp.).

The lack of specialization suggests that the common ancestor had the capability to cope with a broad array of host plant quality, and this could have been important in the splitting and radiation of the *Thaumetopoea* moths. The shift to Gymnosperms occurred just once and it may have been facilitated by similar characteristics in morphology (for example, foliage toughness) and phytochemistry (resins) of these plants with the ancestral broad-leaved host plants. Moreover, ancestral and new host plants belong to the same ecological association of plants adapted to poor soils and first colonizers of disturbed areas.

The shift from broadleaf host plants to Pinaceae was associated with a dramatic loss of nutritional power, as pine needles contain at least three times less nitrogen than Angiosperm leaves (Kramer and Kozlowski 1979). The shift from Angiosperms to Gymnosperms corresponded also to a change of feeding from young to mature leaves: larvae preferably feed on mature leaves on Gymnosperms (clades

B and C) and on young leaves on Angiosperms (clade A). Such a change has been possible because Pinaceae retain leaves for 3 or more years but also because the mature leaves contain less defensive resin compounds than young leaves (Kramer and Kozlowski 1979). In addition, mature needles contain slightly more nitrogen than young needles (Battisti 1988). It is interesting to observe that in the species of clade C the preference for mature needles has been maintained in spite of a spring development of the larvae (Aimi et al. 2008), exactly when the young needles become available, indicating the avoidance of leaves with higher resin content.

Within Pinaceae, the species of clade B maintain a certain degree of polyphagy, being able to exploit host plants in different genera (Stastny et al. 2006; Paiva et al. 2011a), while in clade C there is a specialization for either *Pinus* (*T. pinivora*) or *Cedrus* (the other three species). The shift on *Cedrus* could not be established before the Miocene, provided that this plant genus was not present in the Mediterranean basin before (Qiao et al. 2007). Here we were unable to estimate divergence times due to the absence of calibrating points and we rely only on indirect evidence for our discussion. Irrespective of the exact time of the shift on Pinaceae, its occurrence further favoured the process of differentiation among *Thaumetopoea* moths. Indeed *Pinus* and *Cedrus* became successively isolated in the mountains of the Mediterranean region, during both glacial and interglacial periods.

2.3.3 Life History Adaptations

The shift to Pinaceae also probably led to a longer feeding and larval developmental time in order to compensate for the lower food quality. Thus the developmental time of the ancestor lineage, typically taking 2–3 months in spring, had to extend into summer, i.e. under the high temperatures that occur in the Mediterranean region and that can be fatal to larvae (Santos et al. 2011a). There are two ways by which the species associated to Pinaceae have responded to this strong constraint. The first is the change to the winter feeding observed in clade B, and the second is the extension of the developmental cycle to another year, associated with the retraction of the range to upper elevation and latitude observed in clade C. Both adaptations have a cost consisting in a longer exposure to natural enemies, and in protection from low temperature for species of clade B (tent construction, adoption of a central place foraging strategy), but also an indirect benefit because a longer developmental time is associated with higher body size of the moths, in agreement with the temperature-size rule (Zuo et al. 2012). Actually the species of clade B are those reaching the highest size in the genus, followed by those of clade C and A, respectively (Agenjo 1941; de Freina and Witt 1987). In addition, the shift to winter feeding in clade B may have contributed to reduce the competition with other pine defoliating insects, especially sawflies, which are generally active in spring. As a further matter of facts, the reversion from winter to summer feeding recently observed in a population of coastal Portugal of *T. pityocampa*, and in which a higher tolerance of the larvae to high temperature was demonstrated (Santos et al. 2011a), indicate that the trait is still under selection and likely driven by climatic factors. The shift to winter feeding could also explain the larger egg scales of clade B, as they are functional to achieve an earlier hatching by increasing the egg temperature by several degrees (Milani 1990).

The shift to winter feeding in clade B could be also interpreted as an escape from natural enemies, especially predators and parasitoids active during spring and summer. Although winter colonies are conspicuous and exposed during a long time to generalist predators such as insectivorous birds (Barbaro and Battisti 2011), the mortality is low because of the presence of urticating setae that protect the larvae from vertebrate predators (Battisti et al. 2011). The co-occurrence of social behaviour and defensive urticating setae in the *Thaumetopoea* larvae set them apart from the juvenile stages of all other Lepidoptera species. The advantages of sociality have been described for a number of organisms, including Lepidoptera (Costa 2006). In the case of the processionary moths, it has been shown that not only sociality per se but group size matters for colony performance and survival (Pérez-Contreras et al. 2003; Aimi et al. 2008; Ronnås et al. 2010).

Foraging in group may help circumvent the host plant resistance (e.g. by weakening its defenses) and at the same time lower the probability of being attacked by a predator (Costa 2006); this is particularly true for the pine processionary moth (Fitzgerald and Panades I Blas 2003). Moreover it could represent a further defensive strategy as aposematic signal for vertebrates (Battisti et al. 2011). In the *Thaumetopoea* genus, central place species are always associated with a large tent, which may be used for several months in species overwintering as active larvae (clade B) (Fig. 4.2c); this latter condition resulted to be an evolutionary novelty characterizing clade B. In the other species only temporary tents are produced at the time of moulting, or no tent is produced in species losing gregariousness in later instars (*T. herculeana*). The central place type foraging strategy seems to be an ancestral trait that characterized the *Thaumetopoea* species (Fig. 4.2c). This status was reverted to a patch-restricted foraging strategy, which emerged independently in clade C and in *T. solitaria*. A further shift to the nomadic foraging strategy occurred in clade A for *T. herculeana,* the only species showing this foraging strategy at the larval stage in the genus and, noteworthy, also the less urticating species (Agenjo 1941). Colony movement in head-to-tail lines is instead a typical feature of all larval instars during foraging bouts on the host plant, and it occurs for most species when searching for pupation sites (Fig. 4.2d).

The evolutionary success was further enhanced by the pupation strategy that occurs in the soil in most of the species, while it is performed in the litter in *T. solitaria* or in a well-protected nest in *T. processionea*. This trait was involved for the different *Thaumetopoea* species in protection against vertebrate predation. The pupation habit appears to be linked with major morphological traits of adult moths, as those pupating in the soil have crested front and a prominent spine on the foreleg tibia (Fig. 4.2e). These traits do not seem to be the ancestral trait of the group (Fig. 4.2e). According to the transformation pathway shown in the tree, both characters represent derived traits, that co-evolved independently twice within the genus (clade B+C *vs*. *T. herculeana*). Species that have switched to larval overwintering (clade B) show larger egg scales than those overwintering as an egg, which seems to be the ancestral trait (Fig. 4.2d, e). All larvae of *Thaumetopoea* carry urticating setae on the abdominal tergites starting from the third larval instar, including those of *T. herculeana*.

2.3.4 Taxonomic Implications

The agreement between molecular phylogeny and the most recent taxonomic revision of the former genus *Thaumetopoea*, resulting in three genera (de Freina and Witt 1982, 1987), is high but not complete. While the genus *Traumatocampa* matches perfectly with clades B and C, which include the processionary moths feeding on Pinaceae in winter and summer, respectively, the other two genera, *Thaumetopoea* (corresponding to *T. processionea* and *T. solitaria*) and *Heliantocampa* (including the single species *T. herculeana*), are intermixed within clade A.

Based on a good correspondence between host plant taxonomy and the placement of the species in the identified clades, we may propose hypotheses about the position of taxa that for various reasons were not included in the analysis. Indeed all taxa feeding on Gymnosperms (Pinaceae) form the monophyletic group B+C, while the species associated with Angiosperms are included in clade A. Thus we hypothesize that *T. jordana* and *T. cheela*, both feeding on Anacardiaceae, belong to clade A, as they use the same host plant family as *T. solitaria* (Trougth 1954; Furth and Halperin 1979). The same could be true for *T. dhofarensis*, found in a habitat similar to that of *T. jordana* (Wiltshire 1980) and for *T. apologetica*, restricted to Eastern Africa where there are no native Pinaceae. Conversely, the two recently described species (*T. sedirica* and *T. torosica*, that feed on Pinaceae) are predicted to belong to either clade B or clade C.

Our molecular phylogenies strongly support a parallel evolution of the morphological traits used to divide *Thaumetopoea* in the three distinct genera *Traumatocampa, Heliantocampa* and *Thaumetopoea sensu stricto* (de Freina and Witt 1982, 1987). This result leads us to suggest that all species (included or not in the present work) should be treated as members of a single genus *Thaumetopoea sensu lato*. Further systematic revision should be delayed until a complete taxonomic coverage becomes available and the phylogenetic relationships among all species are fully resolved. There is also a need for identifying new morphological synapomorphies that support the three identified clades, as those characters more commonly used (presence of the crest on the front of the adult and of the spine on the foreleg tibia, size of the egg scales) show evidence of convergent evolution. Indeed those characters are more related to ecological functions such as the emergence from the soil (Démolin 1969) and egg thermoregulation (Milani 1990), and they are present in all clades.

2.4 Summary

Comparing biological traits and distribution of most *Thaumetopoea* species through phylogenetic reconstruction, we outlined the main evolutionary factors leading to speciation in this taxon. The main split inside the genus is associated with the host plant shift from Angiosperms to Pinaceae. This host-plant shift probably implied a longer larval developmental time because of the lower nutritional quality of the leaves, thus leading to different evolutionary responses to this constraint. One of the two clades associated with Pinaceae switched the larval feeding to the cold season (winter pine processionary moths), while the other retracted its range to high elevation and latitude with a development cycle extended over 2 years (summer pine processionary moths). Moreover, recent global warming is affecting all species and seems able to further shape the evolution of the group.

In conclusion, the split in the three major clades inside the genus can be viewed as the result of an adaptive radiation, made possible by an array of life history traits, which allowed a successful evolutionary response to changes in host use and climate. At the present state of knowledge, it is not possible to give full support to the division of the genus into three genera. More taxonomic work and the inclusion of other species will certainly help to solve this issue.

3 Phylogeography of the Pine Processionary Moth Complex: Genetic Structure and Potential Contact or Hybrid Zones

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and Andrea Battisti

3.1 Introduction

Past climate changes, in particular the Quaternary climatic oscillations, have had dramatic impacts on the geographic distribution, demography, and thus the evolution of species. The contemporary distribution of genetic diversity cannot be understood without studying how organisms responded to climate over geological times. The distribution ranges of temperate species were restricted during glacial maxima to a few glacial refugia and the organisms re-colonized northwards, tracking newly suitable habitats, during interglacial periods characterized by the retreat of the ice core. In this case, genetic diversity is supposed to have been retained in the glacial refugia, and to be reduced in the northern, recently colonized areas. Some re-colonization routes could be blocked by geographical barriers or by expansion routes from other lineages (Hewitt 1996). The suture zones formed by lineages originating from different refugia and coming into secondary contact are expected to show higher genetic diversity than other geographic regions (Petit et al. 2003). The "genetic legacy of the Quaternary ice ages" (Hewitt 2000), i.e. the genetic footprint of species' responses to glacial-interglacial successions, has been extensively studied on many species in Europe and North America, that is, in the geographical regions where glaciations were most intense (Hewitt 2004; Schmitt 2007).

The effects of climatic changes on the effective population sizes were more dramatic in northern than in southern regions, meaning that northern populations should bear the signature of a rapid demographic expansion following the climate amelioration, whereas southern populations should evidence marks of more stable, long-term effective population sizes. In most cases, refugial areas were localized in the southernmost regions. Yet, cold-tolerant species may also have survived in northern or altitudinal refugia (Stewart and Lister 2001), such as the Alps, or central, eastern and northern Europe. Moreover, some species strictly depend on other organisms (hosts, mutualists, symbionts, etc.) for their development or dispersal. In that case, the phylogeographic pattern of the dependent species can be influenced by that of its partner. All these characteristics dramatically affected the present-day distribution of genetic diversity and may influence the ability of species to cope with the current global changes.

We here review the data and knowledge concerning the phylogeographic patterns of the pine processionary moth species complex (*T. pityocampa*/*T. wilkinsoni*, i.e., within clade B identified in the previous subchapter) over its whole geographical range, that is, around the Mediterranean basin. The aim of these studies was to characterize the geographic limits of the previously identified clades, and to analyse within-clade genetic structure. As the intensities of the climatic oscillations varied among the different regions, we expect to identify different patterns of genetic diversity. Quaternary climatic variations were most intense in Western Europe, where classical phylogeographic patterns probably occur, while the populations may have been maintained over much longer time spans in the southern rim of the Mediterranean basin as well as in the Middle East. We moreover present new evidence of a hybrid zone occurring in Turkey along a contact region between *T. pityocampa* and *T. wilkinsoni*.

3.2 Phylogeographic Patterns Over the Mediterranean Basin

3.2.1 Three Main Clades Within the Complex

To understand the geographical patterns of the distribution of genetic diversity over the whole range of the species complex, 732 individuals were sampled from 74 localities on various host species. Part of the COI and COII mitochondrial genes were analysed for each individual by SSCP and sequencing. Phylogenetic

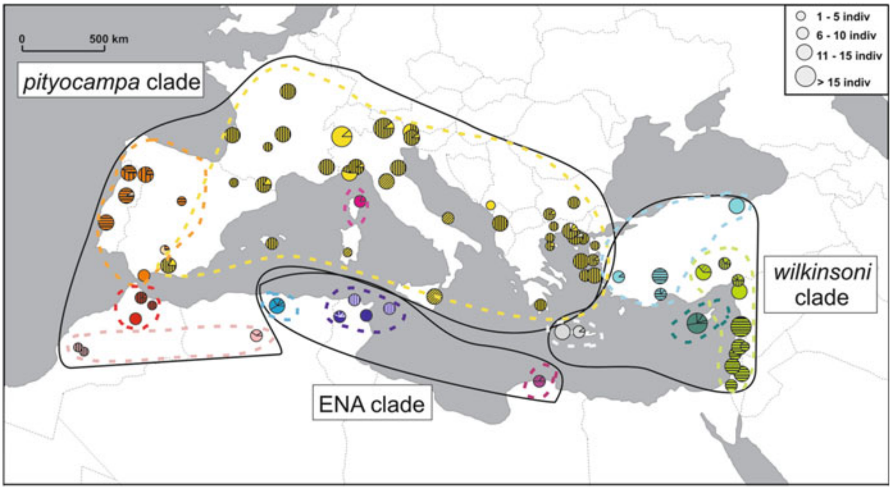

Fig. 4.3 Geographic distribution of the haplotypes found in Simonato et al. (2007) and Kerdelhué et al. (2009), showing the limits of the main clades and sub-clades identified by the phylogenetic analyses and haplotype networks

trees of haplotypes were constructed using a Bayesian approach, and statistical parsimony networks were computed within clades. All details can be found in Simonato et al. (2007) and Kerdelhué et al. (2009).

The results showed a very clear geographical pattern, with three main, parapatric mitochondrial clades (Fig. 4.3). The first clade encompasses all European localities (from the Iberian Peninsula to Greece), Morocco and one Algerian site; it will hereafter be referred to as the *pityocampa* clade, as it probably corresponds to *T. pityocampa sensu stricto*. The second clade occurs in the Middle East (Turkey, Lebanon, Israel and Cyprus), and also includes the island of Crete. It will here be called the *wilkinsoni* clade. A third clade appears to be the sister group of the *pityocampa* clade and is restricted to Eastern North Africa (part of Algeria, Tunisia and Libya). It was named the ENA clade (Kerdelhué et al. 2009).

A Bayesian analysis allowed to estimate the date of the main phylogenetic splits. Even though molecular dating using only mitochondrial markers and without calibration points should be considered with caution, it is interesting to note that the most recent common ancestor (MRCA) of all three clades could date back to 7.5 million years (Myrs) on average, which could correspond to the full opening of the Aegean trench. The existence of the ENA clade was unexpected, and its geographical range does not correspond to any obvious geographical barrier that could have hampered gene flow. It was hypothesized that a conjunction of events may explain this pattern, such as a major biogeographical event (the rise of the Tellian Atlas) combined with the late Tertiary climatic change that could have caused a gap in host availability due to arid phases (Kerdelhué et al. 2009). It also means that the pine processionary moth species complex is ancient, and predates the Quaternary period. Moreover, each clade has diverged before the Quaternary oscillations, and thus independently experienced these past climate changes.

3.2.2 A Strong Within Clade Geographical Structure, with Contrasting Patterns

Each of the three identified clades showed a strong phylogeographical structure (Kerdelhué et al. 2009), and was composed of 3, 4 or 5 well-differentiated sub-clades (Fig. 4.4). With the notable exception of the European range (except a part of the Iberian Peninsula), each sub-clade was restricted to a rather narrow geographical region (Fig. 4.3). However, one should keep in mind that the sampling available in North Africa was too loose to definitely conclude about the exact

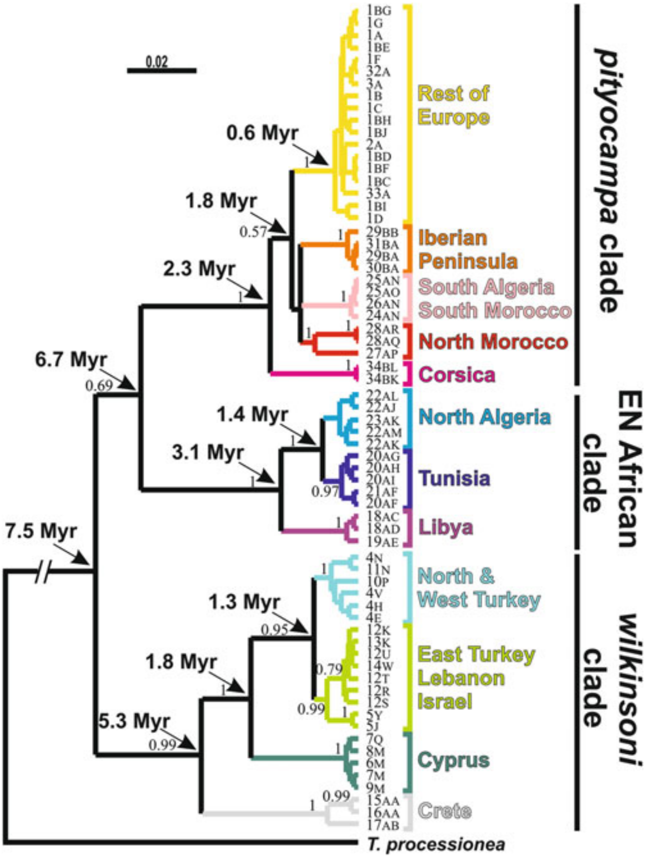

Fig. 4.4 Bayesian phylogenetic tree of haplotypes showing the main geographical clades and sub-clades. Estimated ages of MRCA and Bayesian supports over 0.5 are given (Modified from Kerdelhué et al. 2009)

geographical limits of the identified groups. Interestingly, a vast majority of haplotypes were endemic to one single population, and only five were found in three or more populations. Thus, the pine processionary moth exhibits an extreme spatial structure and a highly reduced mitochondrial female gene flow. Physical barriers as well as ecological characteristics (phenology of reproduction, that is known to differ depending on local climatic conditions (Huchon and Démolin 1970)), or local host adaptations, which in some case can represent a high selective pressure (Zovi et al. 2008) probably recurrently acted to maintain and reinforce the genetic structures. Drift associated to low female migration lead to an increase of the genetic differentiation with time, and to the existence of different mitochondrial lineages in different regions. Moreover, still with the exception of Europe, a majority of the sampled populations in the natural range of the species showed some genetic diversity, even at the rear edge of the distribution. These results suggest that populations were maintained over long periods and demographic changes allowed to retain genetic diversity despite cyclic gradations. The occurrence of potential prolonged diapause in pine processionary moth (i.e. the possible emergence of adults of the same generation over several years) probably further reduces the risk of local extinction and loss of genetic diversity. Such patterns are consistent with the fact that the Quaternary climatic oscillations had only limited effects in these regions. However, only one haplotype was found throughout Lebanon and Israel. This unexpected loss of genetic diversity is due to a very recent origin of the moth in this region, as pine trees were planted there during the afforestation process of the 1910s. The moth populations actually expanded from eastern Turkey during the twentieth century, from a single source of migrant females (Simonato et al. 2007).

In each of the three main clades, the most divergent sub-clades occur in "islands". The Corsican haplotypes were the most differentiated within the *pityocampa* clade, the Cretan and the Cypriot individuals formed the two sister-groups of all other sub-clades within the *wilkinsoni* clade, and the highly isolated moths of Cyrenaica (that can be considered as an "island" in Libya, isolated by the absence of pine hosts in the surroundings) were most divergent in the ENA clade. Based on the estimated ages of their divergence, we can suggest that the PPM survived locally on these remote islands without female exchanges from the continent during few glacial cycles. Thus, they had to evolve locally to cope with at least some Quaternary oscillations and environmental changes (Coope 2004). Yet, the estimates for the age of MRCA within islands were quite recent, and could be due to a founder effect followed by strong genetic drift in small populations. In contrast with the high genetic differentiation of Corsica, Crete and Cyprus, some islands harboured populations of moths that were genetically very close, or even similar, to their closest continental neighbours. This is not surprising for islands that are located very close to the continent, like most Greek islands or Sicily, as they can probably be recurrently colonized from mainland sources. In contrast, in spite of a high distance from the continent, the populations of Sardinia, Pantelleria, or the Balearic Islands bear haplotypes found in Tuscany, Tunisia and eastern Spain respectively, suggesting a recent accidental introduction of the moth.

The genetic patterns found in Europe were drastically different from the results obtained in all other regions (Kerdelhué et al. 2009). Most of the European range, except for the western and central part of the Iberian Peninsula, corresponded to a single sub-clade. Moreover, only one haplotype was found in most of the sampled localities (Fig. 4.3), and occurred from the Atlantic coast to Greece. Further analyses showed that the genetic patterns were consistent with a past demographic expansion. European populations underwent bottleneck events due to the consecutive glaciations and then recurrently expanded after the retreat of the ice. Such results are classically found for temperate and cold-sensitive species in this region (Schmitt 2007). The spatial distribution of the rare haplotypes helps localizing putative refugial areas where the moths survived the glaciations, and possibly also the interglacials as this Mediterranean species is susceptible to both winter cold and summer heat and aridity. Not surprisingly, such refugia were identified in southern Spain, in the Balkans and in Italy, which is typically found for European temperate species. The results also suggested that some genetic diversity was retained in the Pyrenees and in the Alps.

To decipher the role of topography in the past history of the pine processionary moth, Rousselet et al. (2010) designed a specific study in Western Europe, based on a dense sampling including the main mountainous ranges and on the sequencing of a longer fragment of the mitochondrial COI gene. This work showed that the geographical limit between the Iberian and the European sub-clades was not localized along the Pyrenees, but rather occurred in the Ebro basin (on the southern side of the Pyrenean range), where a contact zone was identified, and along the Mediterranean coasts of Spain. Moreover, it showed the existence of three lineages within the European sub-clade. One of them was restricted to the eastern Pyrenees (Pyrenean lineage), one was found in eastern Spain, southern Pyrenees and western France (Spanish-French lineage), while the third was located in Italy, the Alps as well as eastern and central France (eastern lineage, see Fig. 4.8 in the following subchapter). Interestingly, the two main lineages present in France were not separated by the Massif Central as could be expected, but a contact zone was identified on the western slopes of this mountainous region. Similarly, the Alps did not separate different lineages, but all slopes were occupied by a single haplogroup. Moreover, in each region, maximal haplotypic diversity was found at moderate elevations. All patterns thus suggest that mountainous areas did not play a role of physical barrier to dispersal, but rather provided refugia during the Quaternary climatic oscillations, allowing up- and down-movements along the slope to cope with climate change. The Pyrenean lineage was "trapped" and survived locally on montane pines without contributing to the colonization of northern territories after the last glacial maximum. On the other hand, the two other European lineages recently expanded northwards. Details about expansion routes from the main refugial areas are given in the following subchapter.

3.2.3 Nuclear and Mitochondrial Data Are Not Always Consistent

Most of the works reviewed above were based on mitochondrial data, and thus only referred to the maternal lineages. In some cases, limited nuclear data were also available for some regions, and confirmed the patterns identified with the mitochondrial sequences. For instance, ITS1 sequences presented in Santos et al. (2007) showed a differentiation between Iberian and French populations that could reflect the mitochondrial data. Preliminary data using microsatellites in France suggested a clear differentiation between the eastern and the western populations (Kerdelhué et al. 2006), as was suggested above by the existence of two mitochondrial lineages.

Yet, in some cases, we could identify significant discrepancies between markers, which is most probably due to sex-biased dispersal (Petit and Excoffier 2009). Within *T. wilkinsoni*, the mitochondrial data suggested 4 sub-clades, namely [Crete], [Cyprus], [West-Turkey] and [East Turkey, Lebanon and Israel]. In particular, Cyprus was highly divergent from the continental clades (Fig. 4.4). Simonato et al. (2007) genotyped the same populations using 4 microsatellite loci and AFLP markers. The patterns identified were consistent between microsatellites and AFLP, but very different from the results found with the mitochondrial sequences as concerned the Cypriot populations. Nuclear results clearly placed Cyprus as a closely related sister group of southern Turkey, showing genetic similarity between the populations sampled in the island and the closest continental populations (Fig. 4.5).

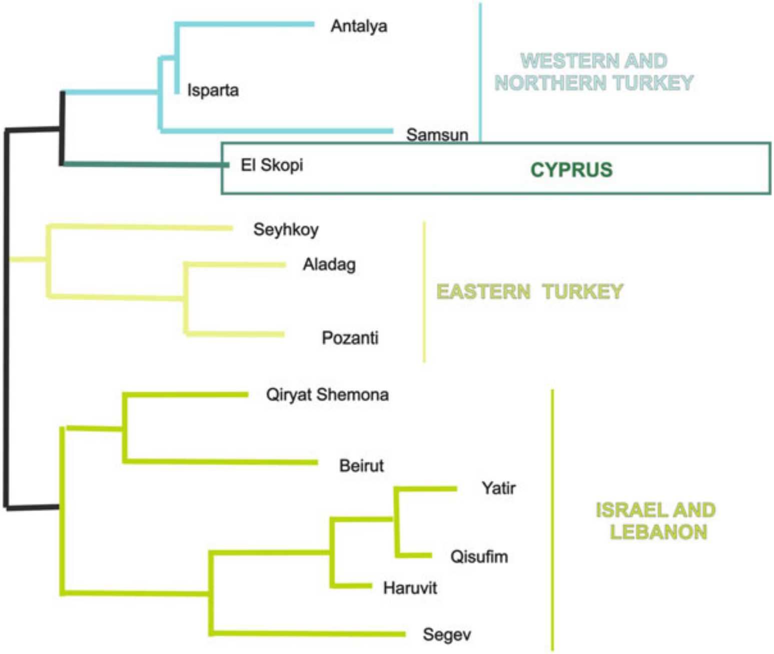

Fig. 4.5 Phylogenetic tree of populations obtained from nuclear markers (AFLP and microsatellites)

Such a pattern can occur if recurrent male gene flow occurred between the island and the continent whereas the female gene pool remained isolated in Cyprus, which is consistent with known differences in males and females dispersion capacities in the pine processionary moth. Similarly, the same study showed that nuclear genetic diversity was found in expanding populations in Israel in which mitochondrial diversity was null. Again, it was supposed that recurrent male gene flow allowed a certain recovery of genetic diversity following site colonization (Simonato et al. 2007).

3.3 Identification and Characterization of a Contact Zone Between **T. pityocampa** *and* **T. wilkinsoni** *in Turkey*

Ranges of *T. pityocampa* and *T. wilkinsoni* meet in Anatolia, as shown in Fig. 4.3. Given that these species exhibit similar habitat requirements, reproductive behaviour, and pheromone chemicals (Frérot and Démolin 1993), the existence of a potential hybrid zone can be hypothesized. Can pine processionary moth be a model organism to study interspecific hybridization, which is currently a popular topic in ecology and evolution? We here present unpublished data that encourage further research about this question (İpekdal 2012). Our objective was twofold: (1) to characterize finely the potential contact zone between both species in Turkey; (2) to compare the patterns brought by a mitochondrial and a nuclear gene to look for traces of interspecific introgression.

Pine processionary moth individuals were sampled either as larvae or male adults from various regions in Turkey, Bulgaria and Greece, including some of the Greek islands close to Turkey. For each sampled locality, the DNAs of 4–10 individuals originating from different nests were extracted, and two genes were amplified and sequenced for each individual, namely the second half of the mitochondrial COI gene (using the primer pair C1-J-2183 (Jerry) and TL2-N-3014 (Pat), Simon et al. 1994), and an exon of a nuclear gene coding for photolyase, hereafter *Pho* (Simonato et al. 2013). Mitochondrial differentiation between both species was found to be highly consistent with the phylogenetic data shown in Fig. 4.4. Mean genetic distance between *T. pityocampa* and *T. wilkinsoni* COI sequences was 0.07 (Maximum Composite Likelihood Model calculated using MEGA 5, Tamura et al. 2011). For nuclear sequences, divergence between *T. pityocampa* and *T. wilkinsoni* alleles was lower than for COI, but interspecific distances were still higher than intra-specific variability. The most parsimonious *Pho* network of alleles is provided in Fig. 4.6. Hence, it was possible for both markers to assign unambiguously each haplotype to one of the two species. We thus could identify (i) individuals characterized by both "*pityocampa*" COI and *Pho* genes; (ii) individuals with both "*wilkinsoni*" COI and *Pho* genes; (iii) individuals exhibiting "*pityocampa*" COI haplotype and "*wilkinsoni*" *Pho* alleles. We could not find any individual bearing "*wilkinsoni*" COI and "*pityocampa*" Pho sequences. Additionally, no F1 hybrids, expected to have a copy from each parent for the nuclear loci, were found in our sampling.

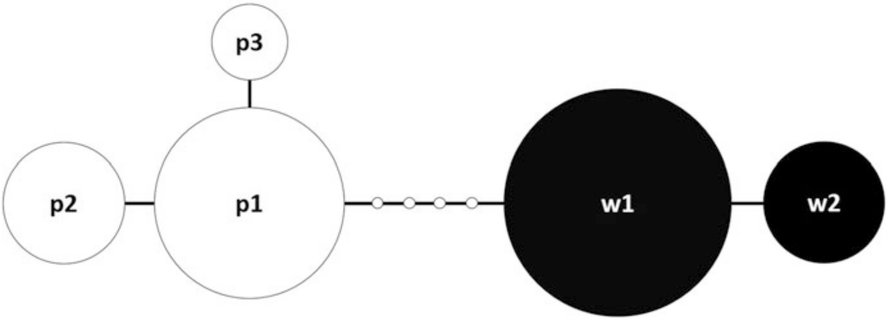

Fig. 4.6 Photolyase haplotype network for *T. pityocampa* (*white*; p1, p2, p3) and *T. wilkinsoni* (*black*; w1, w2) populations in the studied region

The cartography of the results (Fig. 4.7) evidences the existence of a parapatric distribution of the two taxa. Populations from Bulgaria (29 – see the site codes on the map), mainland Greece (28), Thassos (27) and Samothraki islands (26), and western Turkish Thrace (23–25) belonged to the *T. pityocampa* clade for both markers, while populations from Samos (8), Rhodes (7), southern (1–6) and northern (16–21) Turkey were in the *T. wilkinsoni* clade. We also found two localities, one in Tekirdağ (22) and the other in Balıkesir (15) where *T. pityocampa* and *T. wilkinsoni* individuals (i.e., identified as such by both markers) co-occurred. Moreover, introgressed individuals were found in western Turkey (9; 12–14) and the proximate islands Chios (10) and Lesbos (11). Non-introgressed individuals also occurred in each of these localities, recognized as *T. pityocampa* except for İzmir (9) where *T. wilkinsoni* occurs. This narrow region, where characteristic genes from both taxa were discovered either in the same or in different individuals, corresponds to the contact zone. The absence of F1 hybrids in such an area is noticeable, and could be linked either to the rarity of hybridization cases or to insufficient sampling.

However, introgression, characterized here as an inconsistency between mitochondrial and nuclear markers, should result from hybridization events. Cytoplasmic genes are usually exchanged more easily than nuclear genes (Ballard and Whitlock 2004). In pine processionary moth, a sex-biased dispersal has been suggested from genetic markers (Salvato et al. 2002; Simonato et al. 2007; see above, 3.2.3). As better dispersers, males could reach the edge of the distribution range more easily than conspecific females and mate interspecifically. Since mitochondrial DNA is maternally inherited, such a biased dispersal behaviour could favour mitochondrial introgression.

Introgressed individuals always had *T. pityocampa* mitochondrial haplotypes and *T. wilkinsoni* nuclear alleles. Even if more data are needed to confirm these results, this asymmetrical introgression suggests that interspecific matings occurred mainly between *T. pityocampa* females and *T. wilkinsoni* males. Such asymmetric introgression is quite frequent after range expansion, and is modulated according to disturbance, spatio-temporal demographic processes, and intraspecific gene flow (Petit and Excoffier 2009; Excoffier et al. 2009; Currat et al. 2008). Even if the phylogeography of *T. pityocampa* could suggest an eastward expansion (with

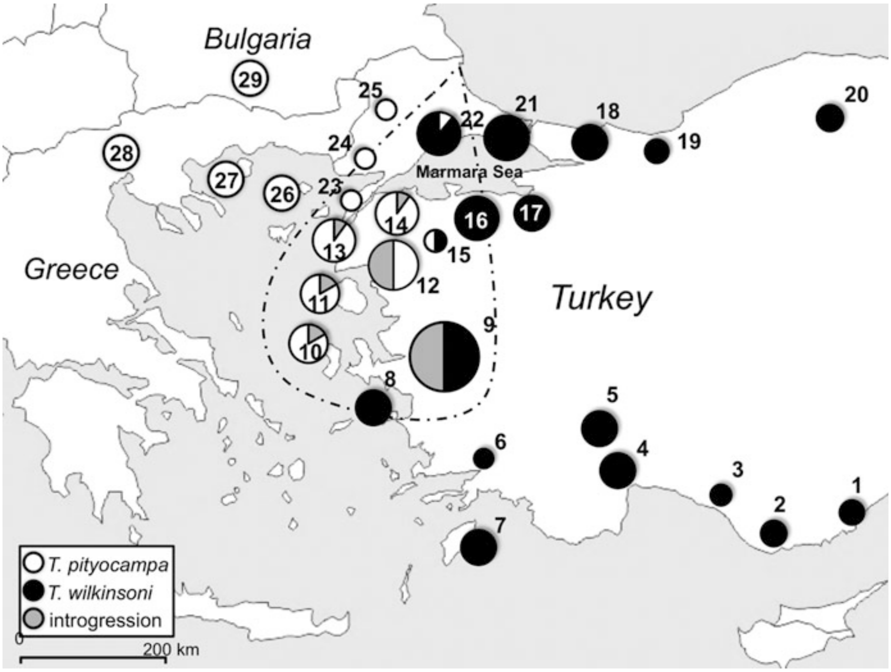

Fig. 4.7 Distribution of sampled pine processionary moth, identified as *T. pityocampa* (*white*), as *T. wilkinsoni* (*black*) and as introgressed samples (*grey*) based on sequence data. *Dotted line* shows the approximate position of the contact zone. The numbers refer to locality codes as cited in the text

reduced genetic diversity), i.e. toward the contact zone, data are less conclusive for *T. wilkinsoni*. Other biological considerations such as Haldane's rule, i.e. less viability of heterogametic hybrids (Haldane 1922; Schilthuizen et al. 2011), presence of sterilizing *Wolbachia* endosymbionts (Turelli et al. 1992; Werren 1997), or differential phenology of sexes and/or species could also be implicated.

In order to describe the present hybrid zone more precisely, more molecular markers and a larger sampling are required. A higher number of markers will make it possible to reveal mosaic patterns of introgression. ITS-1 and microsatellite primers are available for both species (Rousselet et al. 2004; Santos et al. 2007; Burban et al. 2012) and could add valuable insight to the current information. Furthermore, next generation sequencing is promising as it will allow to gather much more genomic data and to bring a precise view of genetic introgression (McCormack et al. 2013; Twyford and Ennos 2012). On the other hand, laboratory hybridization studies as well as spatially characterized bionomic surveys are needed (Bull 1991). The combination of such genetic, experimental and ecological approaches is necessary both to decipher the history of the contact zone and try to predict its future (Buggs 2007). Similar approaches should be also developed in North Africa, where different mitochondrial clades and sub-clades co-occur.

4 Range Expansion in the Pine Processionary Moth: A Population Genetics Approach

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4.1 Range Expansion of the Pine Processionary Moth and Expected Genetic Footprints

In response to the recent climate warming, range expansion of the pine processionary moth to upper latitudes or elevations has been reported in several European countries since the beginning of the 1990s (Benigni and Battisti 1999; Démolin et al. 1996; Hellrigl 1995; Hódar et al. 2003; see Chap. 3). The present-day northern edge of the distribution area extends approximately from the Atlantic Ocean to the Black Sea (Chap. 3) and is mainly controlled by both winter and summer extreme temperatures (Huchon and Démolin 1970; see Chap. 5). The distributional change observed in the last two decades is consequently and primarily due to increased winter temperatures favouring larval survival (Battisti et al. 2005; Buffo et al. 2007; Hoch et al. 2009; Robinet et al. 2007; Chap. 3).

For a large part of Europe, the northward expansion is limited by strong continental climate or mountain chains, although an elevational shift has been observed. In the Italian Alps, the range boundary has thus shifted upwards of 110–230 m over the period 1975–2004 (Battisti et al. 2005). The plains of western France with oceanic climate have offered and still offer the pine processionary moth the widest possibilities of spatial expansion. This insect species has gained about 95,000 km^2 in France, as its range increased from 265,000 km^2 in 1979 (see C.T.G.R.E.F.-I.N.R.A. 1980) to 360,000 km^2 in 2011 (Bouhot-Delduc 2005; Robinet et al. 2010, 2014; Chap. 3).

The current range of the pine processionary moth in France has likely resulted from three major processes of northward expansion since the Last Glacial Maximum: (i) the post-glacial recolonization during the Holocene warming; (ii) the colonization of the climatically suitable areas that have been afforested during the nineteenth and twentieth centuries, especially in north-western France; (iii) the present-day climate-driven expansion observed since the beginning of the 1990s (Chap. 3). Given that pine hosts are largely available in northern France, and that winter temperatures are now favorable in the north of the expansion front, the speed of the on-going spatial expansion is henceforth mainly governed by the dispersal abilities of the moths.

Different dispersal processes can occur during range expansion and the colonization wave front can expand at different speeds according to the proportion of long-distance events (Klein et al. 2006; Kot et al. 1996; Weinberger 1982; Chap. 5). In a homogeneous environment, diffusive expansion, modeled with a thin-tailed dispersal kernel, is expected to lead to a colonization wave of constant speed (Aronson and Weinberger 1975; Kolmogorov et al. 1937), whereas stratified dispersal with long-distance events, modeled with a fat-tailed kernel, is expected to lead to a wave of increasing speed (Garnier 2011; Kot et al. 1996). These different forms of dispersal lead to different genetic structures after spatial expansion (e.g. Bialozyt et al. 2006; Excoffier et al. 2009; Ibrahim et al. 1996; Klein et al. 2006). The rare long-distance dispersers can establish very isolated satellite populations with strong founder effects. This stratified dispersal is generally expected to generate a high spatial differentiation (Klein et al. 2006). In case of very low frequency of long-distance dispersal events, a series of strong bottlenecks or an embolism effect can produce large patches of homozygosity in the newly colonized areas (Bialozyt et al. 2006; Hewitt 1999). Conversely, in the case of diffusive processes, only the individuals in the front of colonization found the new populations. This could imply a more progressive loss of diversity during the range expansion, leading to a weaker differentiation and an isolation by distance pattern (Klein et al. 2006).

In this subchapter, we review the population genetics and phylogeographical data available for the pine processionary moth in Western Europe that allowed to detect the genetic imprints of range expansion and to propose hypotheses about the dispersal patterns that occurred at different time scales. In particular, we will show how the combined analysis of a low mutation rate mitochondrial marker and of polymorphic nuclear loci (AFLP and microsatellites) can shed light about the origins of the currently expanding populations and the on-going processes involved in latitudinal and elevational expansions.

4.2 Past Northward Expansion: Genetic Imprints of a Diffusive Dispersal

In France, the present-day northern edge appears more or less continuous from the Atlantic Ocean to the Alps (Robinet et al. 2007, 2010). The genetic data obtained with a mitochondrial marker (Rousselet et al. 2010) associated to previous field records (Démolin et al. 1996; Chap. 3) revealed that it corresponds to the recent junction of two lineages originating from different glacial refugia and coming into secondary contact in the north of the Massif Central mountains (Fig. 4.8). Details about the phylogeographical pattern in Western Europe and the distribution of each lineage are given in the previous subchapter. While the origin of the eastern lineage, distributed from eastern France to Greece, is still uncertain, the populations distributed from western France to eastern Spain (Spanish-French lineage) likely originated from a glacial refugium located in the eastern Iberian Chain. This lineage is roughly distributed along the Greenwich Meridian and is clearly south-north structured (Fig. 4.8). Its important contribution to the northward post-glacial recolonization opened the possibility to search for genetic signs of range expansion.

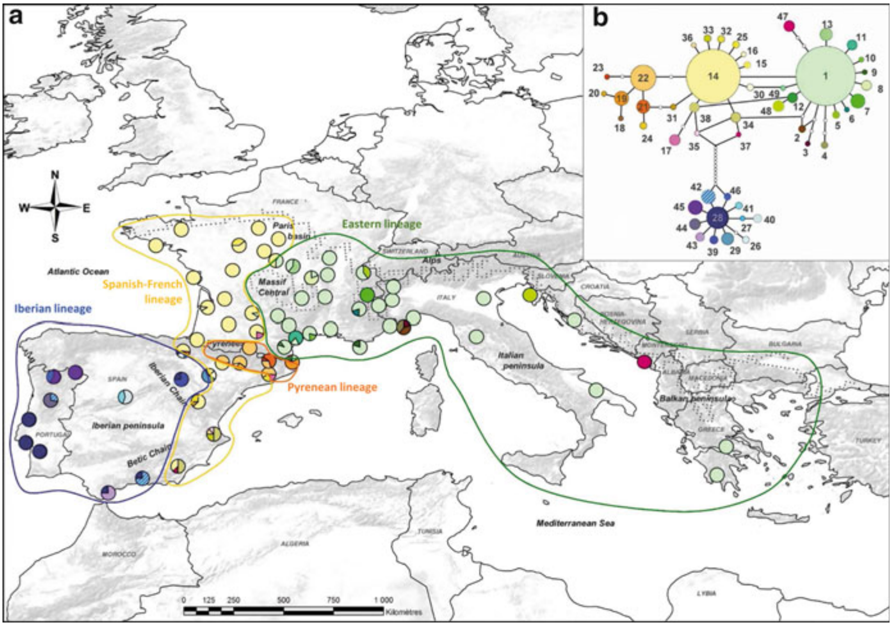

Fig. 4.8 Geographic distribution (**a**) and haplotype network (**b**) of the cytochrome c oxidase subunit I (COI) mitotypes, showing the area occupied by the four main maternal lineages identified in Europe. *Dotted line* indicates the present-day northern and elevational edges (Modified from Rousselet et al. 2010)

4.2.1 A ‘Northern Purity, Southern Richness’ Pattern Within the Spanish-French Lineage

The Spanish-French lineage exhibits a ‘northern purity, southern richness’ pattern as defined by Hewitt (1999). This population genetic structure is a typical genetic footprint of northward post-glacial expansion in cold-sensitive species. The higher genetic diversity and divergence in the southern populations (‘southern richness’) is attributed to their prolonged demographic stability over the Quaternary climatic oscillations, as they occur in regions where environmental conditions were suitable even during the glacial maxima. The ‘northern purity’ is commonly attributed to a loss of genetic variation due to serial bottlenecking associated with pioneer-like dispersal and rapid northward expansion during interglacial periods (Canestrelli et al. 2006; Bialozyt et al. 2006; Hewitt 1999). The pattern of ‘refugia within refugia’ can be an alternative scenario, and is well supported for the Iberian peninsula (Canestrelli et al. 2006; Gómez and Lunt 2006). Multiple, strongly isolated and differentiated refugia could have existed during the ice ages, but they did not all necessarily contribute to the northward post-glacial recolonization. Only a small subset of the overall diversity having occurred in the refugial areas could have been at the origin of the northern populations.

In the case of the pine processionary moth, over the Iberian peninsula, several differentiated refugial areas with different contributions to the northward post-glacial recolonization of Europe were identified. Rousselet et al. (2010) suggested that the different richness in host-plant species might explain these differences of contribution to the present-day range. For example, two mountain pine species, *P. nigra* and *P. sylvestris*, were probably the main continuously available hosts in the northernmost Iberian refugium located in the Pyrenees, while a Mediterranean pine species, *P. pinaster*, was also probably present and abundant in the eastern Iberian Chain (Carrión et al. 2000; De-Lucas et al. 2009). Consequently, the refugial populations of the Pyrenean lineage could have been trapped elevationally by tracking mountain pines and did not contribute to the northward expansion. While these north-eastern Iberian populations only contributed to the upward expansion, the mid-eastern Iberian populations located a little more southerly could have expanded latitudinally by tracking thermophilic lowland pine species. The expansion pathway from eastern Spain to south-western France corresponds to one of the migration routes suggested for *P. pinaster* (Salvador et al. 2000). This would be consistent with the moth following the migration route of one of its hosts, and with a 'northern purity' having resulted from a geographically restricted source of post-glacial recolonization.

However, host-plant relationships might also account for the pronounced loss of genetic diversity observed in the western French populations with the mitochondrial marker used by Rousselet et al. (2010). This oligophagous insect mostly attacks the mountain pine species and, to a lesser extent, the Mediterranean pine species (Buxton 1983; Hódar et al. 2002; Huchon and Démolin 1970; Masutti and Battisti 1990; Montoya 1981). The present-day populations of the Betic Chain in south-eastern Spain exhibited a very low larval survival on *P. pinaster* while first instar larvae were able to develop on *P. nigra* and *P. sylvestris* (Hódar et al. 2002). According to these authors, egg-laying on maritime pine can be considered (in this region) as an "oviposition mistake". The pattern of attacks reported by Montoya (1981) in the eastern Iberian Chain (i.e. mid-eastern mountainous refugial areas) is consistent with these experimental data obtained from the Betic Chain (i.e. south-eastern mountainous refugial areas). Conversely, the French populations seem to exhibit a higher plasticity in host plant use (Huchon and Démolin 1970). In south-western French lowlands, *P. pinaster* is the only native pine species and is moreover considered as a good host (Démolin 1969). In these areas likely colonized during the Holocene warming, this Mediterranean pine was available only along the Atlantic coast until recent afforestation. A host plant shift, associated to a strong bottleneck, might have been at the origin of the maternal lineage that has latitudinally expanded on Mediterranean hosts from a mountainous Iberian refuge to a lowland coastal area. A similar scenario might also explain the low mitochondrial genetic diversity of the populations feeding on *P. pinaster* in the Portuguese lowlands (see Santos et al. 2007; Rousselet et al. 2010).

In conclusion, the variability of the mitochondrial marker was sufficient to suggest a recolonization pathway between the glacial refugia in Spain and the post-glacial areas in France, but not to discriminate between different scenarios leading to a ‘northern purity’ pattern. According to these scenarios, the history of the maternal lineages could be consistent with different dispersal patterns and called for the use of polymorphic nuclear markers.

4.2.2 Genetic Signs of Diffusive Dispersal Within the French Populations

The genetic structure of French populations was further studied at a finer scale using highly polymorphic markers. About 550 individuals from 20 sampling sites covering native post-glacial, afforested and recently colonized areas (Fig. 4.9) were genotyped using five microsatellite markers specifically developed (Rousselet et al. 2004). Populations from the three mitochondrial lineages occurring in France (Fig. 4.8) were sampled, with a special effort for the Spanish-French and the eastern lineages. At these scales of space and time, only population-centred analyses were conducted using the data set from Kerdelhué et al. (2006) and additional data from Robinet et al. (2012).

Genetic differentiation between sampling sites, considered as subpopulations, was analysed using F-statistics (Wright 1951). The pairwise estimates of the fixation index among subpopulations θ_{ST} (Weir and Cockerham 1984) were plotted against geographic distances. The significance of the relationship between genetic and geographic distances ($\theta_{ST}/(1-\theta_{ST})$ against kilometers) was tested using a Mantel test (for more details see Kerdelhué et al. 2006). Genetic diversity within each subpopulation was assessed by calculating the mean number of alleles per locus.

Contrary to Kerdelhué et al. (2006), who studied fewer populations, a statistically significant and positive relationship was found with Euclidian geographic distances, but the relationship was much stronger when geographic distances between sampling sites were calculated as bypassing the Massif Central ($R^2 = 0.72$ against $R^2 = 0.37$). This nonetheless corroborates the main conclusions drawn by Kerdelhué et al. (2006) and means that (i) these nuclear and biparental markers confirmed the east/west separation observed with the maternally inherited marker; (ii) populations that are geographically closer are genetically more similar than populations that are further apart. This so-called ‘isolation by distance’ (IBD) pattern indicates a limited dispersal across space (Wright 1943), as suggested by Démolin (1969). Figure 4.9 indicates the main corridors of gene flows inferred from microsatellite data among the French populations. From north-western to north-eastern France, the pine processionary moth populations are thus gradually differentiated along these two axes. Nevertheless, the populations from the southern Paris basin and from the Saone valley located at each end of these corridors are strongly differentiated (pairwise θ_{ST} are about 30 %), despite the occurrence of a recent contact zone at the north of the Massif Central.

Both in eastern and western France, a linear decrease of the mean number of alleles per locus from the southern to the northern sampling sites seems to be observed (approximately from 8 alleles in the Aquitaine basin to 5 along the western part of the northern edge and from 9 in the Southeast basin to 5 in the eastern part of the northern edge; the highest value, namely 11 alleles, was observed

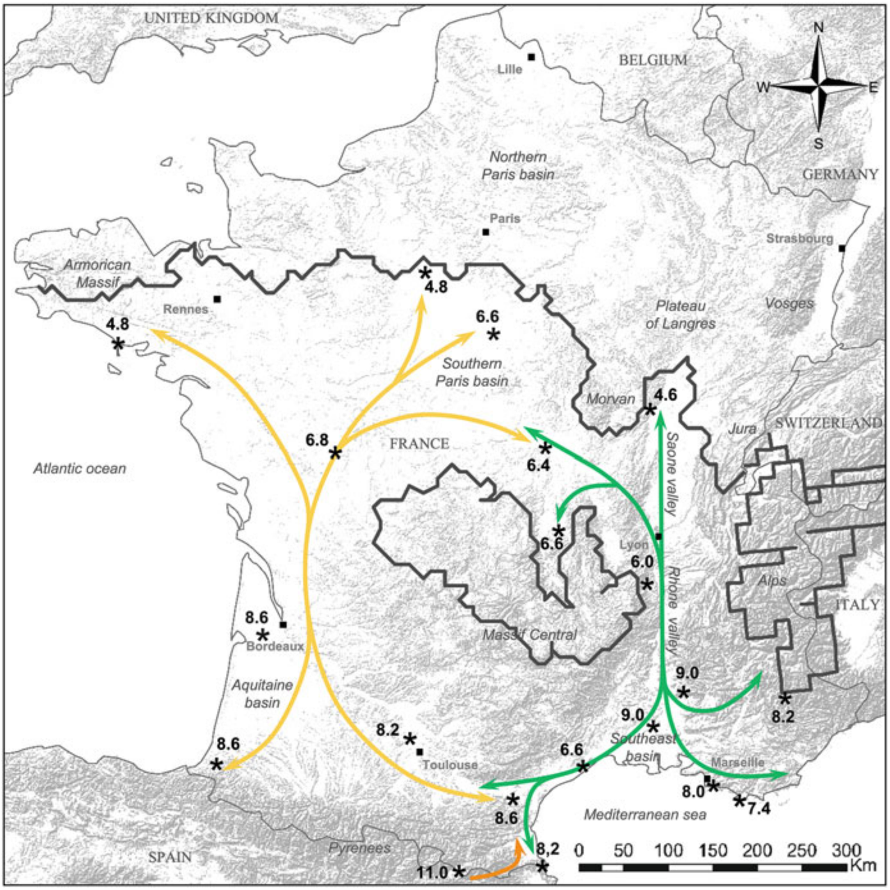

Fig. 4.9 Corridors of nuclear gene flow among the French populations of the pine processionary moth inferred from the analysis of five microsatellite markers. Note that the expansion corridors identified with these markers match the two main mitochondrial lineages shown in Fig. 4.8. *Black stars* indicate the location of the 20 sampling sites, and the values shown beside correspond to the mean number of alleles per locus. Between 25 and 30 individuals were analysed per locality

in an eastern Pyrenean population). This relationship needs to be confirmed with a higher sampling effort and more detailed analyses, but it could result from a gradual loss of genetic diversity during the past range expansion.

In conclusion, both nuclear and mitochondrial markers indicate two major corridors of northward expansion with a recent contact zone in the southern part of the Paris basin. The population genetic structure appeared to be characterized by a gradual loss of genetic diversity and an isolation by distance pattern from the southern glacial refugia to the northern areas colonized once the environmental conditions became suitable. These genetic signs are consistent with a range expansion resulting from a diffusive dispersal, i.e. only short distance individual movements. This result appeared to validate the use of a reaction-diffusion model for modelling the recent expansion of the pine processionary moth (Robinet 2006; Robinet et al. 2014; Chap. 5).

4.3 Current Expansion: A Combination of Active and Passive Dispersal

4.3.1 Pioneer Colonies Beyond the Wave Front and Human-Mediated Long Distance Jumps

During the 2000s, several satellite populations were detected far beyond the northern edge of the main range (Robinet et al. 2012; Chaps. 3 and 5). The first pioneer colonies discovered near Paris were located from 30 to 55 km away from the colonizing front (Robinet et al. 2012). This brings up questions about the active flight capabilities *vs.* passive dispersion of the moth in the expansion areas. Such an apparent stratified dispersal with rare long distance dispersal events was in contradiction with the genetic imprints of diffusive dispersal observed previously at large spatial and temporal scales. The flight abilities of the females measured on a flight mill suggested that these long distance jumps were due to accidental transportation rather than to active flight (Robinet et al. 2012; Chap. 2). The recent establishment of a pioneer colony found close to Strasbourg, i.e. 190 km away from the main range, was clearly incompatible with an active dispersal. Genetic markers were thus used to assess whether the five pioneer colonies occurring near Paris could originate from the expanding front located in north-western France, or likely came from further away.

Twenty individuals from the pioneer colonies were sequenced for the same mitochondrial fragment used by Rousselet et al. (2010) in order to assign them to one of the four maternal lineages described in Europe. To locate the population source more accurately, 705 individuals from 47 sampling sites over Western Europe were genotyped for five microsatellite markers and statistically assigned to their potential source among seven reference groups defined on the basis of population genetic structure (see Robinet et al. 2012).

The individuals from two of the five pioneer colonies (namely Eragny and Aubergenville) exhibited a mitochondrial haplotype belonging to the eastern European lineage rather than the Spanish-French lineage, although this latter was closer. Microsatellite markers showed consistent results (Fig. 4.10). Most of the individuals sampled in these two colonies were clearly assigned to Italy and south-eastern France, or to Italy and north-eastern France. Concerning the three other pioneer colonies (Bailly-Romainvilliers, Nanterre and Saint-Maur-des-Fossés), the haplotypes found belonged to the Spanish-French lineage. Microsatellite markers revealed that most of the individuals from Bailly-Romainvilliers were assigned to the Iberian Peninsula and to south-western France. Finally, only two colonies (Nanterre and Saint-Maur-des-Fossés) were assigned to the nearest and northernmost potential source, namely north-western France.

In conclusion, three of the five studied pioneer colonies probably originated from populations located at least 260 km apart. The precise origin of these three colonies still remains unclear because of large unsampled areas and the limited number of microsatellite markers used. Nevertheless, the result is clearly inconsistent with active dispersal abilities and provides evidence of human-mediated long

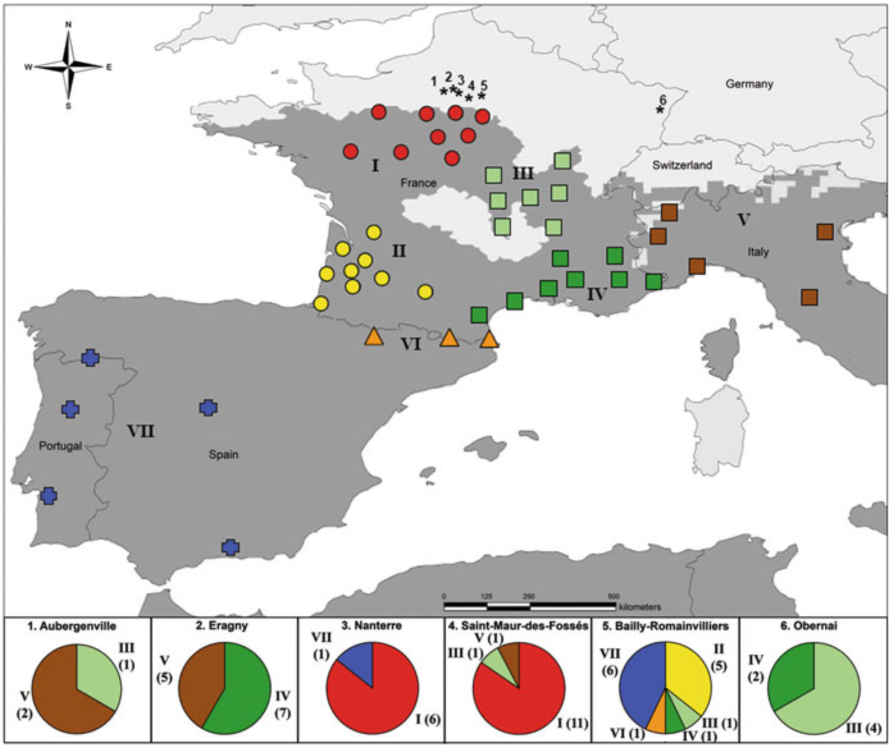

Fig. 4.10 Results of assignment tests for the six studied pioneer colonies. *Pie charts* indicate the proportion of individuals from each colony (1–6) assigned at first rank to each reference population (I–VII) using Geneclass 2.0. *Coloured shapes* on the map show the location of all the sampling sites of each reference population (using the same colour code as pie-charts). The *stars* numbered from 1 to 6 indicate the location of the pioneer colonies. Areas occupied by the moth are indicated in *dark grey* (Modified from Robinet et al. 2012)

distance jumps. To date, no egg parasitoids were detected in the pioneer colonies while some larval and pupal parasitoids were found (Robinet et al. 2012). This could indicate that the pupal stage, which is not easily detectable in the soil, was accidentally introduced into urban and suburban areas with the transplantation of large trees moved with a large amount of soil.

Concerning the two other colonies, which seem to originate from the nearby expanding front, it is difficult to definitely conclude about their colonization pathways. Noteworthy, they are both exposed to the northeastward dominant winds during the flight period in summer. Thus, although these satellite populations are likely still demographically isolated, recurrent male gene flows between them and the main range might have occurred for several generations.

4.3.2 Upward Expansion in the Alps: Impact of Gender Biased Dispersal on the Genetic Diversity of the Leading Edge

Field observations (Démolin 1969), laboratory experiments (Chap. 2) and genetic data (Salvato et al. 2002, 2005) indicate that a male-biased dispersal does occur in the pine processionary moth. Salvato et al. (2002) investigated population genetic structure and gene flow using biparentally (nuclear AFLP) and maternally (mitochondrial DNA) inherited markers. Seven populations in northern and central Italy, including three recently established sites in the expansion zone, were found to be highly spatially structured. Estimates of the absolute number of migrants per generation (Nm) were calculated assuming equilibrium between migration and drift. The twice higher value obtained with the nuclear markers including male-contributed alleles (0.47 *vs.* 0.25) suggested that males disperse more than females. Although these estimates rely on assumptions that can be violated in natural populations, especially in expanding populations, long-distance colonization by adult females appeared to be a rare event. Conversely, males seemed to give a small but constant contribution to the genetic diversity of populations on a relatively wide range. Similar results were obtained for the sister species *T. wilkinsoni* (Simonato et al. 2007; see above, 3.2.3). Dispersing males thus probably reduce the genetic loss associated with bottlenecks that could occur in expanded and/or isolated populations. This assumption was strongly supported by complementary data obtained from the expanding population located in the Western Alps.

Salvato et al. (2005) further compared the genetic diversity of pheromone-trapped males and of larvae sampled in the same stands (hereafter "resident larvae") for the same seven populations. Distribution of mtDNA frequencies revealed substantial homogeneity between trapped males and resident larvae within the six populations located in the core range of the species, including four old native forests and two 50 years old artificial stands that probably were recently colonized. Conversely, in the isolated population of Aosta Ruines Verrès located at the upper edge of the distribution area, the mitotype diversity of trapped males was higher than that of resident larvae. One mitotype found in trapped males was present in other populations but not in the resident larval population of Aosta Ruines Verrès. Consequently, this mitotype was likely transported by migrant males originating from distant and differentiated populations, but was not transmitted because maternally-inherited. Pairwise genetic distances of nuclear data (AFLP) confirmed the same differentiation patterns between adults and larvae. However, due to the dominant nature of AFLP markers, it is not known whether these pheromone-trapped males, especially the putative migrants, successfully bred and contributed to the next generation.

These results, in contrast with those obtained for the six populations located in the core range of the species, can be explained by a number of factors, such as the proximity of moth populations with different mitotypes and an innate tendency of the moths to expand beyond the range's edge, possibly supported by the ongoing increase of the minimum winter temperature. Moreover the outcome of this study underlines the potential for a significant gene flow among populations, driven by male dispersal, existing at least near the edge of the present area of distribution.

4.3.3 Conclusion

The study of the population genetic structure at large spatial and temporal scales in France and in Italy confirmed that the short-lived adults of the pine processionary moth exhibit a limited active dispersal as suggested by Démolin (1969). Genetic differentiation measured by F_{ST} using five microsatellite markers rapidly increases with geographic distance. This isolation by distance pattern and the gradual loss of genetic diversity along the main axis of the past northward expansion is consistent with a preferential exchange of migrants between adjacent demes and a diffusive dispersal. Thereby, only the individuals located at the expanding edge contribute to the advance of the expanding front, and this is expected to lead to a colonization wave of constant speed in a homogeneous environment. However, it will be necessary to investigate the colonization process at a fine scale in the current expansion areas in order to define the patterns of contemporary range expansion in various types of human landscapes (see also Chap. 5).

The contemporary northward expansion appeared to result from a combination of active and passive dispersals. In northern France, especially in urban areas, wide territories have already become climatically suitable for the pine processionary moth and offer abundant host-tree resources thanks to numerous artificial plantations (Robinet et al. 2014). The spread of the populations of the pine processionary moth into these territories appears now mostly limited by the active female dispersal abilities. Accidental introductions can allow to colonize climatically suitable territories beyond the wave front thus accelerating the spread of the insects. It will be crucial to confirm the putative pathway associated to large trees trade in order to avoid accidental transportations.

Males appear to disperse more than females and could contribute to genetic diversity of populations on a relatively wide range, reducing the risk of inbreeding and genetic loss associated with bottlenecks occurring in isolated populations. The identified male-driven neutral gene flow suggests that rapid exchanges of adaptive genetic diversity could occur between genetically differentiated lineages that recently came into secondary contact, and that may also be ecologically differentiated.

4.4 Ongoing Work and Perspectives

4.4.1 The Northward Expansion Area of the Paris Basin: A Melting Pot of Differentiated Lineages

In order to study the genetic imprints of the contemporary range expansion, a sampling grid covering about 60,000 km^2 was designed in the southern part of the Paris basin where the moth has colonized wide territories during the last 20 years (Fig. 4.11a). For this study, additional microsatellite markers were developed (Burban et al. 2012) in order to allow fine-scale and individual-centred analyses. First, 15 individuals collected every 64 km along the grid were analysed using mtDNA, AFLP and microsatellite markers. This study area corresponds to the main current expansion area of the French-Spanish lineage. Its south-eastern part also corresponds to the expected contact zone with the eastern lineage (see Figs. 4.8 and 4.11), allowing to study the pattern of admixture between them.

Surprisingly, the mtDNA marker allowed to identify three rather than two major genetic groups within this expansion area (Fig. 4.11). While the two expected maternal lineages actually co-occurred at this spatial scale (Fig. 4.11b), another

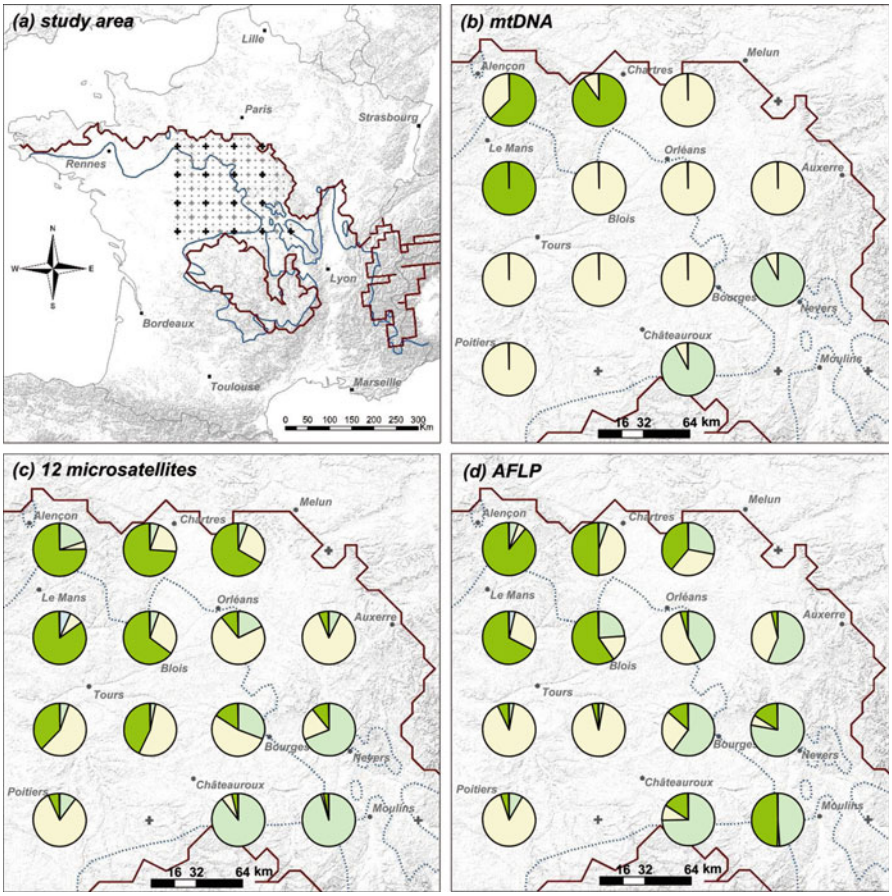

Fig. 4.11 Distribution of the three major genetic groups identified in the expanding area of the southern Paris basin using mtDNA, AFLP and microsatellite markers (**a**) location of the sampling grid (*dark crosses* represent sampling sites of the 64 km × 64 km grid, grey crosses the 32 km × 32 km grid, and *grey dots* the 16 km × 16 km grid) (**b**) each *pie chart* indicates the proportion of individuals bearing a mitotype from the French-Spanish mitogroup (*light yellow*) and from the eastern mitogroup (*dark green* for mitotype 5 and *light green* for the other ones) (**c**, **d**) distribution of the three genetic clusters inferred using Structure 2.3 for the microsatellite (12 loci) and the AFLP data sets respectively. The *red lines* indicate the edges of the distribution area in the winter 2005–2006, the *blue lines* indicate the maximum advance in 1979 according to J.F. Abgrall (CEMAGREF)

mitotype belonging to the eastern lineage (namely mitotype 5, Fig. 4.8) was also found in the north-western part of the grid. To date, this mitotype was found only in the northern French Alps (Rousselet et al. 2010) and its occurrence in the Paris basin likely resulted from an accidental introduction. The north-western corner of our sampling grid was indeed located near an old pioneer colony, reported in 1980 in the vicinity of Alençon (C.T.G.R.E.F.-I.N.R.A. 1980; Abgrall 2001), and now embedded within the present-day northern edge (Fig. 4.11).

The nuclear AFLP and microsatellite markers confirmed the existence of three well-differentiated genetic clusters but also revealed a larger admixture area than that identified by the mtDNA marker, which revealed narrow contact zones (Fig. 4.11b–d). They further suggested that the individuals occurring along the main axis of expansion showed signs of introgression between all the lineages that occurred in parapatry in this area before the climate-driven expansion (Fig. 4.11). This result highlights again the role of the male-driven gene flow at the leading edge.

In order to address the issue of the dispersal pattern in a recent expansion area, microsatellite markers were then used at a finer scale by analysing samples of five individuals collected every 32 km in the same study area. We used the kinship coefficient (F_{ij}) proposed by Loiselle et al. (1995) as a means of measuring the relatedness between each pair of individuals. The plot of the changes of F_{ij} for increasing distance is called the correlogram and reveals the spatial structure of the genetic data (Vekemans and Hardy 2004) (Fig. 4.12).

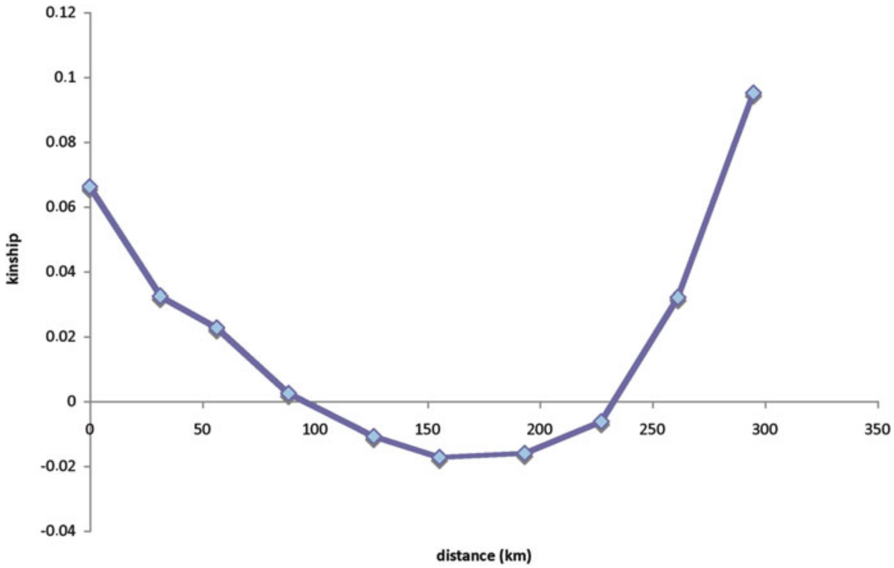

Fig. 4.12 Correlogram showing the large scale spatial variability of microsatellite data. The average of pairwise kinship values between individuals is plotted against the average of pairwise Euclidian geographic distances between them for ten classes of geographic distance

Up to a distance of 150 km, the mean kinship between individuals gradually decreased as geographic distance between them increased. This is consistent with an isolation by distance pattern, and thus with the diffusive dispersal previously found at a larger scale. Above a distance of 200 km, kinship increased as geographic distance increased, but this pattern must be interpreted with caution because of the low number of pairwise comparisons between each corner of the grid. Nevertheless, genetic relatedness between some distant individuals located in the corners revealed by the mean kinship could reflect the complex spatial distribution of the genetic clusters over the grid and the introgression patterns resulting not only from short-distance spread but also from contingent long-distance human-mediated jumps.

4.4.2 "Landscape Genetics" of the Pine Processionary Moth in the Paris Basin: Expansion in a Heterogeneous Environment

The southern part of the Paris basin where the moth recently expanded consists of different land uses, including forests with native broad-leaved trees and exotic conifers, meadow areas, wide open-fields, valleys and wetland areas, and large urbanized territories. The sampling grid in the study area presented above was also designed to cover the different landscapes of this strongly human-affected environment. Supplementary samples consisting of five individuals collected every 16 km will be genotyped for the same microsatellite markers in order to identify landscape features able to account for genetic discontinuities at a fine scale.

We especially aim to assess if the trees outside forests (TOF) can play a role in the dispersion of this species during range expansion, by creating suitable corridors. Considering only the distribution of the host tree resources, the different habitats of the pine processionary moth can be grouped into two main categories: forest lands with numerous and large artificial pine stands and non-forest lands with small stands and scattered ornamental pines. The Beauce region is a vast open-field area recently colonized that did not slow the northward expansion of the moth whereas isolated and scattered pines have been the only available resource (Chap. 5; Rossi et al. 2013). This indicates that TOF can be the sole medium of the spread. Previous field observations (C.-B. Malphettes, 2000, personal communication) suggested that moth expansion could have been accelerated in areas where host trees are scarce whereas large patches of resource like Orléans forest and Sologne could have retained philopatric females and acted as a barrier to dispersal. This also means that some landscapes mainly consisting of TOF might act as filters selecting the better dispersers contrary to more dense and continuous native forests. If true, a part of the spatial genetic structure is expected to be correlated with identifiable landscape features such as host tree abundance or fragmentation.

4.4.3 Concluding Perspectives

The use of neutral genetic markers showed that the population genetic structure in the current expansion areas can result from a combination of active short-distance dispersal and human-mediated long-distance jumps. Moreover, a male-driven gene flow between the wave front and some of the distant satellite populations is very likely. These results question the existence of flows of adaptive genetic diversity occurring at the expanding edge, especially on possible phenological adaptations that might be experienced in the expanding populations (e.g. more frequent prolonged diapause at the edge – Géri 1980 – or phenological shift following admixture between ecologically differentiated lineages). Such a modification of the species climatic envelope would affect the further potential of colonization. Genomic resources are currently being developed for the pine processionary moth, and will soon allow the development of genome-scans approaches. These methodologies, based on high-throughput sequencing, will give access to a tremendous number of neutral genetic markers that can be useful for fine-scale landscape genetics studies, and will at the same time allow to detect the genomic regions under selection, and thus potentially involved in adaptive traits.

5 Global and Local Genetic Structure of the Northern Pine Processionary Moth, *Thaumetopoea pinivora*

Anna Cassel-Lundhagen, Andrea Battisti, Cecilia Ronnås, and Stig Larsson

5.1 Introduction

As opposed to the pine processionary moth *T. pityocampa*, *T. pinivora* is not considered as a major forest pest. It mainly occurs in local populations in mountainous areas in southern Europe and along the coasts of the Baltic Sea in northern Europe. However, like the pine processionary moth, *T. pinivora* causes nuisance to humans, and was recently the focus of attention of the general public because of a major outbreak in a touristic area on the island of Gotland in south-eastern Sweden. A need to gain knowledge about its biology, and particularly its dispersal behaviour, became apparent in order to better understand its abundance and distribution.

As described in the previous subchapters, genetic data can provide information about a species dispersal behaviour. Colonization events tend to result in geographic structuring of genetic diversity so that the dispersal pathways can be revealed (Hewitt 1999; Taberlet et al. 1998). However, in highly mobile species traces from a colonization event (as manifested in haplotypes shared by the founder and founding population) may be blurred by subsequent gene flow from other areas (Ibrahim et al. 1996). In the case of low or no gene flow subsequent to colonization, low genetic diversity is expected to persist in the new populations (Ortego et al. 2011; Whitlock et al. 2003), especially if the population remains small in size (Vrijenhoek 1994). Because dispersal is expected to be most frequent between neighboring locations, and gradually cease as the distance increases, the level of genetic differentiation is expected to increase with geographic distance. However, the correlation between geographic and genetic distance is expected to change over time depending on the rate of dispersal between populations relative to the amount of genetic drift acting within them (Epperson 2003). Over time, new mutations will also accumulate, causing further genetic structuring. Thus, the combined genetic patterns found within and between local populations can be used to reveal the species historic and contemporary dispersal behaviour.

5.2 *The Phylogenetic Position of* **Thaumetopoea pinivora** *in Relation to Other Summer Processionary Moths*

The northern pine processionary moth *Thaumetopoea pinivora* (Treitschke) (Lepidoptera, Notodontidae) belongs to a well-defined clade in the phylogeny of the genus (see beginning of this chapter) that includes the so-called summer processionary moths associated with coniferous host tree species. These species are characterized by larval development across spring and summer, which makes them biologically different from the winter processionary moths. The molecular phylogeny fully justifies such a difference and clearly separates the two clades (Simonato et al. 2013), although the species share the same coniferous host plants.

Four species are included in the clade of the summer processionary moths. *Thaumetopoea pinivora* is the only one associated with *Pinus* spp. whereas the other three species feed on *Cedrus* spp. in various parts of the Mediterranean basin. *Thaumetopoea bonjeani*, which is the most closely related species to *T. pinivora* (although clearly separated based on a large number of mitochondrial and nuclear genes, see the phylogeny subchapter), is monophagous on *Cedrus atlantica* in the mountains of Algeria and Morocco. The other branch of the clade includes *T. libanotica*, which is associated with *Cedrus libani* in the mountains of Lebanon and Syria, and the recently described *T. ispartaensis* from the same host plant is located in the Taurus mountains in southern Turkey.

As far as it is known from natural history (Chap. 2), the four species share the same developmental pattern, pointing at a common origin. However, the geographic data that are currently available do not allow us to locate the most likely geographic area of origin. All four species occupy mountain forests that are well isolated in the Mediterranean basin; thus, we can only speculate that they may be relics of a species that occurred in a former more extended distribution of *Cedrus* forests back in the Tertiary (Qiao et al. 2007).

Thaumetopoea pinivora is the only species that does not feed on *Cedrus* as it has switched to *Pinus*. This could explain why it has been able to expand from the Iberian Peninsula and colonize part of Europe after the last Quaternary glaciation (see below). The lack of *T. pinivora* (or other summer processionary moths associated with *Pinus*) in other parts of the Mediterranean basin where mountain forests of pines are abundant, similar to those of the Iberian Peninsula, supports the notion that the switch probably originated from a species feeding on *Cedrus*. *Thaumetopoea bonjeani* appears to be the most likely candidate as it has a distribution that is geographically close to *T. pinivora* in the Mediterranean area, and because these two species show the shortest genetic distance in the molecular phylogeny. This hypothesis is further strengthened as the two species share the same sexual pheromone (Frérot and Démolin 1993; Frérot et al. 1990), a number of morphological traits (Démolin 1988; Démolin et al. 1994; El Yousfi 1989; Gachi 2004), as well as the species that parasitize their eggs (Schmidt et al. 1997).

A thorough phylogeographic analysis of the clade of summer processionary moths could shed more light on the relationships among the species, especially if other taxa were found in target areas such as the high elevation coniferous forests in the Mediterranean basin. Because these species are much less conspicuous than the winter processionary moths it may be that their occurrence has so far been overlooked.

5.3 Glacial and Postglacial History

Thaumetopoea pinivora has a peculiar global distribution, occurring at high-elevation locations in southern Europe while primarily residing close to sea level in northern Europe. In addition, the distribution is highly scattered and local populations tend to appear more or less isolated (Chap. 3). The main host plant for *T. pinivora*, Scots pine (*Pinus sylvestris* L.), is widespread across Europe (Hultén and Fries 1986). Data obtained from pollen, macrofossil, and phylogeographic analyses of mitochondrial DNA variation across Europe suggest that *P. sylvestris* survived the last glaciation in at least four different glacial refugia: Spain, southern Italy, Asia Minor, and central Europe (Cheddadi et al. 2006; Naydenov et al. 2007; Sinclair et al. 1999), and possibly in cryptic refugia at northern latitudes (Kullman 2002; Larsen et al. 1987). There is evidence that *P. sylvestris* colonized central and northern Europe more than 8,000 years ago, and that the northern pine populations originate from refugia in Italy or central Europe (Cheddadi et al. 2006; Kullman 2008). If *T. pinivora* followed the spread of its host after the last glaciation, i.e., the colonization pathways of *P. sylvestris* mirror the establishment of *T. pinivora,* then we should expect to find significant genetic divergence between the southern and northern European populations of *T. pinivora*. If, on the other hand, all extant populations of *T. pinivora* share the same origin, then we should expect lower levels of genetic divergence across sites (Table 4.2).

The exact habitat requirements are poorly known, and thus the causes of the fragmented distribution are largely unresolved. When knowledge about habitat requirements is limited, as for *T. pinivora,* or when information about the former distribution of the habitat is unavailable, it can be difficult to determine whether geographically separated populations are the result of recent colonization events or if such populations have existed for a long time. A fragmented distribution could also indicate that the populations are remnants of a more widespread distribution

Table 4.2 Suggested large-scale genetic patterns after an expansion event, and subsequent dispersal strategies, of *Thaumetopoea pinivora* depending on time since expansion, the prevailing colonization model and the species dispersal capacity

		Recent events			Ancient events		
Colonisation model	Dispersal capacity	Founder effects	IBD pattern	Unique alleles in colonized locations	Founder effects	IBD pattern	Unique alleles in the colonized location
Long-distance few	High	+	–	–	–	–	–
	Low	+	+	–	–	+	+
Stepping stone	High	–	+	–	–	+	–
	Low	+	+	–	–	–	+

(+) indicates that the pattern is found and (–) that it is not

Founder effect = reduced levels of genetic variation as a consequence of few individuals (few genotypes) colonizing a new location; IBD pattern (Isolation By Distance pattern) = a correlation between geographic distance and genetic distance between pairs of populations. Such pattern occurs if dispersal rate is negatively correlated to distance; Unique alleles = alleles that are found only within a specific population or region

(Habel and Assmann 2010). Finally, such a distribution could also occur if the species has a narrow habitat requirement but is capable of long-distance dispersal, enabling the species to track rare suitable habitat patches (Schroeder et al. 2007).

In order to reveal the mechanism behind the current distribution we evaluated the glacial and postglacial history of *T. pinivora* by using genetic data from both nuclear microsatellite markers and a fragment of the cytochrome oxidase I (COI) gene in the mitochondrial (mt) DNA. A combined analysis of the fast-evolving microsatellites (reflecting more recent processes) and the non-recombining mitochondria (mirroring more ancient events) allowed us to evaluate the species' establishment and dispersal pattern across a wide temporal and spatial range (Table 4.2).

We found that *T. pinivora* exhibits very little mitochondrial diversity across its whole range (Cassel-Lundhagen et al. 2013). Only eight sites within the 633 bp long fragment of the mitochondrial COI gene were polymorphic, and 90 % (116 out of 129) of the analysed individuals, found across the whole range, shared the same haplotype. Thus, the data suggest that the populations have not been present in their current locations long enough for a significant number of mutations to emerge. Data also indicated that *T. pinivora* does not exist as a large and continuous population because such a population should have accumulated genetic diversity over time (Bromilow and Sperling 2011). Because the number of mutations is determined by the length of time that a population has existed, we conclude that all of the analysed populations appear to have a recent history. This was also verified by the microsatellite data which exhibit few unique alleles despite a wide geographic range.

The lack of mtDNA variation across all sites further suggests that the glacial refugium of *T. pinivora* is not associated with any of the studied populations. In general, populations that are older than the last glaciation are typically characterized by high haplotype diversity and possibly deep divergence (Hewitt 1996).

The mtDNA structure of *T. pinivora* stands, for example, in contrast to that of the bark beetle *Tomicus piniperda*, another cold-tolerant species that is also associated with *Pinus sylvestris*. In a study covering the European range of *Tomicus piniperda* a high number of unique haplotypes and accumulated mutations were found in geographically restricted regions (Horn et al. 2009). Horn et al. (2009) also suggested that refugia may occur outside Europe and this could potentially apply also to *T. pinivora* as it is known that several European cold-tolerant species have a distribution that extends into Asia (Schmitt et al. 2010).

As opposed to the mtDNA data, the *T. pinivora* microsatellite diversity was markedly higher in the Spanish populations and was gradually lowered towards the north. The low number of unique alleles in the northern populations supports our conclusion that the colonization was recent (cf. Slatkin 1985) but the differences between the populations were not as pronounced as expected if severe bottlenecks had occurred. The data rather indicate that the colonization process was gradual with most of the variation retained in the expansion front (Ibrahim et al. 1996). The lack of traceable genetic bottlenecks also point against the species having colonized northern Europe through rare long-distance dispersal events with subsequent small population sizes. Simulations of our empirical data compared with a set of suggested scenarios indicate that *T. pinivora* colonized northern Europe approximately 2,000 years ago at least at two separate occasions. Considering the current occurrence, the *T. pinivora* distribution must thereafter have diminished significantly in size leading to the currently fragmented occurrence.

5.4 **Thaumetopoea pinivora** *Outbreak and Local Population Genetic Structure*

Thaumetopoea pinivora was once considered a rare species in Sweden and was until recently red-listed (Gärdenfors 2000). Only a few populations were known to exist in Sweden, one at the southern tip of Gotland Island and one on the neighbour Öland Island, both in the Baltic Sea. In 2004–2006 the density of the Gotland population increased dramatically leading to an outbreak (Larsson et al. 2008). Because outbreaks can lead to resource depletion, and subsequent starvation, they can have drastic effects on insect fitness (e.g. Klomp 1966). One could therefore expect density-dependent emigration to occur into low density and/or unoccupied areas (Berryman 1987; Bowler and Benton 2005; Denno et al. 1995) and this, in turn, may result in new populations being established (Benzie and Stoddart 1992; Nair 1988). When a high-density population is situated at the edge of the species' range, as in the case of *T. pinivora* on Gotland, increased dispersal can also result in an extension of its distribution (Travis et al. 2009; Wilson et al. 2010).

Due to the known high dispersiveness of *T. pinivora* males, and the fact that the food source is readily available throughout Gotland Island, we expected the outbreak to expand the distribution as the competition for resources within the outbreak area increased. To examine if this was actually the case we genotyped recently discovered populations at increasing distances from the high-density area. As neither of these populations had been previously known, and as they were relatively easy to observe due to the aggregating behavior of the larvae and their health impact on humans (Battisti et al. 2011), we assumed them to be newly established from the ongoing outbreak. Using 12 polymorphic microsatellite markers we tested for presence of founder events, if there were reduced allelic richness due to rare long distance dispersal, and if there were signs of recent establishment in terms of sharing of alleles between the outbreak area and the isolated populations (Ronnås et al. 2011).

Contrary to our expectations, three aspects of the results suggest that none of the isolated populations was recently established. First, the distant populations exhibited similar levels of genetic variation to the high-density one and locally unique alleles were found in the isolated sites (Table 4.2). Second, there were no signs of founder events or genetic bottlenecks. Finally, there was significant genetic structuring in the populations located further away from the high-density population. Thus, the outbreak appears not to have resulted in spread into the surrounding areas, despite the high population density (Ronnås et al. 2011). On the contrary, *T. pinivora* appears to have a fragmented local distribution on Gotland Island, possibly the remnant of a former more widespread population similar to what seems to be the case at the larger, continental scale.

5.4.1 Being Rare and Being Common, and the Genetic Paradox

As opposed to *T. pityocampa, T. pinivora* appears typically to reside in relatively isolated populations. From a population genetics view, we expected that this should result in small local effective population sizes with pronounced effects of genetic drift. Therefore, it would be expected that the overall levels of genetic variation were lower on a global scale for *T. pinivora* than for *T. pityocampa* and that the level of differentiation was more pronounced. We did not, however, find this pattern. Although microsatellite data cannot be easily compared among species, it is striking that the levels of heterozygosity are comparable between the two species (Santos et al. 2011b). There is also relatively good agreement in COI haplotype variability within locations. In each genotyped location of *T. pityocampa,* in general, only 1–3 haplotypes were found (Kerdelhué et al. 2009; Rousselet et al. 2010). This was also the case for *T. pinivora* (Cassel-Lundhagen et al. 2013). On a global scale, on the other hand, the pattern was considerably different. In *T. pityocampa,* haplotypes were found in geographically well-defined clusters while all populations across the whole range of *T. pinivora* shared the same main haplotype. The considerably different genetic structure between the two species is likely due to the differences in their current distribution. If a species colonizes a new area, then the same haplotype will spread across all populations. If an area, on the other hand, is already inhabited with a population carrying a certain haplotype, then the spread of an immigrant haplotype is less likely. Thus, the difference in genetic structure may be due to variation in time since establishment. Whether the difference is also due to variation in dispersal behaviour remains to be elucidated.

5.4.2 Conclusions from Genetic Data in Light of *Thaumetopoea pinivora* Distribution

The microsatellite data of *T. pinivora* from Gotland Island revealed some interesting patterns when compared with data from sites across Europe. All microsatellite alleles, except two unique alleles on Gotland, were found across the whole distribution range. Thus, most alleles were found also in Spain, Russia, or Germany. The combined global distribution pattern and genetic structure of *T. pinivora* is puzzling. While it is, as far as we know, a poor disperser, it also has a very scattered distribution. Furthermore, there is an ongoing outbreak on Gotland but this has not yet resulted in any range expansion, or documented new colonizations. We do know that its colonization history in northern Europe is relatively recent. The combined data from genetic studies (Cassel-Lundhagen et al. 2013) rather suggest that *T. pinivora* may be considered as a relict species (Habel and Assmann 2010) where its total distribution is retracting rather than expanding. The habitat requirements of *T. pinivora* appear to be relatively narrow, and populations have not been found in forests managed for wood production. Even though it is not possible to reconstruct the availability of suitable habitats in the past, it is very likely that the intensification of agriculture and forestry during historical time has resulted in a decline in the occurrence of the sparse, slow-growing pine stands that *T. pinivora* prefers.

Glacial relict species are species that had their most restricted distribution during the cold maxima and have expanded since, while interglacial relicts have rather had their more widespread distribution during cold periods with subsequent reductions in interglacial periods. The interpretations of our genetic data do not really support any of these extremes but rather suggest that *T. pinivora* has both expanded and retracted during the interglacial. Thus, it appears that a combination of suitable climate *and* appropriate vegetation was not in place until several thousand years after the ice retreated from northern Europe (Cassel-Lundhagen et al. 2013).

The finding of a relatively high diversity extending across all of Europe, despite the fact that *T. pinivora* appears very locally, suggests that it has had a “burst” of stepping-stone expansion lasting for a limited period, followed by habitat fragmentation and loss of populations. Thus, the combined data suggest that *T. pinivora* can be considered a cold-tolerant relict species residing in habitats appearing irregularly in time and space, with situation-dependent dispersal rather than being widespread and highly dispersive, as could be expected if the species was in general overlooked rather than truly rare.

6 Allochronic Differentiation and Ecological Divergence in a Phenologically Shifted Population of the Pine Processionary Moth in Portugal

Manuela Branco, Helena Santos, Susana Rocha, Maria-Rosa Paiva, Eduardo Mateus, Christian Burban, and Carole Kerdelhué

6.1 Introduction

Speciation is the evolutionary process by which new species arise. The initial reproductive isolation between lineages may occur due to physical separation, such as by a geographical barrier or as a result of habitat fragmentation, in which case speciation is said to occur in allopatry. Speciation can also arise in consequence of ecological specialization and assortative mating within a given geographical region. Most cases of so-called “sympatric speciation” have been studied among either cichlid fishes or phytophagous insects, in which populations primarily diverge through habitat or host-plant specialization (Dres and Mallet 2002; Fan et al. 2012; Kornfield and Smith 2000). A different model of sympatric speciation called “allochronic speciation” was proposed in the 1960s (Alexander and Bigelow 1960). In this particular case, isolation is due to a temporal shift of the reproductive period without geographical separation or habitat change.

In this subchapter, we will review a plausible case of incipient allochronic differentiation in the pine processionary moth in Portugal and provide new evidence about its origin and divergence patterns. We first present a synthesis of the conclusions obtained by the use of molecular markers, we then introduce the results concerning the ecological differentiation observed for various life-history traits, and we finally point out some perspectives and clues for future research.

Thaumetopoea pityocampa is ubiquitous in Portugal, due to a wide distribution of pine trees and mild climatic conditions (see Chaps. 2 and 3). It typically develops with a 1-year biological cycle, with some variation according to latitudinal and altitudinal gradients as observed in other regions. Sexual reproduction occurs between August and September, and larval development unfolds in the fall and early winter. Processions take place in January or February. In August 1997, a huge outbreak of last instar larvae (fifth instar) was observed in “Mata Nacional de Leiria” (Paiva, personal observation), a maritime pine forest located ca. 120 km north of Lisbon. This situation was unexpected, because fifth instar usually occur in December. Field monitoring and observations set up during the following years showed that two different types of processionary moths occurred in Leiria pinewood: some of the individuals develop following the classical life cycle described above, while others reproduce as early as May, then develop as larvae in the summer months and experience the diapause procession in mid-September (Pimentel et al. 2006, see Chap. 2). Based on the timing of larval development, the individuals developing with the classical cycle were called Winter Population (WP) while the individuals with a shifted life cycle were supposed to belong to a divergent Summer Population (SP). Many evolutionary questions rapidly arose from these first observations, and research was undertaken in the fields of phylogeography, population genetics and ecology to bring the first answers. We specifically addressed the following points: (1) Does the SP belong to the same species as the sympatric WP? (2) If so, does it really form a differentiated population? (3) What is the most likely origin of the SP? (4) Is it possible to estimate the age of the SP, and to quantify potential gene flow with the WP? (5) Can we identify key ecological traits that differ between the SP and the WP?

6.2 Evolutionary Scenarios Based on Molecular Data

In order to determine whether the SP actually belongs to the same species as the WP, and should thus be considered a *T. pityocampa* population with a shifted phenology, rather than a cryptic species showing a different life cycle, Santos et al. (2007) first sequenced a part of the mitochondrial COI gene and the nuclear ITS1 marker for a few individuals sampled in Leiria pinewood from the SP and from the WP, as well as in 10 surrounding localities in Portugal, Spain and France. Interestingly, the major COI haplotype and the ITS1 alleles found in the SP were also found in the WP occurring in Leiria, as well as in the other Portuguese populations, and in central and southern Spain. Only one rare mitochondrial haplotype was found exclusively in the SP, being however closely related to the main haplotype found in Leiria pinewood. Results thus demonstrated that the SP did not belong to a cryptic species, and should instead be considered a population of *T. pityocampa*, with a peculiar phenology. Moreover, the genetic data showed that the SP was phylogenetically close to other Iberian populations, evidencing a regional origin for both the mitochondrial and the nuclear markers. The very low nucleotidic divergence observed between the SP and other local populations, further suggested that the phenological shift occurred relatively recently, but did not allow to precisely estimate the time of the divergence. The markers used were not sufficiently informative to identify the closest related sister group in the Iberian Peninsula.

We thus further sequenced the whole mitochondrial COI gene (ca. 1,500 pb), in order to obtain more polymorphic, informative sites and to eventually point to the origin of the SP, at least for the maternal lineage. We sequenced 8 individuals from the SP, 8 from the sympatric WP, and 3 individuals in 12 localities in Portugal, Spain and France. We obtained 21 haplotypes, and the resulting most parsimonious network showed two haplogroups, that corresponded to the Iberian and the European sub-clades previously identified using shorter mitochondrial gene fragments (Kerdelhué et al. 2009; Rousselet et al. 2010; subchapters 3 and 4 above). The geographical distribution of the COI haplotypes and the network are shown in Fig. 4.13. These new data brought significant information concerning the evolution of the SP, as they showed that the main haplotype found in this peculiar population

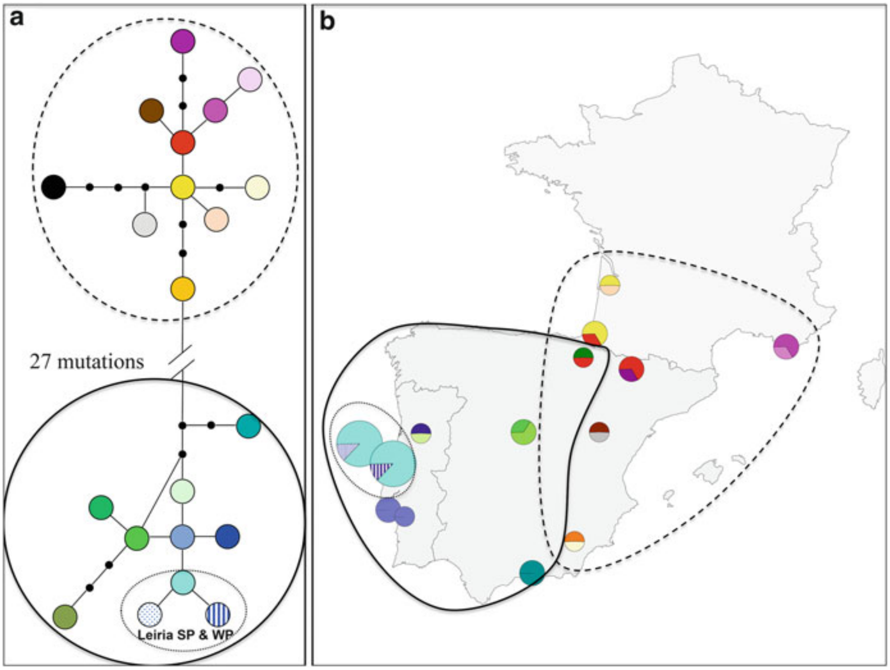

Fig. 4.13 Most parsimonious network of haplotypes (**a**) and geographical distribution of the COI haplotypes in the 14 sampled populations (**b**). Haplotype frequencies and sampling sizes are represented by the area of the *circles* on the map. In the network, each *line* between *circles* corresponds to a mutational step and each small *black circle* to a missing intermediate haplotype

was found only in individuals of the sympatric Leiria WP, and differed by only one or two mutations from the other haplotypes found in Portugal. This strongly suggests that the SP diverged locally, from an ancestral *T. pityocampa* population having a typical "winter" cycle and probably already occurring in Leiria pinewood. According to this hypothesis, the foundation of the SP would have arisen from a sudden phenological shift that rapidly led to a strong limitation of the gene flow with the individuals of the ancestral population.

The next objective was to characterize the genetic differentiation between the SP and the sympatric WP, and to determine if gene flow could still occur in spite of the observed shift in the reproductive period. Santos et al. (2007, 2011b) have monitored the activity of the adults in the field, through male catching with pheromone traps set up in Leiria pinewood from April to October of each year. Results clearly showed the occurrence of two non-overlapping peaks of male emergences, one from early May to mid-June, and another one from mid-July to September, with little inter-annual variations. A period of 1–4 weeks without male catches was observed each year, in early and mid-July. The first peak coincided with the expected reproductive period of the SP, while the second peak corresponded to the period of adult emergence known in Portugal for the WP. Given that the adults of *T. pityocampa* live for 1–3 days only, the flight pattern observed should preclude gene flow between the two populations.

To test the hypothesis that a strong genetic differentiation between the SP and the WP would occur, and to check if the genetic composition of both groups was stable in time, Santos et al. (2011b) further applied a population genetics approach using six microsatellite loci, and genotyped larvae and males trapped over different seasons and years. Females sampled as pupae in the field, that later emerged in the laboratory, were also studied. Very high F_{ST} estimates of differentiation between the SP and the WP were found, reaching 0.18–0.24 in different years. Such values were much higher than the F_{ST} measured between populations of pine processionary moth sampled several hundreds of kilometres apart, as the F_{ST} between populations from Portugal and southern Spain did not exceed 0.15. Individual assignment tests were also performed using a Bayesian framework (Structure software, Pritchard et al. 2000). This approach produced interesting information, as it showed that: (1) The vast majority of the sampled individuals were classified in two clear-cut genetic clusters corresponding to the two phenological classes (SP *vs.* WP individuals); (2) All males trapped in the spring were unambiguously assigned to the SP, showing that the adults emerging in May and June actually gave rise to the next generation of the SP; (3) Most of the males caught in the summer were well assigned to the WP cluster, while few individuals were well assigned to the SP cluster. As the results presented in Santos et al. (2011b) were based on six microsatellites only, including two markers showing high levels of null alleles, we took advantage of recent technological developments (Burban et al. 2012) to genotype the same samples, as well as individuals sampled the following year, using 10 other microsatellite loci and excluding the two problematic markers. Results confirmed the conclusions found in Santos et al. (2011b), with enhanced assignment thresholds (Fig. 4.14).

In conclusion, the population genetics approach confirmed a strong pattern of genetic differentiation between the two sympatric SP and WP, which suggests that gene flow is extremely reduced, in spite of a shared geographical range and continued use of a common host plant. The primary process that probably acted to hamper the genetic exchange between the two populations is a major shift in the reproductive phenology. It is thus likely that the two "phenological populations" that occur in

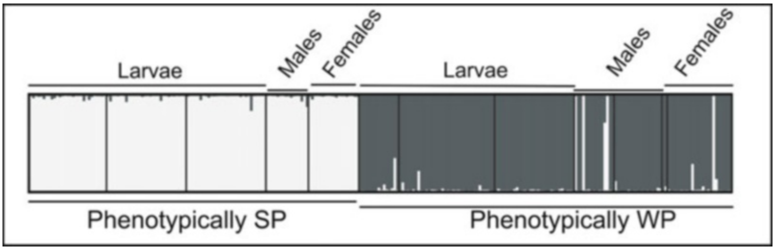

Fig. 4.14 Graphical representation of the individual assignment proportions (estimated membership coefficient for each individual) obtained by running the Structure software with 2 hypothetical clusters and 264 individuals genotyped with 14 loci (larvae, males and females sampled over several years and "phenologically" a priori identified as SP or WP)

Leiria pinewood are under allochronic differentiation and may constitute a unique case of incipient allochronic speciation in a phytophagous insect. Yet, we showed that some “phenologically WP males” actually belong to the SP genetic cluster (light-grey individuals occurring in the dark-grey cluster, see Fig. 4.14).

This result suggests that some individuals originating from the SP cluster can episodically emerge as adults within the period of WP reproduction, after a longer pupal diapause. Such individuals can be seen as SP larvae “reverting” to the WP phenology as adults. Such a mechanism could allow for some gene flow to be maintained, even though the peaks of reproductive activity of the SP and WP are non-overlapping. Analyses are still under way to estimate the levels of gene flow between the two populations, and to test whether recurrent gene flow might have occurred throughout the evolutive track of the SP. Attempts to estimate the time of the SP foundation from a putative WP local ancestor have so far remained inconclusive.

6.3 Evidence for Significant Ecological Differentiation of the Summer Population

Understanding the ecological differentiation occurring during a speciation process is of major relevance in evolutionary biology. Whatever the mechanism involved (local adaptation, drift, plasticity, among others), ecological divergence of key-traits in the separated lineages can even reinforce the ongoing speciation via specialization, or counter-selection of hybrids (Rundle and Nosil 2005). As the molecular data led to the hypothesis of a relatively recent evolution of the SP from a local WP ancestor, we took advantage of this unique model to test whether ecological differentiation could be found in the SP, as compared to the local WP. We focused on key ecological traits involved in reproduction, such as pheromone characterization, fecundity and egg parasitism, as well as on physiological capacities to survive high temperatures, as SP larvae face very hot summer conditions considered lethal for the earlier larval stages (Huchon and Démolin 1970). This research is particularly relevant within the context of global warming, as it also allows for testing the capacity of a species to rapidly adapt to new environmental conditions.

6.3.1 Comparative Study of Reproductive Traits in the SP and the WP

To test whether gene flow between the SP and the WP could be further limited by divergent chemical recognition signals, we compared the female sex pheromone emitted by both populations. The volatile emissions of virgin SP females were collected in the laboratory by SPME (Solid Phase Micro Extraction) and the characterization of the volatiles was performed by gas chromatography and mass spectrometry (Paiva et al. 2011b). Results showed that the pheromone composition

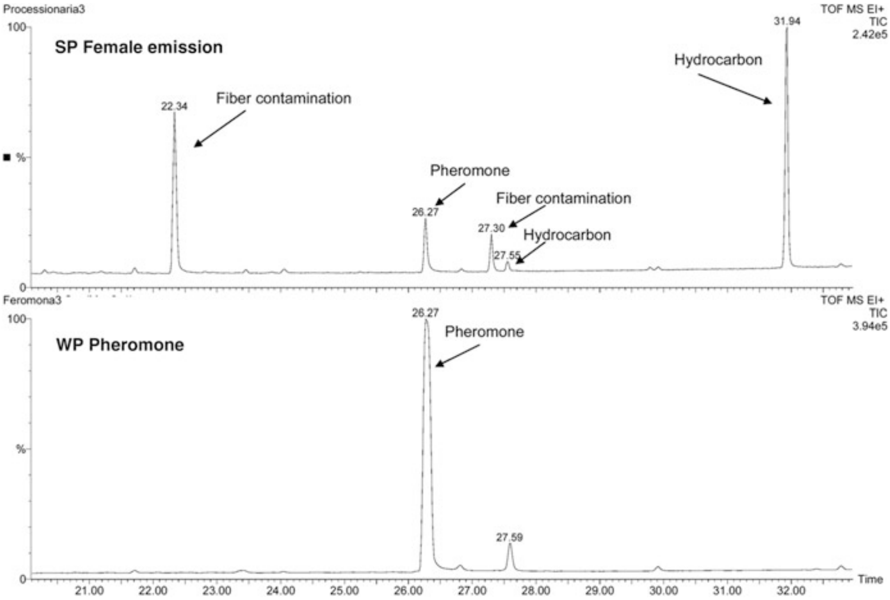

Fig. 4.15 Chromatograms obtained by Solid Phase Micro Extraction (SPME) for the volatile emissions of SP females and for the standard, commercially available, sex pheromone of the WP (Laboratories of FCT, UNL, Portugal, 2010)

of the two populations of pine processionary moth did not differ. Furthermore, no additional compounds could be identified in the volatile emissions of the SP (Fig. 4.15). This work thus indicates that the mechanisms of olfactory communication have not diverged regarding sexual attraction, so that cross mating between the SP and WP probably remains possible.

Pimentel et al. (2012) as well as Santos et al. (2013) further studied the post mating traits involved in reproduction and larval development. The egg batches of pine processionary moth populations have been observed to follow a general latitudinal trend, as they contain numerous small eggs in areas where they are exposed to cold winters and fewer, larger eggs under milder environmental conditions (Pimentel et al. 2010). It was hypothesized that this trend should result from different selective pressures occurring in these two types of environments: pine processionary moth survival to harsh winters is enhanced by the size of the colony (i.e., the number of larvae in a single nest), which favours high fecundity rather than embryo size.

On the contrary, when the selective pressure due to low temperatures is relaxed, selection tends to favour embryo size and survival. A trade-off between the number and the size of the eggs produced by each female would then explain the observed general pattern. As the SP larval development occurs in the spring and summer, it was expected that the selective pressure on colony size would no longer be in operation, and that a lower number of larger eggs would be produced by comparison with the WP. Moreover, due to the shift in phenology, it was also expected that

Fig. 4.16 Phenotypic differences of the scale cover of the egg batches observed for *T. pityocampa* SP (*left*) and WP (*right*), in Leiria pinewood (Modified from Santos et al. 2013)

the SP would escape from the pressure of specialist egg parasitoids. Results confirmed our hypotheses and showed that the SP lays fewer and larger eggs, per egg batch, than the sympatric WP. As final larval dry weight as well as adult size did not differ significantly between populations, total growth was higher in the WP than in the SP. Embryo mortality due to parasitoids and colony extinction before the third larval instar, were shown to be higher in the WP than in the SP (Pimentel et al. 2012). Preliminary results suggest that the SP would be mainly attacked by generalist egg parasitoids, and that the morphology of the scales covering the eggs would be less efficient in protecting the embryo from parasitism, due to a looser scale cover, as a result from differences in the shape of the scales (Fig. 4.16).

6.3.2 Larval Susceptibility to Extreme High Temperatures

Following the phenological shift, “the mutant” Leiria SP became suddenly exposed to new climatic conditions. In particular, larval development shifted from winter to summer, so that SP larvae are subjected to daily temperatures on average 6.6 °C higher than those of the WP. Research was thus conducted to determine whether SP larvae would be less susceptible to extreme high temperatures than WP larvae. Different mechanisms allow insects to overcome unfavourable temperatures, namely physiological and biochemical adaptations (Angilletta et al. 2002; Denlinger and Yocum 1998), behavioural changes such as micro-habitat selection (Breuer et al. 1989), or aggregation (Jones and Oldroyd 2006). To test this hypothesis, two types of parameters were studied by conducting the following experiments: (1) Temperature thresholds: L1 and L2 larvae were reared under controlled conditions at high temperatures, to evaluate the upper thresholds of survival; (2) Larval behaviour: direct observations of larvae placed in potted pine trees, during extreme hot summer days.

For the first experiment, the rearing procedures are given in Santos et al. (2011a). Each treatment consisted of three complete 24 h temperature cycles mimicking three consecutive hot days. In each cycle, the “night” was set 10 °C below the tested maximal temperature (MT), the temperature was then increased

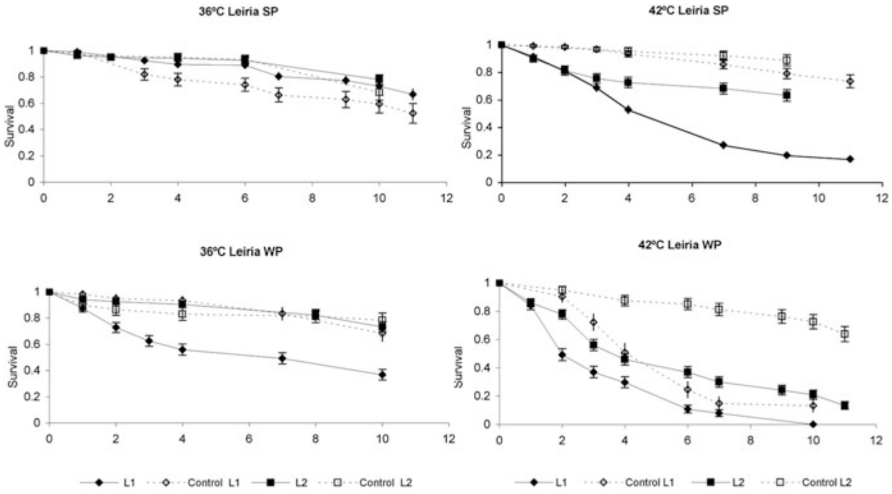

Fig. 4.17 Survival of first instar (L1) and second instar (L2) larvae during heat treatment (3 days) and post-treatment period (7–8 days), for maximal temperatures MT of 36 and 42 °C (From Santos et al. 2011a)

within 6 h to reach the desired MT, which was kept for the next 4 h, and progressively decreased to the night temperature over the following 6 h. After a trial was over, the surviving larvae were placed at room temperature during 1 week. During the whole process, larvae were fed with maritime pine branches planted in Oasis® floral foams. Survival in the tested sets of larvae and in the controls (kept at room temperature) was registered daily. The tested MT were 36, 38, 40 and 42 °C for both populations. Results unambiguously showed that survival was higher in the SP than in the WP, and always higher for L2 than for L1 larvae. Whereas a temperature negative effect upon L1 WP was already observed at 36 °C, a negative effect was only observed for L1 SP at 42 °C (Fig. 4.17). An upper threshold of survival for SP young larvae about 6 °C above that of the WP is thus assumed. At 36 °C there was even a positive effect of temperature on L1 SP survival, which might be related to a release from pathogens (Blanford and Thomas 2000). A high mortality was observed in one of the control groups of L1 WP (Fig. 4.17, low right corner), but the mortality in the heat treated group was still significantly higher. Mortality, estimated by Cox regression model, was for overall heat treatments 108 % higher for Leiria WP in comparison with Leiria SP. Pooling both populations, mortality increased by 24 % for each additional °C, from 36 to 42 °C, and decreased by 53 % from the first to the second larval instar.

We moreover observed behavioural reactions that could contribute to improve larval tolerance to high temperatures and dryness. During the hottest summer days, SP larval behaviour was assessed every hour, and responses categorized using four parameters, namely cohesion, activity, exposure and microhabitat selection, each one with two or three categories, to allow for qualitative analyses. The larvae tended to keep a gregarious behaviour, even at outdoor temperatures of up to 42 °C. Whenever temperatures raised, the larvae showed a significant tendency to abandon the needles and move to shaded areas, either near branching points or to the ground. Similar observations could not be conducted for the WP, as larvae do not occur in summer in this population. Nevertheless, we observed a quite similar behaviour in the field in south-western France particularly during hot days, in October 2009, in a phenologically winter population. Considering the rearing conditions described above, we could also demonstrate for Leiria WP a significant positive effect of the presence of Oasis® floral foam in the rearing boxes in survival at 42 °C, by comparing survival under the conditions tested above, with situations were pine branches were not planted in a floral foam. Conversely, the presence of the floral foam had no significant effect on the controls reared at room temperatures. For logistic reasons, a similar experiment was not conducted for the SP. This result was explained by a tendency of the larvae to aggregate in the vicinity of this humid micro-habitat whenever conditions were unfavourable.

The results obtained thus suggest that the thermal tolerance presently exhibited by SP larvae was quickly acquired, considering the WP as its plausible ancestor. Still, the mechanisms underlying these observations need to be investigated. Within population variability regarding tolerance to high temperatures, is a trait that could rapidly evolve under strong evolutionary constraints (Thuillier et al. 2005). It can be hypothesized that physiological adaptations should be involved, such as divergences in the up regulation heat-shock and stress-related genes, as observed in other insects (Mahadav et al. 2009).

Models forecasting the dynamics of insect species under changing scenarios generally use parameters extrapolated from one, or a few locations only. Models usually underestimate, or even ignore geographic variations of adaptive traits. The results obtained for this peculiar population of pine processionary moth experiencing a phenological change suggest that traits involved in adaptation to the current global warming could evolve rapidly, enabling some species and populations to remain *in situ*, while coping with the resulting environmental changes. The behavioural responses that we observed further enhance the capacity of this species to circumvent unfavourable conditions.

6.4 Perspectives for Future Research

Research is in progress, aiming at a better understanding of the origin of the SP and the evolutionary, ecological and applied consequences of the existence of this population with a shifted phenology. Concerning the molecular approaches, we will develop new programs both on neutral markers and on loci potentially involved in adaptation. Single-nucleotide polymorphisms (SNPs), that can be found all over the genome, will be developed in the near future to complete the microsatellite data that we have so far generated. Gathering information over numerous SNPs will allow research to shift from population genetics to population genomics, and to improve the analysis of various evolutionary scenarios regarding the foundation of the SP. Moreover, this "genome-wide scan" approach will enable the use of new algorithms to identify selected loci, and ultimately to identify the regions of the genome potentially involved in the evolution of the biological cycles and adaptation to new environmental conditions. We could also specifically target candidate genes known to be involved in the phenology of other insect species, and develop SNP genotyping designs focused on this set of genes.

The presence of the SP in the coastal recreational area of Leiria pinewood raises particular concern, since the most urticating larval stages (L4 and L5) develop in the summer months, thus increasing the risk of skin allergies, gastric and respiratory troubles among other health problems, to humans and animals. Since its discovery, the geographical range of the SP has been observed to expand mainly southwards, presently reaching the touristic region of Nazaré, while further expansion can be expected. We are thus planning the development of a species distribution modelling approach, in order to characterize the regions to which the SP could adapt. This approach should contribute to delineate strategies leading to slow its expansion and/or protect susceptible areas. Result dissemination will constitute a priority. In particular residents and visitors to the area should be informed on how to prevent accidents and local authorities involved.

7 General Conclusions

The overview of the main results obtained in phylogeny, phylogeography and population genetics for the genus *Thaumetopoea*, and in particular for *T. pityocampa*, *T. wilkinsoni* and *T. pinivora*, shows that such approaches have brought valuable information in the past 15 years about both the past and contemporary evolutions of populations in front of climate and environmental changes. The field of molecular genetics and phylogenetics is now in front of the genomic and post-genomic era. Genomic resources, based both on genome and transcriptome (i.e., expressed gene sets) sequencing will be available in the near future and will allow to set up new designs to gain precise information both for the neutral history of populations and species (population genomics and phylogenomics) and for the study of specific genes involved in adaptive traits. These perspectives will undoubtedly bring valuable information to understand the fate of populations and species faced to rapid global changes.

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Chapter 5
Modeling the Spatio-temporal Dynamics of the Pine Processionary Moth

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1 Introduction

This chapter presents modeling tools that have been developed to better understand the mechanisms involved in the fast range expansion of the pine processionary moth, and predict the potential spread in the future.

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The geographical distribution of the pine processionary moth in Europe was previously limited by unfavorable temperatures for the feeding activity, which requires at least 9 °C in the tent during the day and 0 °C in the air during the following night (Battisti et al. 2005; Robinet et al. 2007). With recent climate change, the monthly mean of minimum temperatures during the cold season increased by 1 °C between 1972–1981 and 1994–2003 in the northern range of the pine processionary moth in France (Battisti et al. 2005). As a result of this temperature increase, the geographical distribution of the pine processionary moth in Europe has been expanding northward and toward higher elevations (Battisti et al. 2005).

This chapter is divided into five sections. In Sect. 2, we explore how the climate and climate change could affect the species survival and distribution. In Sect. 3, we focus on the potential dispersal of the moth using reaction-diffusion models. Following the results about the moth dispersal and the existence of pioneer colonies far from the main species distribution, we then consider in Sect. 4 long distance dispersal resulting from human accidental transportation to explain the overall range expansion of the pine processionary moth in France. Modeling tools developed in Sects. 2, 3, and 4 successfully explain the spread mechanisms observed at large scale but mostly ignore landscape effects observed at smaller scales. Section 5 is therefore dedicated to these effects and more precisely the effects of the layout of host trees. Lastly, Sect. 6 deals with another issue of the invasion process and focusses on the population dynamics at low population density. In this last section, we explore more particularly Allee effects, which correspond to a decline in the per-capita population growth rate with a decreasing population density. These effects can appear when a few individuals arrive with or without human-assisted means in a new territory.

The models presented in this chapter allow understanding more deeply how climate change has been affecting the population distribution and how it can potentially affect its distribution in the future.

2 Climatic Constraint

2.1 Climatic Factors Involved in the Distribution and Expansion of Pine Processionary Moth

Pine processionary moth is very sensitive to climate and more particularly changes in the temperature because, as all insect species, individuals are poikilotherms and their development rate and survival rate are directly affected by the temperature. One particularity of the pine processionary moth is that its larval development takes place during winter and therefore winter temperatures are more important regarding the colony survival. A second particularity of the moth is that larvae are gregarious and build large white silk tents that are easy to detect when mapping its distribution.

Due to this tent, pine processionary moth is also affected by solar radiation in winter because sunshine can make the temperature increase within the tent (Huchon and Démolin 1970).

There is a threshold temperature below which larvae cannot survive. This lethal temperature depends on the number of larvae in the colony (probably because of thermoregulation, Ronnås et al. 2010, see also Sect. 6.1). For instance, the lethal temperature for a single larva is −7 °C (Démolin 1969) and for a common colony size (a 200-larvae colony) it is −12 °C (Huchon and Démolin 1970) but some larvae in some colonies are actually able to survive at −17 °C (Hoch et al. 2009) and even at −18 °C (field observation in the French Alps, Alain Roques, Personal Communication). However, such extremely low temperatures are not often reached in most parts of Europe and can therefore not be used to predict the potential presence of the pine processionary moth. It is not only the magnitude of the extremely low temperatures which is important but also the duration of moderately low temperatures. Huchon and Démolin (1970) considered a combination of the mean of minimum temperature in January (TNJ) and the annual sunshine duration (SUN). If TNJ $\geq$ 0 °C and SUN $\geq$ 1,800 h then pine processionary moth can potentially be present. If TNJ <-4 °C then pine processionary moth is potentially absent. Between these temperature thresholds, each degree below 0 can be compensated by additional 100 h of sunshine. Huchon and Démolin (1970) proposed a map of potential exclusion of pine processionary moth in France based on these thresholds (Fig. 5.1a). This map was generated using an historical climate and should be updated with current and future climates to explore how these conditions could drive the species distribution under climate change. Since it is not possible to use exactly the same variables (sunshine duration not commonly used in current weather datasets and climate scenarios), it is not possible to use exactly the same approach and simply update the model.

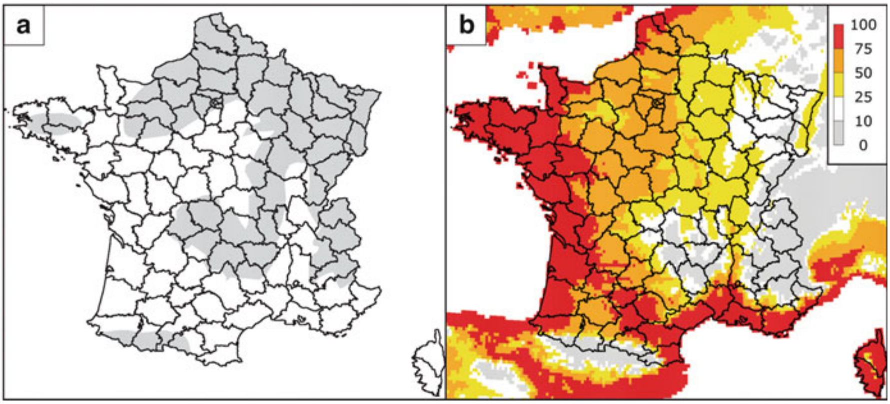


Fig. 5.1 (**a**) Potential exclusion map (in *grey*) of the pine processionary moth (Derived from Huchon and Démolin 1970). (**b**) Potential survival (%) of the pine processionary moth based on a survival function applied to the mean of minimum temperature from October to March during 2001–2010

In addition to this historical model for the pine processionary moth potential distribution, other indicators of the population survival have been considered recently to explore the effects of climate warming. For instance, the mean minimum temperature from October to March is closely correlated with the potential larval feeding and thus with population survival in the northern part of the pine processionary moth distribution in France (Robinet et al. 2007). This indicator may not be valid over all Europe because the time window corresponds to the larval development period in a specific region but it can contribute to a better understanding of the potential range expansion in France and Europe. It is then possible to apply a survival function Sw to derive potential survival rates (see Robinet 2006) (Fig. 5.1b). This survival rate can be calculated with the following function:

$$Sw(x,t) = \frac{1}{1 + \exp\left[s(W_c - W_t(x))\right]},$$

where x is the spatial coordinates of the location, t the winter time (October year t − 1 to March year t), W_t the mean of minimum temperature from October to March (°C), $s = 1$ (sensitivity parameter) and $W_c = 3.3$ °C (critical temperature, i.e., temperature generating 50 % mortality).

Apart from these indicators of potential pine processionary moth presence, it is also possible to consider correlative models to determine the area where the climate is suitable for the species establishment, i.e., the climate envelope. The method consists in finding the climate variables which are the most strongly correlated with presence/absence of the species. However, caution is needed because pine processionary moth is currently extending its range and is therefore not in equilibrium with its environment. Presence of the species indicates that the climate is favourable but absence does not necessarily mean that the climate is not favourable.

At a large scale such as the European scale, the probability of establishment of the species where it is not present is probably low. To explore how the northern limit of the European distribution can help to determine the climatic constraints for the species presence, we applied a regression tree to the distribution currently known in Europe over the 16-km grid (see Chap. 3; map lastly updated on 1st August 2012). We considered 2,755 presence points and 2,122 absence points (supposed to be real absence). We used the mean minimum temperature from October to March, mean solar radiation from October to March, and also the mean of maximum temperature from July to August as explaining variables (source of data: http://www.ccafs-climate.org/download_theme4.html; Baseline 2000). Maximum temperatures could effectively play a role in the species distribution (Huchon and Démolin 1970). The correct classification rate was 82 %. The projection of this model to Europe with current climate and arbitrary temperature rises (+1, +2, +3 °C) provides a preliminary assessment of the area in Europe potentially favourable for the species (Fig. 5.2). This bioclimatic layer should be improved in the future to determine more accurately this area and take into account the variability in the insect phenology across the regions.

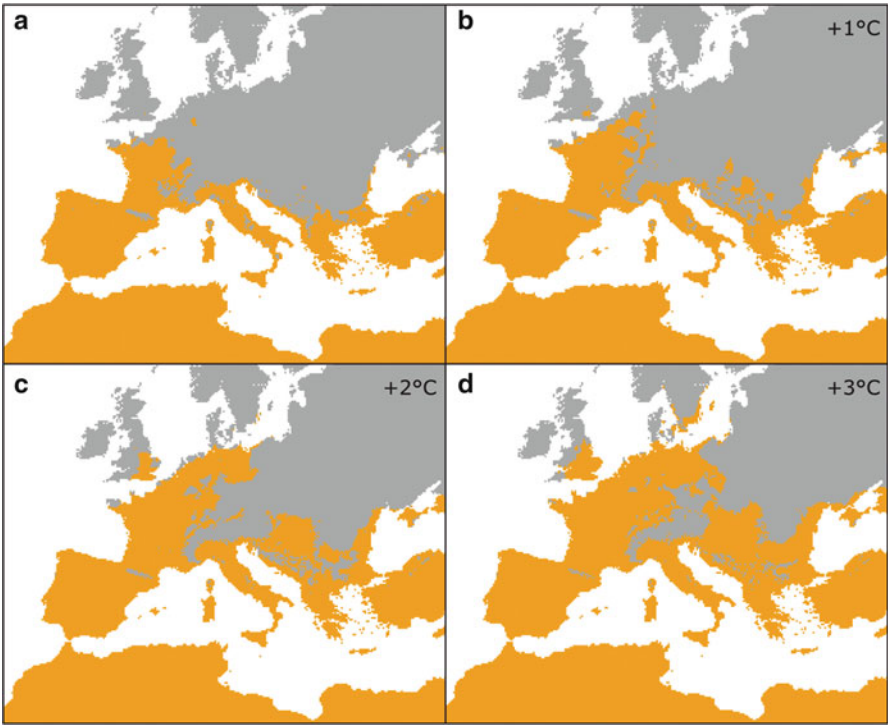


Fig. 5.2 Projection of a regression tree to Europe with (**a**) current temperatures, (**b**) + 1 °C temperature increase, (**c**) + 2 °C temperature increase, and (**d**) + 3 °C temperature increase (preliminary results). The *orange colour* represents the area where the probability of presence given by the model is above 0.5

2.2 Effects of Extremely High Temperatures

The pine processionary moth is extending its distribution in response to the rising trend of winter temperatures. The effects of extreme weather events such as heat-waves were not very well understood until now. It could be important to include them when predicting the future range of the pine processionary moth because their frequency is predicted to increase as a consequence of climate change (Easterling et al. 2000; Meehl et al. 2007). After the heat wave which occurred in August 2003 in Europe, we observed contrasting effects: an acceleration of the range expansion toward higher elevation in the Italian Alps (Battisti et al. 2006) but a population decrease in the northern distribution in France (Bouhot-Delduc 2005). To better understand this population decrease and simulate this effect in the expansion model, we conducted two experiments. First we measured the deviation between temperature recorded in sun-exposed egg masses and temperature recorded by weather stations. In this way, we reconstructed the temperatures experienced by egg masses during the heat wave in 2003 based on temperature and solar radiation recorded by weather stations at that time. Secondly we simulated heat wave conditions in laboratory (in climatic chambers and incubators) and measured the effect on the hatching rate of eggs and the potential delayed effects on larval survival rate. We found no significant negative effects of heat wave conditions on egg masses and no delayed effects on larvae survival. Since the decrease of the population cannot be attributed to a large mortality of the eggs or a delayed effect on larvae, and it can also not be attributed to an outbreak cycle or a disturbance of adults emergence, we conclude that the heat wave has probably affected directly or indirectly the young larvae (Robinet et al. 2013). In the future, it is necessary to understand more deeply the effects of heat waves to be able to develop a model to describe these effects and integrate them in the expansion model.

2.3 Accelerating Propagation During Recolonization Events Linked to Climate Variability

The pine processionary moth range has progressed of 2.7 km/year to the north of Paris between 1972 and 2004, with a notable acceleration since 1992, leading to rates of spread higher than expected on the basis of known dispersal capabilities (average speed of 5.6 km/year between 1994 and 2004 Battisti et al. 2005; average speed of 4.2 km/year between 2007 and 2009, Roques et al. 2011). Since its ability to survive is linked to climate, it is likely that the progression of pine processionary moth consists in a series of colonization-retraction-recolonization events. The aim of this section is to show on a firm mathematical basis that these recolonization events can lead to fast of and accelerating range expansions, in accordance with the observations.

In that respect, we analyzed usual colonization models and we compared them with recolonization models. The main difference between the two approaches lies in the initial condition. In a colonization model, the initial population is generally considered as being localized at a given position. In a recolonization model, the initial population is the result of a previous colonization-retraction event, which can generate a wide variety of population density distributions.

Reaction-diffusion models (see Box 5.1) are traditionally considered to lead to constant spreading speeds. This is for instance the case when the initial condition $u_0(x)$ is compactly supported or rapidly decaying (see Box 5.1 and Kolmogorov et al. 1937; Bramson 1983). Intuitively, we can expect that initial conditions decaying slower than any exponential – *slowly decaying* initial data – will lead to infinite spreading speeds and therefore lead to acceleration phenomena. Such initial data are not classical in the reaction-diffusion framework; however, there are good reasons for considering them as they could help ecologists rethink the role of exogenous constraints on population movements and density distributions.

Box 5.1 Reaction-Diffusion Models

Reaction-diffusion models describe the spatio-temporal dynamics of a concentration $u(t, x)$, e.g., a population density, under the effect of a dispersal operator and a growth function:

$$\frac{\partial u}{\partial t}(t, x) = \nabla \cdot (D(x)\nabla\, u + V(x)u) + f(x, u).$$

The initial concentration, at the beginning of the process, is noted $u_0(x) = u(0, x)$. In most cases, this initial condition is considered to have a fast decay. In the simplified framework of a 1D environment, this means that $u_0(x)$ decays to 0 faster than some exponential function $e^{-\alpha|x|}$, as $x \to \pm\infty$.

2.3.1 Main Results

In the papers (Hamel and Roques 2010; Roques et al. 2010), we considered a classical one-dimensional reaction-diffusion model with slowly decaying initial population densities u_0. The growth function f was assumed to be logistic-like, i.e., f is positive and concave and possesses two equilibriums, 0 and the carrying capacity K. Those assumptions imply that the per capita growth rate $f(u)/u$ reaches its maximum at 0, or equivalently that there is no Allee effect (see Box 5.4). We recall that $u = u(t, x)$ designates the population density at time t and position x.

In sharp contrast with what was known before with classical assumptions on the initial conditions, the results of Roques et al. (2010) show that the density profile u does not converge towards a traveling wave with constant profile and constant speed, and give a precise mathematical description of the evolution of the population range for slowly decaying initial conditions (see Box 5.2).

Box 5.2 Range Expansion

Given a population density $u(t, x)$ in a 1D environment, it is possible to define the (right) population range $x_\lambda(t)$ as the position where the population first falls below a given threshold $\lambda > 0$:

$$x_\lambda(t) = inf\{x > 0,\ u(t, x) < \lambda\}.$$

Then, the (average) rate of range expansion at time t is simply defined by $v_\lambda(t) = x_\lambda(t)/t$.

The results of Hamel and Roques (2010) and Roques et al. (2010) give a precise mathematical description of the evolution of the population range for slowly decaying initial conditions u_0:

$$u_0{}^{-1}\left(\lambda\, e^{-\left(f'(0)-\varepsilon\right)t}\right) \leq x_\lambda(t) \leq u_0{}^{-1}\left(\lambda\, e^{-\left(f'(0)+\varepsilon\right)t}\right).$$

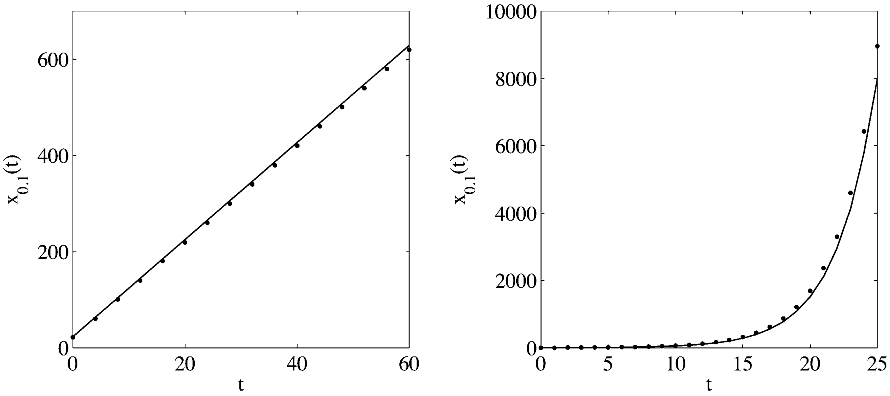


Fig. 5.3 Evolution of the population range $x_{0.1}(t)$ with a logistic growth function $f(u) = u(1 - u)$. (*Left*) with a rapidly decaying initial density $u_0(x) = exp(-x/10)$; (*Right*) with a slowly decaying initial density $u_0(x) = 1/(1 + x^3)$

In particular, it follows from these results that the rate of range expansion can be as large as we want, provided the initial condition is well chosen, and it tends to increase with time, which means that an acceleration of the population range occurs.

Let us illustrate these results on a particular example, with a slowly decaying initial population density $u_0(x) = 1/(1 + x^3)$ and a logistic growth term $f(u) = u(1 - u)$, we get that the population range (here, the level set $\lambda = 0.1$) is close to

$$u_0^{-1}\left(\lambda\, e^{-f'(0)t}\right) = (10\, e^t - 1)^{1/3}.$$

This means that the population range expands exponentially fast! Figure 5.3 illustrates this result and shows the striking difference between this case and the classical case where the initial condition decays exponentially fast.

2.3.2 Discussion

At the beginning of a recolonization event, the population density can take various shapes. In some cases, it is reasonable to assume that the population density decreases slowly in the direction of the range expansion. Our results show that, in such cases, the range expansion can be very fast and even accelerate.

Long distance dispersal hypothesis has also often been used to explain fast spreading and accelerating rates of spread (Clark 1998; Clark et al. 1998; Kot et al. 1996, see also Sect. 4.3). It is certainly a valid explanation in several situations. Our results show that diffusive dispersal can also very convincingly explain such patterns in a recolonization context.

3 Modeling Moth Dispersal in a Heterogeneous Environment

The expansion of pine processionary moth is the result of the dispersal (flight) of female adults which lay their eggs in previously non-infested locations and the survival of this new generation under new environmental conditions. The female flight capability was known to be very limited (Huchon and Démolin 1970). As soon as the females find a suitable pine, they do not disperse further. Therefore the layout of pine trees is very important and isolated pines can play the role of a corridor between pine forests and accelerate the spread. Females can lay their eggs where they have previously made their larval development unless the tree is heavily defoliated. This low dispersal capability is confirmed by the strong phylogeographic pattern of the populations in Europe (see Chap. 4 and Rousselet et al. 2010).

In addition to the mean dispersal capability, it is also important to know the distribution of the dispersal distances (Sect. 3.2) and notably whether the individuals disperse at short distance or some of them can fly over longer distances. Even if long-distance dispersal is not commonly observed, the existence of such stratified dispersal can affect considerably the potential spread of the population because it can create satellite colonies and accelerate the spread rate (see Sect. 4.3). Genetic analysis can help us to determine how the adult moths disperse. The genetic isolation by the distance and the genetic diversity decrease along expansion gradients found in the pine processionary moth populations (see Chap. 4) seem to be consistent with a diffusive dispersal mechanism (Nichols and Hewitt 1994; Ibrahim et al. 1996; Klein et al. 2006). This dispersal pattern is the result at the population scale of individual random walks (Shigesada and Kawasaki 1997). Based on these observations, we used reaction-diffusion models (See Box 5.1) to describe the dispersal and spread of pine processionary moths.

3.1 Forecasting the Expansion of Pine Processionary Moth

To predict the potential expansion of the moth in the future, it is necessary to have reliable data on the historical distribution either at regional or country scales. The pine processionary moth range expansion was first observed in France in the Paris basin. Larval tents are easy to detect and thus mapping their occurrence is relatively straightforward compared to other species. At regional scale (Paris basin), the edge of the moth distribution was reported in 1992 and 1996 (Goussard et al. 1999), and later during the winters 2006–2007, 2007–2008 and 2008–2009 (INRA URZF). At country scale, other maps are available in France: from 1969 to 1979 (CTGREF-INRA 1980; but the method of survey is not known in detail) and during the winters 2005–2006 and 2010–2011 over a 8 km × 8 km grid with a standardized method (INRA, URZF; see Rousselet et al. 2013 for the survey methods on a grid). At continental scale, the limit of the northern distribution in Europe was determined in 2011–2012 (see Chap. 3).

A reaction-expansion model was developed based on historical data at regional and France scale, taking into account the survival rate based on the mean temperature from October to March, the annual fluctuation of this temperature, the pine tree density (surveyed by the French National Forest Inventory, http://www.ifn.fr, in forest stands above 2.25 ha), and the dispersal capability of female moths. When fitting this model to historical edges of the pine processionary moth distribution, we found a spread rate of around 3 km per year (Robinet 2006). This flight distance was well above all previous estimates of this distance, but it was more consistent with an observed spread rate of about 4.2–5.6 km per year over a recent period (Battisti et al. 2005; Roques et al. 2011) and the estimation resulting from a flight mill experiment (Robinet et al. 2012). Based on the climate change scenario B2 (Climat-Arpège regionalized by Météo-France), this model predicts ongoing expansion and pine processionary moth could reach Paris by 2025 based on flight capability only (Robinet 2006, Robinet et al. 2010a, b).

However, this model was not able to predict correctly the spread in the eastern part of the moth distribution near Paris. This issue is due to the junction of the expanding population in the west side of the mountain called Massif-Central (taken into account in the reaction-diffusion model) and another expanding population on the East side of the Massif-Central. The genetic analysis of the moth populations has clearly shown the existence of a genetic lineage from eastern Iberia to western France and second genetic lineage from western Massif-Central to Italy (Rousselet et al. 2010).

This model initially applied to the South of the Paris basin was recently extended to France (Robinet et al. 2014). This model was modified to account for possible long distance jumps due to human-mediated transportation (see Sect. 4). The simulations confirm the role of climate warming in the expansion of moth and forecast an on-going expansion but probably at a lower spread rate. The northward shift of the northern edge of the moth distribution is a bio-indicator of climate change in France. However, even in case of no more warming, the pine processionary moth could continue its range expansion because the warming velocity was higher than its spread rate and therefore large territories which became recently favourable for the moth establishment are not yet colonized. The main barrier for the species' expansion in these regions, where the climatic conditions are favourable but not optimal, could be either related to its dispersal capabilities or to a reduced fitness (see Sect. 3.2). Therefore the pine processionary moth can no longer be used as a simple indicator of climate change but as an integrated indicator of a more complex disturbance which includes climate change and human activities.

There is clear evidence of the impact of higher winter temperature on the species distribution and potential spread in the future but there are several factors that should be more carefully studied in terms of potential mitigation of the spread. Although climate change implies an average increase of temperature, it is also implies an increased frequency of climate anomalies such as heat-waves (Easterling et al. 2000; Meehl et al. 2007). As already mentioned (Sect. 2.2; Robinet et al. 2013), heat-waves can have contrasting effects and reduce the population level. They could have an increasing effect in the future and affect noticeably the species range distribution. In addition, in the northern part of its potential range, the species could encounter less solar radiation and shorter day-time duration (photoperiod) in winter. Further studies are needed to understand how these conditions could affect the temperature inside the tent and limit its establishment in the most northern part of its potential range.

3.2 Estimating the Spatial Variation in the Fitness of Pine Processionary Moth

Extensive measurements that have been carried out by INRA URZF (UR633) at different spatial scales in France show that the northern edge of the pine processionary moth distribution is not flat. This indicates that population expansion is faster in some regions. Determining these regions is of crucial importance for controlling and preventing the species expansion.

One of the main objectives of the model presented in (Roques et al. 2011) was to estimate the local fitness of pine processionary populations and a diffusion coefficient for the adult moths, based on spatial and temporal binary data of presence of tents. Our approach uses a model with main parameters $\boldsymbol{F}(\boldsymbol{x})$ and D, which measure the local species' fitness at each spatial position and the mobility of the adults. Like many other models in ecology these parameters result from the intertwined effects of several factors and cannot be directly measured. However, they can be estimated using observations of the population dynamics of interest (Klein et al. 2008, Soubeyrand et al. 2009a, b); here, we use observations of the position of pine processionary moth tents at the study sites.

The construction of an expansion model that enables parameter estimation raises two non-classical difficulties: (1) the type of data we are dealing with: binary and incomplete observations of the presence of winter tents; and (2) the life cycle of the pine processionary moth: the tent density evolves through a discrete-time process, but this evolution results from the dispersal and laying of adult moths, a continuous-time process.

In (Roques et al. 2011), we proposed a mechanistic-statistical approach (Soubeyrand et al. 2009a, b; Wikle 2003) that combines a statistical model for the observation process with a hierarchical, reaction-diffusion based mechanistic model for the expansion of larval tents. The statistical model bridges the gap between continuous data (tent densities) and binary data (observations) and, conversely, provides a way to estimate the parameters of the mechanistic model based on the observed data. With a mechanistic model we are able to describe the discrete-time evolution of tents as a function of continuous-time adult dispersal and of the environmental effect on the fitness of pine processionary moth.

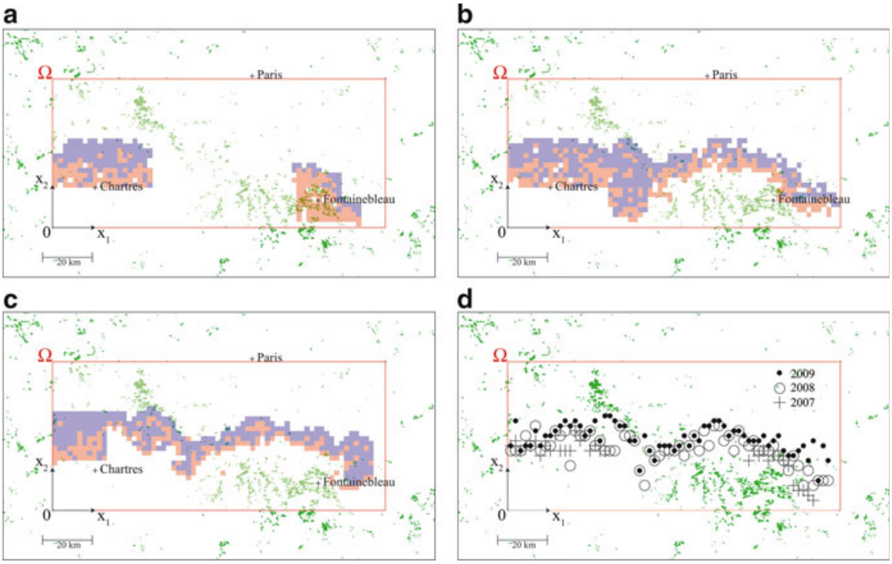


Fig. 5.4 (**a**–**c**): Observation data in 2007, 2008 and 2009 respectively. *Blue squares* correspond to observed cells where pine processionary moths have not been detected. *Red squares* correspond to cells where winter tents have been detected. (**d**): Position of the northernmost points where winter tents have been detected during years 2007, 2008 and 2009

3.2.1 Data

The study site is a rectangular region, located in the Paris basin. This site contains urban, urban fringe, forest and agricultural areas. The moth range has been measured by INRA URZF (UR633) during 2007, 2008 and 2009 (winters 2006–2007, 2007–2008 and 2008–2009) through direct observations of the presence of winter tents. Only binary data (presence or absence of tents) have been recorded (Fig. 5.4a–c). These data indicate a northward range expansion of the pine processionary moth, at an average speed of 4.2 km/year (Fig. 5.4d).

3.2.2 Mechanistic-Statistical Model

The model that we propose combines a statistical model for the observation process with a hierarchical mechanistic model for the expansion of larval tents. The tent density at the end of the adult stage is represented as a function of the adult density during the whole adult stage and of the local fitness $\boldsymbol{F}(\boldsymbol{x})$. Adult density is modeled with a classical reaction-diffusion equation.

Local fitness was defined as $\boldsymbol{F}(\boldsymbol{x})=$ the number of adults who emerge during year $n+1$ (in the absence of demographic constraint) for one (unit of adult density × unit of time) at the position x during year n.

The statistical model for the observation process simply says that pine processionary moth tents are detected with a probability d which depends on the local tent density U:

$$Obs \big| U \ \sim \ Bernoulli\{d(U)\}. \tag{5.1}$$

The reaction-diffusion model for the evolution of the adult density $v(t,x)$ can be written in the form:

$$\frac{\partial v}{\partial t} = D\Delta\, v - \ \frac{v}{\nu} \tag{5.2}$$

where $D > 0$ stands for the diffusion coefficient, Δ is the classical diffusion operator and ν is the adult life expectancy. The initial density v_0 depends on the number of tents of the previous years, through a formula which takes an Allee effect into account, see (Roques et al. 2011) and Sect. 6. Defining $w(x)$ as the *cumulated* adult density at the end of the adult stage and assuming that tent creation at each location x is proportional to the time spent by the individuals at this location and using $\boldsymbol{F}(\boldsymbol{x})$, we can compute the number of tents at the end of the adult stage (in units of the hosts carrying capacity):

$$U(x) = min\{w(x) \times \ \boldsymbol{F}(x),\ Host\ density\ at\ x\}. \tag{5.3}$$

3.2.3 Local Fitness of Pine Processionary Moth

Using the above model and the observation data, we are able to compute the likelihood $L(\boldsymbol{F},D)$ of any couple $(\boldsymbol{F},D)$ of fitness and diffusion parameters. Consider such a couple $(\boldsymbol{F},D)$ and let $U_{\boldsymbol{F},D}$ be the tent density obtained with the model (5.3). This likelihood simply corresponds to the probability $P(Obs|U_{\boldsymbol{F},D})$ that the observation of $U_{\boldsymbol{F},D}$ with the statistical model (5.1) leads to the observations described in Fig. 5.4. Using this likelihood function, a Bayesian framework was used in (Roques et al. 2011) for estimating the effect of the environment on the expansion of pine processionary moth. The posterior marginal distribution of the parameter $\boldsymbol{F}(\boldsymbol{x})$ which was derived in (Roques et al. 2011) is depicted in Fig. 5.5.

We observe that this distribution strongly depends on the position x, which means that there are regions which are clearly more favorable than others for the expansion of the pine processionary moth. Interestingly, favorable and less favorable regions seem to be organized in clusters, which probably means that some spatial covariates play an important role on the distribution of the fitness. Besides, $\boldsymbol{F}(\boldsymbol{x})$ does not seem to be strongly correlated with the host density. This shows that the effect of the host density (other than saturation, which is not taken into account in $\boldsymbol{F}(\boldsymbol{x})$) is relatively small compared to the effect of other covariates.

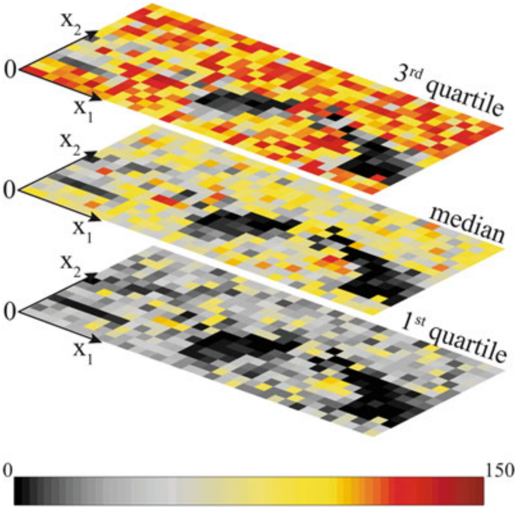


Fig. 5.5 Posterior distribution of the fitness parameter F

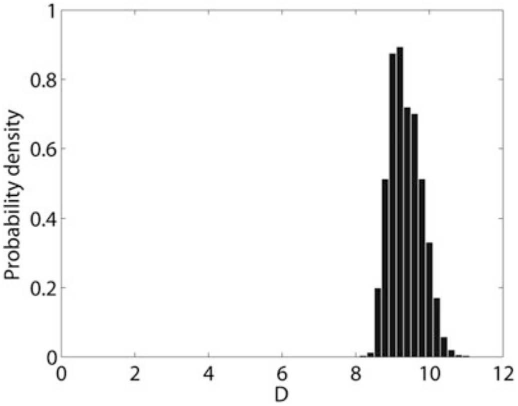


Figure 5.6 Posterior distribution of the diffusion parameter D

3.2.4 Diffusion Parameter; A Clue for the Existence of Long Distance Dispersal Events

The posterior distribution of the diffusion parameter D is presented in Fig. 5.6. The posterior median is equal to 9.3 km^2/day (mean ± SE = 9.4 ± 0.4). D = 9.3 is larger than usually measured for other Lepidoptera species (Kareiva 1983; Shigesada and Kawasaki 1997), but is qualitatively not so far from the value of 5.1 km^2/year which had been obtained previously for pine processionary moth (Robinet 2006), since the life expectancy of adults ν is about 1 day.

Recall that the diffusion model $\partial v/\partial t = D\Delta v$ can be obtained as the limit of a discrete random-walk model (see e.g., Grindrod 1996; Turchin 1998), in which the individuals can change direction at each time step. The diffusion coefficient D can be computed as the limit: $\lim_{\lambda \to 0,\ \tau \to 0} \lambda^2/(4\tau)$, where τ is the time step and λ is the distance crossed in a straight line during τ. If we assume that the direction changes take place every 1 min, i.e., $\tau = 1$ min, we get $\lambda = 2\sqrt{\tau D} = 161\,\mathrm{m}$. This means that the total distance which is travelled by an individual in 1 day is $2\sqrt{D/\tau} = 231\,\mathrm{km}$, which is far more than observed from a flight mill experiment (Robinet et al. 2012). On the other hand, if we assume that this total distance is of 10 km, which is more realistic, we get that direction changes take place every 9 h in average. As a conclusion, the trajectories of the adult moths seem to be made of long straight lines, with few direction changes. This may indicate that the dispersal is not purely diffusive, i.e., that long-distance dispersal events occur (see Sect. 4).

Such a high diffusion coefficient would lead to a high speed of range expansion in a homogeneous favorable environment. However, our study shows that the environment is not homogeneous and the actual speed of range expansion could be mainly limited by the presence of unfavorable regions (i.e. associated with low values of $\boldsymbol{F}(\boldsymbol{x})$) such as the black regions in Fig. 5.5.

4 Existence and Effects of Long Distance Dispersal Events

In addition to the evidence of long distance dispersal events resulting from the previous modelling approach, several pioneer colonies have been discovered between 2003 and 2008 far from the main distribution, near Paris and in Eastern France (Robinet et al. 2012). As the distance between these pioneer colonies and the closest colonies within main distribution was higher than the flight capabilities of female adults (recorded in a flight mill experiment), it is unlikely that females have flown this distance to found these colonies. Furthermore, individuals from at least three pioneer colonies were genetically close to individuals from populations located even further (southwestern France and Spain, or southeastern France and Italy). Thus, individuals which have founded some pioneer colonies came further than the edge of the main distribution and dispersed over very long distances. They were probably accidentally transported by humans with infested materials. When studying specific natural enemies present in pioneer colonies, only a parasitoid emerging from pupae was found, suggesting an accidental transportation at the pupal stage. As pupae are buried in the soil, they have been probably transported when transplanting a tree with a large amount of infested soil. The conclusion of this study is that at least three pioneer colonies could result from human-mediated dispersal, most likely at the pupal stage when transporting large potted trees (Robinet et al. 2012, see Chap. 3). This mode of dispersal is rare and random but it is crucial to take this into account when predicting the potential expansion of the pine processionary moth.

Such dispersal mode is probably not new. In the past, long distance jumps have probably occurred but due to unfavorable climate outside the historical distribution of pine processionary moth, individuals moved outside their native area were not able to establish and found a new population. There is however some evidence that such long distance jumps could have occurred within the historical range or immediate neighbourhood. In fact, the genetic analysis revealed that a population now inside the current moth distribution (Alençon) was totally different from populations nearby and instead was very similar to Spanish populations (Jérôme Rousselet, Personal Communication). These long distance jumps are more problematic now because individuals moved far away from the main distribution have various probabilities to establish and create satellite colonies. The aim of this section is therefore to present different models that can be used to describe this long-distance dispersal and to analyze the possible consequences of long-distance dispersal on the range expansion of pine processionary moth.

4.1 Moth Range Expansion in Presence of Human-Mediated Long-Range Jumps

The first step is to identify the potential drivers of the long distance jumps. For that purpose, we selected 100 points in France outside the pine processionary moth distribution (mapped in 2005–2006) and we compared the mean density of human population and the mean density of host trees between these random points and the locations of pioneer colonies (5 near Paris: Aubergenville, Bailly-Romainvillier, Eragny, Nanterre and Saint-Maur-des-Fossés, and another one in eastern France, at Obernai; Robinet et al. 2012). For the human population density, we used the data in 2005 provided by SEDAC (Socioeconomic data and applications center; http://sedac.ciesin.columbia.edu/gpw). We found that there was an average of 94 persons/km^2 at random locations but 3,434 persons/km^2 at the locations of pioneer colonies. For the host tree density, we used data provided by IFN (French National Forest Inventory; http://www.ifn.fr/) now called IGN (National Institute for geographical and forestry information; http://www.ign.fr/). This institute mainly surveys forest area and not isolated trees (especially in urban areas) at country scale. We found that there was an average of 4,772 pine trees/km^2 at random locations but only 20 pine trees/km^2 at the locations of pioneer colonies. This average was in fact a mean of no host tree over 5 locations and 120 pine trees/km^2 at Bailly-Romainvilliers. These results mean that the location of pioneer colonies is probably not independent of the human population density and that they are more likely to appear in urban areas than in forest areas. Therefore human population density can be used as an indicator of the risk of accidental transportation of the species.

Although we identified clearly a driver for the location of pioneer colonies, there are still a lot of uncertainties because there are very few replicates. This process is stochastic and we do not know the frequency of trees transplanted with large amount of soil coming from an area infested by the pine processionary moth. We therefore propose a simple model to simulate this type of dispersal but further work is needed to estimate correctly the parameters. The process of long distance jumps can be divided into two parts: (1) the frequency of accidental transportation and (2) the location of the introduction.

The first part shows the highest uncertainty. The number of accidental transportations depends on the number of large trees planted beyond the moth distribution and coming from an infested area. We can for instance suppose that this number is $T = 1{,}000$ trees per year but in reality this number could change from one year to another and eventually increase with time. The number of accidental transportations depends also on the number of trees with pupae of pine processionary moth in the soil (among the previous trees). We can for instance suppose that one tree is infested by pupae out of 1,000 trees, and thus we can take a probability $\alpha = 0.001$ to have an infested tree among trees planted beyond the moth distribution and coming from an infested area. Based on these two parameters, T and α, we can estimate the number of introductions each year, N, using the following binomial distribution:

$$N \sim Binom\left(n = 1,\ size = T,\ p = \alpha\right),$$

When considering the values previously given, it means that there is on average one introduction per year.

The second part of the process of long distance jumps is the location of introduction. We found that the location depends on the human population density but there are not enough points to define accurately the function that describes their relationship. Several choices are possible, for instance, the probability of introduction increases linearly with the human population density (simplest choice), or this probability increases with the human population density at power 3 (like for the pine wood nematode, Robinet et al. 2009) (Fig. 5.7).

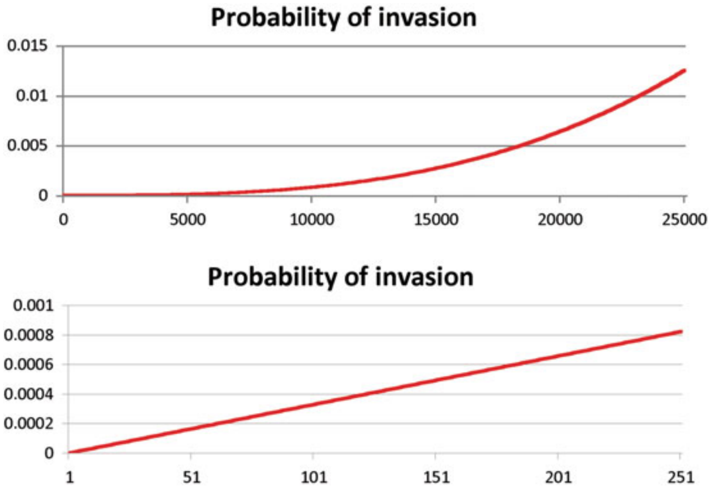
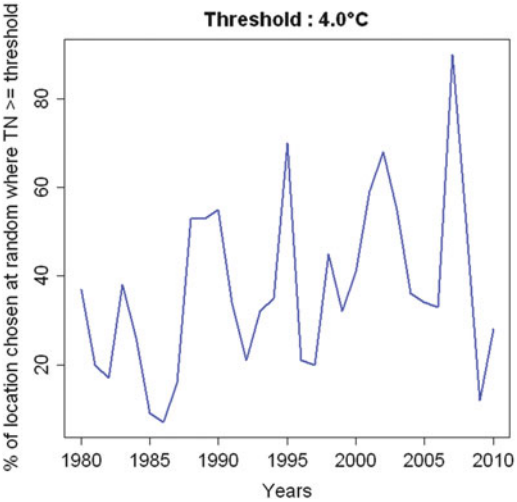


Fig. 5.7 An example function to describe the increase of the introduction probability with human population density

Fig. 5.8 Percentage of random points outside the area where the mean of minimum temperature from October to March was above 4 °C



At this stage, we can simulate human mediated dispersal but then we should consider whether the climate at the place of introduction is suitable or not for the pine processionary moth and thus, whether it can create a pioneer colony or not. Robinet (2006) defined a threshold of 3.3 °C for the mean of minimum temperature from October to March. From experiments in the Paris basin, 50 % of larvae survive at this temperature. The temperature at locations of pioneer colonies is slightly higher (approximately from 4.5 to 7.1 °C near Paris and 3.4 in Obernai for the year of detection). Therefore we considered a threshold of 4 °C for the establishment of pioneer colonies. When selecting at random the points, the percentage of points situated in a suitable area was the highest in 2007 (Fig. 5.8), the year before the detection of four pioneer colonies out of the six.

When we applied the model of long distance jumps previously described with the threshold of 4 °C for the condition of establishment, and then we found that pioneer colonies could mostly appear since 2007 in one case, or since the 1990s in another case (Fig. 5.9).

This study gives a basis to simulate human-mediated dispersal in the case of the pine processionary moth, but as already mentioned, we were not able to estimate several parameters and this model should be used as a tool to test some hypotheses instead of a reliable predictive tool.

4.2 A General Deterministic Approach for Modeling Long-Distance Dispersal

Integro-difference equations and integro-differential equations (see Box 5.3), have been proposed as alternatives to reaction-diffusion models (Fedotov 2001; Kendall 1965; Kot et al. 1996; Medlock and Kot 2003; Méndez et al. 2002;

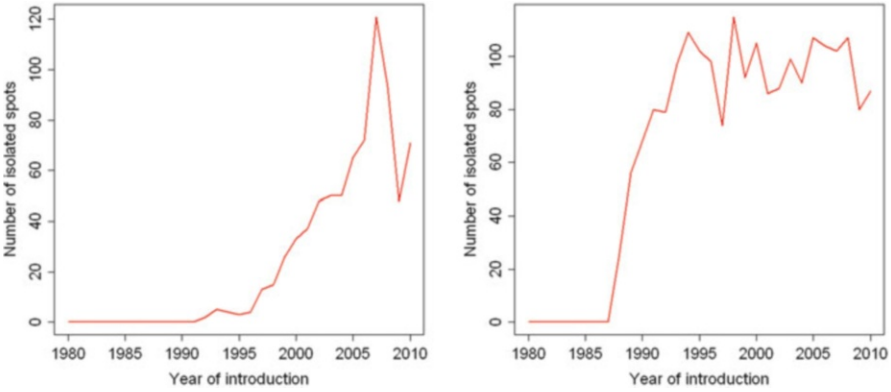


Fig. 5.9 Number of pioneer colonies occurring between 1980 and 2010 over 100 replicate simulations in case of a linear increase of the introduction probability with human population density (on the *left*) and in case this probability increases with the human population density at power 3 (on the *right*)

Mollison 1972, 1977). Those models, also coming from physics (Chandrasekhar 1943; Markoff 1912), can include rare, long distance dispersal events, and can lead to accelerating rates of spread for certain types of redistribution kernels, see (Kot et al. 1996) and Sect. 4.3.

The main difference between these models and the classical reaction-diffusion models is that they are *nonlocal* models, in the sense that the quantity $u(t,x)$ at the position x not only depends on the value of $u(t-1,x)$ (in the integro-difference case) at the same position x, but also on all the values $u(t-1,y)$ for any position y such that $J(|x-y|)$ is positive. Depending on the shape of the dispersal kernel, these models can take long-distance dispersal events into account.

Dispersal kernels are broadly classified in two main classes. The "thin-tailed" kernels are rapidly decaying kernels, i.e., they decay exponentially fast as $x \to \infty$. In the biological literature, such thin-tailed kernels correspond to short-distance dispersion. The "fat-tailed" kernels decay are slowly decaying kernels; they decay slower than any exponential function. With such kernels, long-distance dispersal events can occur with a non-negligible probability.

The qualitative properties of integro-difference and integro-difference models with thin-tailed kernels are close to those of reaction-diffusion models. On the other hand, as we will observe in Sect. 4.3, such models with fat-tailed dispersal kernels can lead to very different results, which shows the crucial importance of taking long-distance dispersal into account.

In the model presented in Box 5.3, the dispersal kernel is assumed to be homogeneous: the probability distribution of jumping from position y to position x only depends on the distance between x and y, through $J(|x-y|)$. However, these models can easily be adapted to more complex situations. For instance, assume as in Sect. 4.1 that human mediated dispersal plays a key role in the propagation of the pine processionary moth. Then, the probability of jumping from position y to position x has to be modulated depending on the human population density at the position x. It can be achieved by replacing $J(|x-y|)$ by

$$g(x)J(|x-y|)\Big/\left(\int g(s)J(|s-y|)ds\right),$$

where g is some increasing function of the human population density.

4.3 Accelerating Propagation with Long-Distance Dispersal Events

Several ecological studies are based on the use of integro-difference and integro-differential models with fat-tailed kernels (Clark 1998; Clark et al. 1998; Kot et al. 1996). For such models, the occurrence of acceleration phenomena had already been reported (Kot et al. 1996). However, there was no clear relationship between the tail of the dispersal kernel and the spreading properties of the model, i.e., the speed at which the range expansion occurs.

Box 5.3 Integro-differential Models

Like reaction-diffusion equations, these models describe the spatio-temporal dynamics of a concentration *u(t,x),* under the effect of a dispersal operator and a growth function:

$$\frac{\partial u}{\partial t}(t,x) = \int J(|x-y|)(u(t,y)-u(t,x))dy \; + f(u(t,x)).$$

Here, the dispersal operator is represented by a spatial convolution between the concentration u and a dispersal kernel J. For any spatial positions x and y, the quantity $J(|x-y|)$ corresponds to the probability distribution of jumping from position y to position x.

Integro-difference models correspond to the time-discrete version of integro-differential equations.

As above-mentioned, recent mathematical works (Coville and Dupaigne 2007) have demonstrated that with thin-tailed kernels, integro-differential models behave in the same way as classical reaction-diffusion models. In particular, the expansion occurs with a constant speed, at least for localized initial population densities.

In (Garnier 2011), we have considered the case of fat-tailed kernels and obtained an accurate description of the spreading properties of these models in that case. The population range $x_\lambda(t)$ and the rate of spread $v_\lambda(t)$ being defined as in Sect. 2.3

(Box 5.2), we were able to obtain an accurate description of the motion of the population range:

$$\left|J^{-1}\left(\lambda\, e^{-\left(f'(0)-\varepsilon\right)t}\right)\right| \leq \left|x_\lambda(t)\right| \leq \left|J^{-1}\left(\lambda\, e^{-\rho t}\right)\right|,$$

for some constant $\rho > f'(0)$. This formula implies that, for any fat-tailed kernel, i.e., any kernel that decays slower than any exponential function, the population range expands with an increasing speed.

Let us illustrate the above formula with two particular examples of fat-tailed kernels: (i) if the kernel decays like $exp\left(-\sqrt{|x|}\right)$ for large $|x|$, then the population range expands at a rate proportional to t^2, which means that the speed of propagation increases linearly with time; (ii) if the kernels decays algebraically, for instance like $1/|x|^3$, then the range expansion occurs with an exponentially increasing speed.

Our results show that incorporating long-distance dispersal in the models drastically modifies their qualitative properties. Starting from localized (i.e., compactly supported) initial population densities u_0, fat-tailed kernels lead to a fast expansion and an acceleration of the population range. On the contrary, thin-tailed kernels and reaction-diffusion models always lead to range expansions with constant speed (but they could also lead to accelerating propagation phenomena for slowly decaying u_0, see Sect. 2.3).

4.4 Enhancement of the Spreading Speed by Vehicle Transportation

It has been observed that invasive species sometimes travel at a higher speed than theory predicts. Such is the case for the pine processionary in Europe or, more recently, for the tiger mosquito in France. One possible explanation for this higher speed would be that some individuals have been carried on by vehicles travelling through infested areas.

We have undertaken a study to understand the mathematical basis for such a claim. The framework we adopt is one in which a very thin region – the road – essentially one-dimensional, has a much faster diffusion than in the rest of the space. The question is to know what is the effect of a one-dimensional line with very fast diffusion on classical Fisher-KPP type invasion in a planar region. Thus, in (Berestycki et al. 2013a, b) we have proposed a new model to describe this phenomenon. There, the road is assumed to be a straight line. Our aim was to understand whether the inclusion of the line with fast diffusion may affect the overall invasion of the species and to further quantify this effect.

In the first paper (Berestycki et al. 2013a) we have considered the case where the two-dimensional environment includes a line on which fast diffusion takes place while reproduction/mortality and usual diffusion only occur outside this line. For a single species, we call v the density of this population in the plane $\boldsymbol{R}^2$ and u the density on the line $y = 0$. Exchanges take place between the two densities. Namely, a fraction m of the density v from the field at the road join the road while a fraction μ of the population u on the road goes in the fields. It is assumed that the population in the field is subject to a logistic type of growth resulting in a Fisher-KPP type of reaction term $f(v)$ in the field. We assume that no such reaction is relevant on the road. The diffusion coefficient in the field is represented by d and by D on the road. By reasons of symmetry, it is enough to consider the upper half plane. We end up with the following system

$$\begin{cases} \dfrac{\partial u}{\partial t} - D\,\dfrac{\partial^2 u}{\partial x^2} = m\,u(x,0,t) - \mu\,u, \quad \mathit{for}\ t > 0,\ x \in (-\infty,\ +\infty), \\ \dfrac{\partial v}{\partial t} - d\,\Delta\,v = f(v), \quad \mathit{for}\ t > 0,\ x \in (-\infty,\ +\infty),\ y > 0, \\ -d\dfrac{\partial v}{\partial y} = \mu\,u - m\,v(x,0,t), \quad \mathit{for}\ t > 0,\ x \in (-\infty,\ +\infty). \end{cases}$$

We have verified that this model conserves the population in absence of reproduction and mortality and preserves order. Then, we have shown that owing to the exchanges taking place between the line and the plane, there is an asymptotic speed of spreading which is the invasion velocity along the line. In order to compute this speed, we have used exponential solutions of the linearised system and compactly supported sub-solutions.

When D, the diffusion on the road, is less than or equal to $2d$, where d is the diffusion in the field, there is no effect due to the road: the propagation takes place at the classical KPP invasion speed. In contradistinction with this case, when D is larger than $2d$, there is an enhancement effect caused by the diffusion on the road resulting in a speed higher than KPP. Lastly, this invasion speed is shown to behave like the square root of D for large values of D.

In the second paper (Berestycki et al. 2013b), we added a transport term and a decay rate on the road. This affects the threshold 2 for the ratio D/d after which the effect of the road is felt (in the sense that the spreading speed is larger than the usual KPP speed).

These studies open up many mathematical questions. The model that we proposed is a very general one that is relevant not only to ecology and population dynamics but also for a wide array of situations in biology.

5 Landscape Effects

5.1 Correlation Between the Spatial Distribution of Pine Processionary Moth and Landscape Characteristics

The results presented in Sect. 3.2 are a first indicator of the landscape effect on the dynamics of pine processionary moth, but the spatial covariates have not been taken

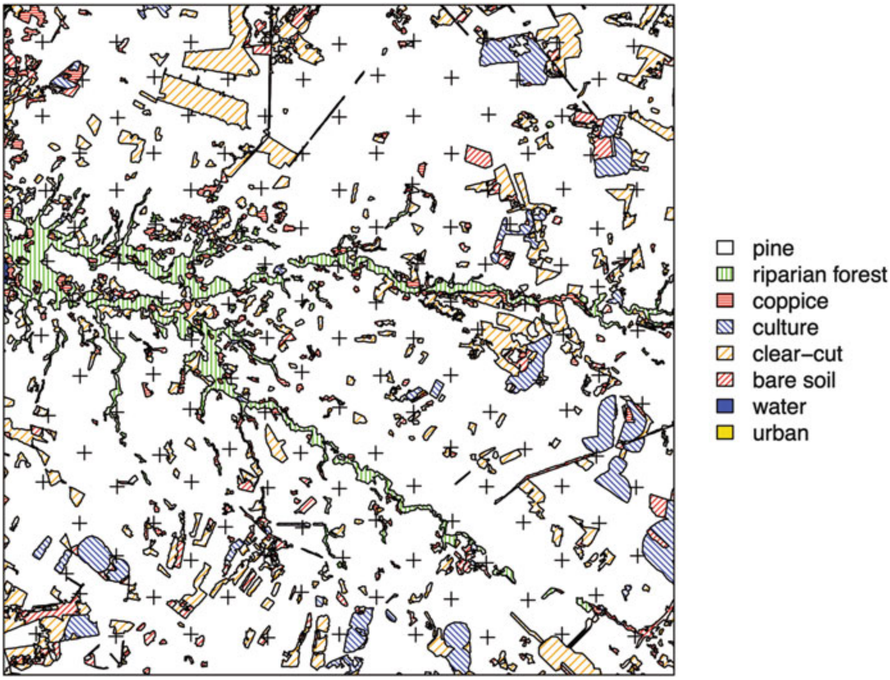


Fig. 5.10 Satellite-based map of the study site. The study site consists of a maritime pine forest (*Pinus pinaster*) with a central elongated riparian forest patch. Sampling localities are distributed along a regular grid and are represented by *black crosses*. At each sampling points, the number of pine processionary moth (*Thaumetopoea pityocampa*) winter tents was assessed in three subsamples located within pine stands and one additional subsample located at the stand edge

explicitly into account. In this section, we focus on the effect of both landscape composition and physiognomy. We report data collected during 4 consecutive years in a pine plantation forest in southwestern France (Samalens and Rossi 2011). Winter tent density was estimated in 145 sampling locations in a 16 × 16 km area (sampling window = 25,600 ha) using a grid size of ca. 2 km (Fig. 5.10).

Count data were used to analyze the spatio-temporal variability of population distribution, which exhibited some marked temporal variability as well as strong spatial structures.

Landscape description was based on a high-resolution and multispectral satellite image (SPOT 5 XS, 10 m) covering the study area (© CNES, distribution Spot Image SA). The landcover of the study site was categorized into eight main land uses by supervised classification (Fig. 5.10; urban areas, water, pine plantations, riparian forest (RF), cultures, coppices, clear cuts, and bare soil).

The landscape analysis consisted of computing landscape metrics around each sampling site of pine processionary moth on the basis of a circular buffer of 1,000 m radius. We used different landscape metrics (Table 2 in Samalens and Rossi 2011) to describe the “local” landscape corresponding to the buffers. The mean proportion of landscape covered by water and urban development was, respectively, 0 and 0.16 % of the buffer area, and therefore, these classes were ignored. We investigated the presence of spatial autocorrelation of population distribution by means of the Moran’s *I* spatial autocorrelation statistic.

The spatial distribution of the density of winter tents exhibited a significant autocorrelation in 2005, 2006, and 2008 but not in 2007, when the average density was at its lowest level. The bivariate correlograms between tent density and landscape metrics were significant in all cases but for clear cuts ($P = 0.05$, Holm’s correction), thus reflecting the correlation between the insect spatial distribution and landscape characteristics. However, correlograms yielded contrasting results according to the spatial scale considered. A negative relationship between tent density and the proportion of landscape covered by riparian forests was observed for distances <4,000 m (Fig. 5.11c). Similar relationships were observed with the percentage of landscape covered by coppices as well as with the PRD

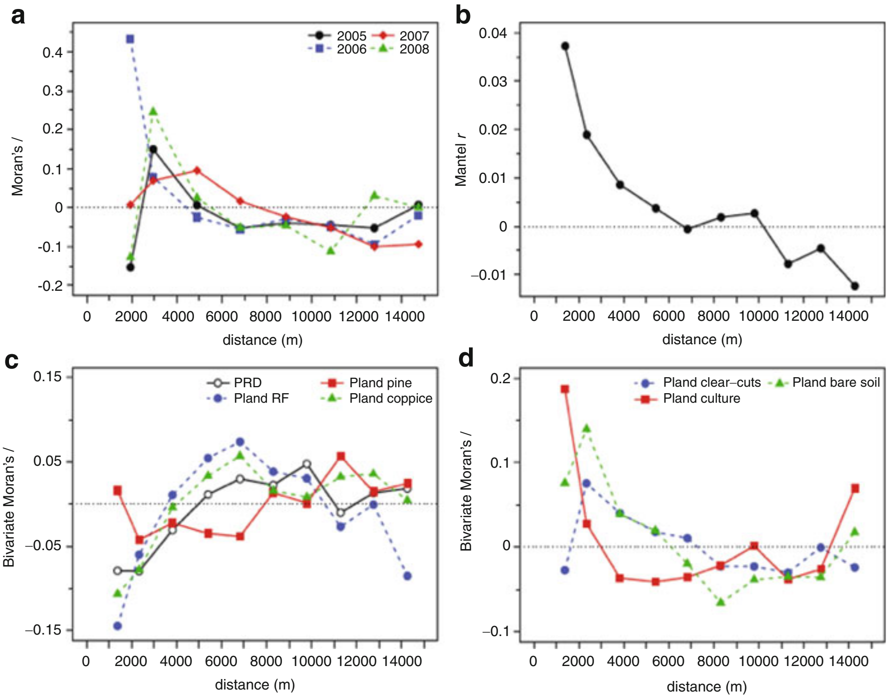


Fig. 5.11 Uni- and bivariate correlograms. (**a**) Univariate Moran’s I correlogram for the winter tent density (tent ha^{-1}) of the pine processionary moth on 4 years of sampling (2005–2008). Spatial autocorrelation is significant in 2005, 2006, and 2008. (**b**) Mantel correlogram computed with the matrix of the multivariate distance derived from a set of landscape metrics (see text for details). (**c**, **d**). Bivariate Moran’s I correlograms computed for the pine processionary moth winter tent density (tent ha^{-1}) and various landscape metrics (all significant at $alpha = 0.05$) (Modified from Samalens and Rossi 2011)

(patch richness density). Interestingly, a positive relationship between the percentage of land covered by culture and tent density emerged for distances <4,000 m (Fig. 5.11c). The relationships between pine processionary moth and landscape metrics (e.g., RF and coppices) changed with the distance lags considered. For example, it was positive for PLAND RF and coppices at scales of >5,000 m. These features mostly reflected the position and sizes of both landscape and population patches with regard to sampling window limits.

Our results indicate that the pine processionary moth winter tent density is spatially structured at the scale of several km and is correlated with certain landscape features. These relationships could be due to direct effects through the modalities of the moth dispersal and a variety of indirect effects implying natural enemies. These results show that accounting for landscape characteristics may be important to understand forest insect pest distribution even in cases where host species are very abundant and homogeneously distributed throughout the study area (e.g. plantation forests).

At the scale of 4 years the density changed markedly due to the natural outbreak cycle of the species. Areas where the density was higher tended to be constant although our ability to describe such a pattern in years where density was at its lowest level is doubtful. The presence of spatial autocorrelation indicates that sampling for monitoring pine processionary moth must be preferentially regular. Further analyses and field work is needed to design optimized sampling design for long-term monitoring, mapping and control.

5.2 Role of Isolated Host Trees in Non-forested Areas

Although the pine processionary moth is a forest pest, it is also present in non forest areas, especially on ornamental pine trees planted along the roads, the motorways, on the roundabouts, in private and public parks and gardens. Beyond its historical distribution in south-western Paris, there is an agricultural region called La Beauce, with a lot of cultivated fields and no forest stand with pines was surveyed by the French National Forest Inventory (IFN) (Fig. 5.12). In this inventory, trees are surveyed if there are located in a forest stand of more than 2.25 ha. Therefore ornamental trees are not surveyed at the country scale. It was initially thought that this region could slow the spread of the pine processionary moth due to a lack of host trees. However, INRA (URZF) georeferenced all isolated pine trees in this region in 2004 and they found an unexpected high number of pine trees (Fig. 5.12). Consequently, the pine processionary moth succeeded in crossing this non forest region in the 2000s.

The distance between each couple of isolated pine trees was calculated. The mean distance was 1.05 km and 97 % of isolated pine trees in this region had a neighbour at less than 3–4 km, which was the supposed flight distance of a female adult (Robinet 2006). Consequently, ignoring isolated pine trees in models that

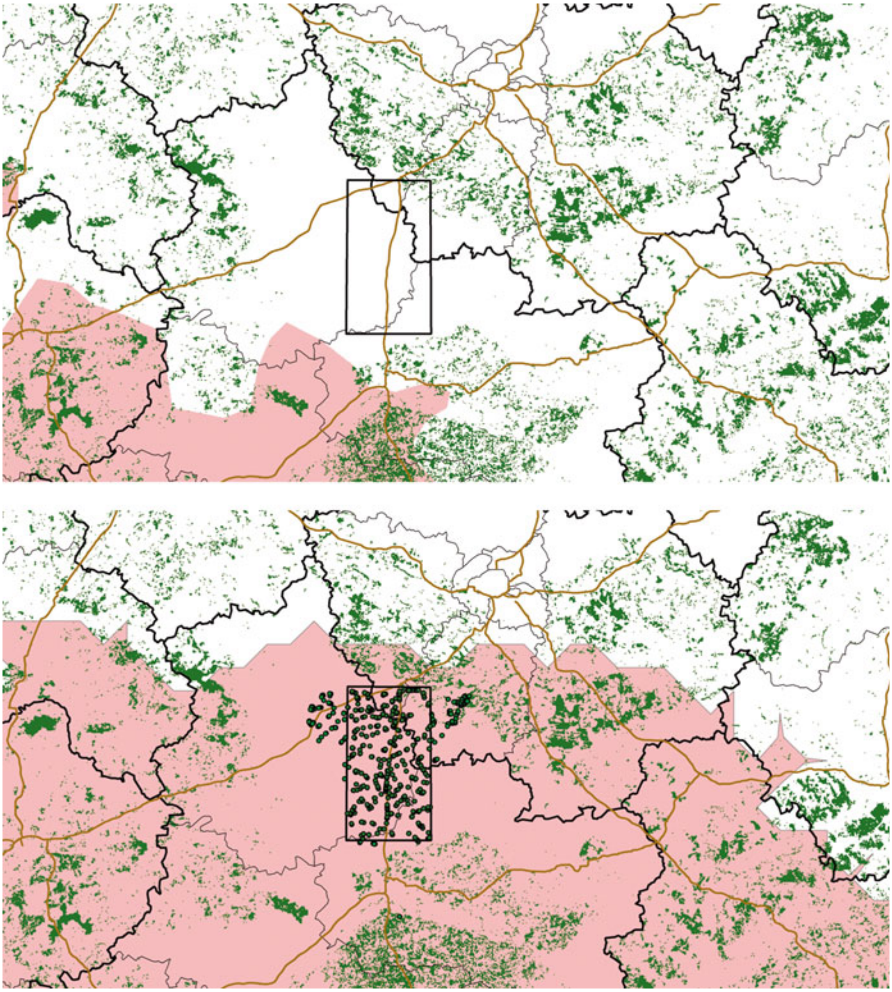


Fig. 5.12 Pine trees surveyed in forest area by the French National Forest Inventory (IFN) (in *green*) and isolated pine trees surveyed by the French National Institute for Agricultural Research (INRA Orléans) (*dark green points*) in the agricultural region called La Beauce (delimited by the *black rectangle*). At the *top* is represented the pine processionary moth distribution between 1969 and 1979 (CTGREF-INRA 1980) and at the *bottom* the pine processionary moth distribution in 2010–2011 (Source: INRA Orléans) (*pink background*)

describe the potential range expansion could be misleading. It is necessary to correct the host tree density in models that describe the potential spread and assume that these trees are present over all the territory (especially in urban areas). This correction was done in the models described in Sect. 3 (Robinet et al. 2014).

6 Causes and Consequences of the Allee Effect

In this section, the results of a preliminary experiment on pine processionary moth are reported, showing that Allee effects can appear. Then, there is a general presentation of how Allee effects can be modelled and how they can affect the population dynamics, either in theory or using another forest pest example.

6.1 Link Between Pine Processionary Moth Survival and Colony Size

The gregarious behavior of pine processionary moth larvae raises the question of the advantages of being in a large group. This strategy can appear particularly in species with Allee effects (see Box 5.4).

Larval performance of a very close species, the northern pine processionary moth, *Thaumetopoea pinivora*, depends on the colony size (Ronnås et al. 2010). In large colonies, the thermal gain is higher and the development is faster. Such thermal gain resulting from metabolic heat production is also observed in other species building tents, such as the small eggar moth, *Eriogaster latentris* (Ruf and Fiedler 2000). Therefore aggregating in tents could offer some advantages to these species. Pérez-Contreras et al. (2003) explored the effects of the colony size for the pine processionary moth, *T. pityocampa*, in Spain under a semi-arid climate and high elevation (around 1,000 m). They measured the larval length and larval mortality in colonies of 25, 50, 75 and 100 larvae. They found a threshold of 32 individuals above which larval length reached its maximal value and they also observed a decrease of the larval mortality with increasing size of the colony from 25 to 75 individuals and no significant difference between 75 and 100 individuals.

Following this preliminary evidence of an effect of the colony size on survival rate, the existence of Allee effects in the pine processionary moth should be carefully examined. If such effects occur, then it would impact the establishment probability and may therefore affect the spatio-temporal dynamics of the populations (see Sect. 6.2.2). To better understand the effects of the colony size on its survival rate, we conducted an exploratory experiment during the winter 2009–2010 near Orléans. We collected pine processionary moth tents in the region of Orléans in early October 2009, and reconstructed artificial tents of 25, 50, 75, 150 and 500 larvae, with 10 replicates for each condition. Over 123 egg-masses collected near Orléans in early July 2010, there were an average of 216 eggs per egg-mass, with a minimum of 102 and maximum of 310. Since several egg-masses can be laid on the same tree and larvae can then gather together to build a single winter tent, it is not unusual to find tents of several hundreds of larvae. Our experiment covered a possible range of colony size, but focused a little more on small colonies. We found no survivors in tents with 25 and 50 larvae. Then the number of surviving tents (Fig. 5.13, left) and the mean number of surviving larvae per tent (Fig. 5.13, right) increased with the colony size.

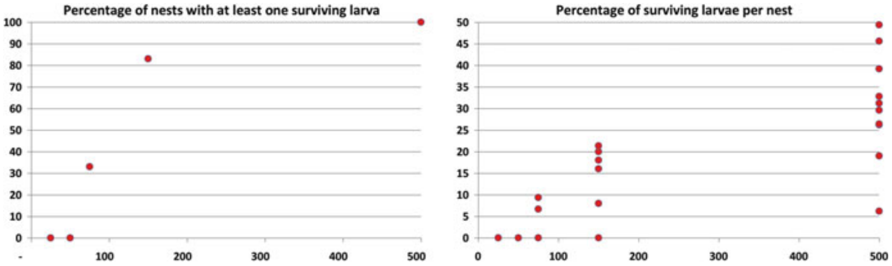


Fig. 5.13 (*Left*) Percentage of surviving tents (with at least one surviving larva). (*Right*) Percentage of surviving larvae in each artificial tent of the 5 conditions

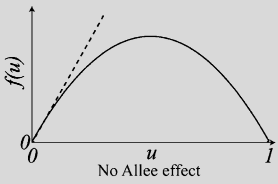
Our study indicates that large colonies likely survive better than small ones. In the following sections we present general methods to model Allee effects and analyse their implications.

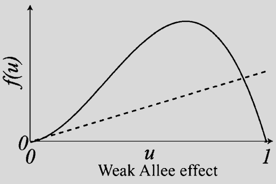
6.2 *Unexpected Consequences of the Allee Effect*

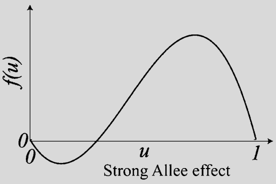
Box 5.4 Allee Effect

The Allee effect corresponds to a lower fitness at low population density. When the growth rate is negative at low population density, i.e., if the birth rate is lower than the death rate, then this is a *strong Allee effect*. Otherwise, if the *per capita* growth rate reaches its maximum at a strictly positive population density, without being negative at low density, this corresponds to a *weak Allee effect*.

In reaction-diffusion models (Box 5.1) and integro-differential models (Box 5.3), three main types of growth terms $f(u)$ are generally considered, depending on the presence of an Allee effect and depending on the type of Allee effect (see Figures below).







Several mathematical approaches have already demonstrated that the Allee effect plays an important role during a species range expansion. For instance, the Allee effect can reduce the speed of colonization (Lewis and Kareiva 1993; Lewis and

Van Den Driessche 1993), and can even stop it in heterogeneous environments (Barton and Turelli 2011). Higher dispersal capabilities in presence of Allee effects could surprisingly lead to lower probabilities to establish and grow (Robinet and Liebhold 2009; Roques et al. 2008). During our study, we carried out an extensive mathematical analysis of the role played by the Allee effect in the context of a range expansion. We have found new and unexpected consequences of the Allee effect, which are detailed below.

6.2.1 Allee Effect Promotes Diversity in Traveling Waves of Colonization

Most mathematical studies on expanding populations have focused on the rate of range expansion of a population (Hastings et al. 2005). However, the genetic consequences of population expansion remain an understudied body of theory (Excoffier et al. 2009). Describing an expanding population as a traveling wave solution derived from a classical reaction-diffusion model (see Box 5.1), we analyzed in the papers (Garnier et al. 2012a; Roques et al. 2012) the spatio-temporal evolution of its genetic structure. In that respect, we assumed that the population was composed of genes or haploid individuals. Its total density u satisfies the above equation. This population is made of N *neutral* genetic fractions v^k. In particular, at initial time $t = 0$,

$$u_0(x) = u(0,x) = \sum_{k=1}^{N} v_0^k(x),$$

where the quantities $v_0^k(x)$ correspond to the initial densities of the different genetic fractions. We assume that the genes (or the individuals) in each fraction only differ by their position and their allele (or their label), while their dispersal and growth capabilities are the same as the total population u, in the sense that the density v^k of each fraction verifies an equation of the form:

$$\frac{\partial v^k}{\partial t}(t,x) = \frac{\partial^2 v^k}{\partial x^2} + v^k \frac{f(u)}{u} \; for \; t > 0 \; and \; x \in (-\infty, +\infty).$$

Thus, the per capita growth rate $f(u)/u$ of each fraction is equal to the per capita growth rate of the total population u. Also note that the sum of the fraction densities verifies the same equation as u. The uniqueness of the solution of this equation implies that, as expected, the sum of the fraction densities remains equal to the total population density at all positive times.

Using this approach, and comparing the case of a function $f(u) = u(1-u)(u-\rho)$ taking an Allee effect into account with the case of a logistic growth function $f(u) = u(1-u)$, we showed that the presence of an Allee effect drastically modifies genetic diversity, both in the colonization front and behind it. With an Allee effect

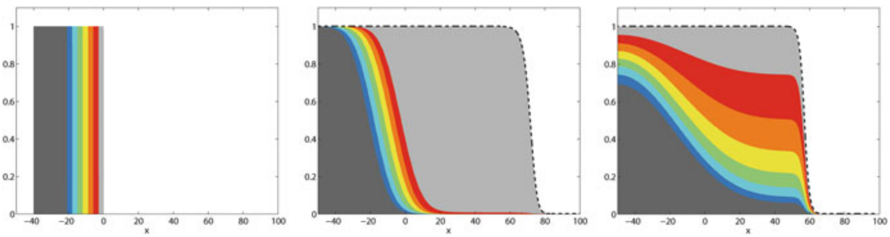


Fig. 5.14 *Left* fig.: initial distribution of the genetic fractions; *middle* fig.: spatial structure of the colonization wave without Allee effect ($f(u) = u(1 - u)$); *right* fig.: spatial structure of the colonization wave with an Allee effect ($f(u) = u(1 - u)(u - \rho)$)

(i.e., pushed colonization waves), all of the genetic diversity of a population is conserved in the colonization front. In the absence of an Allee effect (i.e., pulled waves), only the furthest forward members of the initial population persist in the colonization front, indicating a strong erosion of the diversity in this population (Fig. 5.14). These results diversify the commonly held perspective that the Allee effect possesses net adverse consequences. This perspective is inherited from demographic studies of range expansion, which demonstrate that an Allee effect reduces the speed of colonization (Lewis and Kareiva 1993; Lewis and Van Den Driessche 1993) and can even stop it in heterogeneous environments (Barton and Turelli 2011), see also Sects. 6.2.2 and 6.2.3. Reducing the growth rate of the individuals ahead of the colonization front simultaneously reduces the speed of colonization and enables a diversity of genes coming from the core of the population to remain on the front, as demonstrated by our results. Other mechanisms that reduce the growth rate of the individuals ahead of the front should also result in greater conservation of the genetic diversity of a population. For instance, Pluess (2011) demonstrated how a retreating glacier limited the spread of a population of European larch, thereby functioning as an extreme Allee effect where all of the seeds falling on the icecap die. Given our results, this should lead to high genetic diversity in the colonization front, which was actually observed (Pluess 2011). The Allee effect could be a partial or alternative explanation to the argument of long-distance mixing of genes advanced by Pluess (2011).

The Allee effect also affects the spatial distribution of diversity. As Fig. 5.14 illustrates, this effect leads to a “horizontal pattern” of genetic diversity (i.e., an absence of genetic differentiation in space). Conversely, we observed a “vertical pattern” of genetic diversity in the absence of an Allee effect (i.e., a strongly structured spatial distribution of population fractions; see Fig. 5.14). This genetic structure eventually attenuates due to diffusion in the saturated population and each fraction becomes negligible. However, in both cases the diffusion in the saturated population occurs at a much lower rate than the rate of colonization (sublinear diffusion vs. linear propagation). These two time-scales are consistent with the results obtained in (Austerlitz and Garnier-Géré 2003) with a stepping-stone model.

6.2.2 Fragmentation of the Founding Colony and Success Rate of the Establishment Stage

It is well-known that the Allee effect has a detrimental effect on the establishment of new colonies far from the main population. These new colonies typically consist of a few individuals, and the Allee effect may lead to very low or even negative growth rates, and finally invasion failure.

The success of the establishment phase of these new colonies depends on several endogenous and exogenous factors. Understanding the intertwined roles of these factors is of critical importance to slow down the rate at which biological invasions occur.

Our study, which was presented in (Garnier et al. 2012b) investigates the interactions between founding population characteristics (namely, size and spatial distribution) and the strength of the Allee effect in reaction-diffusion models of the form:

$$\frac{\partial u}{\partial t}(t,x) = D\Delta\, u + \; u(1-u)(u-\rho),\ \textit{for}\ t > 0\ \textit{and}\ x \in (-\infty,\, +\infty),$$

where ρ corresponds to the strength of the Allee effect.

Our study shows that the precise shape of the initial (or founding) population is of critical importance for successful invasion. Using a stochastic model of pattern generation, we constructed a large number of initial conditions with various abundances (measured by an index **p** in [0,1]) and fragmentation rates. Using a new, rigorous definition of the fragmentation rate (measured by the index **fr** in [0,1]), we were able to describe the outcome of an invasion in terms of two attributes of the founding population **p** and **fr** (Fig. 5.15). Interestingly, the outcome of the invasion is indeed almost completely determined by the values of **p** and **fr**; for each value of the Allee threshold ρ we obtained two distinct regions in the parameter space (**fr**,**p**). One region corresponds to successful establishment, and the other one corresponds to establishment failure. The interface between these regions corresponds to a narrow region in the parameter space (Fig. 5.16).

The minimum abundance required for successful invasion tends to increase in a nonlinear fashion with the fragmentation rate. This effect of fragmentation is

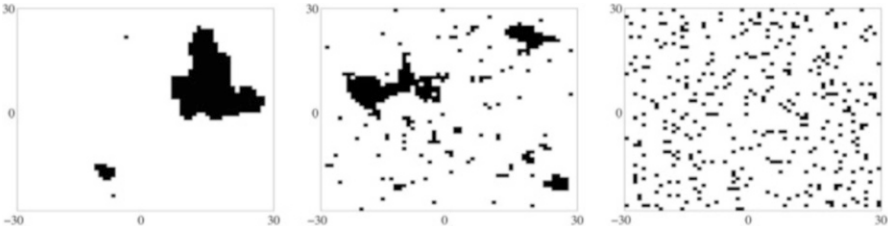


Fig. 5.15 Several configurations: same abundance p = 0.1 and increasing fragmentation rates: fr = 0.05, 0.4 and 0.9

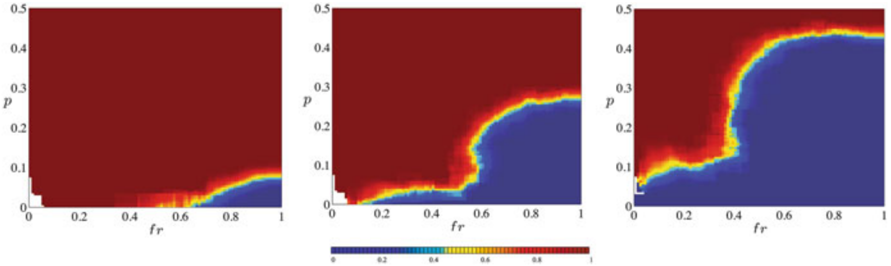


Fig. 5.16 Probability of successful establishment in terms of the fragmentation rate fr and the abundance p of the founding population. From *left* to *right*: $\rho = 0.1$, $\rho = 0.3$ and $\rho = 0.45$ (ρ is the Allee threshold)

enhanced as the strength of the Allee effect is increased. In addition, the relationship between the minimum abundance and the fragmentation rate is highly nonlinear and steep, threshold-like. There is threshold value, say $\mathbf{fr}^*$, where the minimum abundance for successful establishment dramatically increases. On both sides of this threshold, establishment success is almost independent on **fr**. On the one hand, if the rate of fragmentation is higher than $\mathbf{fr}^*$, then the behavior of the model is close to the behavior of a homogenized problem. On the other hand, if the rate of fragmentation is lower than $\mathbf{fr}^*$, the model almost behaves as if the initial condition was replaced by a single ball-shaped group. The existence of such a threshold implies that small changes in the fragmentation rate can therefore drastically modify the outcome of an invasion if the fragmentation rate is close to $\mathbf{fr}^*$.

6.2.3 The Role of Spatial Bottlenecks

As already mentioned, the "climate envelope" of the pine processionary moth, that is, the environmental conditions under which the pine processionary moth can persist, is expanding northward. Following this movement, the pine processionary moth range is also expanding northward. During this migration process pine processionary moth may face absolute boundaries to dispersal, because of external environmental factors. Consequently, not only the position, but also the shape of the climate envelope can be modified. In the paper (Roques et al. 2008), we use a reaction-diffusion model of the same type as in Sect. 6.2.2 to analyze the effects of simultaneous changes in the climate envelope position and shape. When the growth term is of logistic type, i.e., without Allee effect, we show that the ability of a species to follow its climate envelope is principally conditioned by the species mobility and the speed of climate change, but not by the shape of the climate envelope. However, with a growth term taking an Allee effect into account, we find a high sensitivity to the variations of the shape of the climate envelope. In this case, a species which have a high mobility, although it could more easily follow the migration of the climate envelope, would be at risk of extinction when encountering a local narrowing of the boundary geometry. For this reason, the progression of the

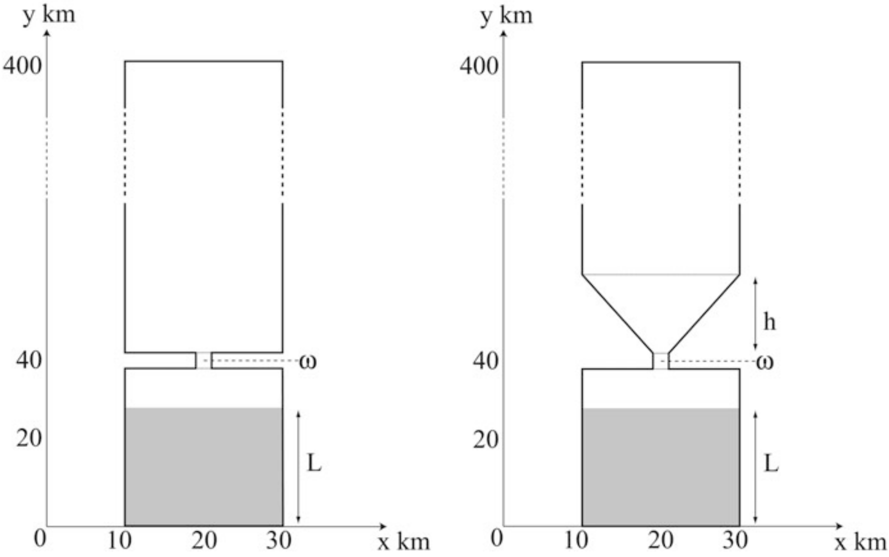


Fig. 5.17 Following the movement of the climate envelope is easier in the right configuration, with a progressive opening of the available space

pine processionary moth could be slowed down in the Alpine valleys, where several corridors can be identified.

This bottleneck effect can be attenuated by a progressive opening of the available space at the exit of the narrowing, even though it transiently leads to a diminished area of the climate envelope (Fig. 5.17).

7 Conclusion

This chapter summarizes several modeling studies conducted on the range expansion of pine processionary moth in a spatio-temporally heterogeneous environment. These studies provide new approaches for analyzing and modeling range expansions and contribute to a better understanding of the effects of a wide variety of factors on the spatio-temporal dynamics of the pine processionary moth. These dynamics mostly depend on the dispersal, survival and reproduction characteristics of the species, and these characteristics fluctuate in time and space, depending on environmental and biological factors. In particular, we have analyzed the role of (1) climate warming (2) landscape characteristics (3) human-assisted dispersal (4) Allee effect. We have shown that both short and long distance dispersal events are very important to consider and we have proposed several approaches to model these events.

A natural conclusion to these studies would be to gather all the results in a single general model, which could be of the integro-differential form proposed in Sect. 4.2, Box 5.3, with a space-time dependent growth function $f(t, y, u(t, y))$ describing the survival and reproduction characteristics of the species and a kernel $K(t, x, |x - y|)$ describing its space-time dependent dispersal characteristics. As explained in Sect. 4.2, this dispersal kernel could be of the form $g(t, x)J(|x - y|)/(\int g(t, s)J(|s - y|)ds)$, where J is a kernel which describes the proportions of short distance and long distance dispersal events and $g(t, x)$ measures the effect of human population density on the probability of introduction at the position x. Estimating the parameters of this general model will be a challenging issue. Although more and more information are collected on the dispersal mechanism in terms of adult flight capability and human-mediated transportation, estimating dispersal kernels, especially in the presence of long distance dispersal events, is a difficult task. To improve our knowledge about dispersal patterns, we should now consider genetics data in the models. Parameter estimation on the basis of genetic data could be achieved by coupling the approaches of Sects. 3.2 and 6.2.1 with the above-mentioned integro-differential models. Regarding the potential effects of climate change on the range expansion of the pine processionary moth, the variability of the species phenology across the regions (Huchon and Démolin 1970) will be important to consider in the future. The large-scale survey conducted over Europe to map the northern edge of the species distribution (Chap. 3) could be used to refine the bioclimatic envelope.

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Chapter 6
Insect – Tree Interactions in *Thaumetopoea pityocampa*

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1 Introduction

The pine processionary moth is, by far, the most important insect defoliator of pine forests in Southern Europe and North Africa, both in terms of its temporal occurrence, geographic range and socioeconomic impact. Monitoring and pest management actions are therefore required on a regular basis, to ensure the detection, evaluation and mitigation of potential risks to forest and public health. However, we still lack some of the basic knowledge required for relevant analyses of the risk posed by the pine processionary moth. Pest risk is defined as a combination of three components:

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(1) pest occurrence, which depends on the spatiotemporal dynamics of populations; (2) plant vulnerability to the pest, resulting in a certain amount of damage; and (3) the socioeconomic impact of damage, depending on the potential value of the plants damaged (Jactel et al. 2012b). The population dynamics of the processionary moth has been extensively studied, in particular within the context of climate change (see Battisti et al. 2014, Chap. 2, this volume). Several studies have recently addressed the question of tree and forest vulnerability to pine processionary attacks but a comprehensive review of evidence was missing. This is the first objective of this chapter. In particular we were interested in a better understanding of the ecological mechanisms responsible for the host tree selection, at both the species and individual tree levels. In a second part we show that pine susceptibility to the pine processionary moth could be reduced by improving forest diversity at different spatial scales. In the last part of this chapter we provide quantitative estimate of the growth losses caused by defoliations of the pine processionary moth. Altogether this information paves the way for quantitative risk analyses on pine processionary moth infestations based on forest growth models.

2 Mechanisms of Host Tree Selection by the Pine Processionary Moth

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2.1 Introduction

It has long been recognized that trees attacked by *Thaumetopoea pityocampa* in conifer stands do not follow a random distribution, infestations being higher near the edges or in isolated trees (e.g. Calas 1897; Démolin 1969b). Furthermore, the intensity of attack observed in the same area can greatly vary between different host tree species (e.g. Buxton 1990; Tiberi et al. 1999; Mateus 2009).

These observations suggest the occurrence of an active process of host detection and selection by adult female moths prior to oviposition and/or differential survival of eggs or immature larvae. According to Bernays and Chapman (1994), females of phytophagous insects should recognize the best food available for their offspring and choose it for oviposition, thus promoting optimal progeny survival. Regarding *T. pityocampa,* although some studies support this hypothesis (e.g. Pérez-Contreras et al. 2008), other results are not conclusive (e.g. Hódar et al. 2002) and research is still in progress.

The objective of this chapter is therefore to review the main patterns of host tree colonization by processionary moths and investigate possible behavioral mechanisms supporting the hypotheses of active host selection by ovipositing adult females vs. differential survival of offspring.

2.2 Spatial Pattern of Tree Infestation at Stand and Landscape Levels

Within a stand, *T. pityocampa* adults preferentially select taller trees for colonization (Démolin 1969a, b), as well as those located at stand edges. Such empirical knowledge was confirmed by Samalens and Rossi (2011) and Dulaurent et al. (2012), who conducted studies on the spatial distribution of *T. pityocampa* infestations and consistently found higher tent density along the border of maritime pine plantations (Fig. 6.1).

The observed tent spatial distribution might reflect favorable micro-climatic conditions near the edges of pine plantations where solar radiation is higher (Buffo et al. 2007). This is confirmed by the observation of heavier infestations along South facing edges (e.g. Démolin 1965; Breuer et al. 1989). Similarly, at high elevations where the pest is expanding, colony survival was higher in South oriented stands, probably due to higher number of hours when feeding activity is possible by comparison to North aspects (Battisti et al. 2005).

Alternatively, higher tent density at stand edge can be due to close proximity with forest tracks where most pupae burials take place (Barbaro et al. 2007). Access to open habitats for larval burial is a decisive factor contributing to higher survival of the overwintering pupae because in this type of habitat soil temperature and humidity are more favorable to the survival of pupae (Dulaurent et al. 2011).

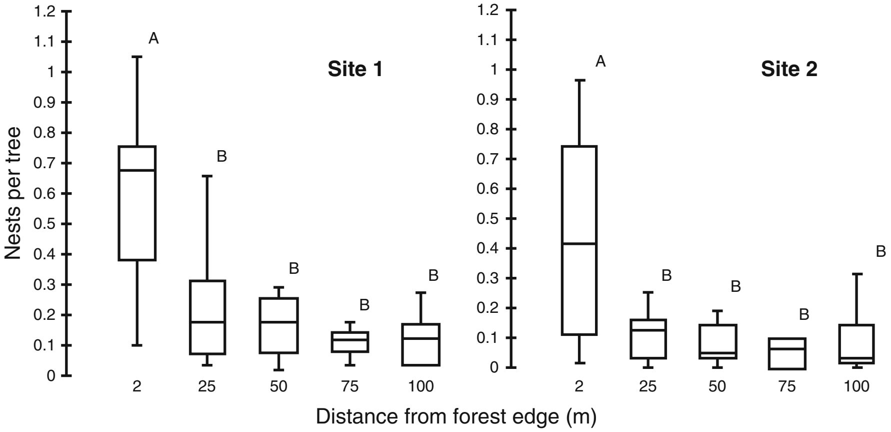


Fig. 6.1 Number of Thaumetopoea pityocampa tents per tree in five groups of trees at various distances from the south-exposed edge of maritime pine stands, at both sites. Different letters above bars indicate significant differences (Wilcoxon paired test) in the number of tents per tree (Modified from Dulaurent et al. 2012)

Géri et al. (1985) found that *T. pityocampa* tent density decreased with increasing tree density in *Pinus nigra* and *P. sylvestris* forests but acknowledged that trees are also higher in low density stands. By contrast, Lombardero et al. (2012) did not observe any significant effect of thinning on the abundance of *T. pityocampa* in stands of *P. pinaster* aged between 17 and 24 years. Similarly Bonsignore and Manti (2013) found no consistent effect of stand density on trap catches of male moths.

At the landscape level, the distribution of *T. pityocampa* tents exhibits a significant spatial autocorrelation over a wide range of scales, with higher tent density in parts of the landscape with higher pine stand density (Samalens and Rossi 2011).

These observations lead to infer that in general, the pattern of colonization by *T. pityocampa* follows similar trends both at tree, stand and landscape levels, resulting into advantageous conditions for the progeny.

Given the reduced mobility of the neonate larvae, preferential egg laying in South facing habitats at tree, row or stand level will largely determine tent location and contribute to colony survival by increasing the absorption of warmth by larval tents. A longer insolation enables the colony to extend feeding periods and contributes to a higher food consumption and better performance of larvae (Démolin 1965; Breuer et al. 1989; Hoch et al. 2009; Battisti et al. 2013). Furthermore, the quality of needles which are exposed to longer photoperiods may also improve, due to increased nitrogen content and decreased foliar defenses (Moreau and Quiring 2011). Higher survival is also probable, since egg-batches and consequently larvae located on branches exposed to sunlight may experience a reduced mortality due to pathogens (*e.g.* Santos et al. 2011). Actually, the fungi *Beauveria bassiana* and *Scopulariopsis* sp. regularly infect the larvae within the tent, or during the larval procession (*e.g.* Géri 1983a, b), and fungi are known to benefit from more humid conditions. However, it remains uncertain whether such location of egg batches or larval tents at stand edges might also trigger higher parasitism or predation~~s~~ which are known to increase along forest borders for other phytophagous insects (De Somviele et al. 2007).

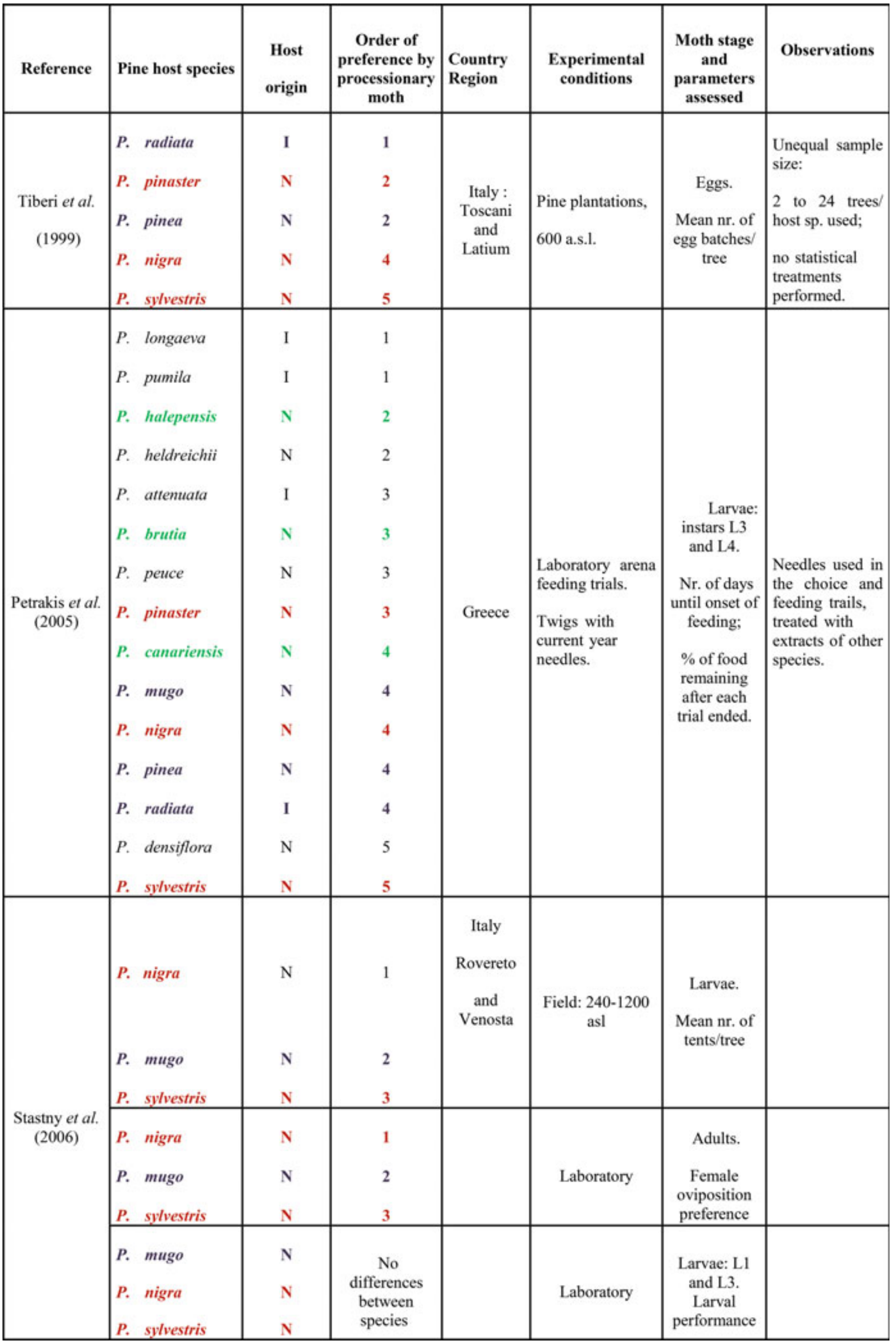
In short, habitat selection by ovipositing females is a key process determining the success of phytophagous insect species (Castells and Berenbaum 2008). Evidence suggests that active selection by *T. pityocampa* adults takes place regarding the location and orientation of host trees at both stand and landscape levels. Pine trees that are isolated, taller or located along stand edges, i.e. more apparent trees, are clearly more often colonized by pine processionary moths. This would contribute to increase the survival and performance of different stages of the progeny mainly through more favorable microclimatic conditions.

2.3 Host Preferences at Interspecific Level

Thaumetopoea pityocampa feeds mainly on pines and occasionally on *Cedrus* spp. and *Larix* spp. A technical diagnostic protocol provided by EPPO (2004) indicated the following decreasing order of host species susceptibility to attack by *T. pityocampa*: *Pinus nigra* var. *austriaca*, *P. sylvestris, P. nigra* var. *laricio*, *P. pinea, P. halepensis, P. pinaster, P. canariensis*, followed by *Cedrus atlantica* and finally *Larix decidua*. However this list did not include exotic pine species.

However different authors do not always agree on the order of host preference which seems to greatly vary between geographical regions or types of experiments. A literature review identified seven papers reporting experiments performed to compare *T. pityocampa* rank order of preference of *Pinus* species (Table 6.1). The number of species compared in each work varied between 2 and 15, most of which were not studied by the other authors. Furthermore, the experiments and observations were conducted in laboratories, insectaries, plantations and natural forests, while the plants used ranged from artificial trees, needles, seedlings and young trees to mature trees. In each study, different parameters were selected as indicators of host preference, namely the number of egg batches per tree, the number of larval tents per tree, the percentage of foliar damage per tree, or the percentage of food not consumed by larvae at the end of the experiments. Out of a total of 20 pine species tested by all authors, comparisons are possible for nine only, each of them being included in at least two studies: *Pinus brutia, P. canariensis, P. halepensis, P. mugo, P. nigra, P. pinaster, P. pinea, P. radiata* and *P. sylvestris. P. canariensis* was considered the least preferred species by the two studies (Petrakis et al. 2005 and Carrillo-Gavilán et al. 2012). However, for the remaining eight pine species, results are not conclusive, as exemplified by *P. nigra*, which emerged as the preferred species in Stastny et al. (2006), as first or second preference in Nicoli et al. (2008) and as the least preferred species in both Tiberi et al. (1999) and Petrakis et al. (2005). Similarly, *P. radiata* ranked as first preference in Nicoli et al. (2008), second in Carrillo-Gavilán et al. (2012), intermediate in Petrakis et al. (2005) and as least preferred species in Tiberi et al. (1999).

Table 6.1 Thaumetopoea pityocampa relative order of preference of *Pinus* species tested under laboratory, insectary and field conditions, reported in seven papers. N – Species native to Europe and the Mediterranean basin; I – Introduced species. Number of studies that included the pine species highlighted: *black*: one; *green*: two; *magenta*: four; *red*: five or six



Reference	Pine host species	Host origin	Order of preference by processionary moth	Country Region	Experimental conditions	Moth stage and parameters assessed	Observations
Tiberi *et al.* (1999)	*P. radiata*	I	1	Italy : Toscani and Latium	Pine plantations, 600 a.s.l.	Eggs. Mean nr. of egg batches/ tree	Unequal sample size: 2 to 24 trees/ host sp. used; no statistical treatments performed.
	P. pinaster	N	2				
	P. pinea	N	2				
	P. nigra	N	4				
	P. sylvestris	N	5				
Petrakis *et al.* (2005)	*P. longaeva*	I	1	Greece	Laboratory arena feeding trials. Twigs with current year needles.	Larvae: instars L3 and L4. Nr. of days until onset of feeding; % of food remaining after each trial ended.	Needles used in the choice and feeding trails, treated with extracts of other species.
	P. pumila	I	1				
	P. halepensis	N	2				
	P. heldreichii	N	2				
	P. attenuata	I	3				
	P. brutia	N	3				
	P. peuce	N	3				
	P. pinaster	N	3				
	P. canariensis	N	4				
	P. mugo	N	4				
	P. nigra	N	4				
	P. pinea	N	4				
	P. radiata	I	4				
	P. densiflora	N	5				
	P. sylvestris	N	5				
Stastny *et al.* (2006)	*P. nigra*	N	1	Italy Rovereto and Venosta	Field: 240-1200 asl	Larvae. Mean nr. of tents/tree	
	P. mugo	N	2				
	P. sylvestris	N	3				
	P. nigra	N	1		Laboratory	Adults. Female oviposition preference	
	P. mugo	N	2				
	P. sylvestris	N	3				
	P. mugo	N	No differences between species		Laboratory	Larvae: L1 and L3. Larval performance	
	P. nigra	N					
	P. sylvestris	N					

(continued)

Table 6.1 (continued)

Niccoli *et al.* (2008)	*P. nigra*	N	1	Central Italy	Field: 2 years old trees, 0.8 -1.5 m height. (generally under minimum size for pine processionary moth attack)	Eggs: mean nr. of egg batches/ tree	Adults introduced in the stands before emergence. Trees treated with monoterpenes. Host species natural bouquets not analyzed.
	P. pinea	N	1				
	P. pinaster	N	3				
	P. radiata	I	4				
Paiva *et al.* (2011a)	*P. brutia*	N	1	Portugal: Setúbal Peninsula	Insectary and Field: *P. pinea* 15 years old plantation	Adults. Female oviposition preferences. Mean nr. of egg batches/ tree	Insectary: artificial *"trees"*. Field: *P. pinea* plantation / *P. pinea* trees emitting *P. brutia* volatiles
	P. halepensis	N	3				
	P. pinaster	N	2				
	P. pinea	N	3				
Carillo-Gavilan *et al.* (2012)	*P. pinaster*	N	1	Spain	Insectary and laboratory	Foliar damage: 3 classes. Pine seedlings (1 year old) used in bioassays.	Mostly non-significant differences; in nature pine processionary larvae do not usually feed on pine seedlings.
	P. coulteri	I	2				
	P. radiata	I	2				
	P roxburghii	I	2				
	P. sylvestris	N	2				
	P. canariensis	N	3				

Although *P. pinaster* was considered as intermediately preferred in four out of the five papers that studied it Tiberi et al. (1999), Petrakis et al. (2005), Nicoli et al. (2008), and Paiva et al. (2011a), it ranked as first preference in Carrillo-Gavilán et al. (2012).

The influence of *Pinus* species origin, native vs. introduced, in determining *T. pityocampa* food preferences was examined inpine seedlings of five native and four introduced *Pinus* species, no significant differences being detected between the two groups of species (Carrillo-Gavilán et al. 2012).

In summary, according to the research conducted in different Mediterranean regions, a fixed rank order of pine species preferences for *T. pityocampa* is not apparent. Hódar et al. (2002) concluded that *T. pityocampa* moths were rather unselective when ovipositing on *P. nigra*, *P. sylvestris nevadensis* and *P. pinaster* and that oviposition on the later species can be considered an oviposition mistake. However, in France *P. pinaster* is highly attacked (Abgrall and Bouhot 1990; Bories et al. 2012), while in Portugal it experienced the highest level of attack among three native and five exotic pine species (Mateus 2009). Several factors, such as use of different methodologies and different response variables may have obscured general patterns. However one may also assume that these discrepancies actually account for true difference in host preference between different populations or genotypes of *T. pityocampa* and/or between genotypes or provenances of *Pinus* species.

Regarding the same pine species, variations in the level of attack by *T. pityocampa* among regions are often observed. This trend can be exemplified by *P. halepensis* which experiences intense attacks over most of the 3.5 million ha occupied in the Mediterranean region, as reported from Spain (Pérez-Contreras et al. 2008), France (Huchon and Démolin 1970) and Algeria (Zamoum et al. 2003). Concomitantly, in eastern Mediterranean regions, the sister species *Thaumetopoea. wilkinsoni* causes defoliation in Israel (Mendel 2000), Lebanon (Talhouk et al. 2001) and Western Turkey (Carus 2009). By contrast, *P. halepensis* is not attacked in Cyprus (Hassan 1971) and Portugal, not even in the vicinity of *P. pinaster* stands attacked by *T. pityocampa* (authors' personal observations).

Co-evolution and adaptation to local pine species is possible. For example *P. halepensis* comprises of two groups, the Eastern Mediterranean, which shows introgression with *P. brutia,* and the Western Mediterranean (Schiller et al. 1986), that have undergone different evolutionary histories (Gómez et al. 2001). In particular the two sub-species are exhibiting contrasting anatomy (Esteban et al. 2010) and/or phenotypic adaptations (*e.g.* Voltas et al. 2008), could explain different susceptibilities to *T. pityocampa*. In accordance, in Greece *P. halepensis* was slightly preferred to *P. brutia* (Petrakis et al. 2005), while in Portugal *P. brutia* ranked as 1st preference and *P. halepensis* as the least preferred species (Paiva et al. 2011a). Evidence therefore indicate that local adaptation of the pine processionary moth is possible (*e.g.* Zovi et al. 2008).

To some extent, *T. pityocampa* population dynamics can be shaped by the host species distribution (Kerdelhué et al. 2009; Samalens et al. 2012). At regional scale, the relative abundance of a host species, as well as the length of its presence in historical time, appear to influence the pattern and level of attack by *T. pityocampa* (Hódar et al. 2002). The fact that pine processionary moth refugia were located in the western part of the Iberian Peninsula, where a specific sub-clade of the *Thaumetopoea* complex is present (Kerdelhué et al. 2009), may further explain variable host preference across the Mediterranean basin.

In conclusion, local adaptation and evolutionary processes probably contribute to explain apparent contradictory results, regarding *T. pityocampa* host preferences in different regions. Differences in the needles physical traits such as needles length, width and toughness (e.g. Pérez-Contreras et al. 2008), or chemical traits, such as concentration of volatiles or antifeedants, could explain different preferences among pine species.

2.4 Use of Visual, Olfactory and Thigmotactic Cues to Select Host Trees

Visual, olfactory and thigmotactic cues, often acting in synergism (*e.g.* Zhang and Paiva 1998; Pérez-Contreras et al. 2008), are central drivers of *T. pityocampa* moth ecology and behaviour.

The role of thigmotactic cues in host selection by *T. pityocampa* females remains poorly studied. Pérez-Contreras et al. (2008) found that *T. pityocampa* females preferentially selected for oviposition the longest and most asymmetrical needles of *P. halepensis*. Démolin (1969a, b) suggested that the width of pine needles should correspond to the size of female moth tarsa, allowing a good hanging during the oviposition process.

The role of visual cues in host selection by *T. pityocampa* was first pointed out by Calas (1897). Démolin (1969a, b) concluded that females use the shape of tree silhouette against a light background, leading to preferential oviposition on isolated or unshaded trees, thus allowing larval tent development under optimal sun light conditions. Preferential selection of larger trees was also emphasized by Pérez-Contreras and Tierno (1997) and Nicoli et al. (2008), while isolation from neighbor trees and thus insulation, has also been recognized as influencing females oviposition behavior (Géri et al. 1985; Dulaurent et al. 2012). In Israel *T. wilkinsoni* displayed a decreasing order of preference of three pine species, *P. eldarica, P. brutia* and *P. halepensis* that could be related to tree shape, taller trees as well as those located at the edges of the stands being preferentially selected (Mendel 1988). At the canopy level, empirical observations indicate that most egg batches are laid in branches facing south (authors' observations).

Larger and more isolated trees are more likely to be infested by the pine processionary moth which suggests a prominent role of visual stimuli in host selection by *T. pityocampa*. However, quantities of pine volatiles emitted by pines are correlated with tree age (e.g. Nicoli et al. 2008) and size (Nicoli et al. 2008; Mateus et al. 2010), so that large amounts of attractants emitted by isolated, larger trees might also result into higher host attractiveness. In consequence, the respective role of visual and olfactory cues is difficult to establish.

Several terpenes have been proposed as host odours recognized by *T. pityocampa*. Electrophysiological experiments showed that the antenna of *T. pityocampa* females responded strongly to four monoterpenes present in the needles of *P. sylvestris*: myrcene, β-phellandrene, trans-β-ocimene and terpinolene. Weaker but repeatable responses were also found to limonene, cis-β-ocimene, and c-terpinene (Zhang et al. 2003). Surprisingly, the most common and major monoterpene in many pine species, α-pinene, 3-carene, and β-pinene were antennally inactive.

In an insectary study, *T. pityocampa* females oviposited on artificial tree dummies, each one baited with an extract from one of four different *Pinus* species. The highest number of egg batches was laid on the dummy baited with a *P. brutia* extract (Fig. 6.2). A field trail was next conducted in a pure *P. pinea* stand attacked by *T. pityocampa*, where an equal number of trees were baited with either an extract of *P. brutia,* or a solvent. The former group received significantly more egg batches than the later, demonstrating that olfactory cues play an important role in host selection by *T. pityocampa*, even when decoupled from visual stimuli – Fig. 6.2 (Paiva et al. 2011b).

Mateus (2009) identified the constituents of the needles of eight *Pinus* species present in an arboretum, evidencing a relationship between the percentage of trees

Fig. 6.2 *T. pityocampa* egg batch laid on plastic needles of a tree dummy, baited with an extract of *Pinus brutia*, in a field insectary (Paiva et al. 2011b)

attacked by *T. pityocampa* and the needles volatile composition. A partial least squares (PLS) regression showed that the first two significant components extracted accounted for over 82.0 % of the variation observed, the most relevant volatiles explaining the differences being β-pinene, terpinolene, limonene + β-phellandrene, myrcene and sabinene (Fig. 6.3). Previous studies showed significant correlations between the contents of the needles of ten pine species in β-pinene, and limonene (Da Silva et al. 2001) and the mean number of larval winter tents/tree of *T. pityocampa* (Paiva et al. 2001).

Two other studies (Tiberi et al. 1999; Nicoli et al. 2008 showed contradictory results (Table 6.2).

For example β- pinene was proposed as repellent by Nicoli et al. (2008), attractant by Mateus et al. (2010) and inactive by Zhang et al. (2003).

Likewise an increase in limonene production by *P. pinea* was observed, both at the start of the flight period and at the beginning of the oviposition period of *T. pityocampa*, which could have a deterrent behavioural effect (Tiberi et al. 1999). In agreement, limonene emulsified with water and sprayed on the foliage of *P. sylvestris, P. nigra, P. pinaster* and *P. radiata* provided a satisfactory degree of protection against oviposition by the moth (Tiberi et al. 1999). However Nicoli et al. (2008) could not reproduce this negative effect.

Moths may use medium/long range olfactory stimuli to locate suitable hosts, since the presence of nonhost trees resulted in a lower *T. pityocampa* infestation of pine stands (Jactel et al. 2012b). Still, generalizations regarding the role of olfactory stimuli in host selection by *T. pityocampa* are not yet consensual. This may be due to the consideration of single compounds whereas it is generally accepted that specific blends of semiochemicals are needed to trigger behavioural responses (e.g. Paiva et al. 2001; Stastny et al. 2006; Jactel et al. 2011, 2011a). Given that 420 volatile substances were identified from the needles of 10 *Pinus* species (Mateus et al. 2010), decoding the composition of such blends will take time.

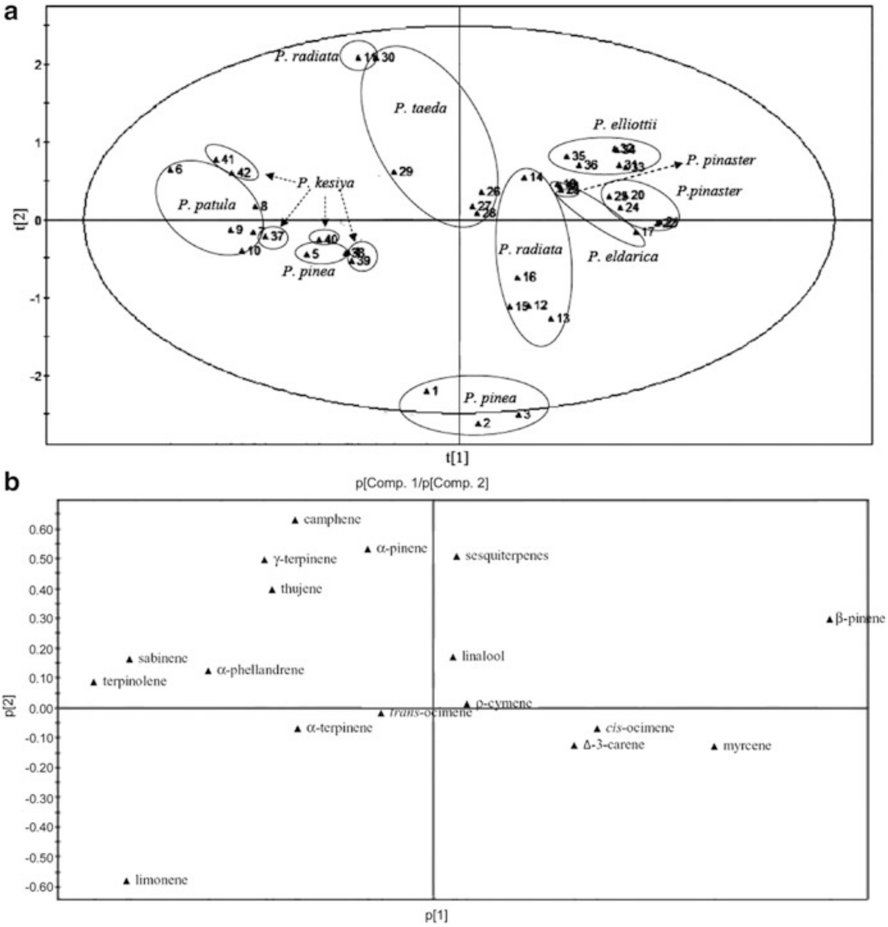


Fig. 6.3 (**a**) Partial least squares scores t_1 and t_2 for eight *Pinus* species, *P. patula*, *P. kesiya*, *P. pinea*, *P. radiata*, *P. taeda*, *P. elliottii*, *P. eldarica* and *P. pinaster* regarding the percentage of attack by *T. pityocampa*. Abrantes, Portugal (Modified from Mateus 2009). (**b**) Partial least squares loadings p_1 and p_2 for the scores data set (limonene = limonene + β-phellandrene)

2.5 Host Tree Exploitation by Larvae

Globally, three main factors related to the needles of host tree may influence larval performance: (i) nutritive quality; (ii) palatability, resulting in amount of ingested food and (iii) toxicity in relation to the ability of the larvae to cope with it. The three factors are determined by the needles physical and chemical characteristics that, to a large extent, affect *T. pityocampa* population dynamics.

Table 6.2 Pine semiochemicals linked to host selection by adult females of *T. pityocampa*, reported in four papers

Reference	Substances	Pine processionary response (0; +; −) *or* presence of substances in host species (V)	Experimental conditions Country	Parameters quantified	Observations
Nicoli et al. (2008)	(R)-(+)-limonene	(0)	Field: *P. nigra*, *P. pinea,* *P. radiata*, *P. pinaster*, 2–3 years old, 0.8–1.5 m height	% of egg batches laid.	Insects introduced in the stands before adult emergence
	(S)-(−)-limonene	(0)	Central Italy	Response to host trees treated with monoterpenes	
	(1S)-(−)-β-pinene	(−)			
Tiberi et al. (1999)	(R)-(+)-limonene	(− −)	Field: *P. pinaster*, *P. nigra,* *P. sylvestris*, *P. radiata* sprayed with semiochemicals	% of egg batches laid	
	(S)-(−)-limonene	(−)	Italy		
Mateus (2009)	β -pinene	(+)	Arboretum: *P. eldarica* *P. elliottii*, *P. kesiya,* *P. patula*, *P. pinea,* *P. pinaster*, *P. radiata,* *P. taeda*	% tree defoliation/ species distribution using a PCA analysis	About 400 pine volatiles were identified
	terpinolene,	?	Portugal		(+) influencing attack
	(−)-limonene and (+)-limonene plus	(−)			(−) influencing absence of attack
	β-phellandrene				
	myrcene	?			
	sabinene	?			

Paiva et al. (2011a)	cis-ocimene	(V) preferred sp	Insectary: dummy trees baited with extracts of *P. brutia, P. pinaster, P. pinea, P. halepensis*	% egg batches laid	Substances found in either the preferred species only, or in the 1st and 2nd preferred species only
	bornyl acetate isomer 1	(V) preferred sp.			
	β- copaene 1	(V) preferred sp	Field: *P. pinea*		
	α- cubebene	(V) 1st and 2nd preferred spp.	Portugal		
	α -bourbonene	(V) 1st and 2nd preferred spp.			

Substances triggering behavioural responses: attraction (+); repulsion (–, - -); (0) no effect. Substances present in the preferred pine species only (V)

2.5.1 Chemical Characteristics of the Needles

The nutritional value of a host for an insect herbivore is related to primary components present in the needles, mainly nitrogen in the form of amino acids, proteins and soluble sugars. A high C/N ratio, representing a high proportion of structural carbohydrates compared to nitrogen, is known to negatively affect larval growth of herbivore insects in general and for *T. pityocampa* larvae in particular. Several experiments on larval performance suggest that the survival of early larval instars is affected by food quality (Hódar et al. 2002; but see Stastny et al. 2006). Hódar et al. (2002) attributed larval mortality in early instars to differences in N contents of needles, whereas larval growth was not affected by this nutrient. A higher survival of both *T. pityocampa* and *T. wilkinsoni* larvae was observed on *P. pinaster* plants grown in a nursery, by comparison with field plants, which was attributed to higher N content in the former (Rocha 2011).

Secondary metabolites, such as phenols, terpenes and resin acids, provide chemical defenses against herbivores, being either constitutive or induced, following attack by herbivores (Fordyce and Agrawal 2001; Kouki and Manetas 2002). These compounds might reduce digestibility and thus negatively affect larval metabolism, or have a possible toxic effect causing acute or chronic individual mortality. Larval ability to detoxify such compounds in part determines its host range. In a study with 14 conifer species, *T. pityocampa* larvae could not complete development on five host species, *P. strobus*, *P. parviflora*, *P. cembra*, *P. wallichiana* and *Larix kaempferi*, although the exact effect of the needles traits on larval performance was not identified (Devkota and Schmidt 1990).

The role of constitutive defenses in host foliage on *T. pityocampa* performance has not been clarified. Still, a direct relationship between previous defoliation of host trees and *T. pityocampa* larval survival has been suggested by several authors (*e.g.* Battisti 1988; Hódar et al. 2004; Zamoum and Démolin 2004; Sbabdji and Kadik 2011). Hódar et al. (2004) for example showed that the highest values of *T. pityocampa* larval survival were observed on undefoliated pines, intermediate survival were found on pines defoliated only in the previous year whereas the lowest values were obtained on trees that had experienced two consecutive years of defoliation. A possible explanation would be a strong physiological response of host pine following defoliation, that would notably alter needles characteristics (Sbabdji and Kadik 2011) such as secondary metabolites, resulting in lower larval performance (Hódar et al. 2004). Still, none of the needles traits analyzed showed a clear relationship with larval survival.

Among secondary metabolites, resin acids may act as feeding inhibitors and cause low larval performance and survival in several species developing on *Pinus* spp. (*e.g.* Saikkonen et al. 1995; Pasquier-Barre et al. 1999), although some insects may sequester them for their own protection against predators (Larsson 1989). Further research is needed to assess the relevance of resin acids for *T. pityocampa* larval development.

As a result of co-evolutionary history, herbivore insects are expected to be better adapted to the chemical and physical traits of their native host species, than with those of exotic species. Therefore, for *T. pityocampa* a high degree of adaptation to Mediterranean European pines could be expected. Complementarily, non-native species may lack defenses against specialized herbivores, thus presenting a higher susceptibility. Such is the case of *P. radiata* plantations in Europe which are heavily attacked by *T. pityocampa*. Lombardero et al. (2012) compared stands of a native species, *P. pinaster* with an introduced one, *P. radiata*, regarding tree nutritional quality and oleorosin flow, considered as a host defense indicator. It was concluded that stands of the exotic pine were more suitable for *T. pityocampa* than stands of the native *P. pinaster*. Moreira et al. (2013) exposed juvenile trees of *P. pinaster* and *P. radiata* to herbivory by *T. pityocampa* larvae. Constitutive defenses were measured in the stem and needles of control plants, while in chewed plants the herbivore-induced concentrations of total polyphenolics, volatile and non-volatile resin, as well as the profile of mono- and sesquiterpenes were quantified. Results showed no major effects of folivory on needles defensive chemistry, but a strong increase in the concentration of polyphenolic compounds in the stem. However opposite examples exist, i.e. exotic pine species that are resistant, i.e. poor host for *T. pityocampa* such as *Pinus aristata, P. arizonica, P. flexilis, P. massoniana,* or *P. resinosa* (authors' observations).

Thompson and Pellmyr (1991) proposed that host trees selected by females should coincide with the best nutritional food for the offspring, guarantying optimal larval survival. Consequently adults behavioural responses to host stimuli should be related to the quality of host plant tissues. Yet, lack of co-evolutionary history with specific host plant species, or trade-offs with other environmental factors such as natural enemies, might determine a mother's choice for host plants less favorable for their offspring (Randlkofer et al. 2007). A discrepancy between female host choice and larval performance has been observed for *T. pityocampa*, since under no-choice conditions, females remained discriminating in spite of time limitation, while the relative growth rate (RGR) and mortality of the larvae did not differ significantly among three host pine species (Stastny et al. 2006).

2.5.2 Needle Physical Characteristics

In addition to chemical characteristics of host plant foliage, physical morphological defensive traits may hinder larval performance (*e.g.* Fordyce and Agrawal 2001; Kouki and Manetas 2002). Regarding *T. pityocampa,* several studies concentrated on the effects of leaf toughness on larval mortality. Schopf and Avtzis (1987) could relate larval mortality to the toughness of needles (measured in terms of silica content), while the concentration of soluble carbohydrates, amino acids and phenolic compounds had no influence.

A positive correlation was evidenced between needle toughness and C/N ratio in four pine species (Branco et al. unpublished). Still, no detrimental effect of needles toughness was observed on larval performance in the same study. The highest

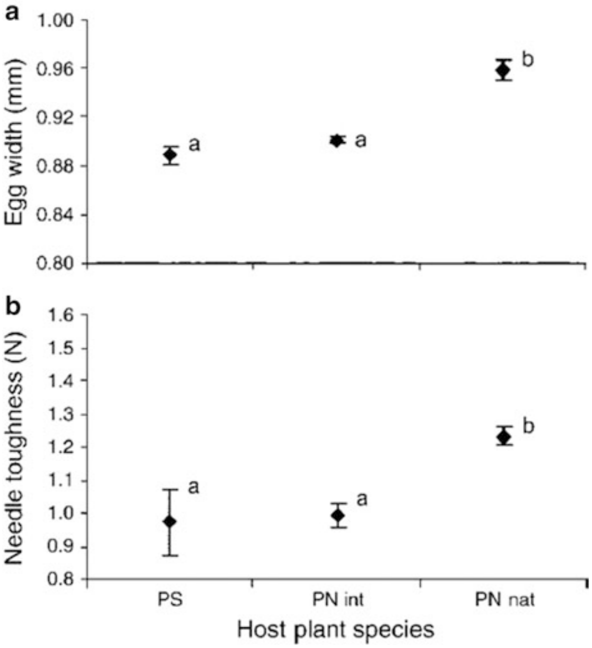


Fig. 6.4 (**a**) *T. pityocampa* larvae feeding on *Pinus sylvestris* PS; *Pinus nigra* PN, introduced (int); *Pinus nigra* (PN, native stands (nat). (**a**) Egg size (12–30 egg batches per site, 10 eggs measured per batch); (**b**) Needle toughness (in newtons) of the three types of host pines (n = 20 trees for each host type). Different lowercase letters indicate significant differences in pairwise comparisons of means (Tukey test, P, 0.01) (Modified from Zovi et al. 2008)

consumption (i.e. ingestion) occurred on *P. pinaster*, which had the hardest needles, suggesting a compensatory effect of higher metabolic costs for *T. pityocampa* larvae (Branco et al. unpublished). Mendel (1988) found similar results in a *Pinus* spp. – *T. wilkinsoni* system.

In the Italian Alps, *P. nigra* and *P. sylvestris* differed in needle toughness across an East – West gradient. Concomitantly, a size gradient of *T. pityocampa* eggs and larvae was observed, matching the pattern of foliage toughness in the respective local host plants (Zovi et al. 2008) (Fig. 6.4).

2.6 Conclusions

In summary, host tree selection by the pine processionary moth involves a large range of physical and chemical cues acting at different spatial and temporal scales. Female moths seem to distinguish first between suitable vs. unsuitable habitats using long range volatile organic compounds signaling the presence of large masses of pine trees that will supply larvae with edible foliage. Then at closer proximity adult moths would mainly rely on visual cues to focus on isolated or taller trees that are more likely to provide optimal microclimatic conditions (high solar radiation) for eggs survival and successful development of larvae. Once landed on more apparent host pine tree, thigmotactic stimuli, based on needle width and toughness, would trigger ovipositing but also inform on leaf palatability for young larvae. Depending on local adaptation to the relative amount of host pine species or genotypes, these processes would evolve, leading to variable host preferences.

3 Effect of Tree Species Diversity on Associational Resistance to *Thaumetopoea pityocampa*

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3.1 Introduction

There is a growing body of evidence to support the assumption that biodiversity provides forest ecosystem services, including natural pest regulation. Recent reviews (Jactel and Brockerhoff 2007; Vehviläinen et al. 2007; Castagneyrol et al. 2012) have demonstrated that particular forests with higher diversity of tree species are less prone to forest insect damage, a phenomenon known as associational resistance. The effect of forest diversity on insect herbivory significantly depends on two main factors, (i) the host specificity of herbivores and (ii) the quantitative and qualitative characteristics of tree species assemblages. Mixed forests provide strongest associational resistance to mono- and oligophagous insect herbivores, those able to feed on tree species within the same genus or family respectively. By contrast, the effects of tree mixtures on polyphagous insects (feeding on tree species from different families) are neutral or even positive, i.e. leading to higher damage than in pure forest stands (associational susceptibility). The relative proportion of the focal tree amongst other associated trees is also a critical driver of resistance because the dilution of host trees limits the ability of insect herbivore to find and exploit their feeding resources (Castagneyrol et al. 2013). Finally, the composition of tree mixtures seems to be more important than species richness *per se* because diversity effects on herbivory are often greater when mixed forests comprised taxonomically (Jactel and Brockerhoff 2007) or phylogenetically more distant tree species (Yguel et al. 2011; Castagneyrol et al. 2012).

The pine processionary moth, *Thaumetopoea pityocampa*, can be considered as an oligophagous insect, mainly feeding on pine within the *Pinus* genus and sometimes on other tree species from the Pinaceae family, e.g. *Cedrus* (Devkota and Schmidt 1990; Masutti and Battisti 1990). Although pine species such as Scots pine (*Pinus sylvestris*), black pine (*P. nigra*), Aleppo pine (*P. brutia*) and maritime pine (*P. pinaster*) are often grown as pure stands in forest plantations, they also co-occur with many broadleaved species such as oaks and birch in semi natural forests of the native range of pine processionary moth. There are therefore objective reasons to believe that the management of the main host trees of the pine processionary moth in admixture with other, phylogenetically different tree species might result in lower infestation level by pine processionary moth. And yet, as early as in 1980, Géri (1983a, b) observed in Corsica significantly less pine processionary moth damage on the Corsican black pine (*P. nigra laricio*) growing in admixture with beech trees (*Fagus sylvatica*) than in pure stands of Corsican pine. Since then several studies have addressed the relationship between tree species diversity, both at the stand and landscape scale, and resistance to pine processionary moth defoliation.

The objective of this chapter is therefore to present the knowledge that has accumulated on this functional relationship. The main ecological mechanisms underlying associational resistance to insect herbivory will be reviewed and tested for their relevance to pine processionary moth. Then we will suggest several implications of these results for the preventive control of moth populations.

3.2 Disruption of Host and Habitat Location Cues for Pine Processionary Moth (Bottom-Up Processes)

Increased host availability is often cited as the main reason for the higher rates of insect herbivory in tree monocultures (Jactel and Brockerhoff 2007; Barbosa et al. 2009). According to the resource concentration hypothesis (Root 1973) insect herbivores are more likely to find their host plant if it is present at high density and in more diverse plant communities, host plants are proportionally less frequent (Hambäck and Beckerman 2003) leading to reduced likelihood of host finding and exploitation. In his Corsican study, Géri (1983a, b) observed a reduction of 35 % of pine processionary moth defoliation on Corsican pines when the proportion of beech equalled 50 % in the mixed stands and of 96 % when this proportion of non host trees reached 75 %.

This local effect was also observed at the landscape scale. An intensive spatial monitoring of mothtent density was carried out over a 16 × 16 km area (ca. 25,000 ha) of pine plantation forests. Even in this ecosystem mostly covered by the host pine species, the study clearly showed that landscape composition is an important driver of the spatial distribution of pine processionary moth (Samalens and Rossi 2011). The strongest landscape component negatively correlated with tent density was the percentage of non-host tree species within a surrounding landscape of 1 km radius. Subsequently, in order to quantify the independent effect of those broadleaved forests on infestation by pine processionary moth, pairwise comparisons were made between pine stands within heterogeneous forest landscape vs. within pine monoculture (Dulaurent 2010). Paired stands were selected independently, controlling for stand characteristics and taking into account for the spatial correlation of pine processionary mothtent density throughout the landscape. The presence of more than 15 % of broadleaved riparian forests in surrounding landscapes resulted in a reduction of ca. 90 tents/ha in the central pine stands (Fig. 6.5) which represented on average 60 % less tents than in similar stands

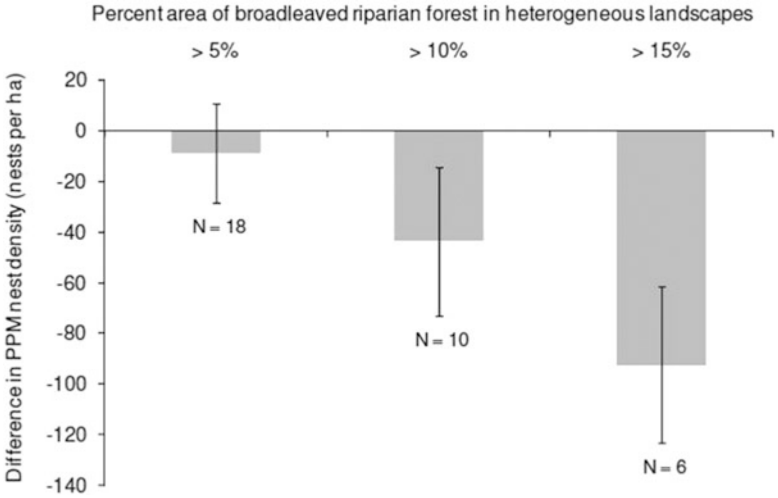


Fig. 6.5 Mean difference in tent density of pine processionary moth between pine stands within heterogeneous landscape and paired stands within pine monocultures, for different samples of stands corresponding to increasing percent of broadleaved forests in heterogeneous landscapes

located within pine monoculture. This reduction was observed above a threshold of 15 % of broadleaved forest in the pine plantation forest landscape.

3.2.1 Visual Cues

Besides the quantitative reduction of host resources, the adjunction of non host tree species might also result in the disruption of host finding cues, i.e. in reduced host apparency. Host apparency has been defined as the probability of a plant being found by herbivores (Endara and Coley 2011) and several recent studies have shown that it can be a main driver of associational resistance (Giffard et al. 2012; Castagneyrol et al. 2013). Visual attraction to hosts has been demonstrated for several phytophagous insects (see Prokopy and Owens 1983). In particular, the use of host shape contrast by insects has been recorded for another processionary moth, *Ochrogaster lunifer* on acacia trees (Floater and Zalucki 2000). Since the seminal work of Démolin (Démolin 1969a, b), it is currently admitted that female moths use the shape of a tree silhouette against a clear background to select the host tree prior to egg laying. This behaviour is consistent with the common observation of higher infestation levels of pine processionary moth at forest stand edges than in forest interiors (Dulaurent et al. 2012). The presence of non host vegetation may then hide host trees from the vision of insect herbivores (Watt 1992) as already suggested for the pine tip moth *Rhyacionia frusfrana* (Sun et al. 2000), the spruce budworm *Choristoneura fumiferana* (Bergeron et al. 1995), or leaf-tying larvae on *Quercus alba* (Marquis et al. 2002). It was therefore hypothesized that non host, e.g. broadleaved trees standing in front of pine stand edge could hide host tree

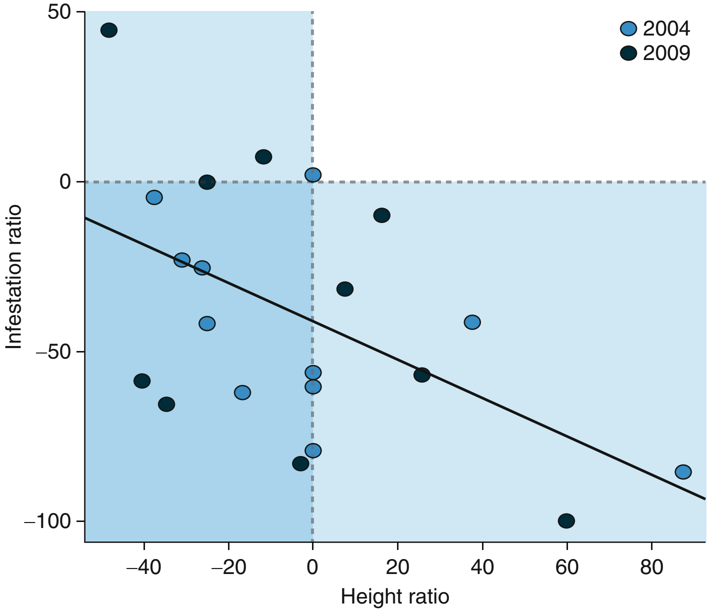


Fig. 6.6 Relationship between relative infestation ratio (IR) of pine processionary moth and tree height ratio (HR). IR was calculated as the difference between moth infestation on pines behind the hedgerow and moth infestation on pines along pine stand edge (control) divided by moth infestation on pines along pine stand edge. HR was calculated as the difference between height of hedgerow and height of pines divided by height of pines (see Dulaurent et al. 2011 for details)

from ovipositing female and ultimately reduce the risk of defoliation by offspring larvae. This hypothesis was tested in a quasi experimental setting. Twenty one pure, even-aged maritime pine stands were selected in the Landes de Gascogne forest (France) with a part of their edge hidden by a broadleaved hedgerow while the rest of the edge remained totally visible. Winter tents of pine processionary moth were counted on trees located on the first rows of the sampled pine stand edge, both behind the hedgerow and on the exposed part of the edge, over the same edge length (Dulaurent et al. 2011). The presence of a broadleaved trees hedgerow resulted in a decrease of 40–90 % moth infestation on pine edge when the hedgerow was higher than the pine canopy whereas no significant reduction in pine processionary moth infestation were detected behind smaller hedgerows (Fig. 6.6).

This pattern might be explained by an active choice of the most apparent trees by female moths, based on visual cues. However it may alternatively resulted from lower egg survival behind the hedgerow due to the effect of predation and parasitism by natural enemies benefiting from complementary habitat, or unfavourable microclimatic conditions in the shade of broadleaved trees. In a subsequent experiment, sentinel egg masses obtained from a laboratory rearing were installed on pine trees behind broadleaved hedgerows or on the exposed part of the pine stand edge. Egg masses were either protected from predation by a net or left unprotected

(Castagneyrol et al. 2014). Automatic data loggers were used to monitor microclimatic conditions. No significant differences in egg mortality due to predation or microclimatic conditions were detected on pine trees situated on exposed edge or behind the broadleaved hedgerow. It is therefore more probable that the reduced pine processionary moth infestation observed on tree hidden by broadleaved non host trees resulted from the disruption of cues used by female to select the host tree prior to oviposition.

3.2.2 Olfactory Cues

However, plant odours seem to play the major role in insect host-recognition and location processes (Tasin et al. 2006). Non-host plant odours might then disturb olfactory-guided host choice by specialist herbivores as suggested by the "semiochemical diversity hypothesis" (Zhang and Schlyter 2003). Several studies have shown that non-host plant volatiles can chemically "hide" neighbouring trees and deter pest insect herbivores such as bark beetles (Zhang and Schlyter 2004) and moths (McNair et al. 2000). It has also been shown that the emission of non-host volatiles can reduce the attacks of conifer bark beetles on host trees (Jakuš et al. 2003; Schiebe et al. 2011; Schlyter 2012) and the response of spruce seed moth to sex pheromone (Bédard et al. 2002). Olfactory cues released by conifers also seem to play a role in the host selection process of female moths. Adult female antennae respond to volatiles emitted by pine trees in electrophysiological tests (Zhang et al. 2003) and behavioural trials have shown that *T. pityocampa* females can discriminate among bouquets extracted from different host pine species which can drive oviposition preferences (Paiva et al. 2011b). Presence of non-host neighbouring trees may then also result in high release of non-host volatiles that would disturb host-pine recognition by female moths.

This hypothesis was experimentally tested by exposing cut branches of birch (*Betula pendula*) at the base of pine trees during the oviposition period (summer) of pine processionary moth. The following winter, pine trees with cut branches of birch at their base had significantly fewer larval tents compared to non-manipulated control trees within the same maritime pine stand (Jactel et al. 2011, 2012a). Further gas chromatography – electro antennography tests showed that both male and female antennae of pine processionary moth reacted to several compounds found in volatile collections of birch branches in a way similar to the response to pine odours (Zhang et al. 2003). Several volatiles were common to maritime pine extracts but another one was only found in aerations from birch and was identified as methyl salicylate (Jactel et al. 2011, 2012a). This compound inhibited significantly the male response to standard female pheromone traps, as did natural oak and birch materials. In a third experiment, the dose-response effect of methyl salicylate (MeSa) was tested in the field by placing release devices of synthetic MeSa along 25 m long edges of maritime pine stands. The next winter the number of larval tents was counted on the canopy of all pine trees located on treated edges vs. neighbouring control edges of the same size within the same stand. A clear

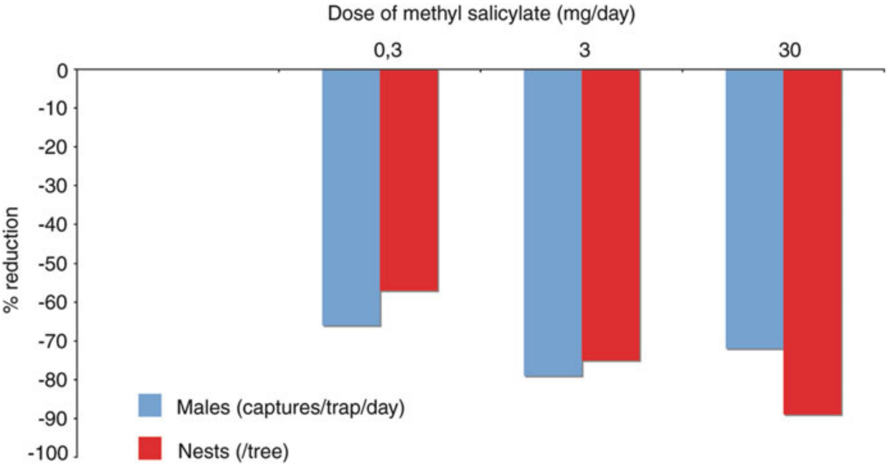


Fig. 6.7 Relative (to the control) percentage of reduction in male moth capture and winter tents of pine processionary moth along maritime pine stand edges (n = 12) where dispensers of different release rates of methyl salicylate (MeSa) were activated during the adults' summer flight period (see Jactel et al. 2011, 2012a for details)

reduction of larval winter tents with the dose of MeSa was observed (Fig. 6.7). The pine processionary moth infestation rate was reduced by ca. 80 % with the highest dose of 3 mg MeSa per m of forest hedge per day in treatment edge compared with the blank control edge.

All these results provide experimental support for the implication of non-host volatiles in associational resistance to pine processionary moth. Females were able to perceive several angiosperm non-host volatiles as shown by GC-EAD although the pine processionary moth is specific to conifers. This suggests that *T. pityocampa* had evolved the sensory capabilities to distinguish between suitable (pine) and unsuitable (broadleaved) trees or habitats since it has long lived within natural forests ecosystems associating the two types of tree. MeSa seems to play a critical role in the beneficial association of broadleaves to pines. MeSa is a very common volatile already identified from several tree genera but which are all deciduous (see Goff and Klee 2006). It has shown direct repellent effects on many insect herbivores including the forest moth *Lymantria dispar* (Marković et al. 1996). It has also been found as a volatile involved in indirect plant defense, where leaves damaged by herbivore attract predators and parasitoids (Turlings and Ton 2006). Furthermore recent studies have shown that associational resistance can be elicited by interplant communication *i.e.* eavesdropping (Barbosa et al. 2009) through the release of volatile organic compounds by damaged plants. Interestingly, one of the most common primers of this acquired resistance is methyl salicylate (Heil and Ton 2008).

MeSa naturally released by broadleaved trees where it is highly concentrated such as in birch, or artificially released in its inexpensive commercial form via dispensers might then offer an environmentally friendly method of control of pine processionary moth, notably in urban areas.

3.2.3 Microclimatic Cues

Changes in microclimate caused by neighbouring trees or vegetation can also influence the behaviour and survival of forest insect herbivores (Barbosa et al. 2009). In spring, late instar larvae of pine processionary moth make a procession to descend from the crown of pine trees before they bury into the soil and pupate. Prior to entering the soil they can crawl several tens of meters, searching for sunny exposed soil, notably in gaps or forest edges, probably to find optimal survival conditions for pupae. Most forest landscapes form a mosaic of pine stands, deciduous woodlands or hedgerows and patches of open area, resulting from clearcuts or along forest roads. Pine processionary larvae have therefore many opportunities to find preferred pupation sites in open areas. However, on some occasions, they may venture into neighbouring broadleaved stands or hedgerows that resemble open areas because they are without leaves in winter at the time of larval procession. Because the pupation phase lasts until the next summer, these deciduous trees have time to produce new leaves and microclimatic conditions can change from those of open areas to those of broadleaved forest cover. If these conditions of temperature and humidity are not favourable to pupae survival, neighbouring broadleaved habitats may act as ecological traps (Robertson and Hutto 2006). Larvae of pine processionary moth may be then mislead by microclimatic cues, such as warm temperatures and high insulation, to pupate in broadleaved habitat that can later prove to provide unsuitable soil or microclimatic conditions for pupae survival.

To investigate this question, pine processionary moth larvae were artificially forced to bury into three different soil origins, i.e. from pine stand, oak forest and grassland, which were further transplanted under the same three types of land cover using a complete factorial design (Dulaurent et al. 2011). A significant effect of the cover type, but not of the soil origin, was detected on the proportion of emerged pupae, i.e. of adult moths. The highest rates of moth emergence were observed in open areas and the lowest under forest covers (Fig. 6.8).

This is consistent with common observations of pine processionary larvae making procession towards forest gaps, clear cuts, edges or forest trails to bury into the soil (Démolin 1971). The main microclimatic characteristics explaining higher moth emergence in the experiment with larvae forced to burry were the soil temperature and relative humidity in April and May, the months that just followed the burying of larvae (in March). These findings are consistent with those of previous studies showing that microclimatic conditions right after pupation of pine processionary larvae are decisive for their survival (Démolin 1974; Markalas 1989). In the most favourable soil habitat, within open areas, edaphic temperatures were on average higher than 19 °C and humidity above 30 %. Too cold and dry soil habitat may be then detrimental to pupae survival. Of course extreme values in soil temperature and moisture, whether high or low, have also been found to have negative impact on the survival of pine processionary pupae (Démolin 1974; Markalas 1989).

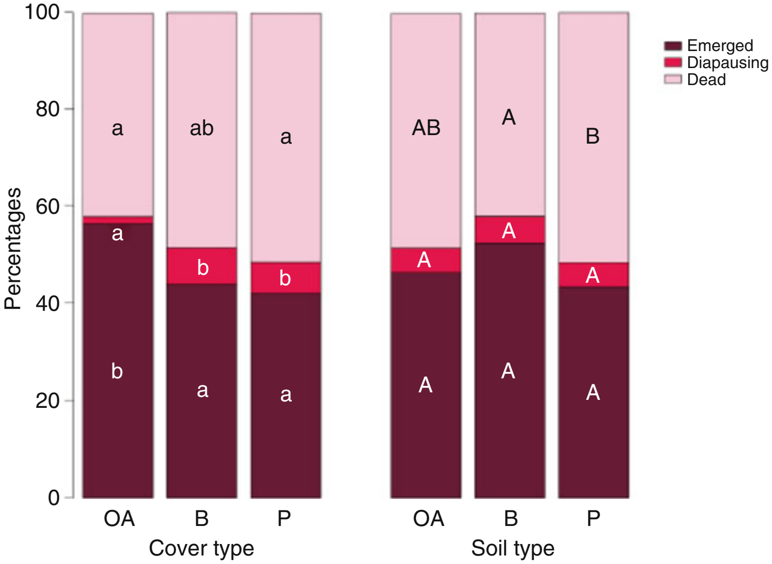


Fig. 6.8 Mean proportion emerged pupae, diapausing and dead pupae of pine processionary moth (%) for two classes of land cover and soil types. Different letters indicate significant differences between types (see Dulaurent et al. 2011 for details)

Active habitat selection by arthropods to gain shelter from adverse climatic conditions for the overwintering stage is well documented (Purtauf et al. 2005; Geiger et al. 2009). Pine processionary larvae seem to use the same behaviour by leaving pine stands with closed canopy, and so very few gaps, in the search of cooler open habitats. However they may also migrate in neighbouring broadleaved forests or hedgerows which no longer have leaves in canopy trees. And yet, broadleaved habitat proved to be unsuitable for pupae survival compared to open areas, notably because of colder temperatures in spring when the tree canopy closes again. The maintenance or plantation of broadleaved tree species next to pine forests might then act as an ecological trap, providing natural control of pine processionary moth populations.

3.3 *Reinforcement of Natural Enemies of Pine Processionary Moth (Top-Down Processes)*

The second main ecological mechanism explaining associational resistance is the "natural enemy hypothesis" which suggests that more diverse plant communities offer a greater array of complementary food and habitat resources that benefit natural enemies which can, in turn, control herbivores more effectively (Root 1973; Russell 1989; Barbosa et al. 2009). Generalist parasitoids and predators are likely to encounter a higher availability of alternative prey or hosts in mixed forests because they provide habitat for more herbivorous species (Castagneyrol and Jactel 2012). Richer plant communities can also provide a better supply of complementary food such as pollen, nectar and honeydew that improve the fitness of specialised parasitoids (Russell 1989; Cappucino et al. 1999). Finally, due to their higher structural complexity, mixed forests may provide predatory birds with more suitable tenting sites (Bibby et al. 1989; Donald et al. 1998; Najera and Simonetti 2010).

3.3.1 Reinforcement of Egg Parasitoids

Parasitism by two Hymenopteran species is the main mortality factor in the egg stage in pine processionary moth (Santos et al. 2008). *Ooencyrtus pityocampae* (Hymenoptera, Encyrtidae) is a generalist species which emerges 2 months earlier than the adult moth (Masutti 1964), and is known to parasitize other host insects feeding on broadleaved tree and shrub species (Masutti 1964; Battisti et al. 1988). Another main parasitoid of pine processionary eggs is *Baryscapus servadeii* (Hymenoptera, Eulophidae), a specialist species with emerge at the same time as the oviposition period of the pine processionary moth (Géri 1983a, b).

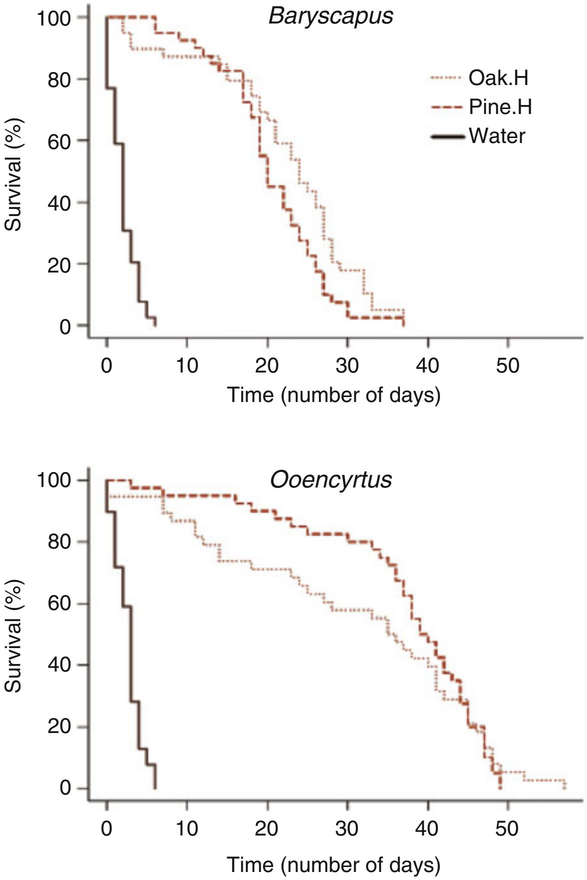
Mixtures of tree and plant species can provide a consistent supply of honeydew because different species host different aphids which produce at different times and so complement each other (Zoebelein 1957). Because honeydews differ in sugar and amino acid composition between aphid species and their host plants (Völkl et al. 1999), mixed forests may also provide insect parasitoids with more various food supplies. Sugar-rich foods may help generalist parasitoid species to increase adult longevity and allow them to alternate on several host species with different periods of occurrence. In specialist species, honeydew can be important for improving adult fecundity or mobility, thus improving their ability to find and parasitize their hosts.

The longevity of the generalist *O. pityocampae* and the specialist *B. servadeii* parasitoids of pine processionary eggs was compared under laboratory feeding conditions including water and honeydew from aphid species growing on maritime pine (*P. pinaster*) or pedunculate oak (*Q. robur*). The longevity of both parasitoid species increased when adult individuals were fed with honeydew (Fig. 6.9).

The specialist parasitoid longevity was increased by 23 days on averaged when fed with honeydew of oak aphids. The lifetime of adult *O. pityocampae* was increased by 32 days which allows an overlap of two weeks with the period of pine processionary eggs presence in pine forest, versus no overlap when no supplementary food was provided.

These findings support the hypothesis that mixed forests, associating pine and broadleaved trees or shrubs, can provide both specialist and generalist parasitoids of with complementary food resources such as honeydew which ultimately may improve their fitness and ability to locate and parasitize eggs of pine processionary moth.

Fig. 6.9 Kaplan–Meier estimates of the survival functions of the specialist species *Baryscapus servadeii* and the generalist species *Ooencyrtus pityocampae* according to trophic resources supplied to the parasitoid females. *W* Water (control), *O.H* Oak aphid honeydew, *P.H* Pine aphid honeydew



3.3.2 Reinforcement of Vertebrate Predators

At least eight bird species and five bat species are known or likely predators of the pine processionary moth (Barbaro et al. 2014, Chap. 7, this volume). These avian and chiropteran predators have either a specialist or generalist diet and included the barbastelle bat (*Barbastella barbastellus*), long-eared bats (*Plecotus austriacus* and *P. auritus*), Kuhl's pipistrelle (*Pipistrellus kuhlii*), serotine bat (*Eptesicus serotinus*), great spotted cuckoo (*Clamator glandarius*), common cuckoo (*Cuculus canorus*), European (*Caprimulgus europaeus*) and red-necked nightjars (*C. ruficollis*), Eurasian hoopoe (*Upupa epops*), and three tits (*Parus major, Lophophanes cristatus* and *Periparus ater*) (Barbaro and Battisti 2011). They all have particular foraging techniques that allow them feeding on pine processionary moth in spite of the urticating setae of the larvae and the protection offered by silky tents (larvae) or the soil (pupae) (Barbaro and Battisti 2011). Cuckoos have soft gizzard wall structure allowing to regurgitate urticating setae, great tits (*Parus major*) are able to discard the urticating integument of larvae before swallowing, hoopoes have a long curved beak to dig out buried pupae and break the cocoons, bats and nightjars can feed on flying adults of pine processionary moth which are not urticating (Barbaro and Battisti 2011).

As generalist predators, forest bats and passerines such as the great tit may benefit from alternative prey insects and tenting cavities that can be found in richer tree species communities and they are actually more abundant in mixed than in pure forest stands (Barbaro et al. 2007; Sweeney et al. 2010; Boughey et al. 2011). However, generalist birds can exhibit a significant numerical response to pine processionary moth (Barbaro et al. 2013), especially during cold winters, as well as generalist bats in summer during adult moth emergence (Barbaro et al. 2014, Chap. 7, this volume).

The foraging ecology of the specialist ground probing hoopoe, *Upupa epops*, has received more attention (Battisti et al. 2000). In south-western Europe, Eurasian hoopoes specialize in pine processionary pupae and are therefore particularly abundant in forest landscapes that provide a complementation of suitable habitats, i.e. pine forests that provide a large supply of prey insects and oak forest fragments where they can breed and find tenting cavities (Barbaro et al. 2007). At the home-range scale (Fig. 6.10), hoopoes show strong selection for short grassland

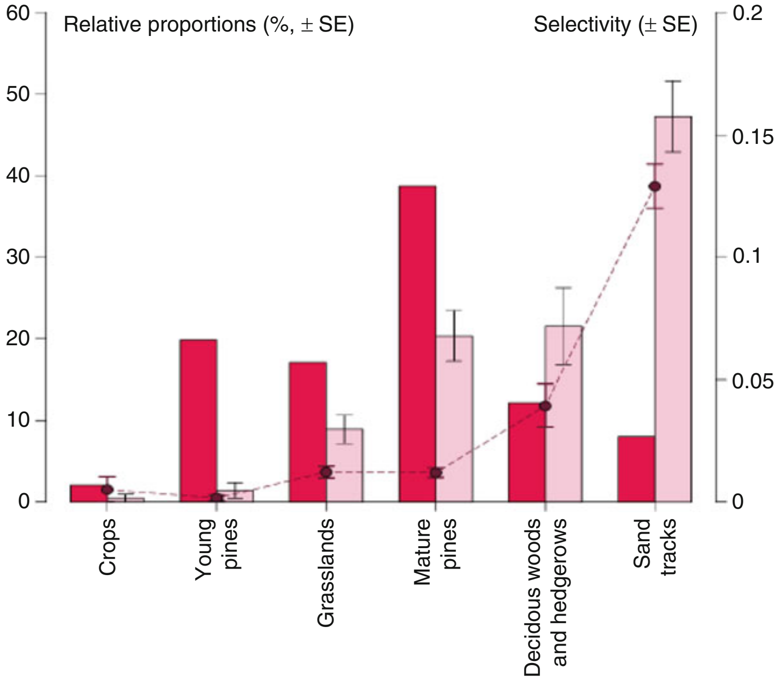


Fig. 6.10 Relative proportions (%) of habitat types available within the study area (*red bars*), mean proportion of hoopoe relocations per habitat type within home ranges (*pink bars*) and mean forage ratio per habitat type (*black line*): young pine, mature pine, deciduous woods and hedgerows, sand tracks, grasslands, and crops

vegetation along pine forest edges where most pine processionary pupae are buried (Barbaro et al. 2008).

Hoopoe foraging intensity and pine processionary moth abundance covary significantly, suggesting a functional response to prey abundance and a significant potential for pest control (Barbaro et al. 2008). Hoopoe conservation requires the maintenance of adjacent breeding (deciduous woods) and foraging habitats (pine plantation and adjacent sward edges), and consequently depends on the improvement of tree species diversity at the landscape scale along with the line of the concept of biological conservation control.

3.4 Implications for the Preventive Control of Pine Processionary Moth

It emerges from this review that all life stages of the pine processionary moth may be affected by presence of non-host, broadleaved species, in the neighbourhood, possibly leading to associational resistance. All of the main associational resistance mechanisms, i.e. reduced host tree accessibility and increased top down control by natural enemies, would be involved.

Female of pine processionary moth seem to be deterred from laying eggs on pine tree crowns due to host finding disruption, via interferences with both visual and olfactory cues. The presence of broadleaved hedgerows, particularly when they comprise birch trees, can reduce by up to 80 % the percentage of infested trees. Adult moths are also exposed to predation by patrolling nightjars than benefit from heterogeneous forest landscapes.

Once laid, egg-masses are exposed to parasitism and predation by natural enemies which are better supplied in complementary feeding resources (honeydew for parasitoid wasps and alternative prey for tits) by mixed forests of pine and broadleaved trees.

Pine processionary larvae may also be prayed within winter tents by avian predators like tits which are also more abundant in pine and deciduous trees admixtures. Broadleaved hedgerows along pine stand edges may represent ecological traps for late instar larvae as they might be selected as pupation habitat which turns to be unsuitable for pupae survival due to adverse microclimatic conditions. The rate of increased pupae mortality would average 20 %. Furthermore buried pupae can be preyed upon by hoopoes which require deciduous forest fragments to breed and tent.

Due to the lack of quantitative data it remains difficult to estimate the effectiveness of each of these processes in terms of damage reduction. However the maintenance or improvement of tree species diversity as a control method for pine processionary moth has several advantages. First, because it involves several ecological mechanisms targeting all life stages (Fig. 6.11), it accumulates each of their individual effects and may then significantly limit pine processionary moth infestations.

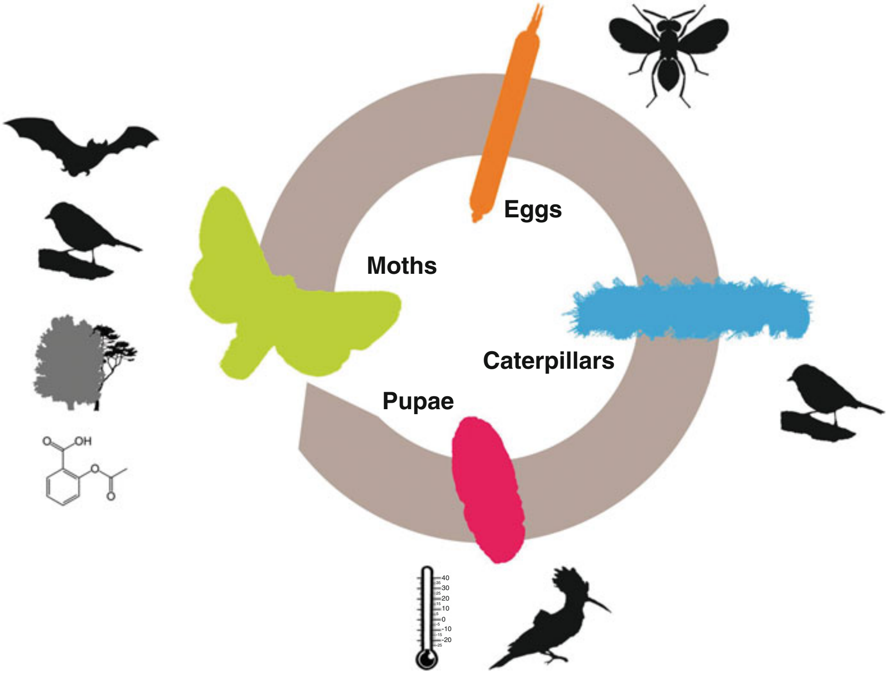


Fig. 6.11 Conceptual diagram showing the main biological control processes of pine processionary moth mediated by tree species or habitat diversity, at different life stages

Second, it is in principle a preventive approach, thus designed to avoid damage rather than to try to reduce populations of pine processionary moth once defoliations have already occurred and caused growth loss. Third it has long term effects, relying on broadleaved tree growth and survival and thus does not need to be replicated each year following pine processionary moth outbreak.

It is for management policy important to realise the different ecological scales at which different mechanisms operate. The bottom-up biotic and abiotic processes seem to predominate at a finer grain, while larger carnivores (insectivores) clearly are affected by variation up to landscape level scale, as there seems to be a scaling of predator behaviour and mobility with their trophic position (Eveleigh et al. 2007). At the smaller scale of habitat or forest compartment (stand) an admixture of trees planted will incur difficulties in planting, thinning, and harvesting. In contrast, diversity on ecosystem (here forest) could be more easily accomplished by forest management of having many stand types.

However, more studies are needed to better estimate the relevance of improving forest diversity for control of pine processionary moth. First further investigations should focus on the composition of mixed pine forests that can better prevent pine processionary moth infestations, notably on the choice of broadleaved species according to their functional traits i.e. growth rate to provide visual barrier, volatile organic compounds for repellence, leaf palatability for honeydew producing aphids, provision of trunk cavities for tenting birds, etc. Second, more research effort should be devoted to optimizing the relative share of host (pine) and non-host tree species in mixed forests. This question is crucial because trade-offs have to be evaluated when considering the establishment of mixed-species plantations or the management of semi natural mixed forests. Depending on the tree traits taken into consideration, the functional diversity of mixed forest may have different consequences for different ecological processes and then ecosystem processes. Tree species admixtures designed to prevent damage by pine processionary moth may be less productive or more costly to manage. Cost-benefit analyses are therefore needed to balance the amount of money saved by reducing growth loss due to defoliation by pine processionary moth against the investment and maintenance of mixed forests.

4 Impact of Pine Processionary Moth Defoliation on Tree Growth

Jean-Sébastien Jacquet, Alexandre Bosc, Andrea Battisti, José A. Hódar, and Hervé Jactel

4.1 Introduction

Forest ecosystems are major terrestrial carbon sinks (Hyvönen et al. 2007) and may then help to mitigate the detrimental effects of climate change (Luyssaert et al. 2010). In this context, the maintenance of sustained tree growth is crucial. However, a number of abiotic disturbances may directly impact tree growth such as droughts (Allen et al. 2010). Among the biotic risks, defoliation and mortality by insects can have strong adverse effects on wood biomass production. Large outbreaks of bark beetles for example have been shown to transform forest ecosystems from carbon sink to carbon sources (Kurz et al. 2008). And yet, insect defoliations are known to be enhanced by increasing temperatures (Robinet and Roques 2010) and drought (Jactel et al. 2011, 2012a). Climate change may then trigger a vicious cycle due to negative feedbacks on carbon sequestration by trees. It is therefore of critical importance to improve our understanding of the defoliation impact on tree growth, including in interaction with abiotic stresses.

Pine processionary moth is the main insect defoliator of pine and cedar species in Southern Europe and North Africa (Devkota and Schmidt 1990; Masutti and Battisti 1990). In response to rising winter temperatures, its geographic range has spread towards higher elevations and latitudes (Battisti et al. 2005; Robinet et al. 2007). The processionary moth larvae prefer to feed on mature needles but may also shift onto young needles, potentially resulting in defoliation up to 100 % during outbreaks. Such damage on tree crowns may have dramatic effects on individual tree growth and but also on stand productivity and more generally on forest ecosystem health. It is therefore of great importance to peri-Mediterranean pine and cedar forests to better understand and predict the impact of defoliation by pine processionary moth on tree growth. We review in this chapter the accumulated knowledge on the relationships between processionary moth defoliation and individual tree growth, considering different *Thaumetopoea* species and different tree species. We also analyze the interaction with tree age and water stress and provide some possible ecophysiological mechanisms to explain the observed response of trees to processionary moth defoliations.

4.2 Quantitative Relationships Between Defoliation Intensity and Tree Growth Loss

A first qualitative examination of all available published papers (27 articles published between 1897 and 2013) on the effects of pine processionary moth indicates that, in all but one case (in Barrento et al. 2008, but probably due to an artifact), tree growth was reduced by processionary moth defoliation. The magnitude of growth loss greatly varied between studies, for example ranging from 20 to 80 % for complete defoliation (100 %) (Jacquet et al. 2012). However, these studies concerned different *Thaumetopoea* species (*T. pityocampa*, *T. wilkinsoni*, *T. bonjeani*), different tree species (*Pinus pinaster, P. sylvestris, P. nigra, P. brutia* and *Cedrus atlantica*) and many different methods have been used to quantify these losses (e.g. through tree diameter, height or volume measurements). To estimate the overall effect of processionary moth defoliation across these different publications we updated the meta-analysis conducted by Jacquet et al. (2012). This meta-analysis was based on 88 pairwise comparisons between defoliated and undefoliated trees, derived from 15 publications or reports published between 1977 and 2013. It showed an important growth loss in defoliated trees which significantly and linearly increased with increasing intensity of defoliation (Fig. 6.12). The relative growth loss varied from ca. 30 % in trees with low defoliation to about 70 % in severely defoliated trees.

In this meta-analysis we did not detect any significant effect of tree species ($P = 0.42$) or tree age ($P = 0.61$) on the impact of defoliation on tree growth. However, the influence of tree age had never been examined simultaneously with that of defoliation intensity within the same experiment. We took advantage of an outbreak of *T. pityocampa* in the Landes de Gascogne Forest during the winter 2009–2010, when maritime pine trees (*P. pinaster*) were defoliated up to 100 % to set up a large field experiment. There we controlled for both the age and the defoliation rate of trees to quantify the impacts of defoliation by pine processionary moth on tree growth dynamics through measurement of annual girth increment. Again this experiment clearly demonstrated that defoliation by pine processionary moth can cause significant radial growth losses in *P. pinaster* and that this effect lasts at least 2 years (Jacquet et al. 2013). In this study, stem growth losses increased linearly with increasing defoliation intensity ($R^2 = 0.97$, $P < 0.001$), reaching ca. 90 % in 100 % defoliated trees the next year (Fig. 6.13). The following year (i.e. after the second growing season following defoliation) growth losses were still

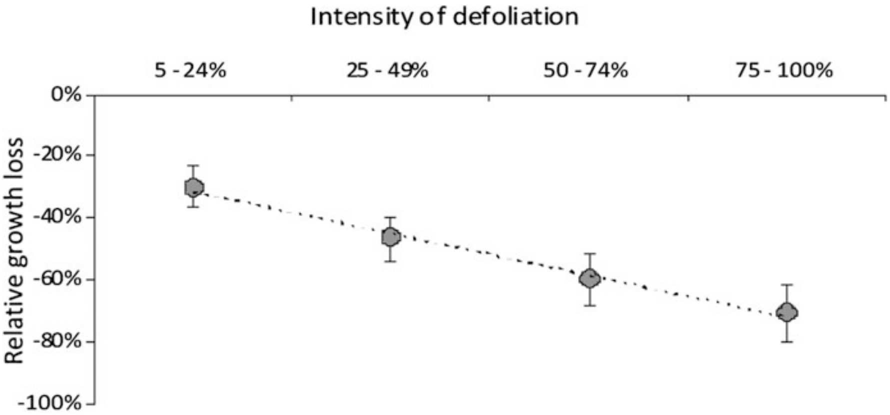


Fig. 6.12 Effect of defoliation intensity by processionary moths on growth loss in defoliated trees as reported in the literature from 1977 to 2013

important, significantly correlated with defoliation intensity ($R^2 = 0.95$, $P < 0.001$), with ca. 70 % reduction in 100 % defoliated trees (Fig. 6.13).

The two approaches (meta-analysis and experiment) therefore confirmed that (1) even low level of defoliation by pine processionary moth (from 5 to 25 %) significantly reduce tree growth, (2) growth loss increased linearly with defoliation intensity, (3) completely defoliated trees can lose as much as 90 % of their growth potential, the adverse effect on growth last at least 2 years.

4.3 Effect of Additional Factors: Tree age and Water Stress

4.3.1 Tree Age

In most of the existing studies on the effect of insect defoliation, juvenile trees were used because they are easier to measure or to artificially defoliate. Only little is known about the extent to which defoliation affects crown architecture of older trees (Buck-Sorlin and Bell 2000; Ericsson et al. 1980; Krause and Raffa 1996 and Puntieri et al. 2006), their capacity to reallocate biomass (Krause and Raffa 1996) and resources (Boege 2005 and Ericsson et al. 1980). The reasons for this lack of information are probably associated with their architectural complexity (Puntieri et al. 2006) and long recovery time after a defoliation event (Haukioja and Koricheva 2000; Krause and Raffa 1996 and Puntieri et al. 2006). And yet ontogenetic changes occur while tree ages, and also the carbon–nutrient balance, storage capacity so that in general shoot/root ratio increase while growth rates and metabolic activity decrease in older trees (Medhurst et al. 1999). All these modifications may affect the response of mature trees to defoliation.

In a recent experiment (Jacquet et al. 2013), the effect of pine processionary moth defoliation on *Pinus pinaster* annual growth was assessed across a 40-year

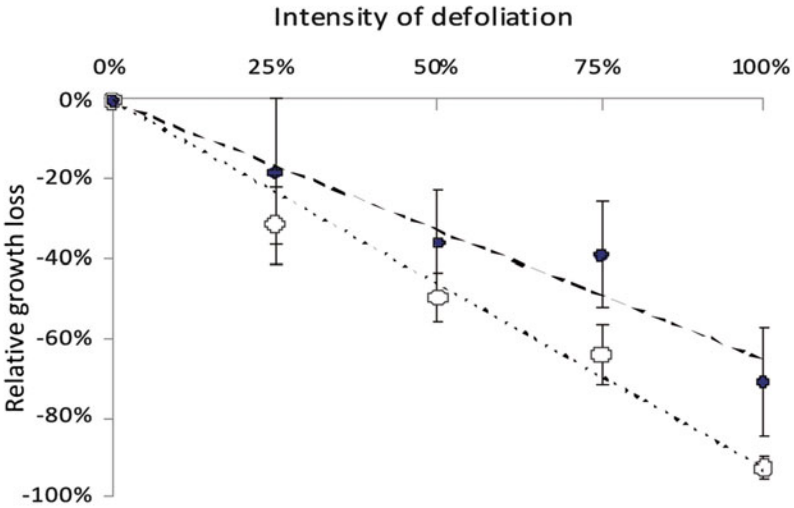


Fig. 6.13 Annual radial growth loss (%) of *Pinus pinaster* (mean ± CI 95 %) in relation with natural pine processionary moth defoliation intensity, the following year (*empty dots*) and the next year (*solid dots*)

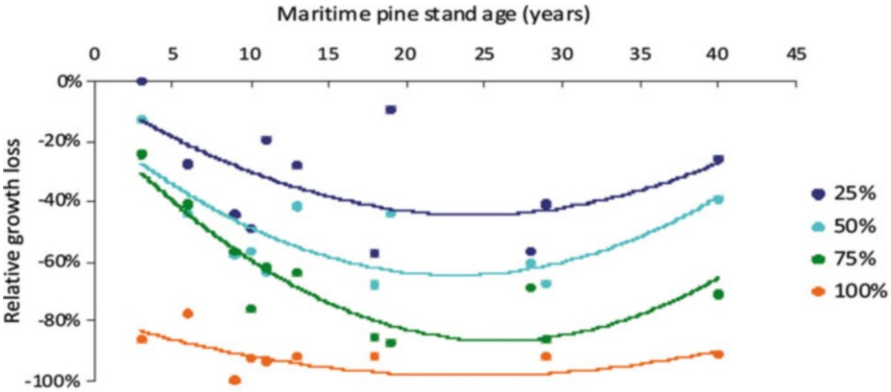


Fig. 6.14 Curvilinear relationships between radial growth losses due to defoliation by pine processionary moth varying from 25 to 100 %) and tree age (3–40 years) in *Pinus pinaster*

chronosequence, while controlling for defoliation intensity within each class of tree age. There was no significant interaction between tree age and defoliation intensity on tree growth. Regardless of the defoliation level considered, we observed a curvilinear relationship between tree age and annual growth loss induced by natural defoliation by pine processionary moth (Fig. 6.14). The highest growth losses were observed for trees between 15 and 30 years old, which correspond to the period of complete canopy closure in maritime pine stands.

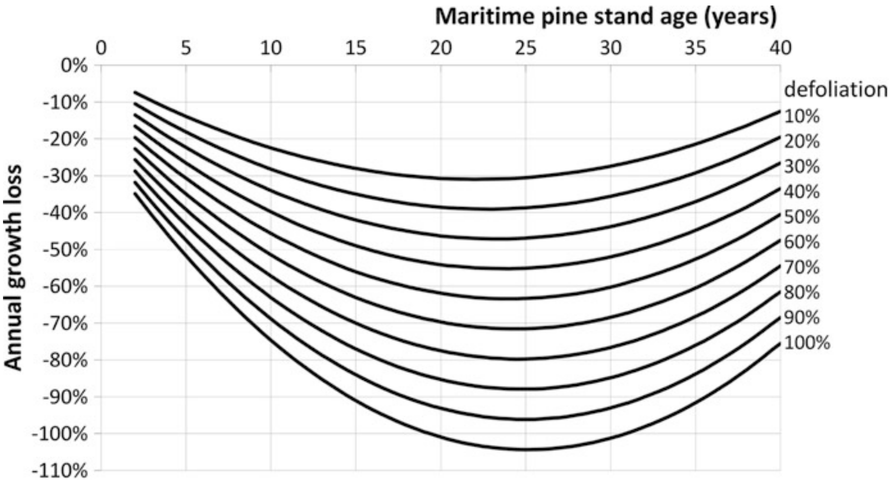


Fig. 6.15 Abacus providing the estimate of annual growth loss of *Pinus pinaster* trees from 2 to 40 years old when defoliated from 10 to 100 % by *Thaumetopoea pityocampa*

We modeled the relationship between relative annual growth loss and stand age for each level of defoliation using a curvilinear relationship ($y = a_1 x^2 + a_2 x + a_3$). We managed to demonstrate that the three parameters a_i were linearly dependant from the percentage of defoliation. Using these linear correlations we built models of growth loss prediction for the four defoliation intensities that we observed. The predicted values of growth loss were significantly correlated with observed losses ($P = 0.1$, 0.01, 0.0002 and 0.03 for % defoliation = 25, 50, 75 and 100 % respectively). Using these statistical relationships we were then able to build an abacus that can provide an estimate of annual growth for maritime trees between 2 and 40 years old that are defoliated from 10 to 100 % by *T. pityocampa* (Fig. 6.15)

4.3.2 Water Stress

Defoliation by pine processionary moth and drought are likely to occur concomitantly in the future due to increased probability of severe droughts (Blenkinsop and Fowler 2007) and positive effect of climate warming on *T. pityocampa* populations (Battisti et al. 2005; Netherer and Schopf 2010). There is therefore a need to better understand the combined effects of water stress and pine processionary moth infestations on tree growth in order to predict the effect of climate change on productivity of forest ecosystems where processionary moths occur or may colonize.

In a recent meta-analysis, Jactel et al. (2011, 2012a) demonstrated that damage by insect defoliators were significantly higher under dryer conditions. Similarly, an ecological review (Valladares et al. 2007) reported additive effects of harsh environmental conditions and insect herbivory on plants and several observational studies showed significantly larger defoliation effects on stem growth in low-productivity (low nutrient) sites (Ovaska et al. 1993; Pinkard and Beadle 1998; Antonnen et al. 2002; Pinkard et al. 2007). In contrast, other reviews predicted antagonist effects of biotic and abiotic stresses on growth in trees (Hawkes and Sullivan 2001; Wise and Abrahamson 2007). Thus, it is not clear whether the effect of several interacting stresses would be additive, synergistic or even antagonistic. Very few experiments have manipulated in the same time water supply and defoliation to examine their combined effects and they provided contrasting results. Kolb et al. (1999) found antagonist effects of water stress and defoliation with higher stem biomass in potted Douglas-Fir seedlings submitted to western spruce budworm defoliation in low moisture than in high moisture conditions. In *Eucalyptus globulus* (Quentin et al. 2011; Eyles et al. 2009) and in red oak seedlings (McGraw et al. 1990), tree growth was unaffected by defoliation under different water treatments which might be due to compensatory responses to defoliation and drought.

Recently, Jacquet et al. (2014) developed a manipulative study under field conditions to examine the combined effects of artificial defoliation (which correctly mimics the effects of natural defoliation by pine processionary moth; Jacquet et al. 2013) and water stress on tree growth. Both defoliation rate and water treatments significantly affected annual stem growth with no significant interaction between the two factors, indicating an additive effect of the two stresses (Fig. 6.16).

In the well watered plots, annual radial growth was significantly reduced by 88 % in 100 % defoliated trees compared with control undefoliated trees. The

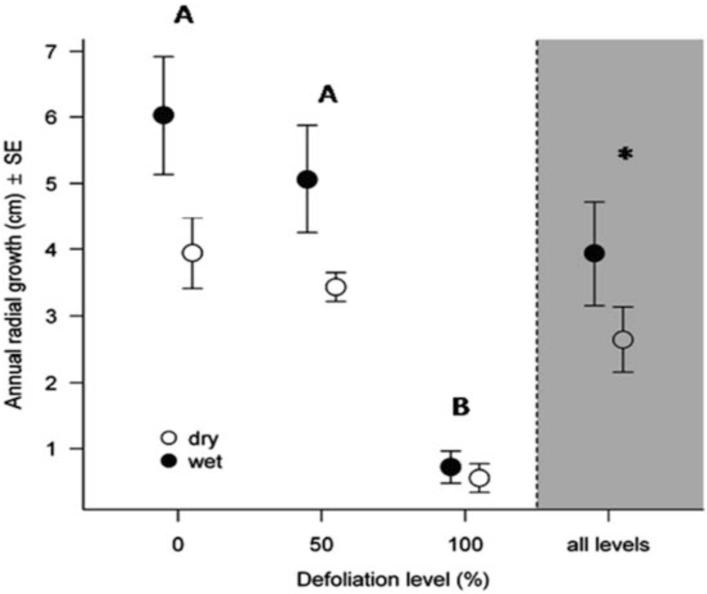


Fig. 6.16 Effects of defoliation and water treatments on annual radial growth of *Pinus pinaster*. Dots with the different letters corresponded to significantly different mean values (Tuckey's tests, $\alpha = 0.05$)

relative growth loss in water stressed trees compared with non stressed trees remained constant across the defoliation classes and of −30 % on average. Growth losses associated with additive effects of defoliation and water stress reached 91 % in 100 % defoliated water stressed trees. The defoliation effect of pine processionary moth is therefore likely to increase under dryer climate conditions.

4.4 Ecophysiological Mechanisms Involved in Tree Growth Response to Processionary Moth Defoliations

Many ecophysiological models consider that defoliation results in reduced carbon fixation through disruption of photosynthesis (Roxburgh et al. 2004). This seems to be consistent with the linear relationship observed between defoliation by pine processionary moth and maritime pine growth losses 1 year following the attack. However, Jacquet et al. (2013) observed that annual growth losses 2 years following defoliation were larger than those predicted by such a fixed carbon allocation model once the establishment of new 1-year-old needles had been taken into account (Fig. 6.17). This suggests that relative growth losses in the second year could not be fully explained by reduced photosynthates supply.

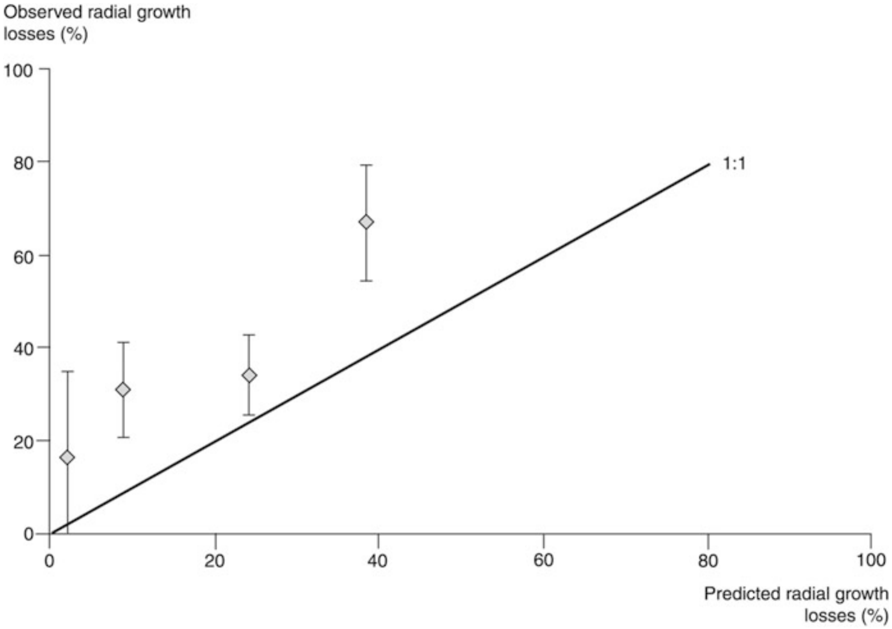


Fig. 6.17 Predicted radial growth losses (*solid line*, based on the regression model built with year 1 data from the same plots as those observed in year 2 following defoliation event) plotted against observed radial growth losses in year 2

Defoliation effect on stem growth might be also mediated by a shortage in carbon storage (Vanderklein and Reich 1999). Indeed, defoliation result in both a net loss of stored carbohydrates due to needle consumption (Li et al. 2002) and a decline in carbohydrates reserves in all organs (Hudgeons et al. 2007; Eyles et al. 2009). Despite this, several studies have shown that stem carbohydrates were only temporary reduced following defoliation (Palacio et al. 2008, 2012; Jacquet et al. 2013) suggesting a short duration of C source limitation for stem growth even after a severe defoliation.

Maintenance or even increase of carbohydrates pools observed in defoliated trees (Jacquet et al. 2014) could be then considered as a consequence of another resource limitation for stem growth. Indeed, a characteristic of evergreen conifers is that they store nutrients such as nitrogen in their needles (Millard et al. 2001). Nutrients in old needles are remobilized each spring to supply the growth of new foliage. Defoliation, particularly of old needles preferred by pine processionary moth, may then have led to significant nitrogen shortage which can in turn result in reduced tree growth.

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Chapter 7
Ecological Responses of Parasitoids, Predators and Associated Insect Communities to the Climate-Driven Expansion of the Pine Processionary Moth

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1 Introduction

This chapter aims at analyzing how the expansion of the pine processionary moth with climate warming is expected to change its trophic interactions with the associated arthropod and vertebrate communities of parasitoids, predators and competitors (i.e., other pine-feeding Lepidoptera). Although parasitoids and

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predators are known to influence moth outbreak dynamics, the evolution of host-parasitoid and predator-prey interactions under ongoing climate change is still subject to considerable uncertainty and may impede biocontrol efficiency. Moreover, the pine processionary moth expansion may also cause unprecedented damages on biodiversity if it rapidly spreads in pine forests with high conservation value outside of its previous range. Despite a large amount of mostly empirical literature available on predators and parasitoids of *Thaumetopoea pityocampa*, there had been no previous attempt to synthesize that information and replace it in the context of the climate-driven expansion of the moth. There is for example a lack of studies on the differential parasitism rates experienced by the moth in core areas of its former distribution range compared to newly-colonized areas. A first section presents some recent results obtained about the response of egg parasitoids to moth expansion. Then, we investigate how insectivorous vertebrates may or not be efficient predators of *T. pityocampa* on the range expansion gradients, by successively quantifying numerical and functional responses of specialist birds, generalist birds and generalist bats to *T. pityocampa* density for several moth life stages, including late-instar larvae, pupae and imagos. Finally, we will discuss whether the expansion of the moth in inner Alpine valleys may become a serious threat to the endangered Spanish moon moth *Actias (=Graellsia isabellae)* by competing for the same pine needle resource.

2 Expansion of Pine Processionary Moth and Parasitoid Responses

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2.1 Introduction

The “Enemy Release Hypothesis” suggests that the success of invasive species could be linked to the absence of their natural enemies in the invaded environment (Colautti et al. 2004; Keane and Crawley 2002; Liu and Stiling 2006). It was primarily developed in the context of biological invasions caused by individuals transported from remote areas, where the probability of transport of natural enemies together with the host is quite low (Colautti et al. 2004; Nicholls et al. 2010). Indeed, Cornell and Hawkins (1993) showed that phytophagous insects had reduced parasite species richness and parasitism rates in invaded areas compared to their native range. Following colonization, the subsequent expansion capacities of the invasive species would thus be enhanced because they are released from natural enemy pressures (Keane and Crawley 2002; Mitchell and Power 2003). Some recent studies suggest that the Enemy Release Hypothesis could also apply to species increasing their natural range by gradual geographic expansion, even without long-distance colonization (Menendez et al. 2008). A strong relationship between parasitism rate, parasitoid species richness and time since the colonization date of a given area by the host was shown for several expanding Lepidoptera (Grabenweger et al. 2010; Grobler and Lewis 2008). In Europe, the example of *Cameraria ohridella* Deschka and Dimic (Lepidoptera: Gracillariidae) that feeds on the horse-chestnut (*Aesculus hippocastanum* L.) is particularly meaningful. This species has spread over 20 years almost everywhere its main host is present at a speed of 60 km per year (Augustin et al. 2009a, b). The success and expansion speed of this species could be explained among other reasons by quite low predation and parasitism rates (Augustin et al. 2009a), which even decreased in the recently colonized areas (Hernández-López et al. 2011). Moreover, the observed parasitism in recently colonized areas was mostly due to the shift of local parasitoids (Hernández-López et al. 2011), rather than to the tracking by natural enemies from the native range which appeared largely delayed compared to host expansion (Gebiola et al. 2014). On average, native parasitoids shifted to this new host after ca. two decades (Grabenweger et al. 2010).

As regards the pine processionary moth, its present and rapid geographical expansion (see Roques et al. 2014, Chap. 3, this volume) is likely to affect the distribution of its associated enemies. Consistent with the “host-tracking hypothesis” (Kohnen et al. 2012; Stone et al. 2012), interacting species can be expected to follow the distribution shifts of their host species, either concomitantly or with a temporal delay due for instance to lower dispersion capacities, or limited ability to detect the host when it is still at low densities. In this latter case, parasitism rates will be significantly reduced near the new boundaries of the host range. Moreover, the different parasitoids associated with a given species may not all be able to track their host at the same speed or with the same success, therefore altering the community composition and structure along the expansion routes. Conversely, parasitoid richness may also increase with time either because the invading host continuously encounters new parasitoid species during its spread (geographic spread-hypothesis) or because local parasitoids need different periods of time to adapt to the novel host (adjustment-hypothesis) (Grabenweger et al. 2010). In any case, geographic expansions and/or host shifts experienced by the associated parasitoids are expected to impact their genetic diversity and spatial genetic structure. Depending on the type of interaction and the level of specialization, these phenomena can result in differentiated populations along the expansion corridor (in case of repeated founder effects due to long distance dispersal), or in a continuous distribution with an isolation by distance pattern (in case of diffusive dispersal). Parallel evolution and diversification can generate synchronism between spatio-temporal phylogeographic patterns under the “Contemporary Host-tracking Hypothesis” (Becerra 2003), while temporal discrepancies can occur under the “Delayed Host-tracking Hypothesis”, in which the natural enemy can display more recent diversification patterns than its host (Kohnen et al. 2012; Stone et al. 2012).

All over the Mediterranean basin, a rich community of insect parasitoids and predators is associated to the pine processionary moth (see Battisti et al. 2014, Chap. 2, this volume). Most of these species specifically attacks a particular developmental stage of the host, i.e., embryos in eggs, any of the five instar larvae in the nest, mature larvae in procession, pupae, or adults. Among the parasitoids, the hymenopteran chalcids infesting pine processionary moth eggs have extensively been studied because they may act as biocontrol agents modulating pine processionary moth eruptive dynamics through an induced decrease in the number of larvae per nest and in the subsequent damage (Arnaldo and Torres 2006; Mirchev et al. 2004; Perez-Contreras and Soler 2004).

The many studies conducted around the Mediterranean basin on pine processionary moth egg parasitoids (Mirchev et al. 1998, 2004; Mirchev and Tsankov 2000; Schmidt et al. 1999; Tsankov et al. 1995, 1998, 2006) revealed an overall dominance of two thelytokous chalcid species, the eulophid *Baryscapus servadeii* Domenichini, considered as a pine processionary moth specialist, and the encyrtid *Ooencyrtus pityocampae* Mercet, which is supposed to be a generalist parasitoid attacking various lepidopterans and hemipterans (Battisti 1989; Géri 1980; Lopez-Sebastian et al. 2004). Two more chalcid species were usually found but at much lower densities, namely the eupelmid *Anastatus bifasciatus* Geoffroy and the trichogrammatid *Trichogramma* sp., sometimes identified as *Trichogramma embryophagum* Hartig (Tsankov and Mirchev 2003). These four species are the only pine processionary moth egg parasitoids commonly found in France, where they can present two generations per year. In Central France, adults of the generalist species, *O. pityocampae,* emerge in spring, well before the period of pine processionary moth egg laying but they can survive for long periods and use intermediate hosts before attacking pine processionary moth eggs (Battisti et al. 1988). In contrast, adults of the specialist species, *B. servadeii,* emerge in summer concomitantly with the pine processionary moth egg-laying and they immediately oviposit in the freshly laid eggs (Biliotti 1958; Géri 1980). The larvae of both species then develop at the expense of the young host embryos, and a new generation of adult parasitoids emerge before processionary moth larvae hatch. They immediately parasitize again pine processionary moth eggs but at a more advanced embryonic stage. The parasitoid larvae of this second generation then enter diapause to overwinter and the subsequent adults emerge the following spring or summer. However, a variable proportion of these larvae may remain in prolonged diapause for 1 more year (Biliotti 1958; Géri 1980).

Ancient data already suggested that parasitism rates and species richness of parasitoid communities are reduced near moth range boundaries. Hence, Biliotti (1958) observed a very low rate of egg parasitism, which was only attributed to *Trichogramma* sp., at the northern edge of pine processionary moth distribution whilst Géri (1980) noticed a similar phenomenon in a 1,300 m-high mountain pass in Corsica. These lower parasitism rates may favour pine processionary moth expansion because colony size may be subsequently higher near the expanding front, thereby increasing individual survival in this gregarious species (Perez-Contreras et al. 2003). In order to confirm and quantify egg parasitoids responses to pine processionary moth expansion northwards and upwards, and to compare parasitoids and host population structures, the variation in parasitism rates and species composition has been assessed along three gradients corresponding to the main pine processionary moth expansion pathways in Western Europe, from the historical native range to recently established populations on the leading front edge. The macroclimatic variations along such gradients can be viewed as natural laboratories to study the possible impact of climate warming on both pine processionary moth and parasitoids. The gradients were designed to compare latitudinal and altitudinal expansion, elevational gradients presenting the advantage to include a steep temperature variation over short geographical distances, thus reducing the confounding effects of different local environmental conditions. The genetic structure and diversity of the two main parasitoid species were simultaneously investigated along these gradients.

2.2 *Species Composition and Parasitism Rates: Do Expanding Pine Processionary Moth Populations Escape Egg Parasitoid Pressures?*

2.2.1 Definition of the Altitudinal and Latitudinal Gradients Used in the Survey of Parasitoid Responses

The three studied expansion gradients are shown in Fig. 7.1. The south-north gradient, corresponding to the pine processionary moth latitudinal expansion, was drawn from Spain (Eastern Iberian chain corresponding to a putative glacial refugia of pine processionary moth, see Kerdelhué et al. 2014, Chap. 4, this volume) to the current expanding front in the Paris basin in north-central France, including the pioneer populations identified above the front (see Roques et al. 2014, Chap. 3, this volume). One of the altitudinal gradients stretched along the Durance valley in the Southern French Alps, while the other was located in the South-Western part of the French Massif Central. In each gradient, sampling sites were selected in (i) the “core area”, i.e. the historical native range of the pine processionary moth, (ii) the “newly colonized area”, reached by the pine processionary moth between 1990 and 2000, and (iii) the “front area”, invaded by the pine processionary moth less than 5 years ago. For each gradient, whenever possible, egg batches were sampled on the same tree species to avoid any host plant effect (Arnaldo and Torres 2006). Emerging adult parasitoids were collected every week, identified and stored in alcohol for future genetic studies, while already emerged individuals were identified following Tanzen and Schmidt (1995). The rearing and identification methods are detailed in Imbert (2012). Species composition and parasitism rates could thus be reliably estimated. The study was conducted for 2 consecutive years, corresponding to egg batches laid in 2008 and 2009, in order both to assess the inter-annual variability in parasitism rate. The results were also compared with those from previous surveys done along the same gradients in the Alps (2003 and 2004) and the Massif Central (2007).

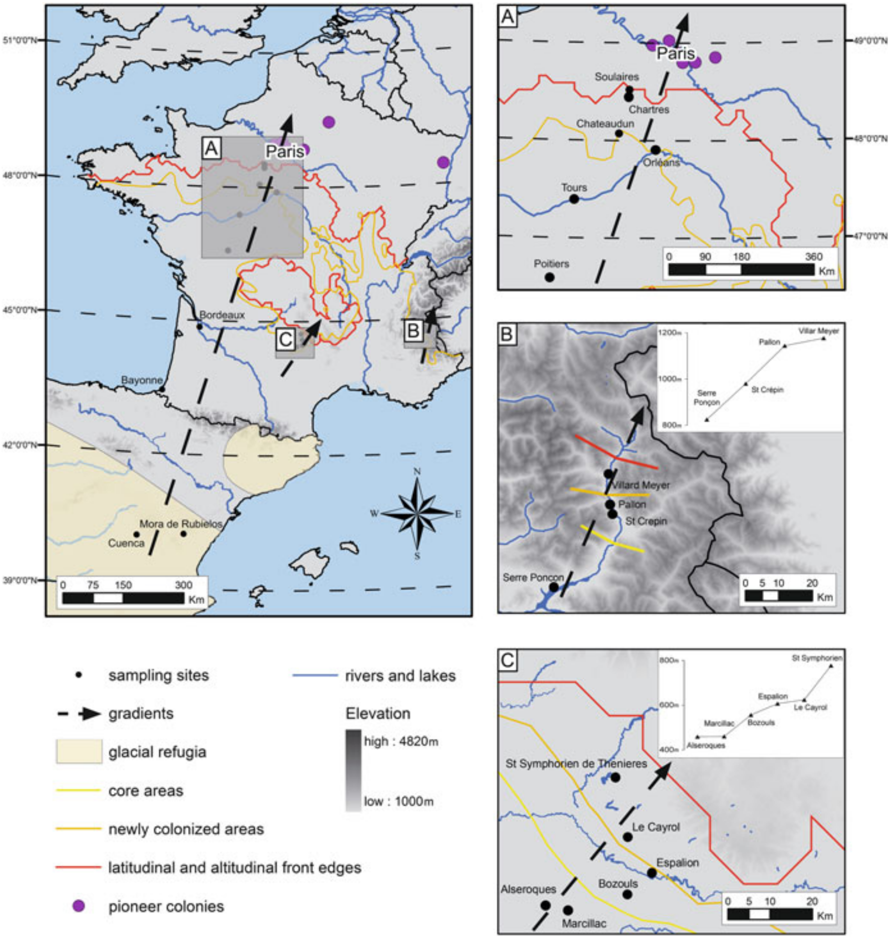

Fig. 7.1 Sampling sites of pine processionary moth egg batches along the three gradients studied in 2008–2009

2.2.2 Variation of Total Egg Parasitism Along the Expansion Gradients

Parasitism rates of pine processionary moth egg batches are known to be highly variable in space and time over the moth's distribution range. It typically ranged from 6 % to ca. 40 % in previous studies conducted in Southern Europe (Mirchev et al. 1999; Schmidt et al. 1999; Tiberi 1990; Tsankov et al. 1996, 1998).

Consistently, the parasitims rates measured along the three studied gradients varied both between sites and between years (Fig. 7.2.). Yet, spatial and temporal patterns could be noted. In all three regions, total parasitim rates were higher in 2009 than in 2008. Egg batches were always more parasitized in the Alps than along the other two gradients. However, whatever the year or the gradient total parasitism was significantly lower at the front edge than in the core and the newly- colonized areas.

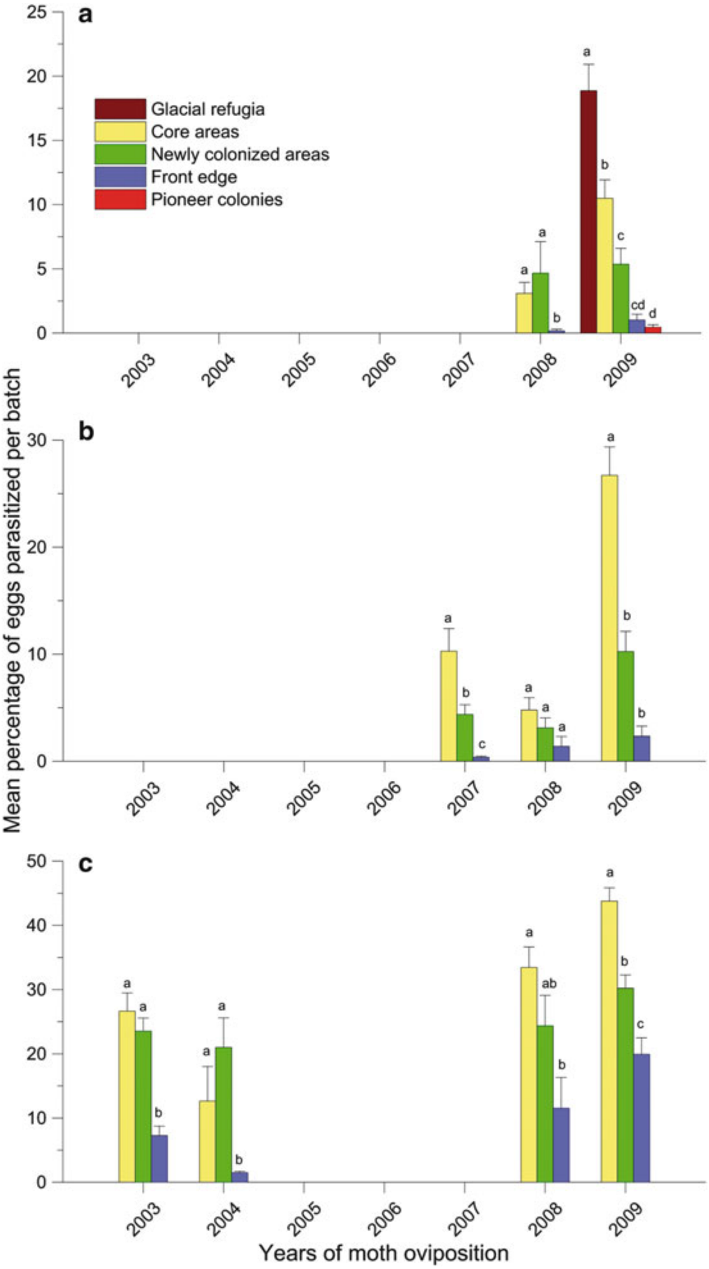

Fig. 7.2 Variation in total parasitism of pine processionnary egg batches by chalcid parasitoids along gradients from core areas to front edge and pionneer, isolated colonies beyond the front. (**a**) Latitudinal gradient, from glacial refugia in Spain to Paris basin in 2008 (no. analyzed batches from 25 to 51 according to area) and 2009 (n = 50–114); (**b**) Altitudinal gradient in the Southern Massif Central in 2007 (n = 18–127), 2008 (n = 12–49) and 2009 (n = 33–62); (**c**) Altitudinal gradient in the Southern French Alps in 2003 (n = 54–91), 2004 (n = 15–30) 2008 (n = 11–20) and 2009 (n = 29–60); Different letters show significant differences between locations during the same year and the same gradient following a Kruskal-Wallis test ($P < 0.05$)

The most recent, expanding populations were therefore always less affected by natural enemies, while the parasitism rates were usually already rather high in the areas colonized between 1990 and 2000. Unpublished data gathered by the authors in 2003–2004 (i.e., 5 years earlier) over the same Alpine gradient already showed a similar trend but with a much lower parasitism at the front edge. Thus, parasitism of egg batches at the front averaged 7.3 % in 2003 and dropped to 1.5 % in 2004 whereas it reached 11.5 % in 2008 and up to 19.9 % in 2009. The survey of the annual variations in moth populations at the front edge using both qualitative visual estimations of nest densities and pheromone trappings of male moths revealed that nest density significantly increased between 2003 and 2004, simultaneously to a threefold increase in male captures (from an average of 27 per trap in 2003 to 82 in 2004). This could explain the observed decrease in the percentage of parasitized egg batches in 2004. In contrast, nest density strongly decreased between 2008 and 2009 but moth captures in 2009 (33 moths per trap) as well as nest densities were quite similar to the values observed in 2003 whereas these of 2008 (96 moths per trap) matched the 2004 observations. The much higher rate of parasitism observed in 2008–2009 compared to 2003–2004 may suggest that egg parasitoids tend to follow the expansion of the pine processionary moth but with a short time lag allowing the moth to escape from its main enemies during the first steps of the expansion. However, larger samplings are needed to confirm this hypothesis because host egg masses are highly clustered in space, especially in the expansion areas, and it is likely that the relation between host density and parasitism rates is not linear. An alternative explanation could be a de-synchronisation between the life cycles of pine processionary moth and its main egg parasitoids due to specific environmental conditions prevailing at the front edge (see below). As our data also show that the embryos' mortality due to other factors is similar between sites, we conclude that more pine processionary moth larvae successfully hatch per egg batch at the front edge of the expansion areas, if the sizes of the egg masses are similar. In addition, pine processionary moth colony size is associated with the capacity to resist winter temperatures. A high density of larvae in the nest both increases individual survival to low temperatures (Huchon and Démolin 1971) and enhances growth rate (Perez-Contreras et al. 2003). The observed decrease of parasitism rate near the expanding front could thus lead to nests containing more larvae, and to a higher than expected individual survival in spite of harsher climatic conditions in the northernmost and upmost populations.

2.2.3 Variation in Parasitoid Communities Along the Gradients

As expected, the four species of pine processionary moth egg parasitoids known from France were present along the three gradients. The majority of sampled individuals belonged to either the pine processionary moth specialist, *Baryscapus servadeii,* or to the generalist, *Ooencyrtus pityocampae*. *Anastatus bifasciatus* and *Trichogramma* sp. were found occasionally but never at high frequencies. A few additional specimens, which may belong to the genus *Eupelmus* according to their

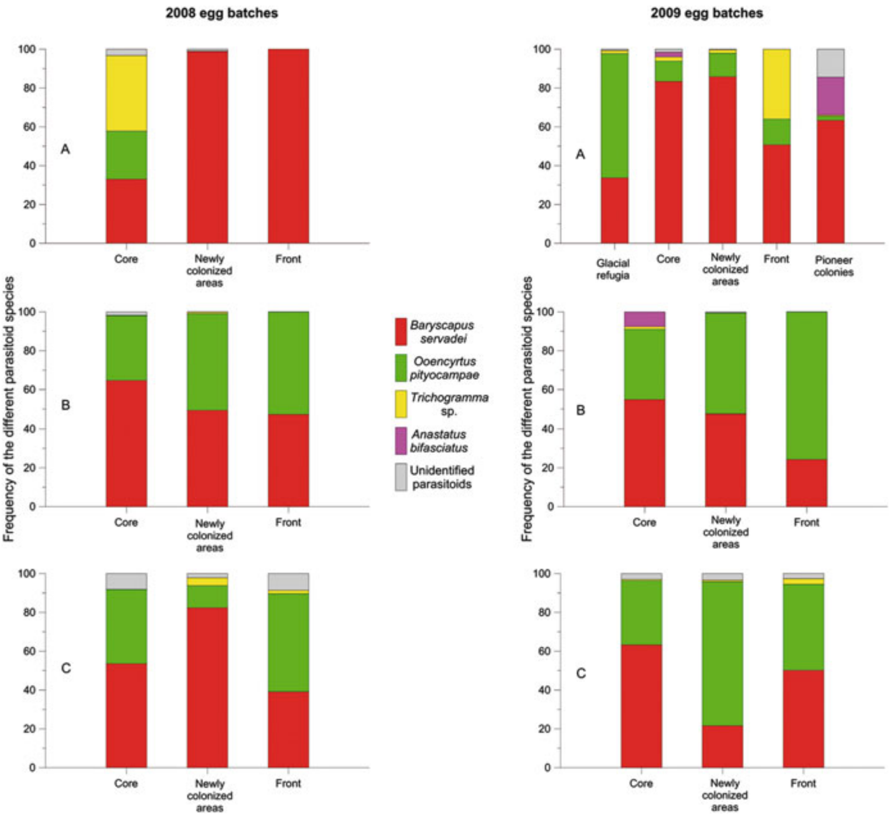

Fig. 7.3 Variation in the specific composition of the egg parasitoid complex along the different gradients in 2008 and 2009. (**A**) Latitudinal gradient, from glacial refuges in Spain to Paris basin; (**B**) Altitudinal gradient in the Southern Massif Central; (**C**) Altitudinal gradient in the Southern French Alps

barcode sequence (Auger-Rozenberg, personal observation), were observed in 2009 but they could not be identified at species level.

Species richness of parasitoids and relative abundance of the sampled species were highly variable between years and localities, and the observed patterns were not consistent between gradients (Fig. 7.3).

Baryscapus servadeii was predominant all along the latitudinal gradient except in the refugial area of Spain in 2009 where most emerging parasitoids were *O. pityocampae* (Fig. 7.3A). Interestingly, *B. servadeii* was even dominating the few specimens emerging from the pioneer colonies located beyond the front edge that seemed until recently free from egg parasitoids (Robinet et al. 2012). These results suggest that the specialist species could track its host with a limited delay, and that the generalist species did not efficiently shifted to this new resource in the Paris basin. Along the altitudinal gradient studied in the Massif Central, *B. servadeii* was mostly found in the core region, while *O. pityocampae* was the main species sampled at higher elevations (Fig. 7.3B). This is consistent with ecological hypotheses suggesting that *O. pityocampae* would be adapted to cooler climates while *B. servadeii* would be more susceptible to frost (Masutti 1964), which could impede its local expansion. Yet, this pattern was not confirmed in the second altitudinal gradient studied in the Alps, where the dominant species was different between years in most sites, especially in the recently colonized areas (Fig. 7.3C).

2.3 Host-Parasite Synchronisation and Survival in Different Environmental Conditions

As pine processionary moth is currently expanding towards higher latitudes and elevations, it reaches regions were climatic conditions tend to be more severe than in the historical range. For instance, we measured a difference of 1.7 °C in average winter temperatures between the core and the front areas in the Southern French Alps. Because warming temperatures may affect differently the phenology of host and parasitoids, this can alter the synchrony between interacting species (Parmesan and Yohe 2003; Root et al. 2003; Visser and Both 2005). This could explain the lower parasitism rates in the front areas documented above. It is also possible that parasitoids are more susceptible to low temperatures than pine processionary moth, and cannot survive the environmental conditions in the front areas. To test these hypotheses, *in situ* cross-translocation experiments were carried out in the Southern French Alps in order to compare (i) the emergence curves of adult parasitoids in the core vs. the front areas; (ii) the emergence curves of adult parasitoids issued from eggs laid in the core area that were artificially moved to the front edge before winter, and vice-versa (hereafter, "translocated parasitoids"); (iii) the pine processionary moth flight periods using *in situ* male pheromone trapping at both sites (Imbert 2012).

Indeed, the two major parasitoid species did not emerge simultaneously with pine processionary moth emergence peak, as already documented by Dulaurent et al. (2011) in South-Eastern France. Individuals of the generalist *O. pityocampae* emerged 3 weeks to a month before their host, while the emergence of the specialist *B. servadeii* started about a week before egg laying of pine processionary moth and continued throughout the pine processionary moth flight period (Fig. 7.4).

Both species naturally emerged about 2 weeks earlier in the core area than at the front edge. Translocated parasitoids of both species emerged as adults at the same time as their native conspecifics. This suggests that the difference in parasitoid phenology observed between core and front areas is mostly due to a plastic response to local winter conditions.

Actually a smaller gap between parasitoid and pine processionary moth emergence was noticed at the front edge compared to the core area. Thus, in the front

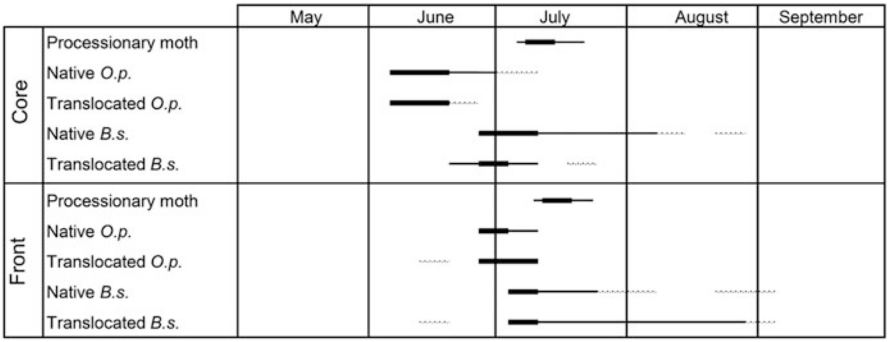

Fig. 7.4 Flight period of parasitoids and pine processionary moth in the two sampling sites in the Southern French Alps (front and core areas): *Bold lines* represent peaks emergence, *solid lines* represent mass emergence, and *dotted lines* represent sparse emergence. For each site, native species correspond to species which emerged from egg-batches sampled in the same sites and translocated species to egg-batches sampled in one site but moved in the other site for winter

area, the emergence of the two major parasitoids is still (and even better) synchronized with the egg laying period of the moth. Moreover, Dulaurent et al. (2011) showed that egg parasitoids may survive longer by feeding, e.g. on honeydew, and can thereby compensate a delay in host availability. Since the translocated parasitoids are capable to survive overwintering and emerge as adults at the front area, they are able to resist cooler temperatures than in the historical range. The decrease of parasitism rates along the expansion pathways of the pine processionary moth are thus probably not due to a de-synchronisation with their host, nor to a very high mortality due to harsher conditions.

Therefore, it could be so far hypothesized that the delay in parasitoid expansion as compared to the pine processionary moth may be explained by a lower dispersal capacity, or by difficulties in locating their host in the newly colonized areas, where the egg batches are probably more scattered in the landscape. Nevertheless, it cannot be excluded a sampling bias due to low densities of parasitoid populations in processionary moths expansion areas.

2.4 Parasitoid Genetic Diversity Along Pine Processionary Moth Expansion Pathways

Range expansions may have consequences on richness, abundance or phenology of species, but also on the genetic diversity of their populations. Just as we studied the variations of genetic diversity of the pine processionary moth along its main expansion pathways (Kerdelhué et al. 2014, Chap. 4, this volume), we also used molecular data to examine the genetic consequences of the expansion on egg parasitoids. As observed in several cases, invasive or expanding populations may exhibit reductions in genetic diversity along the colonization routes (Excoffier et al. 2009; Rousselet et al. 2010; Smith et al. 2011) due to founder effects, or to the fact that a fraction of the existing population contribute to the expansion at each generation. Contemporary processes and species life history and ecological traits (reproductive system, generation time, fecundity, dispersal modes, etc.) can affect the spatial distribution of genetic diversity in various ways. As explained in Kerdelhué et al. (2014, Chap. 4, this volume) for the processionary moth, dispersal potential can lead to various patterns of genetic variation and structure. Long-distance dispersal events can result in large patches of homozygosity and conversely, diffusive processes can lead to the maintenance of genetic diversity, usually with a spatial pattern of isolation by distance. Moreover, the egg parasitoid species studied here have an asexual reproduction (thelitokous parthenogenesis), which can also affect the genetic structure because it strongly affects gene flow.

In order to evaluate if the expansion affects the patterns of genetic diversity in pine processionary moth-associated parasitoids, and to compare the host/parasitoid patterns, the variability in mitochondrial DNA sequences was analysed along two of the gradients presented above. In the future, attempts will be made to develop highly polymorphic nuclear markers such as microsatellites, which are relevant to study genetic structure at regional spatial scales. Yet, this will necessitate species-specific development, and a much higher sampling effort.

A total of 13 sites ranging from northern Spain to Paris basin could be considered for the latitudinal gradient, and 6 sites in the Southern French Alps for the altitudinal one. In the Massif Central, the too limited number of emerged parasitoids allowed molecular analysis only in a single site of the core area. Following species identification using adult morphology, DNA was extracted from five individuals per species and per sampling site, reared from different egg masses and different pine trees to reduce the risk of collecting siblings. For each individual, a part of the Cytochrome Oxidase I (COI) mitochondrial gene was sequenced. We then could analyse the distribution of haplotypes and the spatial genetic diversity found for each species, and a parsimony network was built to infer gene genealogies.

The specialist species *B. servadeii* showed 13 haplotypes along in the latitudinal gradient whereas 12 were observed along the altitudinal Alpine gradient. However, no haplotype was shared between these two gradients, indicating a strong spatial genetic structure (Fig. 7.5). In the single site studied in the Massif Central, three haplotypes were observed, among which two were also found in the latitudinal gradient but none was also present in the Alps. In both gradients, the genetic diversity was significantly higher in the core areas, with ten haplotypes found in the Spanish sites and eight in the core area of the Alpine gradient. In contrast, only three haplotypes were observed in the newly-colonised areas and at the front edge of the latitudinal gradient whilst it decreased to a single haplotype in the corresponding areas of the altitudinal gradient. The patterns observed in the specialist egg parasitoids are thus consistent with a loss of genetic diversity along both northwards and upwards expansion routes. These results are quite similar to the patterns exhibited by the host (Kerdelhué et al. 2014, Chap. 4, this volume), and consistent with a diffusive dispersion of the parasitoid tracking its host. In addition,

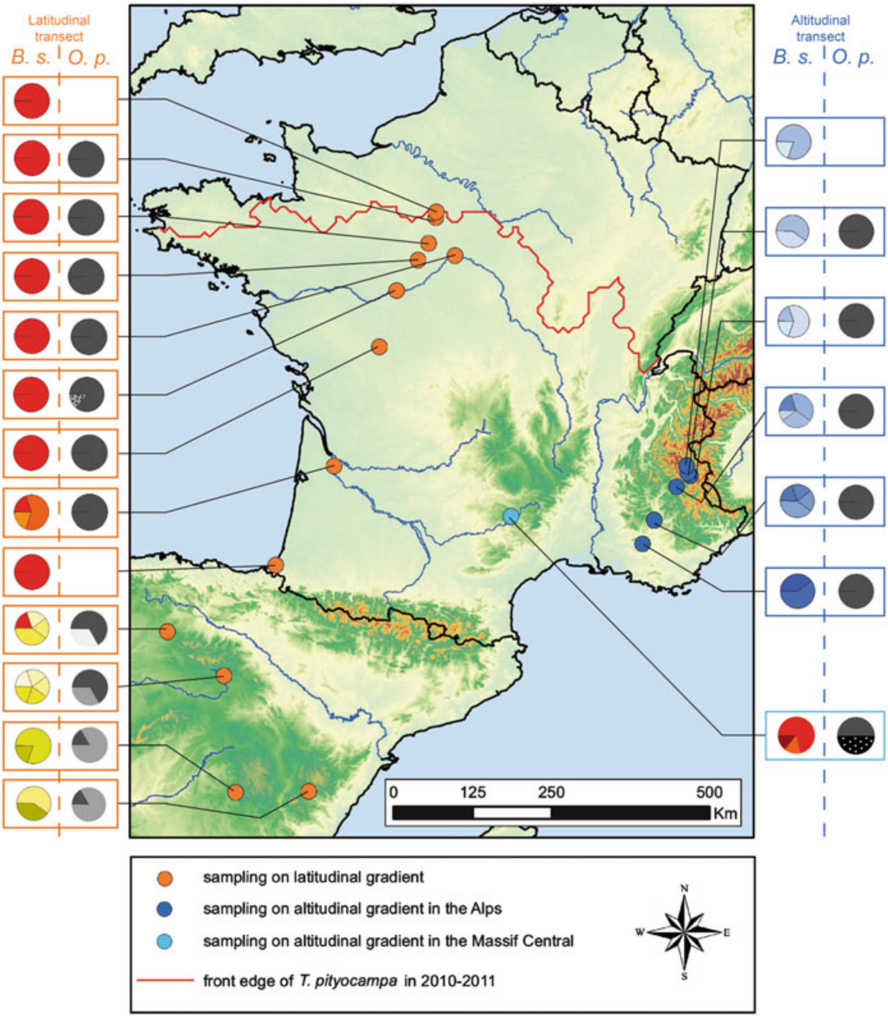

Fig. 7.5 Geographical distribution of mitochondrial haplotypes of the two parasitoid species in the latitudinal and altitudinal gradients. *B. s.* = haplotypes identified in *Baryscapus servadeii* populations and *O. p.* = haplotypes identified in *Ooencyrtus pityocampae* populations

the spatial structure discovered for that species, with specific haplotypes found in both studied gradients, suggests that *B. servadeii* exhibits a strong phylogeographic structure, with a high genetic diversity retained in the southern part of its natural distribution.

The generalist *O. pityocampae* presented only five haplotypes throughout the two gradients. One of these haplotypes was present at high frequencies. It corresponded to the major haplotype along the latitudinal gradient, it was the only one found in the altitudinal one and it also occurred in the Massif Central.

Three other haplotypes were restricted to the core area of the latitudinal gradient, and one was only found in the Massif Central. These results indicate that *O. pityocampae* exhibits a quite limited genetic diversity compared to *B. servadeii*, despite the fact that they have both asexual reproduction (thelytoky), and that this species is not significantly structured at the studied geographical scale (Fig. 7.5). The low variability of the considered mitochondrial marker did not allow to assess if the genetic patterns are consistent with a recent expansion of the parasitoid, or could correspond to a shift from local populations already present in the regions recently colonized by the pine processionary moth but developing upon other hosts. Range-wide studies of mitochondrial genetic diversity will be necessary to confirm these observations and fully understand the patterns observed (Torres-Leguizamon et al. submitted). Moreover, a fine scale study of the genetic variation along the gradients will be developed using highly polymorphic microsatellites markers in both species to better analyse the changes in genetic patterns along the expansion routes.

2.5 Conclusion and Perspectives

The studies presented here showed that four species of parasitoids are present throughout the distribution range of the pine processionary moth, no new species being observed in newly colonized areas. A specialist species, *Baryscapus servadeii*, and a generalist species, *Ooencyrtus pityocampae*, were by far the most frequent species. Quantification of parasitoid species richness and frequencies along three expansion gradients showed that parasitism rates were much lower at the front edges, which may be due to a delay in host tracking because parasitism rate significantly increased with time in this area whatever the moth population dynamics. This time lag may allow the host to experience significant population growth, which can further enhance its expansion rate. Moreover, the generalist parasitoid could be present beyond the pine processionary moth expansion front and associated there to other hosts. Thus, the parasitism due to *O. pityocampae* in newly colonized areas could be due to a local shift of this species to the pine processionary moth host rather than to parasitoid populations expanding from the core areas. In this case, the delay observed would be due to the time necessary for the parasitoid to adapt to the new host.

New research will now be necessary to fully understand the processes acting along the expansion routes on the pine processionary moth-parasitoid relationships. In particular, little is known about the environmental requirements and ecological niches of the different parasitoid species. The direct effects of climate warming and land use changes upon parasitoids remain unknown, which impedes understanding the host-tracking mechanisms. Data are also needed about host preference and host localization of the generalist parasitoids to infer their capacity to shift to the new, expanding hosts near the front edge. Range wide studies of phylogeographic patterns and genetic diversity will also help understanding the present-day situation by shedding light on the evolutionary histories of the multiple partners.

3 Numerical and Functional Responses of Predatory Birds and Bats to the Pine Processionary Moth

Luc Barbaro, Yohan Charbonnier, Fabrice Vetillard, Sébastien Blache,
and Andrea Battisti

3.1 Introduction

3.1.1 Numerical and Functional Responses of Predators to Outbreaking Insects

The strength of predator-prey interactions is the main factor shaping the numerical and functional responses of predators to prey abundance (Abrams and Ginzburg 2000). While the numerical response of the predator can be defined as an increase in abundance with prey density, the functional response is the increase in prey consumption by predators with prey density. The efficiency of the biological control of pest insects by predators is therefore directly related to the shape and magnitude of their functional responses (Abrams and Ginzburg 2000). The most widespread functional response is the ‘type II’, in which consumption rate first increases with prey density and then decreases or remains constant irrespective of prey density. For outbreaking herbivorous insects, several authors have highlighted the beneficial influence of predators on prey outbreak frequency and magnitude (Klemola et al. 2002; Barbosa et al. 2012). However, there is still considerable uncertainty regarding the evolution of predator-prey relationships under ongoing climate change (Berggren et al. 2009; Bretagnolle and Gillis 2010). In particular, spatial and temporal mismatches between a given predator and its prey may impede the future efficiency of biocontrol in agro-ecosystems (Thomson et al. 2010). The current range expansion of *Thaumetopoea pityocampa* with climate warming (Battisti et al. 2005), therefore questions the potential role of vertebrate predators, together with parasitoids and other mortality factors, on pine processionary moth dynamics in time and space.

3.1.2 Biological Control of Pest Insects by Birds and Bats

The key functional role played by predatory vertebrates feeding on forest pest insects is acknowledged for a long time (Morris et al. 1958; Buckner 1967). Insectivorous birds and small mammals are especially efficient predators showing numerical and functional responses to pest insect abundance (Buckner 1967; Dempster 1983; Glen 2004). Among efficient predators of forest arthropods, birds and bats are together considered to provide a valuable ecosystem service of pest insect biocontrol (Whelan et al. 2008; Kunz et al. 2011). While forest birds have long-term been considered key insect predators, the role of insectivorous bats as natural enemies is less documented, although bats have large diet spectrum and foraging tactics (Vaughan 1997; Schnitzler and Kalko 2001) and can affect insect populations as much or more than birds in cross-taxa experiments (Kalka et al. 2008; Williams-Guillén et al. 2008; Karp and Dialy 2014). The role of bat echolocation in the evolutionary responses of tympanate moths to escape bat predation is actually well-known (Schnitzler and Kalko 2001; Waters 2003; Windmill et al. 2006). The predation by insectivorous vertebrates allows maintaining prey populations at low densities but this effect becomes negligible during prey outbreaks because of a predominant type II functional response (Crawford and Jennings 1989; Glen 2004). However, generalist and specialist predators do not exert the same biological control on pest insects because their functional responses to prey abundance differ in intensity and shape (Klemola et al. 2002). Specialists and generalists generally feed on different prey life stages and their spatio-temporal predation patterns are highly complementary within complex food webs (Hanski et al. 2001; Symondson et al. 2002). There is consequently a need for maintaining the functional diversity of insectivorous vertebrates at the landscape scale, including both generalist and specialist predators, to allow long-term biological control of this urticating moth (Tscharntke et al. 2007; Philpott et al. 2009).

3.1.3 Pine Processionary Moth as a Special Case of Predator–Prey Interactions

Recent studies have brought evidence for a rapid range expansion of the pine processionary moth upwards and northwards in Europe (Battisti et al. 2005), and for a correlation between the magnitude of moth outbreaks and the NAO index (Hódar et al. 2012). This climate-driven expansion has been proven to depend on the number of feeding hours allowed to overwintering larvae, or its surrogate, daily mean minimum temperature during the coldest period (Buffo et al. 2007). The moth expansion is strengthened by a highly efficient strategy of predation avoidance due to both morphological and behavioural adaptations: eggs are covered with scales by the female, late-instar larvae are covered by urticating setae and overwinter in silk nests where they hide during the day, and pupae are buried into the soil (Halperin 1990; Battisti et al. 2000). Moreover, adults of *T. pityocampa* are among the moth species that have evolved tympanic organs adapted to detect efficiently bat echolocations (Sierro and Arlettaz 1997; Waters 2003; Windmill et al. 2006). Predatory birds and bats have developed counter-efficient strategies to feed on urticating Lepidoptera such as *T. pityocampa* with morphological and behavioural adaptations to avoid prey defences (Waters 2003; Barbaro and Battisti 2011). Moth species experience vertebrate predation throughout their seasonal life-stages, although mortality at late-instar larval and pupal stages is the most likely to impact moth population dynamics on the long-term (Dempster 1983; Crawford and Jennings 1989; Tanhuanpää et al. 2001). Four main predation periods succeeding in time and space can be distinguished for *T. pityocampa*, corresponding to main moth life-stages and associated predator strategies (Barbaro and Battisti 2011): (i) generalist

Fig. 7.6 A breeding adult hoopoe carrying a pine processionary moth pupa during the breeding season. Aquitaine, France, 29th May 2011 (Alain Laborde). Breeding hoopoes can consume up to 74 % of buried pupae (Battisti et al. 2000)

passerines, including mixed-species flocks led by Paridae tits, prey on eggs and early-instar larvae in late summer and early autumn; (ii) a small generalist, the great tit *Parus major*, and two large specialists, the great spotted cuckoo *Clamator glandarius* and the common cuckoo *Cuculus canorus,* prey on urticating late-instar larvae, especially in late winter and early spring; (iii) the specialist Eurasian hoopoe *Upupa epops* prey on below-ground pupae in late spring and early summer (Fig. 7.6) and (iv) nocturnal predation of adult moths occurs in summer during moth emergence period, by generalist bats (at least *Pipistrellus kuhlii* and *Eptesicus serotinus*), European nightjar *Caprimulgus europaeus* and red-necked nightjar *C. ruficollis* (Table 7.1).

3.2 Predation Strategies Used by Vertebrates to Feed on Thaumetopoea pityocampa

3.2.1 Strategies of Specialist Insectivorous Birds

Large insectivorous birds feeding on aposematic and toxic insects, including those carrying urticating setae, can be considered as dietarily specialized, i.e., they have both homogeneous diets and particular foraging behaviours (Sherry 1990). These species have evolved efficient strategies to feed on urticating Lepidoptera,

Table 7.1 Bird and bat species feeding on *T. pityocampa* (TP) within its circummediterranean range

Predator species	Body mass	Consumed stages	Period	Foraging methods	Diet specialization
Birds					
Clamator glandarius	130–192 g	Late-instar larvae	II–IV	Ground and canopy gleaning	Specialist (TP is up to 100 % of diet)
Cuculus canorus	95–140 g	Late-instar larvae	III–IV	Ground and canopy gleaning	Specialist (hairy larvae are 75 % of diet)
Caprimulgus europaeus	51–101 g	Moths	VII–VIII	Aerial hawking or flycatching	Specialist (moths are 80–90 % of diet)
Caprimulgus ruficollis	60–120 g	Moths	VII–VIII	Aerial hawking or flycatching	Specialist (moths are a large part of diet)
Upupa epops	47–87 g	Pupae, larvae	III–VI	Ground probing and gleaning	Specialist (TP can be up to 74 % of diet)
Parus major	14–22 g	Eggs, larvae, moths	IX–V	Canopy and ground gleaning	Generalist (TP in up to 60–90 % stomachs)
Periparus ater	9.5–12.5 g	Eggs, larvae	X–IV	Canopy gleaning	Generalist (TP in up to 66 % stomachs)
Lophophanes cristatus	10–13 g	Eggs, larvae	IX–IV	Canopy gleaning	Generalist
Bats					
Barbastella barbastellus	6–14 g	Moths	VII–VIII	Aerial hawking	Specialist (moths are up to 90 % of diet)
Plecotus austriacus	6–14 g	Moths	VII–VIII	Aerial hawking or gleaning	Specialist (moths are up to 90 % of diet)
Plecotus auritus	6–14 g	Moths	VII–VIII	Canopy and ground gleaning	Generalist (moths are 20–100 % of diet)
Pipistrellus kuhlii	5–10 g	Moths	VII–VIII	Aerial hawking	Generalist (moths are 15–38 % of diet)
Eptesicus serotinus	18–35 g	Moths	VII–VIII	Aerial hawking	Generalist (moths are 10–15 % diet)

Modified from Barbaro and Battisti (2011)

Predation periods are indicated by months (II = February, III = March, IV = April, V = May, VI = June, VII = July, VIII = August, IX = September, X = October)

including *T. pityocampa*, for example by banging late-instar larvae on branches to discard the head capsule and the integument, and eat only the viscera (Gill 1980; Gonzalez-Cano 1981). The late-instar larvae can also be cleaned from their setae by cuckoos and hoopoes rubbing them on the ground before ingesting the prey (Barbaro and Battisti 2011). Moreover, cuckoos of several genera (*Cuculus, Chrysococcyx, Clamator* and *Coccyzus* spp.) are well-adapted to feed on urticating larvae (Gill 1980). Their gizzard inner layer has evolved towards a soft, thick and non-keratinoid structure that allows the larva setae to be kept inserted in the gizzard wall and to be regurgitated as mixed pellets of mucous membrane, setae and gut contents, including pine needle fragments.

Cuckoos (*Coccyzus* spp., *Clamator glandarius, Cuculus* spp.) are also known for their post-migratory nomadic phase when returning from wintering grounds in early spring, during which they are likely to locate moth outbreak areas (including *Lymantria dispar*, *Malacosoma* spp. or *T. pityocampa*) before establishing their breeding territory (Hoyas and Lopez 1998; Barber et al. 2008). Great spotted *Clamator glandarius* and common cuckoos *Cuculus canorus* can locally specialized on urticating fifth instar larvae of *T. pityocampa*, typically preyed on during pre-pupation processions in early spring (Valverde 1971; Hoyas and Lopez 1998). Another high predator specialization on *T. pityocampa* pupae during below-ground spring diapause is found in the Eurasian hoopoe *Upupa epops*. Hoopoes' long and curved bill allows the birds to dig out buried cocoons, separate the pupae from the urticating skins of the last larval moult, and ingest or carry out pupae for chicks (Battisti et al. 2000; Barbaro et al. 2008; Fig. 7.6). Finally, adult *T. pityocampa* moths are likely preyed on during their summer emergence by two specialists, nocturnal aerial feeders, European nightjar *Caprimulgus europaeus* and red-necked nightjar *C. ruficollis*, where they geographically co-occur with the moth in their respective ranges (Cuadrado and Dominguez 1996; Sierro et al. 2001; Table 7.1).

3.2.2 Strategies of Generalist Insectivorous Birds

Generalist insectivorous forest passerines such as tits (family Paridae) can aggregate in areas with high food availability, including outside the breeding season (Diaz et al. 1998). The great tit *Parus major* is particularly able to forage on temporarily available food resources provided by defoliating Lepidoptera, including some urticating species such as *T. pityocampa* (Pimentel and Nilsson 2007; Garcia-Navas et al. 2013). Empirical evidence for great tit predation on the pine processionary moth, including regular feeding on urticating late-instar larvae, is acknowledged for a long time (Biliotti 1958; Geroudet 1963). Great tits can feed both upon egg clusters, early-instar and late-instar larvae of *T. pityocampa* throughout the moth distribution range from south-western Europe to North africa and the Middle East (Gonzalez Cano 1981; Halperin 1990; Pimentel and Nilsson 2007; Barbaro and Battisti 2011). To feed on overwintering fifth instar larvae of *T. pityocampa*, great tits can dig holes in winter nests to collect larvae and remove their head capsule and most of the integument carrying the urticating setae to eat only inner parts of the larval body (Gonzalez Cano 1981). Most predation events occur in winter, when numerical responses of great tits to moth density can be observed (Barbaro et al. 2013). A previous study in central Spain has shown that up to 90 % of great tit stomachs and faeces contained residues of *T. pityocampa* larvae in winter (Gonzalez Cano 1981; Table 7.1).

The coal tit *Periparus ater* and the crested tit *Lophophanes cristatus* are two conifer-dwelling species that are also able to feed on eggs and early-instar larvae of *T. pityocampa* in summer and autumn in central Spain (Gonzalez Cano 1981). The same study provided evidence for predation of the coal tit on late-instar larvae of *T. pityocampa* using holes made by great tits in winter nests. Although the coal tit is known to feed mainly on pine seeds ouside the breeding season (Brotons and Herrando 2003), up to 66 % of its stomachs and faeces contained pine processionary moth with peak predation periods in October–December and April–May (Gonzalez Cano 1981). Finally, two deciduous forest specialists, the blue tit *Cyanistes caeruleus* and the long-tailed tit *Aegithalos caudatus* have also been reported as occasional, and maybe regular, predators of *T. pityocampa* eggs and early-instar larvae in fall and winter (Gonzalez Cano 1981). However, there is a lack of knowledge regarding the vertebrate and invertebrate predators of these early life-stages of the moth, potentially involving several insectivorous bird species, but also orthopterans and coleopterans (Hódar et al. 2013).

3.2.3 Strategies of Insectivorous Forest Bats

Using mostly echolocation to locate their prey, European bats (Microchiroptera) form a guild of nocturnal insectivores foraging on night-flying invertebrates in various habitats, including forests and their edges (Schnitzler and Kalko 2001; Kunz et al. 2011). Bats can consume over half of their body mass in insects nightly and each foraging guilds use different hunting techniques to feed on a wide spectrum of invertebrate prey, including forest moths (Kalka et al. 2008). Bats, especially open-habitat foragers, are also able to concentrate on locally abundant food resource by aggregative responses to increasing prey density (Müller et al. 2012). Adult moths are mainly active at night and therefore constitute a significant part of bat diets, albeit moths can also be predated by bats during their larval stage (Wilson and Barclay 2006). Numerical responses of bats have been studied to date by comparing total insect availability and bat activity or by nocturnal exclusion experiments (Kalka et al. 2008; Williams-Guillén et al. 2008; Müller et al. 2012; Karp and Dialy 2014). Functional responses of bats have been mostly demonstrated through faeces analysis (Vaughan 1997; Goiti et al. 2003; Kervyn and Libois 2008; Ashrafi et al. 2011).

Among the main bat species occurring in circum-Mediterranean pine forests, two species have particularly specialized foraging methods and diets on nocturnal Lepidoptera, the barbastelle bat *Barbastella barbastellus* (Sierro and Arlettaz 1997) and the grey long-eared bat *Plecotus austriacus* (Ashrafi et al. 2011). Both species are moth specialists with Lepidoptera representing up to 90 % of the diet (Vaughan 1997), which is similar to the proportion found on another nocturnal moth specialist, the European nightjar (Sierro et al. 2001). Two horseshoe bat species (*Rhinolophus ferrumequinum* and *R. hipposideros*) are also significant predators of Lepidoptera (20–90 % of the diet; Vaughan 1997), but they seldom use pine forests for foraging and are thus unlikely to feed on *T. pityocampa*. Three other species, the brown long-eared bat *Plecotus auritus* (Ashrafi et al. 2011), the Kuhl's pipistrelle *Pipistrellus kuhlii* (Goiti et al. 2003) and the serotine bat *Eptesicus serotinus* (Kervyn and Libois 2008) are generalist predators whose foraging methods allows them to feed on moths within pine forest or edge habitats. As opportunistic feeders, their diet is composed of a significant part of Lepidoptera

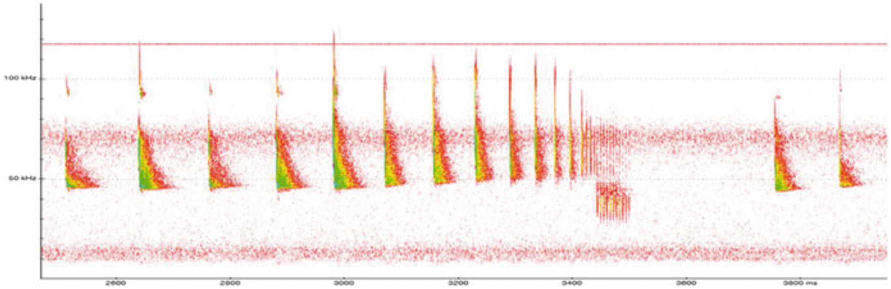

Fig. 7.7 An echolocation sequence including a typical 'buzz' signal emitted by a Kuhl's pipistrelle when capturing a prey such as a pine processionary moth during summer emergence. Kuhl's pipistrelles were responsible for ca 75 % of bat foraging activity recorded during a study in south-western France (Charbonnier et al. 2014)

(Table 7.1) that are likely consumed in proportion with their availability. The latter two species, Kuhl's pipistrelle and serotine bat, showed significant numerical and functional responses to experimentally increased density of pine processionary moths in pine plantations of south-western France (Charbonnier et al. 2014). Moreover, the strongest numerical and functional responses to *T. pityocampa* density were found in the Kuhl's pipistrelle (Fig. 7.7), a Mediterraneo-atlantic bat that experienced a recent expansion of its distribution range with climate warming (Sachanowicz et al. 2006; Rebelo et al. 2010).

3.3 Functional and Numerical Responses of Predatory Birds and Bats

3.3.1 Functional Responses of a Pupae Specialist Bird

The Eurasian hoopoe *Upupa epops* is a specialist insectivore foraging on below-ground invertebrates by ground probing in short sward structures including patches of bare ground (Barbaro et al. 2008; Tagmann-Ioset et al. 2012). Hoopoes are local specialists of *T. pityocampa* late-instar larvae and especially below-ground pupae in circum-Mediterranean pine forests (Battisti et al. 2000; Barbaro et al. 2008). A quantitative study of hoopoes' functional responses to the moth has been conducted in pine forests of northern Italy, showing that hoopoes can consume up to 74 % of buried moth pupae (Battisti et al. 2000). Quantifying pupae predation was based on the number of depredated cocoons left on the ground by hoopoes after pulling out the pupae (Battisti et al. 2000; Fig. 7.6). A telemetry study of foraging adult hoopoes during the breeding season has been performed in pine plantations of south-western France (Barbaro et al. 2008). The study revealed that breeding hoopoes selected pine plantation edges with short sward structures (<7 cm) and important bare sand cover (>25 %) to forage mainly on pine processionary moth

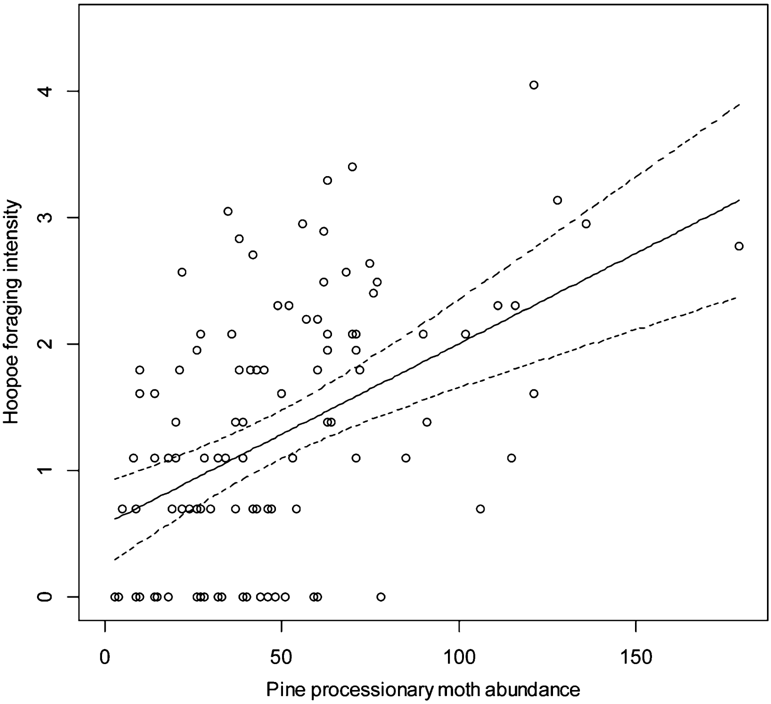

Fig. 7.8 Linear mixed model linking the log-transformed abundance of foraging hoopoes to winter nest abundance of pine processionary moth along pine plantation edges in south-western France (Modified from Barbaro et al. 2008)

pupae and *Gryllus campestris* (Barbaro et al. 2008). Hoopoe foraging microhabitats matched narrowly with those used by *T. pityocampa* for below-ground pupation. As a result, we found a significant increase in hoopoe foraging intensity and nesting success during 3 consecutive years with increasing winter nest density of *T. pityocampa* measured along pine stand edges (Barbaro et al. 2008). The functional response of foraging hoopoes to moth density was analyzed by means of a linear mixed model with pine plantation edge as a random intercept effect and the 3 consecutive years of the study and pine processionary moth nest abundance as fixed effects (Zuur et al. 2009). The year effect on hoopoe foraging intensity was not significant but moth abundance significantly increased hoopoe foraging irrespective of year, indicating a marked functional response of *U. epops* to *T. pityocampa* ($t_{1,67} = 4.95$; $P < 0.0001$; Fig. 7.8).

We further estimated the efficiency of hoopoe predation on moth survival by pheromone trapping in paired stand edges located inside or outside hoopoes' foraging areas during two summers in 2004 and 2006 (Fig. 7.9). We calculated the ratio of trapped moth abundance on winter nest counts in a given pine stand edge to estimate moth mortality due to hoopoe predation. There was a trend for a lower moth survival in preyed than in unpreyed stand edges, although the effect of

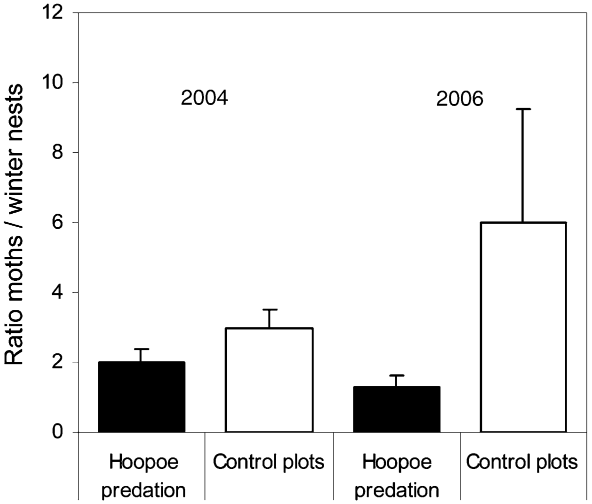

Fig. 7.9 Mean (±SE) moth survival (ratio of trapped moth on winter nest abundances) in paired pine stand edges located within and outside foraging areas of breeding hoopoes' home ranges in 2004 (n = 12) and 2006 (n = 16)

hoopoe predation on the emergent moth/winter nest ratio was not significant (Fig. 7.9). However, the effect of hoopoe predation might be blurred by confounding effects of uncontrolled predation and parasitism and/or incertitude on true abundance of moth population estimated by male pheromone trapping.

3.3.2 Numerical Responses of Generalist Insectivorous Birds

The numerical responses of insectivorous bird assemblages to *T. pityocampa*, including generalist avian predators such as the great tit *Parus major*, have been studied within the moth expansion areas in France (Barbaro et al. 2013). Insectivorous bird communities and moth nest density were sampled on the same 250 m-long linear transects during two consecutive winters in 48 pine forests located along altitudinal (Mont Ventoux) and latitudinal gradients (Aquitaine and Orléans forests) of moth expansion in France. We hypothesized that the numerical reponses of winter bird communities to moth nest density, including foraging tit species flocks, would differ among core (i.e., at lower latitudes and elevations), and expansion areas of the moth distribution (i.e., at higher latitudes and elevations). We recorded foraging bird abundance and richness as the number of individual birds and species observed at least once in foraging activity during 10-min periods at the end of each transect (Brotons and Herrando 2003). Foraging bird assemblages were largely dominated by foraging Paridae tits on both elevation and latitude gradients (respectively 78 % and 55 % of foraging bird species). Dominant foraging species were the great tit and the crested tit *Lophophanes cristatus* on the latitude gradient and the coal tit *Periparus ater* on the elevation gradient (Barbaro et al. 2013).

On the elevation gradient (Mont Ventoux), we analysed the responses of foraging bird abundance and richness by Poisson generalized linear mixed models with elevation belts as a random factor to take into account the uncontrolled variation of moth density with elevation (Zuur et al. 2009). We found a significant effect of moth nest density on bird foraging abundance and richness only during the severe winter of 2009 ($z = 4.17$; $P < 0.0005$ and $z = 4.34$; $P < 0.0002$ for bird abundance and richness respectively; Fig. 7.10a). The significant predictors included in the best models for foraging bird abundance and richness were moth density and dominant tree species after multi-model inference at stand and landscape levels (Barbaro et al. 2013). Foraging bird abundance and richness were also significantly higher in pure Austrian pines (*Pinus nigra* ssp. *nigra*), the favourite host tree for *T. pityocampa*, and lower in mixed pine forests ($z = 4.20$; $P < 0.0003$ and $z = 2.95$; $P < 0.003$ for bird abundance and richness respectively). There was also a significant winter numerical response of *Parus major* to moth nest density on the elevation gradient, suggesting that great tits are able to profit from a somewhat abundant, albeit more difficult to handle, food resource in winter (Barbaro et al. 2013; Garcia-Navas et al. 2013). On the latitudinal expansion gradient (Aquitaine and Orléans forests), we found a similar numerical response of foraging bird abundance and richness, but only during an important *T. pityocampa* outbreak in winter 2010 ($z = 3.53$ and $P < 0.0005$ for foraging bird richness; Fig. 7.10b). The separate effect of host pine species (*Pinus pinaster, P. nigra* and *P. sylvestris*) on foraging bird abundance and richness along the latitude gradient was not significant.

3.3.3 Numerical and Functional Responses of Foraging Bats

To study the numerical and functional responses of forest insectivorous bats to the pine processionary moth, we used an experimental design coupling pheromone traps and ultrasound bat recorders along pine stand edges in south-western France (Charbonnier et al. 2014). We estimated foraging bat activity in response to increasing abundance of mating male moths attracted by pheromone lures along a gradient of pine stand infestation by *T. pityocampa*. We quantified bat species abundance (numerical response) as the number of echolocation calls recorded per species and bat foraging activity (functional response) as the number of buzz signals indicating effective feeding attempts recorded per species (Fig. 7.7). Pheromone lures were used to simulate male moth aggregations after emergence at pine stand edges used by foraging bats in summer. We used linear mixed models to link the log-transformed abundance of echolocation calls with the nested effect of sampling night within the plot as a random intercept factor (Zuur et al. 2009).

Foraging bats showed both numerical and functional responses to increased abundance of adult pine processionary moths for two generalist species: the Kuhl's pipistrelle *Pipistrellus kuhlii* ($z = 3.39$; $P < 0.001$ for the numerical response; $z = 3.38$; $P < 0.001$ for the functional response; Fig. 7.11a) and the serotine bat *Eptesicus serotinus* ($z = 2.51$; $P < 0.02$; for the numerical response; $z = 2.30$; $P < 0.05$ for the functional response; Fig. 7.11b). By contrast, the responses of the moth-feeding bat specialists recorded, *Barbastella barbastellus*

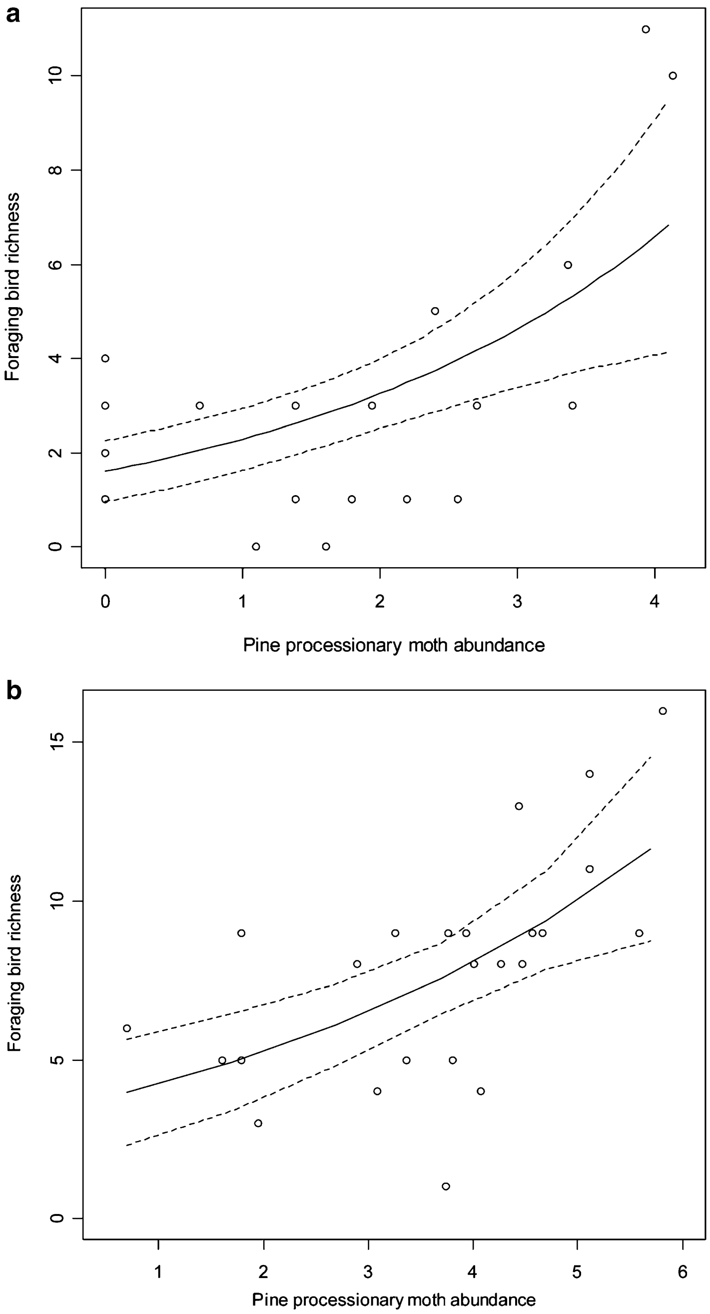

Fig. 7.10 Poisson generalized linear mixed models linking foraging bird richness to log-transformed nest abundance of pine processionary moth; in (**a**) winter 2009 on an elevation gradient of moth expansion (Mont Ventoux forest); (**b**) winter 2010 on a latitudinal gradient of moth expansion (Aquitaine and Orléans forests)

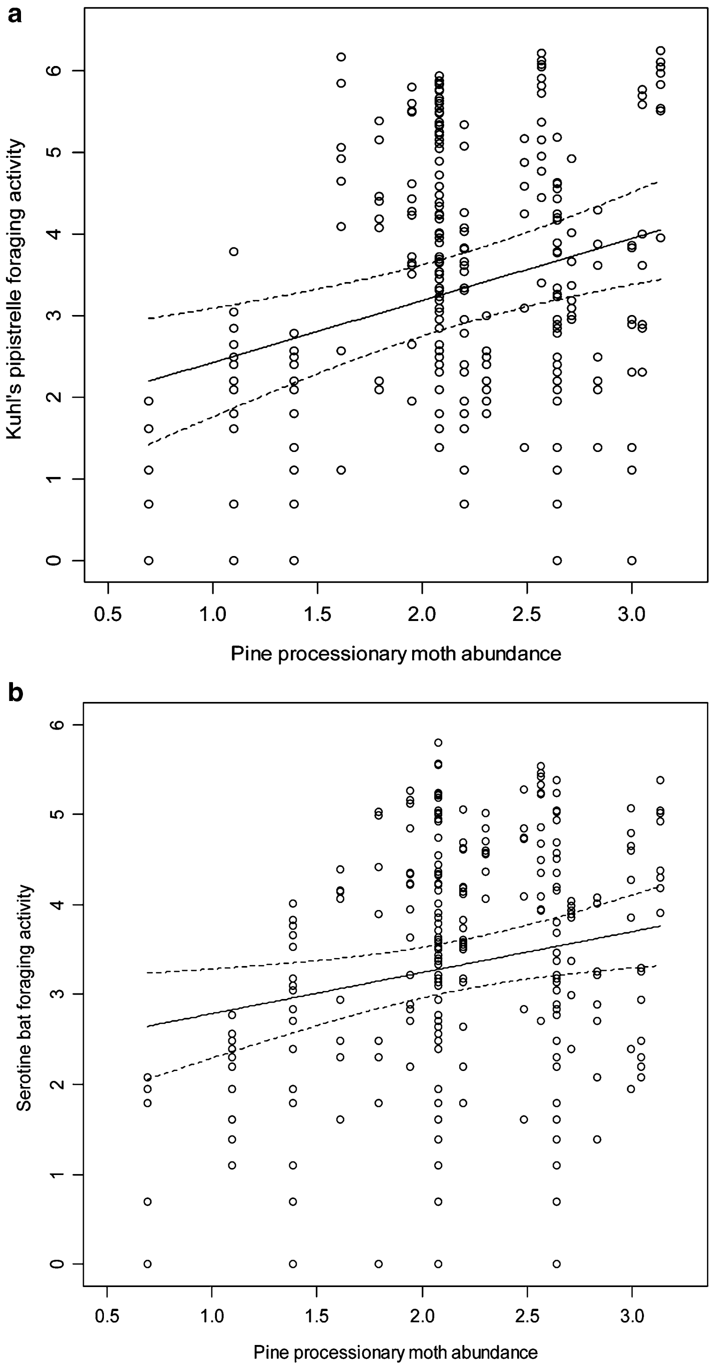

Fig. 7.11 Linear mixed models linking log-transformed foraging activities of generalist bats for; (**a**) *Pipistrellus kuhlii* and; (**b**) *Eptesicus serotinus* to log-transformed moth abundance monitored by pheromone trapping (Modified from Charbonnier et al. 2014)

and *Plecotus* spp., were not significant despite a trend for increased foraging with *T. pityocampa* abundance. Moth-feeding bat specialist occurred at much lower overall abundance in the study site compared to generalist bats *P. kuhlii, P. pipistrellus* and *E. serotinus*, which may explain the lack of significant responses observed for specialist bats compared to generalists, together with distinct prey selection strategies (Charbonnier et al. 2014). Generalist forest bats also exhibited significant functional responses to mating aggregations of male pine processionary moths, since their foraging activities were significantly higher close to moth pheromone lures than in control plots (Charbonnier et al. 2014). Nocturnal activity periods of foraging bats and mating adult moths were also both higher during the first 4 h after sunset, indicating a narrow temporal matching between flying bats and pine processionary moths.

3.4 Discussion and Conclusion

Both insectivorous birds and bats are efficient predators able to track prey fluctuations and to aggregate in places where prey density is higher (Crawford and Jennings 1989; Diaz et al. 1998; Barber et al. 2008; Müller et al. 2012). In temperate forests of the northern hemisphere, predatory vertebrates can especially aggregate in highly-defoliated forest areas caused by the collective feeding behaviour of outbreaking forest moths such as *Choristoneura fumiferana, C. occidentalis, Ennomos subsignarius, Epirrita autumnata, Operophtera brumata, Lymantria dispar* and *T. pityocampa* (Morris et al. 1958; Haney 1999; Gale et al. 2001; Hogstad 2005; Wilson and Barclay 2006; Pimentel and Nilsson 2007; Barbaro et al. 2013). Such aggregation of predators in high prey density areas are found both in specialist and generalist insectivores and is especially documented in the *Coccyzus* cuckoos (Gale et al. 2001; Barber et al. 2008) and the Parulinae warblers in North America (Crawford and Jennings 1989; Patten and Burger 1998; Venier and Holmes 2010). The most efficient predators of target lepidopteran pests (spruce budworm *Choristoneura fumiferana* and elm spanworm *Ennomos subsignarius*) constitute a species-rich pool of specialist canopy-gleaners including bay-breasted *Dendroica castanea*, Cape May *D. tigrina* and Tennessee warblers *Vermivora peregrina* (Morris et al. 1958; Patten and Burger 1998; Haney 1999; Venier and Holmes 2010). Birds from this key foraging guild can consume up to 84 % of budworm pupae and larvae when prey populations are low, and up to 22 % at higher prey density (Crawford and Jennings 1989). In European forests, numerical responses of forest passerines, including the brambling *Fringilla montifringilla*, to geometrid moth outbreaks have been demonstrated (Hogstad 2005). However, a similar functional role such as the one played by Parulinae warblers in North America is mostly provided in Europe by Paridae tits, which are resident canopy gleaners able to exploit rapidly a new food resource locally and temporarily abundant, during the breeding season as well as in winter (Diaz et al. 1998; Brotons and Herrando 2003; Velky et al. 2011; Kaunisto et al. 2012; Carrascal et al. 2013).

The most significant generalist predator of *T. pityocampa* outside the breeding season is the great tit *Parus major* (Gonzalez-Cano 1981; Pimentel and Nilsson 2007; Barbaro and Battisti 2011). Its rapid responses to spatial and temporal fluctuations of food resources is linked to efficient foraging and feeding behaviours allowing to benefit from prey more difficult to handle than usual, such as urticating moth larvae (Gonzalez-Cano 1981; Velky et al. 2011; Garcia-Navas et al. 2013). According to the ideal free distribution, the winter occurrence of foraging great tits is mainly driven by food availability and accessibility (Diaz et al. 1998; Kaunisto et al. 2012; Carrascal et al. 2013). As predicted by optimal foraging theory, overwintering nests of *T. pityocampa* larvae may constitute large, abundant and aggregated protein-rich prey allowing a temporary specialization, especially during cold periods (Barbaro et al. 2013; Carrascal et al. 2013). The high adaptive plasticity of great tits makes them efficient biocontrol agents in agroecosystems and plantation forests, including for newly occurring or expanding pest insects (Kaunisto et al. 2012). Another generalist predator, the Kuhl's pipistrelle *Pipistrellus kuhlii* also exhibited marked numerical and functional responses to adult pine processionary moth density in summer. The Kuhl's pipistrelle is a Mediterraneo-atlantic bat that experienced a recent expansion of its distribution range with climate warming (Sachanowicz et al. 2006; Rebelo et al. 2010). It may thus be potentially able to track more than other predators the current range expansion of *T. pityocampa* northwards (Battisti et al. 2005).

Although generalist predators alone can be efficient for pest insect biocontrol (Symondson et al. 2002), the occurrence of the complete vertebrate guild of *T. pityocampa* predators would provide a biotic insurance through functional complementarity between predators succeeding along the entire moth life cycle, in the absence of marked intraguild competition between moth predators (Philpott et al. 2009; Barbaro and Battisti 2011; see Table 7.1). The predation of pine processionary moth by specialist predators occurs mostly in spring during the critical late-instar larval and pupal stages (Hoyas and Lopez 1998; Battisti et al. 2000). However, specialist bats (barbastelle and long-eared bats) and birds (cuckoos, hoopoe, nightjars) exhibit lower density than generalists due to higher habitat requirements, including resource complementation needs at the landscape scale (Nakamura and Miyazawa 1997; Sierro and Arlettaz 1997; Sierro et al. 2001; Barbaro et al. 2008; Ethier and Fahrig 2011). Promoting silvicultural practices for the highest possible coexistence of generalist and specialist predators within European pine forests at stand and landscape scales is therefore critical to ensure a sustainable management of this key defoliator (Cayuela et al. 2011; Hódar et al. 2012). Such practices would include keeping understorey forest structure compatible with aerial foraging of bats and nightjars on adult moths in summer (Sierro et al. 2001; Jung et al. 2012), favouring stand edge diversity in pine plantations for stopover insectivore migrants potentially feeding on eggs and early-instar larvae during autumn migration (Rodewald and Brittingham 2004), and maintaining short sward structure along pine stand edges for large ground-gleaning insectivores such as the hoopoe (Barbaro et al. 2008; Tagman-Ioset et al. 2012). As a concluding remark, we advocate for considering the pine processionary moth as a keystone species in European pine forests for both forest health and biodiversity rather than an oversimplistic view of a forest pest insect that need to be fully eradicated by non-sustainable practices such as insecticide spraying (Müller et al. 2008; Cayuela et al. 2011).

4 The Expansion of the Pine Processionary Moth in the Southern French Alps and Its Impact on the Populations of the Endangered Spanish Moon Moth

Charles-Edouard Imbert, Francis Goussard, and Alain Roques

4.1 Introduction

In a number of insect species, the recent warming up has relaxed the thermal barriers previously delimiting the species' natural range, thus allowing a more or less rapid expansion of this range (Parmesan 2006; Parmesan et al. 1999). Those species are thus entering areas where they were excluded until now. Their arrival is susceptible to affect severely the structure and composition of communities as well as the functioning of ecosystems in the newly colonized areas (Walther et al. 2009). Actually, the presence of an additional organism in an ecosystem can have huge consequences on local species, as it is rather well documented for exotic invasive species introduced into a new continent where they may behave as predators or competitors for the resource, or both, for native species (Gurevitch and Padilla 2004; Hill and Lodge 1999; Kenis et al. 2009). Bøhn et al. (2008) thus listed as possible consequences of such competitive interactions: (i) niche shifts in habitat or diet; (ii) decrease in population density or extinction; (iii) reduced individual growth rate; (iv) reduced food intake; (v) alteration of prey community towards smaller species; and, (vi) altered size structure of prey populations towards smaller individuals.

However, unlike invasive species, the possible impact of expanding populations of native insects on local communities inhabiting the areas they are colonizing with warming up, has been little studied. One of the best documented examples of the effect of climate warming on the release of thermal thresholds constraining species distribution is the pine processionary moth, *Thaumetopoea pityocampa* (Den. & Schiff.) (Lepidoptera: Notodontidae), a major pine defoliator in southern Europe (Hódar et al. 2003). Since the mid-1990, populations of this winter- developing insect of Mediterranean origin are expanding towards higher latitudes and elevations in Southern and Western Europe (see Roques et al. 2014, Chap. 3, this volume). On the average, the moth progressed northwards by 5.6 km per year in the Paris basin (Robinet et al. 2007, 2012), and its mean upper distribution in elevation in the Italian Alps advanced by 70.1 m per decade (Battisti et al. 2006). Thus, *T. pityocampa* is entering new bioclimatic and bio-ecological areas where it may affect the resident fauna through eg., novel competitive interactions for pine resources, indirect effects on host quality, indirect cascading effects through shared parasitoids, and virus/disease transmission. The recent penetration of pine processionary moth into some high Alpine valleys of the Southern French Alps offered the possibility of assessing the possible impacts on a remarkable, resident competitor for pine needle resource, the endangered Spanish moon moth, *Actias* (=*Graellsia*) *isabellae* (Graells, 1849) (Lepidoptera: Saturniidae).

4.2 Pine Processionary Moth Expansion Lead to Face New Competitors for Pine Resources

4.2.1 Expansion of Pine Processionary Moth in the Upper Durance Valley

The Upper Durance valley of the Southern French Alps hosts one of the expansion leading edge in altitude of pine processionary moth. The pine processionary moth was historically present in the south of this valley, below 1,000 m elevation, but its presence in the upper areas was limited by the harsh climatic conditions prevailing there. Since the early 2000s, it has entered the sub-alpine mountainous climatic level, colonizing stands of Scots pine (*Pinus sylvestris* L.) located at 1,200–1,400 m elevation in the Natural park of Queyras (Imbert et al. 2012). At present, the moth has crossed more than 4 km onto the park. The pine processionary moth has thus penetrated the natural range of another moth developing on Scot pines, the Spanish moon moth (Goussard and Roques 2007; Maurel et al. 2013). The natural ranges of the two moth species were contiguous and did not overlap until this moment. In this area, *T. pityocampa* feed on pine foliage from August on throughout winter and leave the colonized pines by March–April to pupate in the ground (Huchon and Démolin 1971).

4.2.2 A Native Competitor for Pine Foliage, the Spanish Moon Moth, *Actias isabellae*

The endangered Spanish moon moth, *Actias isabellae*, is restricted in France to a few upper valleys of the Southern Alps (Goussard and Roques 2007; Maurel et al. 2013). The French Natural park of Queyras, situated in the Guil valley of the Southern French Alps, shelters a large part of the moth populations. This beautiful moth is protected by the Habitats' Directive and the Bern Convention (revised by Procter and Harding 2005), and included in the French and Spanish official red lists of endangered fauna (Vila et al. 2009).

A. isabellae develops on Scots pine, and probably mountain pine. There is 1 generation per year. The adults emerge, mate and lay eggs in May–June. The hatching larvae feed solitarily on mature needles produced during the previous years but they do not consume the needles of the current year (Goussard and Roques 2007). The larvae pass through five larval stages until August when they finally pupate in the ground where they overwinter (Chefaoui and Lobo 2007).

Thus, the flight and egg-laying period of *A. isabellae* just follows the departure of *T. pityocampa* larvae in spring, which leave host pines partially defoliated and showing large white nests. Since 2007, such processionary nests have frequently been observed on pine trees known to regularly host larvae of *A. isabellae* in the lower part of its range in the Queyras natural park (Imbert et al. 2012). *A. isabellae* populations usually remain at low density and do not inflict any visible defoliation on Scots pines (Goussard and Roques 2007) in contrast to the defoliation caused by the gregarious larvae of *T. pityocampa* (Hódar and Zamora 2004).

4.3 Possible Effects of Pine Processionary Moth Expansion on the Choice of Oviposition Sites by Spanish Moon Moth

4.3.1 Pine Processionary Arrival Modifies the Pine Tree Habitat for Spanish Moon Moth

In phytophagous insects, selection by females of a site adequate for egg-laying is crucial for the survival and development of offspring. Often, first-instar larvae are not highly mobile and cannot move to another host if the one on which they have emerged is not adequate (Renwick and Chew 1994). During the search for an oviposition site, the choice of host plant is determined by multiple stimuli. At first, long- distance orientation is governed by visual and/or olfactory signals. Vision has a major role for host plant localization in a number of insect species. Visual cues may include color (e.g., in bark beetles *Dendroctonus frontalis* Zimmerman; Strom et al. 1999), spectral reflectance and reflectance contrast with the background (e.g., larch cone flies; Roques 1988), but also host shape or silhouette such as in the pine processionary moth (Démolin 1969; see Chap. 5). Volatiles emitted by the host plant also have a major role in the orientation of phytophagous insects and for alimentation and oviposition (Visser 1986) although it appears difficult to get a general pattern in a number of species including pine processionary moth (see Roques et al. 2014, Chap. 5, this volume). However, no data still exist about host selection process in Spanish moon moth, and the possible associated cues. Therefore, the observations could be only empirical at this moment.

The colonization of a pine tree by processionary moths has both direct and indirect consequences. Under temperate and mountainous climates, the gregarious larvae of this winter-developing insect progressively build a large white, silky nest as a protective shelter during the winter period. The final size of this nest can be up to 20 cm in diameter (Démolin 1969). In the Alps, the nest is built by November and it remains on tree, although discolored, several months after the larvae left it by early spring for pupation in the soil. Depending on population density of both insects and hosts, a variable number of nests can be present on the same tree, thus changing drastically its visual aspect. Second, needle consumption by developing larvae can result in a severe defoliation, which can sometimes exceed 90 % of the foliage (Hódar et al. 2003), thus also affecting tree visual appearance. Besides, defoliation by pine processionary larvae results in modifying the chemical composition of the needles (Hódar et al. 2004), and is likely to change as well the profile of volatile emissions by the attacked tree such as it has been observed in other defoliators (Haukioja 1990; Mumm et al. 2003).

4.3.2 In Situ Study of the Response of Spanish Moon Moth to the Arrival of Pine Processionary Moth

The egg-laying behavior of *Actias isabellae* has not yet been precised. However, in any case, in the areas newly colonized by pine processionary moths females of *A. isabellae* foraging for pine trees have at present to cope with the presence of white nests and a more or less heavy defoliation due to the processionary larvae which have just left these trees. As soon as the pine processionary moth was first detected in the natural range of *A. isabellae* in the Queyras valley, the latter species was no more observed on several individual trees where it was frequently recorded before (Goussard, Personal observation). Various factors may be involved, of which annual variations in population density and population displacement in response to climate change – but nothing is yet known about these processes –, but also a response to the habitat disturbance induced by the arrival of pine processionary moth.

To test whether females of *A. isabellae* avoid trees previously colonized by pine processionary larvae, we translocated in autumn colonies of second instar larvae of pine processionary moth in an area of the natural range of *A. isabellae* where processionary moths were still absent (vallon du Fournel, near L'Argentière la Bessée, southern French Alps). In spring 2009, a systematic survey of pine trees in the area using feces traps on the ground allowed to select 40 trees on which *A. isabellae* was present (for details, see Imbert 2012). During autumn, one to five colonies of pine processionary larvae were grafted on half of these trees, the others being used as a control. The previous presence of pine processionary larvae on a tree did not seem to affect significantly the further occurrence of *A. isabellae* larvae. Developing larvae of *A. isabellae* were found again in 2010 on 11 of the 40 surveyed trees, proving that females of Spanish moon moth used at least these trees for egg-laying although mortality factors could have eliminated larvae or eggs laid on other trees. These 11 colonized trees included four ones with no grafted processionary colonies but three of them had one colony and four had five colonies.

Therefore, mated females of *A. isabellae* apparently lay eggs on pine trees whatever their defoliation status. In phytophagous insects, egg- laying and host choice behavior can help to precise population dynamics. A selective behavior may allow females to avoid an overexploitation of the resource. On the other hand, a lack of selectivity in host choice does not allow the species to cope with an altered food resource and its impact on the offspring development; this could be a reason for the eruptive phases observed in some populations (Tammaru et al. 1995). Mated females of *A. isabellae* lay approximately 90 eggs within several days (Chefaoui and Lobo 2007). A 15-year survey of their populations in this Alpine area did not reveal any eruptive patterns, or any strong defoliation of the host trees. This could suggest a selective behavior for the egg-laying site. However, under laboratory breeding conditions, mated females can lay eggs on dead or alive branches of any tree species, suggesting a non- selective behavior for the egg- laying site.

In Scot pines, defoliation results in large changes in the physico-chemical composition of needles as well as in the qualitative and quantitative of their volatile emissions (Honkanen et al. 1999; Poykko et al. 2005; Smits and Larsson 1999; Smits et al. 2001). Because hatching larvae of *A. isabellae* must feed on the tree where the eggs were laid, a non- selective behavior for the oviposition site may be problematic in case of large previous damage by processionary larvae.

4.4 Impact of Previous Defoliation by Pine Processionary Moth on Survival and Development of Actias isabellae

4.4.1 Change in Food Quality Induced by Defoliation Due to Pine Processionary Larvae

Defoliation by an herbivore may induce a defensive response from the attacked plant (Haukioja 1990; Nykanen and Koricheva 2004). This reaction, called ‘Induced Response’, may lead to a modification of the food quality for the defoliators (Smits et al. 2001), and have an impact on their population dynamics (Kaitaniemi et al. 1999; Nykanen and Koricheva 2004; Tscharntke et al. 2001; Williams et al. 2005). Thus, winter defoliation by *T. pityocampa* larvae is known to affect directly the quality of the juvenile foliage to be produced the following spring (Battisti 1988). Hódar et al. (2004) actually showed a direct relationship between the survival of *T. pityocampa* larvae on a pine tree in a given year and its defoliation by the previous generations of processionary moths, the more defoliation, the lower the larval survival. Indeed, pine trees generally compensate for defoliation by producing new foliage to restore resources for photosynthesis, but these renewed plant tissues usually show modifications in primary or secondary compounds (Poykko et al. 2005). Hódar et al. (2004) observed that the needles of defoliated pines present higher nitrogen levels and a lower content in fibers, tannins and phenolics than those of undefoliated pines, but they consider it difficult to identify the substances causing a detrimental effects on herbivores. Similarly, Battisti (1988) showed that complete tree defoliation by *T. pityocampa* significantly modified the physico-chemical characteristics of the subsequent needles in Austrian pines (*Pinus nigra*), therefore negatively affecting survival and development of the next generation of larvae feeding on the branches that had been previously defoliated. Increased death among the newly-hatched larvae feeding on trees previously defoliated might be an important driver of herbivore populations (Zalucki et al. 2002), and more especially the main cause of the collapse following the eruptive phase in several outbreaks of forest insects (Haukioja 1990; Hódar et al. 2004). Hódar et al. (2004) also showed that the most abundant terpenes of Scots pine foliage in Sierra Nevada Mountains had lower concentrations in trees previously defoliated by *T. pityocampa*. β-pinene contrastingly increased in pines defoliated the year before but not in these defoliated 2 years before or having two consecutive defoliations. They concluded that terpenes may be more constitutive than inducible in Scots pine. However, the relationships between the chemical profile of a plant and the response of the insects feeding on that plant remains still controversial (Hódar et al. 2004),

4.4.2 Do the Changes in Food Quality Induced by Processionary Larvae Affect Survival and Development of *A. isabellae* Larvae?

To investigate how the degree of previous defoliation by processionary larvae undergone by host pines might later affect the survival and development of *Actias isabellae* larvae, manipulative experiments were carried out under semi-natural conditions in a Scots pine nursery at INRA Orléans (Imbert et al. 2012). Sixteen trees from the same clone, and the same age, were manually implanted with processionary colonies during autumn 2009. Four treatments were applied in order to get an increasing rate of defoliation, from control trees without defoliation (0 %), to trees with little defoliation (5–25 %), medium defoliation (25–50 %), and heavy defoliation (more than 50 %). Then, in the following spring groups of 10 larvae *Actias isabellae* were reared from the first instar until pupae on twigs cut from these 16 test trees in order to assess the survival rate and the development time of each larval instar.

A daily survey revealed that the defoliation rate, whatever its magnitude, did not result in a significant change in the survival rate of *Actias isabellae* larvae (Fig. 7.12) whereas Hódar et al. (2004) observed an effect of the previous defoliation by pine processionary on the survival of conspecific larvae the year after. However, feeding on foliage of heavily defoliated trees (>50 %) resulted in a significant increase in the development time of *A. isabellae* larvae and a decrease in relative growth rate compared to feeding on foliage of undefoliated trees (Fig. 7.13a). A longer development time may have an indirect effect on the survival of larvae. The "slow growth, High mortality" hypothesis suggests that herbivores feeding on plant with low nutritional quality are likely to increase the time of their development, and so the window of vulnerability to natural enemies attack and/or climate is enlarged (Benrey and Denno 1997; Williams 1999; Cornelissen and Stiling 2006). However, lower defoliation levels did not result in significant differences in larval performances of *A. isabellae* compared to control (Imbert et al. 2012).

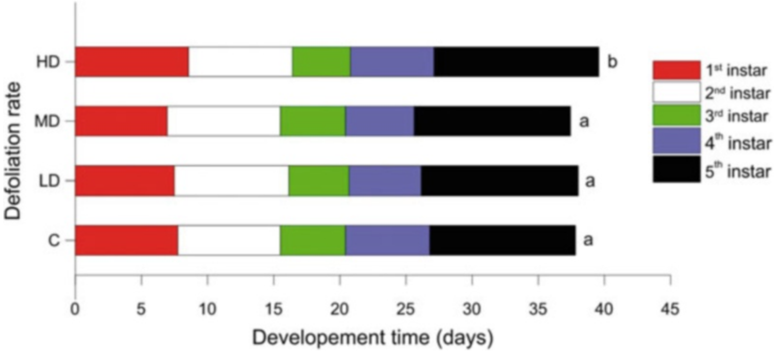

Fig. 7.12 Mean time of the five larval instars of *A. isabellae* with regard to the degree of previous defoliation by *T. pityocampa* of the pines trees on which they are reared. Defoliation groups: C: no defoliation; LD: 5–25 % defoliation; MD: 25–50 %; HD: >50 % defoliation. Letters on the right indicate the differences in total development time according to defoliation groups at αB = 0.008 using multiple pairwise Mann-Whitney test (From Imbert et al. 2012)

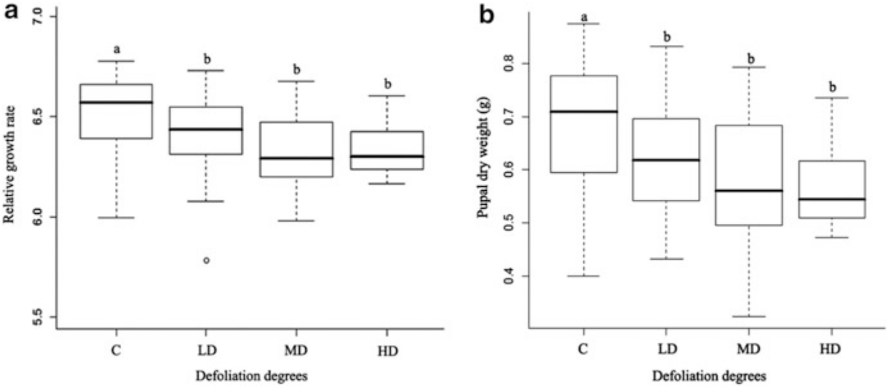

Fig. 7.13 Effect of the degree of previous defoliation of Scots pine trees by *T. pityocampa* on (**a**) the relative growth rate of larvae of *A. isabellae* fed with needles from these trees; (**b**) the dry weight of pupae of *A. isabellae* issued from these larvae. Defoliation groups: C: no defoliation; LD: 5–25 % defoliation; MD: 25–50 %; HD: >50 % defoliation. Boxes topped with the same letter are not significantly different at αB = 0.008 using multiple pairwise Mann-Whitney tests (From Imbert et al. 2012)

Dry weight of pupae was also significantly decreased when the larvae were fed with foliage of defoliated trees whatever the defoliation degree (Fig. 7.13b), and this may affect imago performances. Pupa weight is considered to be correlated with adult performances and especially the reproductive potential by influencing flight capabilities of males and mating process (Wigglesworth 1972) as well as female fecundity. Defoliation has already been shown to influence negatively the reproductive potential in other species (e.g., larch budmoth, Benz 1974). In females, the egg mass is a part of the adult body and it is related to the female size. In a number of species, smaller females were considered to lay a fewer number of eggs and therefore to present a reduced fecundity (Honek 1993; Pimentel et al. 2011). *A. isabellae* does not feed during the adult stage and then, the resources to be used during this stage for reproduction directly depend on these obtained during the larval stage (Heisswolf et al. 2009). Therefore, the consumption of needles from trees defoliated by pine processionary moth may reduce the number of eggs carried by females as well as the flight capacities of males. Since high degree of *T. pityocampa* defoliation is to be expected during the colonization phase, its arrival in the subalpine pine stands may effectively affect the populations of the endangered *A. isabellae*.

4.5 Are the Parasitoids Arriving with Pine Processionary Moth Susceptible to Affect Actias isabellae *Populations?*

4.5.1 Apparent Competition Between Pine Processionary Moth and Spanish Moon Moth?

Apparent competition is defined as the reduction of the fitness of a species caused by another species' natural enemies (Holt 1977). For example in California vineyards the decrease in population density of a native leafhopper, *Erythroneura eleganta* Osborn, was not directly caused by the introduction of an invasive congeneric species, *Erythroneura variabilis* Beamer, but by an increase in the parasitism rate following the arrival of the invasive one (Settle and Wilson 1990). Another striking example is the parasitoid complex associated to the invasive gypsy moth, *Lymantria dispar* in the United States, including more than 60 introduced species (Kenis et al. 2009) of which the dipteran *Compsilura concinnata* (Meigen), which parasitizes larvae and turned later to be responsible for the extinction of several species of Saturniidae (Boettner et al. 2000). Péré et al. (2010) also showed that apparent competition mediated by shared natural enemies accompanying the spatial invasion in Central and Western Europe of the horse- chestnut leafminer, *Cameraria orhidella* Deschka & Dimic, affects species richness and abundance of other native leafminers. Such a process can be expected with the generalist parasitoids associated to pine processionary moth which could switch on other species, especially lepidopterans, in the newly colonized areas. Although their rate of expansion is lower than that of the pine processionary moth (see above 7.2.; Imbert 2012; Robinet et al. 2012), the presence of such parasitoids, those affecting moth egg at least, have now been ascertained near the expansion fronts (see 7.1) whereas pupal parasitoids are already present in isolated colonies beyond the front (Robinet et al. 2012). Thus, it can be wondered wether some of these generalist parasitoids can switch on Spanish moon moth.

4.5.2 The Native Parasitoid Complex Associated to Spanish Moon Moth

The natural enemies of *Actias isabellae*, especially these attacking the larval stages, are quite unknown, in France at least. In Spain, larvae were observed to be attacked by several parasitoids species such as the hymenopterans *Pimpla robusta* Rondani (Hymenoptera, Ichneumonidae) and *Ichneumon microsticus* Wsm. (Hymenoptera, Ichneumonidae) and the dipterans *Compsilura concinnata* (Meigen) (Diptera, Tachinidae), *Masicera silvatica* (Fallén) (Diptera, Tachinidae) and *Drino inconspicua* (Meigen) (Diptera, Tachinidae) (Peigler 1996). Tachinid and ichneumonid larval parasitoids have also been observed on other saturniid species (Boettner et al. 2000). Unlike processionary moths, no egg parasitoids have yet been detected. The adults, and principally males looking for females and attracted by their sex pheromones, are predated by bats during the night (Imbert, Personal observation).

4.5.3 Experimental Survey of a Possible Switch of Egg Parasitoids of Pine Processionary Moth on Spanish Moon Moth

Among the numerous parasitoids of *T. pityocampa* recorded in the Alps (Biliotti 1958), these associated with eggs are more easy to survey, sample and manipulate; an additional interest being that they are known to be capable of affecting largely the host population dynamics. Three of the four species observed in the Southern French Alps are generalists (*Ooencyrtus pityocampae*. *Anastatus bifasciatus* and *Trichogramma* sp.) whilst the last one, *Baryscapus servadeii,* is specialized on the processionary moth (see 7.2.). *O. pityocampae* and *B. servadeii* largely dominate the egg parasitoids in the expanding processionary moth populations found near the expansion front in the Upper Durance valley (see Fig. 7.3.). The generalist *Ooencyrtus pityocampae* is the first species to hatch, from early June on. This timing perfectly matches the end of the flight period of *A. isabellae* and, subsequently, the period where its eggs are laid. The eggs of Spanish moon moth largely differ from these of pine processionary moth by both their larger size, their blue-grey color and the much smaller size of the clutch, which corresponds to a tiny pack of ca. 10 eggs. In order to investigate the egg parasitism in *A. isabellae* under natural conditions and the possible sharing of parasitoids with *T. pityocampa*, eggs of *A. isabellae* were artificially offered to parasitoids in three experimental sites of *Pinus sylvestris*, selected along the Upper Durance valley according to the simultaneous presence or not of both moth species. A first site was located in the core range of *A. isabellae* where the pine processionary moth was not yet present (06°46′08.7″E; 44°44′15.8′N) whilst the second site located in the subalpine expansion range of processionary moth hosted both species (06°41′52.8″E; 44°40′ 33.8″N), and the third one was located much southern in the core area of the pine processionary moth (06°20′11.3″E; 44°31′38.7″N), where *A. isabellae* was not present. The last site could be considered as a control site to appreciate the capability of egg parasites to attack *A. isabellae* egg under high density of pine processionary moth. The eggs used for this experimentation were obtained through manipulative matings realized under natural conditions in the same area of the Alps between females issued from INRA laboratory breedings and wild males naturally attracted by these females. It allowed to expose three series of 20 eggs per site for a total of 60 eggs by site. Each group of 20 eggs was tied to a branch of a different Scots pine tree. The eggs were installed less than 24 h after laying and were left for 10 days on site. Then, the eggs were brought back to the laboratory in order to assess the relative proportion of moth larvae hatching vs. the possible emergence adult parasitoids. Eggs without any hatching were finally dissected to check for dead parasite larvae.

Whatever the site, no parasitism was finally observed on the exposed eggs whilst the percentage of hatching larvae of *A. isabellae* varied from 56.7 to 68.3 % but did not significantly differ between sites. *O. pityocampae* was successfully reared in Spain on eggs of *A. isabellae* eggs but only under controlled conditions, with no simultaneous offering of eggs of another species (Lopez-Sebastian et al. 2004). Even if this generalist parasitoid is present in the natural Alpine range of *A. isabellae*, it may be prevented to parasitize its eggs because of behavioral and/or physiological incompatibility (Menendez et al. 2008) or it may be unable to identify *A. isabellae* eggs in the pine forest. Actually, Battisti (1989) showed that *O. pityocampae* is attracted by the sex pheromone of pine processionnary moth, which allows it to locate the host. However, it has been observed to parasitize eggs of a number of other lepidopteran and hemipteran species of which several also develop on pine trees (e.g. the pine-tree lappet moth, *Dendrolimus pini* (L.), the pine hawk moth, *Sphynx pinastri* L.; Noyes 2003), indicating that it is capable of identifying those eggs.

Finally, even if the pine processionary moth has penetrated the natural range of *A. isabellae* in the Alps, its egg parasitoids do not seem to attack the eggs of the protected moth. However, it is likely that several of the numerous other parasitoid species associated with the larval and pupal life stages of pine processionnary moth (see Battisti et al. 2014, Chap. 2, this volume) have followed the expansion of their host although no precise assessment yet exists. Thus, a thorough study of the parasitoid complex associated to all life stages of *A. isabellae* seems urgent to be realized in order to both understand its role in the population dynamics of this specie and compare its composition with that of pine processionary moth in the expanding areas.

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Chapter 8
Medical and Veterinary Impact of the Urticating Processionary Larvae

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1 Introduction

This chapter presents recent findings on the impact of processionary moths on human and animal health. The data obtained demonstrate that setae can be dispersed kilometers away from their origin, a fact that now explains why some sensitized subjects experience symptoms without a direct contact with larvae.

The use of molecular biology has made possible the study of some allergens present in the setae and Tha p 2, a major setae allergen from *T. pityocampa*, probably corresponds to thaumetopoein described many years ago. Therefore, setae must be considered as a source of allergens and not only as producers of irritant or toxic reactions.

The sensitizing capacity of moth allergens is clearly demonstrated with the help of epidemiological studies. Frequent contact seems to be the most relevant factor for sensitization and occupationally exposed workers should be carefully checked for sensitization in order to avoid further exposure to the allergens.

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Processionary moths constitute also a health hazard for animals. This chapter describes the results of epidemiological studies carried out to measure the relevance on different animal species, the main symptoms after contact and the degree of knowledge among veterinarians about this risk.

The relative risk of sensitization in France has been calculated and a program allows now to estimate the zones with highest danger. In this way medical and veterinary professionals as well as the whole population could be made aware about the danger of these moths and the preventive measures necessary to avoid contact with the setae.

Taking all these facts in consideration, the chapter updates our knowledge about the impact on health of *T. pityocampa*. Most of the findings will be useful for the remaining processionary moths, but the most relevant fact is that climate change will affect other territories where this problem was not previously known. It is therefore necessary that animal and human health professionals working in newly colonized areas are instructed about this emerging health hazard.

2 Comparative Structure of the Urticating Apparatus in Processionary Moths

Andrea Battisti, Paolo Paolucci, Edoardo Petrucco Toffolo, and Alain Roques

2.1 Introduction

Urticating setae are common in Lepidoptera, both larva and adult, and are generally considered to act as a defense against vertebrate predators (Gilmer 1925; Pesce and Delgado 1971; Kawamoto and Kumada 1984). Incidentally, these setae also pose a serious threat to human health when they get in contact with the skin or other parts of the body (Specht et al. 2008; Hossler 2009; Mullen 2009; Battisti et al. 2011).

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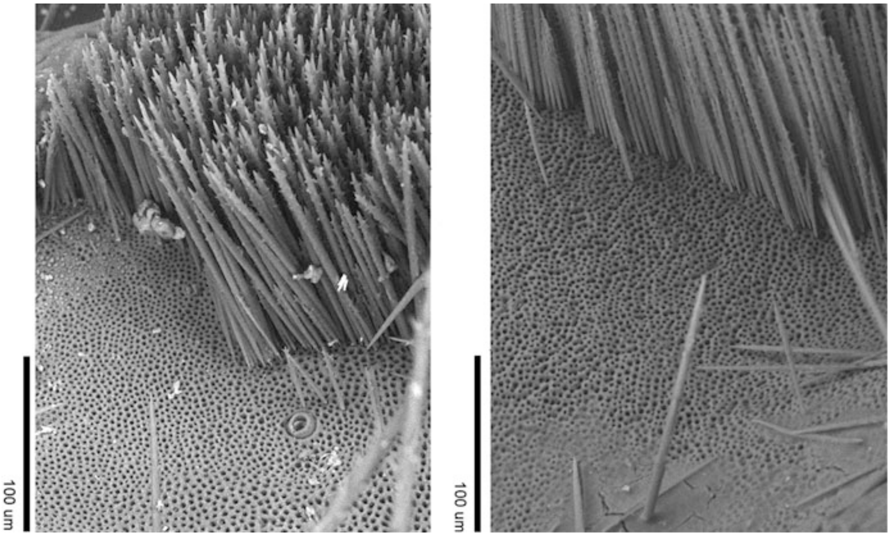

Fig. 8.1 Scanning electron photographs of the urticating setae in Thaumetopoea pinivora (*left*) and pityocampa (*right*). The setae are packed on special integument areas on the upper part of the abdomen. The holes indicate the sockets were their sharp proximal ends are implanted, while barbs indicate the distal ends of the setae. The penetration in the skin of the target organisms is made by the sharp proximal end, helped by the barbs of the distal end

Their nature is very different from other defensive hairs occurring in Lepidoptera, which are part of the integument and require contact with the larva to cause the reaction (e.g. the larvae of Saturniidae, Megalopygidae and Limacodidae), while they are similar to urticating setae released by some spiders from America (Theraphosidae) (Battisti et al. 2011). Setae are readily dehiscent from the integument and can disperse in the environment, often far away from the infested trees (Werno and Lamy 1990; Maier et al. 2003).

All studied species of the Thaumetopoeinae subfamily of Notodontidae are known to carry urticating setae, either as larva (genus *Thaumetopoea*) or adult (e.g. genus *Anaphe* from Africa and *Ochrogaster* from Australia) (Lamy et al. 1984; Floater 1998). The urticating setae of the larvae of a few *Thaumetopoea* species, namely the pine processionary moth *Thaumetopoea pityocampa* (Denis and Schiffermüller 1775), the northern pine processionary moth *Thaumetopoea pinivora* (Treitschke 1834), and the oak processionary moth *Thaumetopoea processionea* (Linnaeus 1758) (Lepidoptera, Notodontidae), have been well described (Fig. 8.1) and are reviewed in this chapter.

Setal production and morphology was first studied in the pioneering work of Fabre (1899), continued by Démolin (1963), Lamy et al. (1982) and Novak et al. (1987). The urticating setae are produced from the third larval instar or fourth larval instar, depending on the species, on integument areas of the abdominal tergites that are called "mirrors," owing to their property to reflect light (Figs. 8.2, and 8.3).

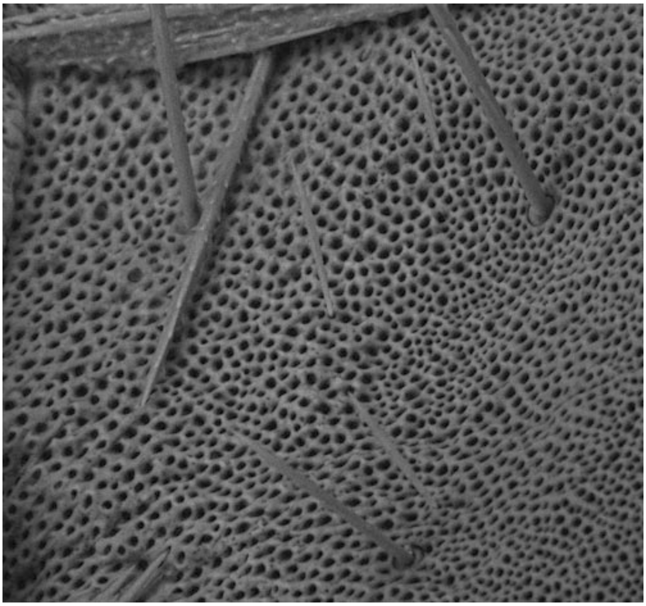

Fig. 8.2 Scanning electron photographs of the seta field of *Thaumetopoea pityocampa* with detached urticating setae laying on the floor and true hairs firmly implanted in the integument. The latter are identifiable by a collar at the base of the hair and are distributed all over the integumental field carrying the setae, having a role in the detachment of the urticating setae from the integument (see also Fig. 8.5)

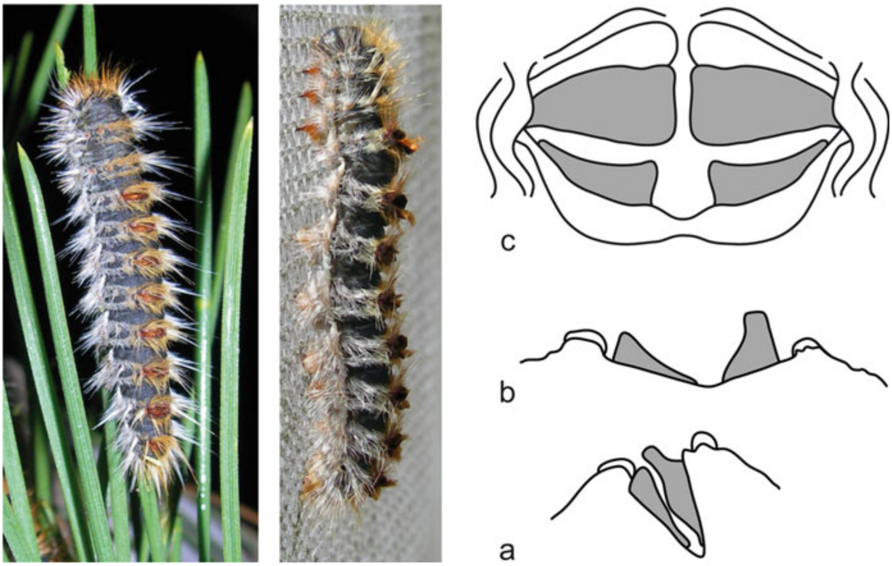

Fig. 8.3 Schematic drawing of the seta field of *Thaumetopoea pityocampa* when closed (*a*) and open (*b*) seen laterally, and open but viewed from *above* (*c*). On the left a fifth instar larva with the fields closed, with the longer setae protruding out of the fold like in (*a*). The setae are *bright orange* and are surrounded by *orange* and *white* hairs

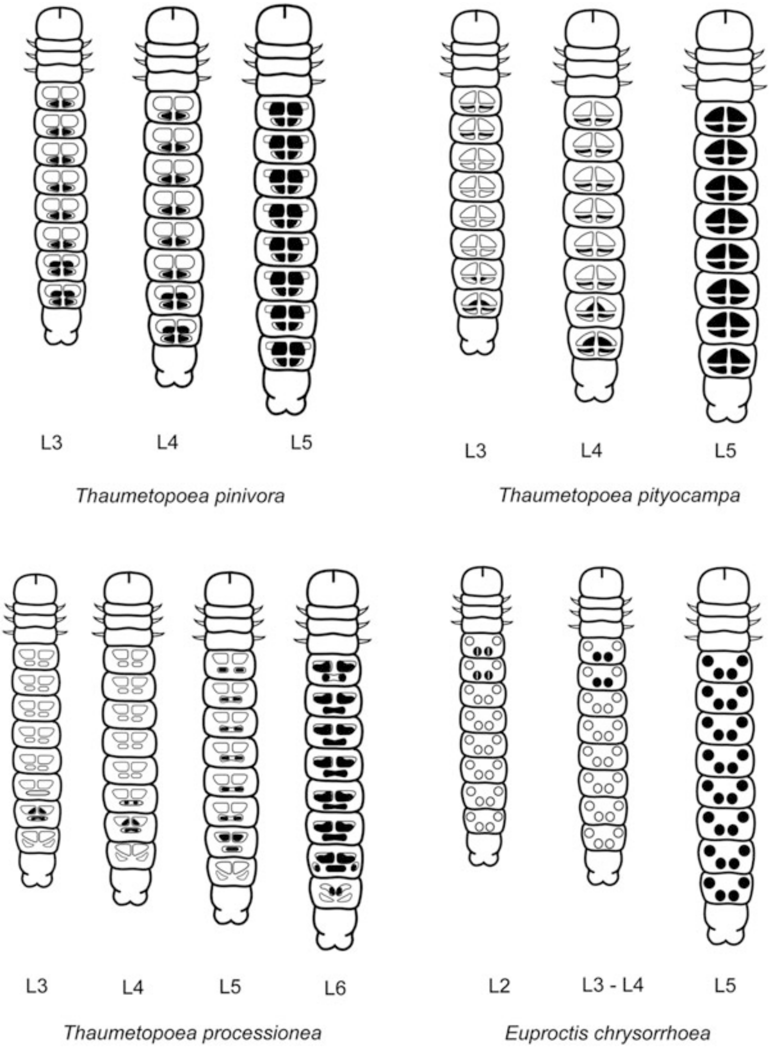

Fig. 8.4 Schematic drawing of the distribution of the seta fields in larvae of different instars of three *Thaumetopoea* species, compared with one lymantriid species

These mirrors increase in number with larval molts until the last larval instar, in which they occur on 8 abdominal segments (Fig. 8.4).

At this stage there are approximately 1,000,000 setae/larva in *T. pityocampa*, with a density of 60,000 setae/mm^2; setae are a few hundred micrometer long, with a sharp proximal end and pointed barbs directed distally (Lamy 1990). These setae are renewed at each molt and many are left with the old skin, so that they occur in a high number in tents used by larval colonies on trees as well as at pupation sites.

The release of setae by the larvae was explored by Démolin (1963), who showed that the larvae may actively open the integument mirrors when disturbed (Fig. 8.5).

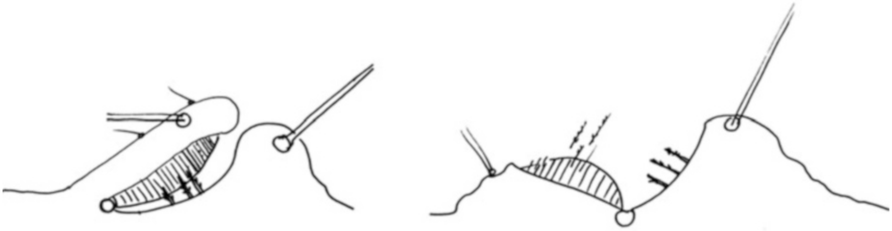

Fig. 8.5 Scheme of the opening of the setae field and release of the urticating setae by the action of normal hairs implanted in the field (*Thaumetopoea bonjeani*, modified from Démolin (1988))

Werno and Lamy (1990) found setae in pollen traps, with the abundance of setae progressively decreased moving away from the infested forest. Fenk et al. (2007) develop a setal dispersion model for the oak processionary moth, *T. processionea*, based on their physical properties in relation to prevailing wind. This is important because most reactions in humans are associated with airborne setae (Maier et al. 2003; Fuentes et al. 2006; Gottschling and Meyer 2006; Vega et al. 2011a, b). An aggravating factor is the long persistence of the setae in the environment even after exposure to rather extreme conditions: Hase (1939) demonstrates that dried insects retain their irritating power after 12 years of preservation and after treatment with temperature as high as 110 °C.

2.2 *Comparative Analysis of the Urticating Apparatus of* Thaumetopoea

To obtain samples of urticating setae of the 3 *Thaumetopoea* species, we collected larvae in the last instar from rearing in Padova University campus or from colonies in natural conditions. Samples were collected in 2008 from Tregnago (Italy) (45°30′N, 11°11′E, m 477) for *T. pityocampa*, from the island of Gotland (Sweden) (56°56′N, 18°16′E, m 7) in 2009 for *T. pinivora*, and from Caprino Veronese (Italy) (45°35′N, 10°47′E, m 245) in 2009 for *T. processionea*. To explore the length and diameter of setae, we randomly selected 10 individuals, each from a different colony, which were directly frozen after collection. Setae were randomly extracted with forceps from mirrors under stereomicroscope and were measured using a scanning electron microscope (SEM Hitachi TM-1000, Tokyo Japan) ($n = 108$ for *T. pityocampa*, $n = 120$ for *T. pinivora* and $n = 175$ for *T. processionea*). To setae were studied through their aerodynamic diameter, which is the hypothetic diameter that a water droplet would have in order to settle with the same velocity as the particle under consideration (Petrucco Toffolo et al. 2014). Last instar larvae of the 3 species were also used to observe the distribution of the setal length classes in the urticating apparatus. Larvae from the freezer were kept on ice under a stereomicroscope and dissected transversally to the fields carrying the setae. The specimens were observed using an SEM (Hitachi TM-1000) equipped with a cool stage unit (MK3 model, Deben United Kingdom), which maintained the specimens at temperature below zero to avoid water evaporation.

In *T. pityocampa*, the distribution of seta length showed a bimodal distribution (Fig. 8.6). The hypothetical horizontal distance traveled for a seta released at 20 m height in a day with a wind velocity of 2 m/s is 6.5 km for the short setae and 2.4 km for the long setae. The distribution of the length of *T. pinivora* is also bimodal (Fig. 8.6), and the corresponding dispersion distances are 21 and 7.4 km. In *T. processionea*, the distribution of length is unimodal, resulting in a dispersion of 8 km for a release at 20 m of height and a wind velocity of 2 m/s. It must be mentioned that the velocities and distances given above are for the mean aerodynamic diameter. Because the velocity is inversely proportional to the square aerodynamic diameter, the smaller setae will spread much further. Setal diameter and length were highly correlated in the three species according to a logarithmic function, with a higher slope for short setae. The picture of the setae in the mirrors showed differences among the three species. In *T. pityocampa* and *T. pinivora*, there were two well-defined levels of setae length that cohabit on the whole surface of the mirror, whereas this was not the case for *T. processionea* (Fig. 8.1).

2.3 General Considerations and Future Studies

Although the setal system of processionary moths has been the subject of a large number of studies, for both morphological and functional traits (Fabre 1899; Scheidter 1934; Démolin 1963; Lamy et al. 1982), the present analysis shows a markedly different pattern of setae length from that expected, with important implications for the dynamical properties. In particular, short setae like the ones that occur in two of the three species are able to spread farther away than long setae. The results showed a wide variation in setal length. In the case of *T. pityocampa*, the longest (680 μm) were approximately 14 times longer than the shortest (50 μm), whereas in *T. pinivora* (47–492 μm) and in *T. processionea* (56–351 μm) the same ratios were equal to 10 and 6 times, respectively. Previously published measures of the range were much lower for: *T. pityocampa*, 80–160 μm (Scheidter 1934), 93–415 μm (Hase 1939) and 150–250 μm (Lamy 1990); *T. pinivora*, 60–260 μm (Démolin 1963); and *T. processionea*, 150–250 μm (Lamy 1990) and 85–290 μm (Fenk et al. 2007). These differences may be ascribed to differences in setal extraction methods and sample sizes.

In *T. pityocampa* and *T. pinivora* the distribution of setal length can be considered bimodal, with a first peak in the class of 50–100 μm, and a second in the class of 200–250 μm, while it is unimodal in the oak processionary moth *T. processionea* (Fenk et al. 2007). Bimodality in *T. pityocampa* and *T. pinivora* can be explained by the overlapping of 2 normal distributions for each of the length classes. In fact, the short and long setae are intermixed throughout the mirror (Fig. 8.1). There are a few published examples of variation in setal size, for example, in the adult female of *Anaphe venata* Butler 1878 (Notodontidae) (Lamy et al. 1984), but no

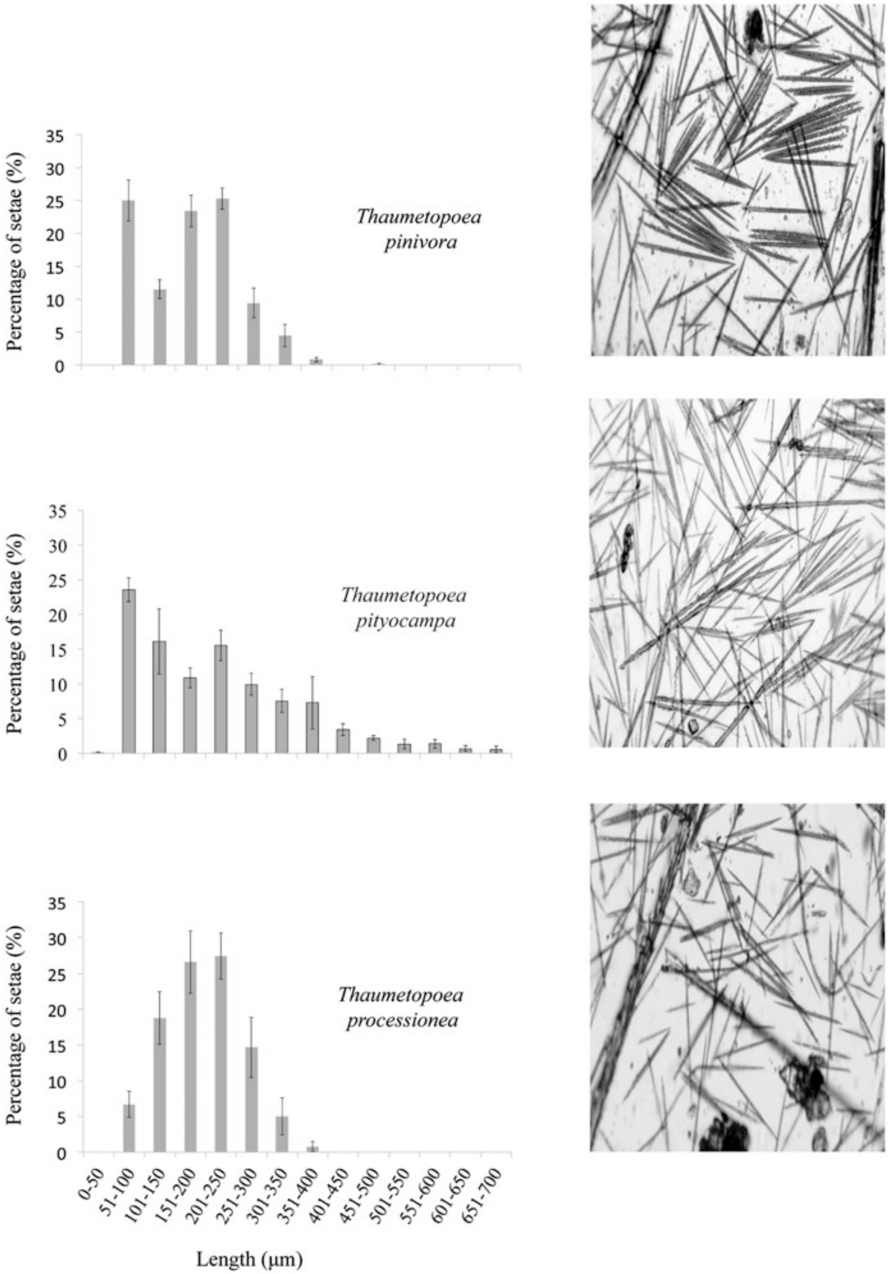

Fig. 8.6 Distribution of the length of setae in three species of *Thaumetopoea*, with photographs of the setae when they are removed from the integument with a forceps. Fragments of normal hairs are also visible

interpretation of the importance of setal size is given. As in the studied species of *Thaumetopoea*, the general shape of the seta is the same; the different size, however, may affect both dispersion and skin penetration. In other arthropods, however, such as the brown tail moth *Euproctis chrysorrhoea* (Linnaeus 1758) (Kemper 1955) and South American tarantula spiders (Cooke et al. 1972), the setae display a high variation of shape that could be potentially linked to a different function (Battisti et al. 2011). The absence of bimodality in *T. processionea*, despite a large interval of variation, remains unexplained and it is possibly related to a different evolutionary history of this species, the only species in the genus feeding on oaks (*Quercus* spp.) over all of Europe (Groenen and Meurisse 2012).

The role of seta size in protection from predation can be discussed in relation to what is known about the defense mechanism. Battisti et al. (2011) point out that the urticating setae provide an efficient defense system for the colony but not for the individual, as the symptoms appear with a delay of time, when the larva has already been killed. Although these conclusions have been made based on the reaction development in humans, it is unlikely that birds or mammalian predators would respond differently. As setae disperse as a cloud around the colony (Fenk et al. 2007), with high concentration of short setae up to 6 km (during the day) and 12 km (during the night), their function could be to keep away predators (Fig. 8.7). In this case, the larger and denser is the cloud, the stronger is the protection; the diversity of seta size may extend such a barrier much farther, with a direct benefit for the colony. Therefore, one could speculate that other prey of vertebrate predators could indirectly benefit from the protection, and, thus, competition among insect herbivores should increase. Although the mechanism needs to be elucidated with appropriate experiments, the large investment in urticating setae made by these species of processionary moths indicates that the benefits from extended protection are higher than the costs possibly imposed by competition.

In conclusion, the awareness of a great variation in size of urticating setae may open the way for better modeling of both the ecology of the systems and the risks to which humans and domestic mammalians are exposed. In the case of processionary moths, such a risk is very high due to the wide distribution of host plants in both urban and forest areas (EFSA 2009). This is emphasized by a continuous release of setae from the soil or from tents, because of their high persistence. The information provided in the present paper may offer an opportunity to explore the importance of setal size for protection from predation and for risk assessment toward non-target vertebrates and humans. In addition, it may be useful to pest managers and decision-makers in planning the control operations of these forest and urban tree pests.

3 Human Immune Responses to *Thaumetopoea pityocampa*

Ana-Isabel Rodríguez-Mahillo, Miguel González-Muñoz, Jose María Vega, Alain Roques, and Ignacio Moneo

Fig. 8.7 Relationships between insectivorous birds and larvae and pupae of the pine processionary moth *Thaumetopoea pityocampa*. A winter tent with a hole made likely by tits (Parus spp.) to extract the larvae, which are eaten by cutting off the head and taking the inside, thus leaving the skin with the urticating setae. A pupa inside the cocoon where the last larval skin carrying the urticating setae is present. When the hoopoe (Upupa epops) takes the cocoon (photo Z. Mendel), they open it and take only the pupa. For more information about bird predation of processionary moths (see Auger-Rozenberg et al. 2014, Chap. 7 in this volume)

3.1 Introduction

Stinging insects are known to cause allergic reactions, because they inject allergens that are recognised by the immune system, leading to a specific immune response with the synthesis of specific IgE against the injected allergens. After a new contact, these allergens cause the bridging of specific IgE located on the surface of basophils and mast cells. This induces the release of inflammatory mediators and initiates an allergic response. However, non-stinging insects, such as Lepidoptera, raise still today doubts about their mechanism of sensitization and many authors think that the lesions seen after contact with larvae are due to non-immune toxic mechanisms.

The pine processionary larva's ability to induce cutaneous lesions is well known since the first descriptions of Reamur in 1736 and Fabre in 1899 (described by Ducombs et al. 1981*). Thaumetopoea pityocampa* larvae induce skin lesions such as urticaria or dermatitis, conjunctivitis and rarely respiratory symptoms or even anaphylactic shock. These responses are caused by urticating hairs called setae disposed on cuticular plates and dispersed around the larvae as a defence mechanism. It is quite clear that the mechanical lesion induced by the penetration of the setae in the skin can be responsible for the pruritus that is always present, but setae store toxins and probably enzymes causing an additional injury that contributes to an increase of the inflammation observed in individuals who were in contact with larvae. Therefore, the dual additive mechanical-toxic effect was considered as a sophisticated defence mechanism (Ducombs et al. 1979).

3.2 Pine Processionary Moth Allergens

The first article that describes the antigens and proteins of the *T. pityocampa* setae was published in 1983 (Lamy et al. 1983). They described the protein content of the setae as a complex mixture of 16 proteins. Among them, they studied a 28 kDa protein, exclusive to the setae as it was present neither in the haemolymph nor in the cuticle. This protein was not associated to carbohydrates or lipids. It could be further separated in two subunits of 13 and 15 kDa. They called it thaumetopoein and proved its urticating properties in guinea pigs. Thaumetopoein induced mast cell degranulation by a non-immune mechanism. (Lamy et al. 1985)

Several years later, the same scientific group described a homologue of thaumetopoein in the setae of the oak processionary larva (Lamy et al. 1988). This protein exhibited the same urticating effect as thaumetopoein in the guinea pig's skin.

An IgE mediated mechanism of sensitization to allergens present in *T. pityocampa* setae was demonstrated by ELISA and western blotting in 1993 (Werno et al. 1993). Two proteins bound IgE from the sera of exposed workers and one of them, a 28 kD allergen, was identified as thaumetopoein. Additionally a 45 kDa protein gave also a strong reaction with IgE. The authors, therefore, describe the presence of specific immune responses to allergens present in setae as potential relevant contributors to the lesions induced by these larvae, as well as the IgE-binding properties of thaumetopoein, previously described as a specific mast cell activator.

Some years later, our group described the presence of specific IgE antibodies in the serum from a patient suffering severe reactions after contact with *T. pityocampa* larvae. The allergen used for diagnosis was a whole body larvae's extract and this positive result suggested that the IgE-mediated mechanism found could be much more relevant than previously suspected.

3.3 Specific Antibodies to Crude Larval Extracts

A pilot study was designed by our group several years ago in order to evaluate the allergenicity of the crude whole larval extract and to characterize the principal allergens. Figure 8.8 shows how IgE from 15 patients with symptoms related to *T. pityocampa* exposure was able to bind proteins of a crude whole larval extract. The molecular weight of these proteins ranges from less than 6 kDa to more than 100 kDa, being the one around 15 kDa the most frequently recognised.

This protein could be the major allergen Tha p 1, described for the first time in 2003 (Moneo et al. 2003). In this paper, more than ten different proteins of the extract were able to bind patients' IgE, being the most frequently detected a protein of around 15 kDa. This protein was purified by ethanol fractionation by differential precipitation of a whole larval extract followed by separation by a reversed-phase high performance liquid chromatography (RP-HPLC). The amino terminal sequence GETYSDKYDTIDVNEVLQ for Tha p 1 was obtained, but, at that time, no similarities with other proteins were found using the web interface BLAST of the USA National Centre for Biotechnology Information (NCBI). Several years later, the complete sequencing of the silkworm *Bombyx mori* genome led to classify Tha p 1 as a chemosensory protein, similar to those found in this species (Picimbon et al. 2000).

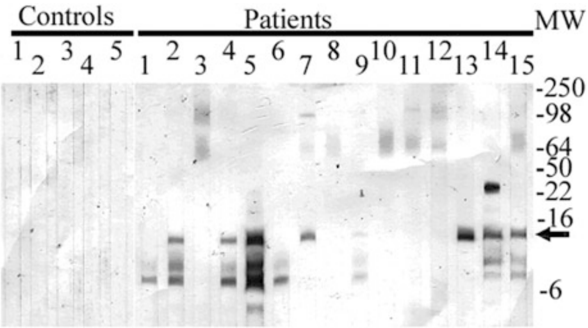

Fig. 8.8 Immunoblot of a crude whole body *Thaumetopoea pityocampa* extract revealed with sera from 5 healthy donors used as controls and 15 patients with allergic symptoms related to larva exposure. Estimated molecular weights are indicated. Tha p 1 is outlined by an *arrow*

```
                                            cggggacagccagacg
aaggatcgtgcagttatcacgcggcgattgttaaaatgaaacttcttatcttagcgtta
                                    M  K  L  L  I  L  A  L
acgtgcgcggcggccgtctgggccagacccggtgaaacttactcagacaagtatgacacc
 T  C  A  A  A  V  W  A  R  P  G  E  T  Y  S  D  K  Y  D  T
atcgatgtgaatgaagtcctccagtccgagcgtttgttgaaaggctacgtggagtgcctg
 I  D  V  N  E  V  L  Q  S  E  R  L  L  K  G  Y  V  E  C  L
ttagataagggacggtgcacaccggacggcaaggagctgaaggacaccctccctgatgcc
 L  D  K  G  R  C  T  P  D  G  K  E  L  K  D  T  L  P  D  A
ctggaacacgaatgcagcaaatgtaccgagaaacagaagtccggcgcggacaccgtcatc
 L  E  H  E  C  S  K  C  T  E  K  Q  K  S  G  A  D  T  V  I
agacacctggtgaacaagcgcccggagctgtggaaagagttggcggttaagtacgacccc
 R  H  L  V  N  K  R  P  E  L  W  K  E  L  A  V  K  Y  D  P
gagaacatctaccaggagagatacaaggaccggctggaatcggtgaaggaacattaaacg
 E  N  I  Y  Q  E  R  Y  K  D  R  L  E  S  V  K  E  H  -
gtccaacagcaatccgattttaatgctgggtggaggagatggctcacgtaatactgatat
tataagaataaaagacgcaatatgtaaaaaaaaaaaaaaaaaaaaaa
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Fig. 8.9 Complete sequence of Tha p 1 mRNA and its translation to amino acids. Stop codon is identified as a dash. Signal peptide is underlined (European Nucleotide Archive accession number HE962022)

3.4 Tha p 1: Cloning and Amino Acid Sequence

Mature Tha p 1 mRNA (Fig. 8.9) could be sequenced isolating the larva RNA using the traditional method of TRIzol and performing a retrotranslation followed by a polymerase chain reaction (RT-PCR).

Tha p 1 was modelled upon the crystalline structure of the chemosensory protein 10 from *Bombyx mori*, using the web interface Fist approach mode of Swiss-model (available at http://swissmodel.expasy.org/). The predicted model (Fig. 8.10) showed that Tha p 1 was folded into 6 α-helices joined by random coils, with two possible disulfide bonds between Cys 56/Cys 58 and Cys 29/Cys 36.

Despite the high homology between the chemosensory proteins of *T. pityocampa* and *B. mori* (Fig. 8.11), patients sensitized to the pine processionary larva did not recognize any protein of a silkworm whole body crude extract (data not shown).

3.5 Allergens Present in Setae

To obtain a protein extract, setae were isolated from the larva body using forceps and a magnifying glass. We designed an especial extraction method which included several consecutive steps in order to measure differences in solubility of the potential allergens contained inside the setae or present on their surface.

Fig. 8.10 Predicted 3D model of Tha p 1, modelled upon the crystalline structure of *Bombyx mori* chemosensory protein 1. Cys residues are highlighted in *pink*

```
BAF91712        MKLFMVCALLCVA    AVA WGK PASTY TDK WDY INV DEILESQRL LKGYV DCL MDRGRCT ADG  60
AAM77040        MKFIVAVALLCLV    AES W-- AASTY TDK WDN INV DEILESQRL LKAYV DCL LDRGRCT PDG  58
CAJ01513        MKTVILVALMCLE    AAA WGK PASTY ADK WDN INI HEILESNRL LKGYV DCL LDRGRCT SDA  60
AAF16721          MKMLLLV  -ISCCV ALP WAL SASTY TDK WDN INV DEILESDRL MKGYV DCL LDKGRCT PDG  59
NP_001037064      ---------  MACV AVT WAR PESTY TDK WDN INV DEILESNRL LKGYV DCL LGKGRCT PDG  51
ABH88203        MKILIIV    -VMACV AVT WAR PESTY TDK WDN INV DEILESNRL LKGYV DCL LGKGRCT PDG  59
Thapl           MK   LLILA --LTCA AAV WAR PGETY SDK YDT IDV NEVLQSERL LKGYV ECL LDKGRCT PDG  58

BAF91712          KTLKETMPDALE HECSKCT EKQK ESSDKVI RF LINKR PE LWKEL ATKYDP DNVYQQRYKD  120
AAM77040          KALKETLPDALE NECSKCT EKQK AGSDKVI RY LVNKR QD LWKEL SAKYDP NNIYQDRYKD  118
CAJ01513          KTLKETLPDALE HDCNKCT AKQK SGSDKVI SH LVNKR PE LWKEL SVKYDP NNIYQEKYKD  120
AAF16721          KALKETLPDALE HDCSKCT EKQK VGSEKVI RN LVNKR PA LWKEL SAKYDP NNLYQEKYKD  119
NP_001037064      KALKETLPDALE HECVKCT GKQK SGADKVI RH LVNKR PD LWKEL AVKYDP DNIYQARYKD  111
ABH88203          KALKETLPDALE HECVKCT GKQK SGADKVI RH LVNKR PD LWKEL AVKYDP DNIYQARYKD  119
Thapl             KELKDTLPDALE HECSKCT EKQK SGADTVI RH LVNKR PE LWKEL AVKYDP ENIYQERYKD  118

BAF91712          KIE AVKEH -  128
AAM77040          KIE AVKGQ -  126
CAJ01513          KLQ TIKA --  127
AAF16721          KID SIKGQ -  127
NP_001037064      KID AVKGSA 120
ABH88203          KID ------  122
Thapl             RLE SVKEH -  126
```

Fig. 8.11 Alignments of the chemosensory proteins' sequences of several moths and butterflies: *Bombyx mori* (NP_001037064 chemosensory protein 3 and ABH88203 chemosensory protein 10), *Papilio xuthus* (BAF91712 chemosensory protein), *Heliothis virescens* (AAM77040 chemosensory protein 2), *Heliconius melpomene* (CAJ01513 hypothetical protein) and *Manduca sexta* (AAF16721 sensory appendage protein 4). The alignment was performed using the web interface ClustalW available at http://www.ebi.ac.uk/Tools/clustalw2/index.html. *Red* indicates identical amino acids, *green* indicates semi-conserved substitutions and *blue* indicates conserved substitutions

1. As a first washing step, the setae were resuspended in PBS and after a short incubation at room temperature (5 min), setae were centrifuged and supernatant 1 (SP1) was reserved.
2. The pellet containing the setae was redissolved in PBS and sonicated. Sonication induced the fragmentation of the setae, exposing in this way its internal content. After centrifugation, supernatant 2 (SP2) was reserved.

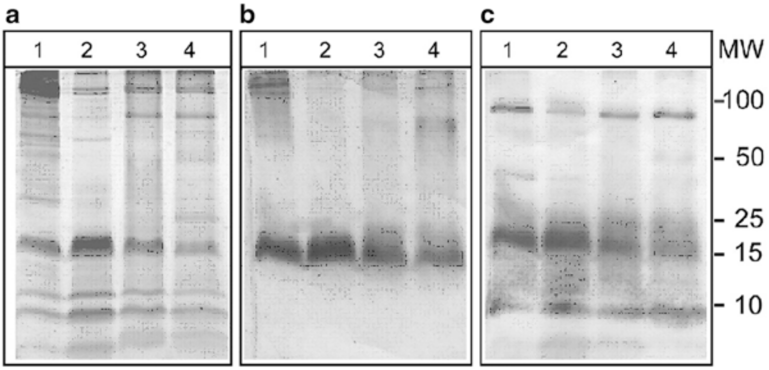

Fig. 8.12 Setae protein and allergen content studied by sequential extraction in different solutions. Coomassie stained SDS-PAGE (**a**), rabbit polyclonal immunoblot (**b**) and human IgE (**c**) immunoblot using a pool of positive sera. *Lane 1*: washing in PBS (SP1). *Lane 2*: SP2 supernatant obtained after sonication. *Lane 3*: SP3 extraction in SDS. *Lane 4*: SP 4 proteins obtained after extraction of the setae in hot SDS. Estimated molecular weights are indicated

3. The pellet was further redissolved in an ionic detergent solution (2 % SDS), incubated at RT and centrifuged to obtain supernatant 3 (SP3).
4. The pellet was redissolved again in the same detergent solution and then boiled and centrifuged to obtain supernatant 4 (SP4). This step tried to elute tightly non-covalently bound proteins attached to insoluble matrices, for instance to chitin.

The protein content of the different fractions was similar, ranging from 252 μg/ml (SP1) to 190 μg/ml (SP2).

After running the supernatants in a SDS-PAGE, proteins were visualized by Coomassie staining or transferred to nitrocellulose to perform Western blot (Fig. 8.12). The immunoblots were revealed with a rabbit anti-setae antiserum or a pool of *T. pityocampa* sensitized human sera. More than 25 different proteins were observed by Coommassie staining of the consecutive extracts (Fig. 8.12a). Some of these proteins (for example, the one of around 25 kDa, see Fig. 8.12a lane 4) were only extracted by boiling in detergent solution. A 15 kDa allergen was strongly detected when revealing the western blot with the rabbit antiserum (Fig. 8.12b). When revealing the Western blot with the pool of human sera (Fig. 8.12c), three proteins were mainly detected: a high molecular weight protein of around 90 kDa, a medium molecular weight protein of around 15 kDa and a low molecular weight protein of around 10 kDa.

The whole study demonstrated that allergens could be detected after an extraction that minimally broke setae and that sonication induced the release of an additional amount of protein. Harsher extraction conditions such as the use of high amounts of ionic detergents and the combined use of high temperature and detergents released further amounts of allergens from the setae, indicating that these allergens remained attached to the chitin core and were not solubilized by conventional extraction conditions. This fact led us to believe that after skin penetration, allergens could be delivered to the immune system in a dual way: a fast release of allergens present in the outside of the setae and a slow or very slow release that must occur after degradation of the setae by chitinases. Macrophage chitinases could directly deliver allergen to the macrophages and these cells could now present the allergens for optimal immune response, especially for IgE synthesis.

A second finding of the sequential extraction was that a protein of around 15 kDa was the most abundant component found in the different extracts, especially after mincing the setae by sonication (Fig. 8.12a). Furthermore, this protein bound specific antibodies from a rabbit antiserum obtained after immunization of rabbits with a whole setae extract (Fig. 8.12b) (Rodríguez-Mahillo et al. 2012). It was also by far the allergen most strongly detected by a pool of sensitized human sera (Fig. 8.12c). All these data suggested that this allergen could in fact correspond with thaumetopoein described by the group of Lamy several years ago (Lamy et al. 1985).

Figure 8.13 shows the IgE and IgG recognition patterns of 18 *T. pityocampa* sensitized patients. Again, several allergens present in the setae extract were detected, although the IgG recognition patterns of the whole body and the setae extracts were much weaker than the IgE recognition patterns. This fact implies that, for unknown reasons, sensitized subjects only produced IgE antibodies. In the IgE immunoblots, the 15 kDa protein was recognized by 72.2 % of the patients, while the low molecular weight allergen (10 kDa) was only detected by 27.7 %. Although the molecular weight of the 15 kDa setae allergen (Fig. 8.13, asterisk) was similar to that of the major body allergen Tha p 1 (Fig. 8.13, arrow), recognition of both allergens was not always paired (Fig. 8.13, patients 4 and 12), a fact that demonstrated that they are different proteins. The 15 kDa setae allergen, registered as Tha p 2, has been sequenced recently (Rodríguez-Mahillo et al. 2012). It has not similarity with Tha p 1 and it may correspond to the thaumetopein described in 1985, but unfortunately no information about the sequence of this allergen was provided. It is interesting to note that Tha p 2 showed similarity in the carboxy terminal region to a hypothetical protein of *Acyrthosiphon pisum*, the pea aphid (Fig. 8.14). This fact suggested that both proteins could be members of an unknown family of insect proteins and that more allergens of this family could be found in the future.

The proteins of the setae extract (SP1, Figure 8.12) were purified by reverse phase HPLC using a C18 column. More than 60 proteins were resolved (Fig. 8.15).

The amino end of the low molecular weight setae allergen (Tha p 3) has been sequenced (LAVETPEPISSN) and some other internal sequences have been obtained by the novo sequencing and MALDI-MS (EKDVHEWTGANWK ($m/z = 1{,}698.832$) y DVHEWTGANWK ($m/z = 1{,}441.685$) y VHVEWKGDN, where K can also be Q). None of these sequences had similarities with any other described protein.

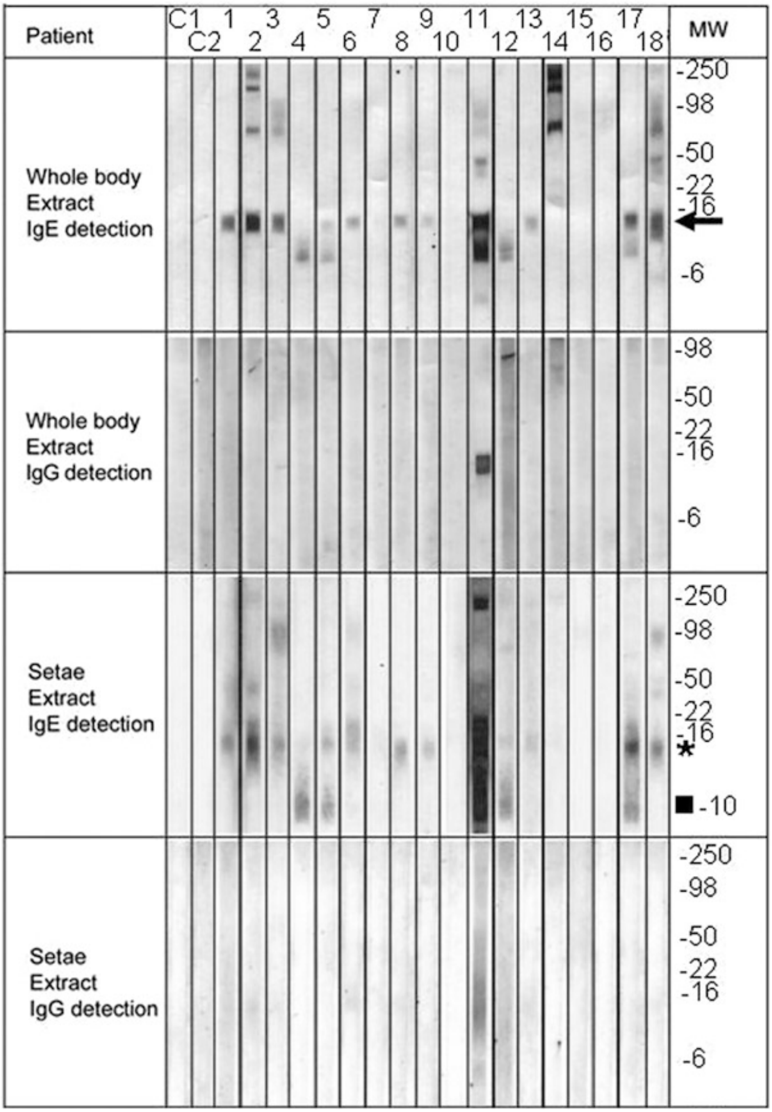

Fig. 8.13 IgE and IgG detection of proteins of *Thaumetopoea pityocampa* whole body and setae extracts. Individual sensitized patients (1–18) and healthy donors (C1 and C2) sera were tested. Tha p 1 is marked with an *arrow*. Tha p 2 is marked with an *asterisk*. Tha p 3 is marked with a *square*

3.6 Allergens Present in Larvae from Different Geographical Origins

When comparing the protein content of *T. pityocampa* from Spain (Valladolid and Madrid) and France (Charters, Orleans, Tours) by SDS-PAGE and immunoblot, we could find that they presented some differences. Figure 8.16 shows that although the

```
XP_001947225        MFAVVIFVLICAHAVHPSTVISGNTLTNRGSDKDNAAAGAAAAGDVIAATGGIIDEGSLA 60
Tha p 2             -----MKLLIFATLIALSSSVP--QLSEK-------------AEEAIDLT---------- 30

XP_001947225        AEHESDTDHALTKRGSGTDHAAQGAGTAGDVIAATGGIIAAGSLATGPLAPVVAGIGGVT 120
Tha p 2             ----YQEKNNLFDLGS----------VAGDILSRDG------------------------ 52

XP_001947225        AAVGGLVSVISKAADQSCREFGCHKNYCWSYC-------SLGNQWCYTTKTYSQSFEYVS 173
Tha p 2             CHVS----------------FGCHKGYCWAGCGNPTNPWSWGENWCYTTKSYSQSYSYVQ 96

XP_001947225        CTRDDECNGCWKCAGSCTL 192
Tha p 2             CTQDSECNGCWKCGGPCSA 115
```

Fig. 8.14 Alignment of the Tha p 2 sequence and a hypothetical protein from *Acyrthosiphon pisum*, a pea aphid (accession number XP_001947225). The alignment was performed using the web interface ClustalW available at http://www.ebi.ac.uk/Tools/clustalw2/index.html. *Red* indicates identical amino acids, *green* indicates semi-conserved substitutions and *blue* indicates conserved substitutions

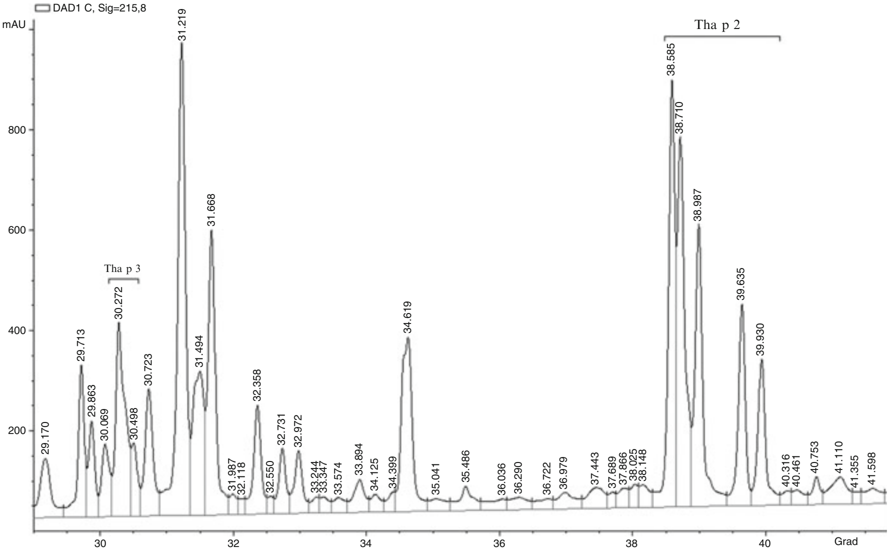

Fig. 8.15 RP-HPLC chromatogram ($A_{215\ \text{nm}}$) of the setae extract obtained in PBS after sonication. Detail from 20 to 67.5 % acetonitrile (ACN). Retention times of each peak are included. Tha p 2 corresponds to the peaks with retention times 36.586–39.930. Tha p 3 corresponds to the peaks with retention time 30.272 and 30.498

Coomassie stained SDS-PAGEs may be similar, patients with allergic symptoms related to exposure to larvae were able to detect different proteins from larvae collected in Spain and larvae collected in France. We do not know at present if this finding could have any clinical value or if it simply reflects normal variations in antigenic content of the different larvae.

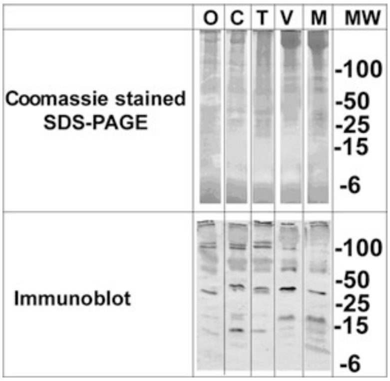

Fig. 8.16 Protein content of *T. pityocampa* from different origins in Spain and France. Coomassie stained SDS-PAGE and immunoblot revealed with a pool of *T. pityocampa*-allergic patients' sera. The whole body extracts were obtained using larvae from Orleans (*O*), Tours (*T*), Chartres (*C*), Valladolid (*V*) and Madrid (*M*). Estimated molecular weights (*MW*) are indicated

3.7 Differences Between Immune and Non-immune Reactions to Setae

As previously shown, around half of the people with suspected *T. pityocampa* larvae reaction showed positive skin prick test responses and clinical differences with respect to non- sensitized subjects indicating that an immune response was responsible for the symptoms (Vega et al. 1999). Therefore, the presence or not of immune reactions to larva allergens should be diagnosed early in order to avoid the progressive increase of the sensitization that occurs after new contacts with the allergen/s. The normal sensitization process implies that the sensitized subject responds to an allergen that he previously tolerated and that during the development of the immune response the symptoms appear after shorter exposure times or even after decreasing allergen exposure levels. As the immune response has a genetic background, not all the individuals show symptoms after exposure to setae, whereas toxic or irritant mechanisms normally affect all exposed subjects. However, the most practical way to demonstrate the presence of an immune response is the finding of positive skin tests or the presence of specific IgE antibodies on symptomatic subjects.

3.8 Factors Influencing a Specific IgE Response

One of the most intriguing findings of the immune response to this insect is the shift of the immune response to the IgE compartment. It is clear that other aspects of the immune response, such as non-antibody mediated cellular responses have not been yet explored, but the question remains unanswered: why are specific IgE antibodies synthesized in the absence of a specific IgG response? In other words, why are allergic responses preferred as a defensive response in spite of a classical IgG response as observed in a typical response to bacteria or viruses?.

Ducombs calculated that a single larva carries inside the mirrors around 1 million setae (Ducombs et al. 1979). This fact implies that a subject can be exposed to a high number of setae after direct contact to larvae, for instance after occupational exposure (pine cone collectors, etc). But the chronic exposure to low or very low number of setae can also occur. People living in the proximity of infested areas can be exposed to a low number of wind-carried setae for long time periods and this could lead to a high number of sensitized people such as found by us in epidemiological studies. The prevalence of positive skin prick tests reached 12 % in rural areas, 9.6 % in semi-urban areas with nearby pine forests and 4.4 % in urban areas (Vega et al. 2011a, b). Furthermore, this study demonstrated that 83.3 % of patients that fulfilled the criteria for a convincing reaction presented symptoms merely by walking or passing by pinewood areas without direct contact with larvae.

In addition to a long time exposure to low antigenic doses two other reasons can explain the shift towards an IgE response to setae antigens: the intradermal delivery and the presence of chitin or even the binding to chitin of the proteins present in the setae. Both conditions have been previously found to be especially relevant for IgE production (reviewed in Rodríguez-Mahillo et al. 2012) in animal models.

3.9 Relevance of the Immune Response

The presence or absence of an immune response to setae allergens is a relevant issue, because a sensitization to setae allergens changes the perspectives of the affected individuals. Toxic or irritant lesions produced by these larvae are usually more self-restricted to the contact areas. On the contrary, immune reactions can present systemic reactions that can require treatment at emergency rooms. Treatment of IgE-mediated reactions is similar to other allergic diseases and early diagnosis is required in order to avoid the development of the immune response.

3.10 Immune Reactions to Other Processionary Moths

Due to the close phylogenetic proximity between members of the Thaumetopoideae family, the presence of common allergens in other members of this family should be considered. A protein with similar molecular weight and showing cross-reactivity to the pine processionary was described to be present in the setae from the oak processionary larva (Lamy et al. 1988). Furthermore, workers exposed to oak processionary larvae presented severe anaphylactic reactions during work, a fact that suggests that IgE-mediated mechanisms were the cause of these reactions. It is therefore likely that other members of the same family could also have sensitizing properties (Bosma and Jans 1998; Licht and Jonker 1998).

3.11 Conclusions

The most relevant data about immune responses to larvae of pine processionary moth obtained so far can be summarized as follows:

- Both the whole larvae and the setae contain IgE-binding proteins (allergens).
- Some of them are restricted specifically to either the larva or the setae.
- In endemic areas, the IgE-immune response occurs in a high proportion of exposed subjects
- If present, the immune response is near always restricted to IgE, being the specific IgG response absent in most cases.
- Cell-mediated immune responses have not been tested so far and could be operative in some subjects.

4 Epidemiology and Clinical Symptoms of Human Reactions to Processionary Moths

Jose María Vega, Jesús Vega, José Carlos García-Ortiz, Ignacio Moneo, and Alain Roques

4.1 Introduction

In Europe and the Middle East, processionary moths (*Thaumetopoea* spp.) are among the main urticating Lepidoptera. From their third larval instars, they are armed with hair-like material called setae that can cause a variety of cutaneous reactions, ocular lesions, rhinitis and more rarely dyspnea and anaphylaxis. These reactions are attributable to a combination of non-allergic and allergic factors. IgE-mediated hypersensitivity reactions may be implicated when the process is rapid, recurrent and progressively more severe.

4.2 Epidemiology

4.2.1 *Thaumetopoea* Reactions are Underestimated: Possible Reasons

Although *Thaumetopoea*-related disease is common in the Mediterranean area, currently its importance is underestimated in both clinical practice and the scientific literature. This fact may be attributable to several factors including:

1. probably because most reactions are mild and transient;
2. in endemic areas, often the patient is aware of the cause and self-treats the condition;

3. there are not specific symptoms or signs of *Thaumetopoea*-related disease;
4. low knowledge of this pathology or inability of physicians to identify the suspected larvae;
5. diagnostic allergy tests are not commercialized.

However, we should also bear in mind that more serious reactions may occur and these are treated symptomatically without a diagnosis of the cause or without providing the patient with the necessary information to avoid future recurrences.

4.2.2 Epidemics of *Thaumetopoea* Reactions Can Occur

Another factor to take into account is that, although the reactions usually occur in isolated patients, at times, epidemics may occur. These can be related to exposure in areas of heavily infested tree forest or in communities located close to infested trees, the biological cycle of the insect or weather conditions, particularly strong winds.

4.2.3 Epidemiological Studies

Few epidemiological data have been published on reactions caused by species of the genus *Thaumetopoea*. Most studies describe isolated cases or series of patients attending in a hospital or incidence studies after outbreaks, such as one of *T. processionea* (6 % of 1,025 persons living in a radius of 500 m from infested trees in town) (Maier et al. 2003) and one of *T. pinivora* (18 % of 4,300 persons living in an infested area of about 3,500 ha) (Holm et al. 2009). However, two prevalence studies of reactions by *T. pityocampa* in general population have been reported and their results confirm that these reactions are common in endemic areas. In the first one, 9 % of 653 children living in a rural area had reactions with this Lepidoptera (Vega et al. 2003a, b). In the second, a cross-sectional study was carried out in 1,224 adults, the prevalence of skin reactions to *T. pityocampa* was 12 % in rural areas, 10 % in semi-urban areas with nearby pine forest and 4 % in urban areas (Vega et al. 2003a, b).

Children are particularly susceptible to Lepidoptera related conditions, this fact may be related to frequent outdoor activity; their natural curiosity leads them to touch the larvae or play with sand or vegetation that contains rests of them. As the article previously mentioned shows, these reactions are common in children from rural areas. However, peripheral urban areas with nearby pine/oak trees are also areas with a high incidence of *Thaumetopoea* reactions and where the treatment of the pest is particularly difficult (Maier et al. 2003; Gottschling et al. 2007; Artola-Bordás et al. 2008; Vega et al. 2011a, b).

4.2.4 Risk Factors

Exposure to the Larvae

The main risk of skin reactions to *T. pityocampa* is directly related to exposure to the larvae. This risk is significantly higher in people with daily exposure (Vega et al. 2011a, b).

Influence of Sex, Area of Residence, Age and Atopic Status

In adults, the reactions are more frequent in men from rural or semi-urban areas because they are more frequently exposed to larvae due to occupational exposure or hobbies. However, age influence or atopic status has not been found (Gottschling et al. 2007; Vega et al. 2011a, b).

Seasonal Influence

Thaumetopoea-related disease is usually seasonal. Most of the reactions occur in the months corresponding to urticating larval stages (*T. pityocampa*/*T. wilkinsoni*: January-April; *T. processionea*: May-July; *T. pinivora*: June-August). Within these months, the last larval stage has the highest risk because the number of setae and their allergenicity is maximal (Rebollo et al. 2002). In addition, the processionary larvae whose nymphosis occurs in the soil (all the species except *T. processionea*), in their last stage in which they descend from the trees, they cause a bigger exposure and a higher number of reactions (Vega et al. 2011a, b).

However, an out-of-season contact with setae can occur through dead larvae, tents, debris from an infested pine forest or with setae present in spit or hair from pets or livestock (Vega et al. 2004; Maronna et al. 2008). In addition, setae shed by the larvae can persist in the environment for many years. On the other hand, patients with hypersensitivity to the larvae can have symptoms with a minimal exposure to setae. These facts can explain why some people have recurrences of the reactions throughout the whole year.

Occupational Exposure

Exposed workers have a major risk of *Thaumetopoea*-related disease due to a major frequency and intensity of the exposure to setae. This risk is up to 5 times higher in forest workers exposed to *T. pityocampa* (Vega et al. 2011a, b). The jobs at greatest risk are pinecone collectors and lumberjacks (Vega et al. 2004; Vega et al. 2011a, b). Moreover, epidemic affectation of soldiers exposed to *T. processionea* has been reported (Hesler et al. 1999).

4.3 Clinical Manifestations

4.3.1 Dermatological Manifestations

Clinical Patterns

Cutaneous reactions are the most frequent clinical manifestation. The main symptom is an intolerable itching sometimes without visible lesions. Skin lesions by *Thaumetopoea* larvae are of two different types: immediate wheal and flare reaction (contact urticaria, Fig. 8.17) and delayed and persistent itchy eruption, usually reported as a papular eruption (Fig. 8.18). On the other hand, an overlapping of these skin lesions or a dual reaction can happen.

Most of the patients with contact urticaria by *Thaumetopoea* larvae are allergic (IgE-mediated) (Vega et al. 2000). The eruption appears within 30–60 min after exposure to larvae and disappears within 24 h and usually within a few hours. The whealing reactions can be strictly confined to the area of contact but they can also appear as generalized urticaria, facial oedema and sometimes can associate extracutaneous symptoms and anaphylactic reactions.

Delayed reactions do not appear until 2–24 h after exposure. The most frequent type, consist in infiltrated papules similar to insect bites that persists for several days. Sometimes, an eczematization of the lesions occurs due to the scratching or when the outbreaks are repeated. Less frequently, it has been described as pin-sized red papules, pustules and erythematous streaks which clear within 3–5 days (Maier et al. 2003); or pustular lesions on the palms of the hands of small children (Vega et al. 2003a, b); or vesicular dermatitis (Bogaerts-Rosbergen and van Wijk 2010); or blistering dermatitis, more frequently reported after *T. pinivora* exposure (Fagrell et al. 2008; Holm et al. 2009). In these delayed cutaneous reactions

Fig. 8.17 Intense contact urticaria with associated angioedema on the face and neck of a 5-year-old girl after playing in a sandpit close to pines infested with *Thaumetopoea pityocampa*. The allergological study showed a positive skin prick test with setae and whole larval extracts (Reprinted with permission of the authors and the editor (Vega et al. 2011a, b)

Fig. 8.18 Papular-erythematous rash on the anterior face of the wrist and the palm of the hand of a 7-year-old girl. Reprinted with permission from the authors and the editor (Vega et al. 2011a, b)

it is thought that an irritant mechanism is responsible, although a possible a delayed-type allergic reaction could also be present.

Distribution: *Thaumetopoea* larvae usually cause an airborne disease (Maier et al. 2003; Vega et al. 2011a, b). Skin lesions are more frequently located on exposed areas, typically on the neck and limbs, and in particular the wrists, forearms, flexure areas and ankles, although covered areas of the body may also be affected. Physical activity and scratching may increase the intensity of the dermatosis.

The palms of the hands and the interdigital spaces are more often affected in children, probably due to direct contact with larvae when playing on infested places (Vega et al. 2003a, b).

Ocular Manifestations

Ocular involvement due to processionary setae is also frequent and it may or may not be accompanied by dermatological involvement. It happens in about 11–30 % of individuals with *Thaumetopoeae* reactions (Maier et al. 2003; Holm et al. 2009; Vega et al. 2011a, b).

The setae can cause different ocular pathologies, which are aggravated by scratching. After setae exposure, immediate or delayed signs as conjunctivitis, keratitis and uveitis can appear (Fig. 8.19). Three cases of ophthalmia nodosa by *T. pityocampa* setae have been reported (Watson and Sevel 1966). Moreover, late signs (cataract, vitritis and retinitis) by an intraocular migration could happen (Trincao et al. 2012), although other authors with years of experience in ocular lesions induced by *T. pityocampa* have not found any case (Portero et al. 2013).

As in dermatological involvement, a combination of non-allergic and allergic factors can be responsible of the ocular manifestations. Patients with IgE-mediated hypersensitivity show often ocular itchiness with or without redness of the eye that disappears spontaneously or after treatment with antihistamines in minutes or few hours.

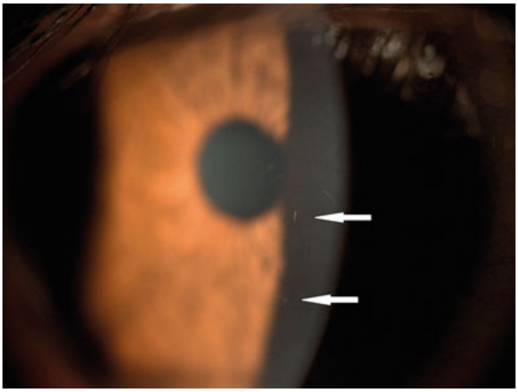

Fig. 8.19 Higher magnification, slit-lamp images of the cornea, showing the setae of *T. pityocampa* larvae (*white arrows*) (Image obtained by courtesy of A. Portero)

Other Manifestations

Respiratory involvement is less common and include rhinitis, dyspnea, cough and wheezing occasionally associated with an anaphylactic reaction with multiorgan involvement as described in several case reports (Licht and Jonker 1998; Bosma and Jans 1998; Vega et al. 1997, 1999; Shkalim et al. 2008).

Other systemic symptoms, such as fever (Gottschling et al. 2007; Maronna et al. 2008; Holm et al. 2009), vomiting, abdominal pain or hypertension (Kozer et al. 1999) have only rarely been reported. Moreover, a 15-month-old boy with severe orofacial edema after ingestion of a processionary larva has been reported (Inal et al. 2006). Up to date, fatal cases caused by *Thaumetopoea* species have not been informed, as it has happened in rare cases of lonomism by other Lepidoptera.

Hypersensitivity Reactions

In addition to mechanical irritation, Lepidoptera are capable of causing hypersensitivity reactions in susceptible individuals. The term hypersensitivity is used when a reaction causes objectively reproducible symptoms or signs, initiated by exposure to a defined stimulus at a dose tolerated by normal subjects. It can be classified in allergic (immunologic mechanism -IgE or not IgE mediated-) and nonallergic (Johansson et al. 2001).

With respect to *Thaumetopoea*-related disease, experimental application of setae cause a local inflammatory reaction in all subjects showing different intensity among them (Fagrell et al. 2008). Moreover, within the same population or workers group with similar exposure, stands out the great variability between subjects. There are cases practically free of symptoms, but others present severe reactions (Vega et al. 2011a, b; Holm et al. 2009). To date, there is evidence of a type I hypersensitivity (IgE-mediated) to *Thaumetopoea* setae, however, there has been no conclusive data of the participation of other types of hypersensitivity mechanisms, although cellular immunity is probably involved in some cases (Vega et al. 2011a, b). It also seems that chitin and its degradation products, which are powerful promoters and regulators of immune reactions, may play a role in the variable sensitivity to these insects (Battisti et al. 2011).

A difficulty to apply the term hypersensitivity to *Thaumetopoea* reactions is that in non-experimental conditions it is not possible to quantify the exposure (the number or amount of fixed setae) and therefore, there is a lack of definition in the magnitude of the reaction that could have a normal subject (not hypersensitive) after setae exposure. Moreover, an overlapping of pathogenic mechanisms (non-allergic and allergic) can happen, existing difficulties to value the clinic relevancy of each one.

IgE-Mediated Hypersensitivity

- Prevalence
  In endemic areas, approximately half of the adults with dermatological reactions due to *T. pityocampa* are allergic (IgE-mediated) (Ruiz 2011). In children from a rural area, a lower prevalence of allergic reactions has been found (7 % from 60 cases) (Vega et al. 2003a, b). However, this prevalence increases in children from communities located close to infested trees, as peripheral urban areas (data not shown).
- Risk factors
  The frequency and intensity of exposure to the larvae facilitates the sensitization to their allergens. Therefore, the main risk factor to IgE *T. pityocampa* hypersensitivity is the male sex because males are more frequently exposed to larvae by an occupational exposure or by some hobbies (Ruiz 2011).

  The atopic predisposition has not been found as a risk factor, as in the case of allergic reactions to other insects as Hymenoptera. The age and the presence of relatives with reactions to *T. pityocampa* were not found to be risk factors (Ruiz 2011).
- Clinical pattern
  The clinical pattern of patients with IgE-mediated hypersensitivity to *T. pityocampa* shows significant differences with respect to nonsensitized patients. Patients with IgE-mediated hypersensitivity experience immediate and progressively more severe reactions but of a lower duration. In addition, IgE-mediated reactions can appear even after a minimal exposure as walking through a pine forest. Moreover, the symptoms may occur throughout the year including the months in which the insect has not setae (Vega et al 1999; Ruiz 2011). In these patients, the characteristic skin manifestation is contact urticaria accompanied by angioedema -particularly on the eyelids- in half the cases. Rhinitis occurs more frequently and the most of cases of anaphylactic reactions have been reported among allergic individuals. Table 8.1 shows the differences between individuals with IgE-mediated and non allergic reactions to *T. pityocampa*.

Table 8.1 Differences between individuals with IgE-mediated and non allergic reactions to *T. pityocampa* larvae

	IgE-mediated	Non allergic
Affected people	Some	All
Prior contacts with the larvae (prior immunization phase)	Necessary	Not necessary
Intensity of the exposure	Minimal	High
Latency period	<1 h	>1 h
Number of reactions	Several	Few
Characteristic skin manifestation	Contact urticaria	Papular dermatitis
Distribution of cutaneous lesions	Exposed areas/ generalized	Exposed areas
Severity of the clinical manifestations	Greater	Lower, except for extensive exposure
Skin prick test	Positive	Negative
Specific IgE	Yes	No

Abbreviation: *IgE* immunoglobulin E

4.4 Diagnosis

There are no specific clinical signs of reactions to *Thaumetopoea* larvae. Diagnostic suspicion is based on several observations.

4.4.1 Criteria of Clinical Suspicion (Vega et al. 2011a, b)

- A history of exposure in the previous 24 h in an area with trees infested with these insects is essential. Although *Thaumetopoea*-related disease has a seasonal importance, it can also cause symptoms throughout the whole year.
- Presence of urticaria, with or without angioedema, or papular eruption that are very pruritic and tend to appear on the neck and flexure and distal areas of the limbs. In children, the palms and interdigital spaces in particular should be checked for lesions. Keratoconjunctivitis is also frequent.
- Identification, whenever possible, of urticating hairs on the skin or clothes of the patient by applying an adhesive strip or directly through use of a dermatoscope.
- Reactions should not appear in other circumstances, and other differential diagnoses that may be associated with similar signs and symptoms should be excluded. These include reaction to bites of other insects, nodular or atopic prurigo, scabiosis, other contact eczemas and urticarias, photodermatoses, etc.
- Criteria for suspicion of an IgE-mediated allergic component include immediate and progressively more severe reactions, even with minimal exposure.

4.4.2 Pathologic Anatomy

Microscopic assessment of the different skin reactions to *Thaumetopoea* is also nonspecific and cannot be used for diagnosis. The microscopic pattern of the most characteristic delayed cutaneous manifestation, papular eruption, shows a nonspecific inflammatory reaction with epidermal oedema and a perivascular lymphohistocytic infiltrate with eosinophils, as seen in bites and reactions to other insects. There are not histopathological descriptions about vesiculopustular or blistering dermatitis.

4.4.3 Allergy Diagnostic Tests

Confirmation of an IgE-mediated mechanism would be made by a positive result in the skin prick tests with extracts to non-irritative allergen concentrations and/or specific IgE determination in serum using setae and whole body extracts from larvae in their last larval stage.

4.4.4 Skin Tests

Several studies have shown the safety and diagnosis usefulness of the skin prick tests using whole larval and more recently setae extracts. Biological standarization with both extracts has been performed and an extract concentration of 5 mg/ml was adequate for diagnosis (García-Ortiz et al. 2010; Ruiz 2011). When whole larvae and setae extracts have been compared by skin testing and immunoblotting, both extracts have demonstrated to be useful and complementary for diagnosis (Rodríguez-Mahillo et al. 2012; Ruiz 2011).

Patch testing with extracts at non-irritative concentrations can be a useful test in the investigation of *Thaumetopoea* delayed reactions such as has been demonstrated with other Lepidoptera.

4.4.5 Serological Determinations

IgE immunoblotting is a less sensitive technique than the skin prick test but it is very specific. Previous studies have shown a positive result in 72–74 % of the patients with positive skin prick tests (Vega et al. 1999; Ruiz 2011), thereby demonstrating the usefulness of this test. Specific IgE determination to *T. pityocampa* larvae by EAST method has been also reported (Fuentes et al. 2006).

Up to date, two major allergens from *T. pityocampa* have been described: Tha p1 from whole larvae extracts (Moneo et al. 2003) and Tha p2 from setae extracts (Rodríguez-Mahillo et al. 2012). These findings open the possibility of the molecular diagnosis for urticating Lepidoptera.

4.5 Treatment

Table 8.2 shows some of the preventive measures to avoid reactions to these insects. If a contact with these larvae has happened, washing with soap and water and removal of contaminated clothing is necessary. Scratching should be avoided as far as possible as this will exacerbate cutaneous symptoms or it will be able to cause ocular complications. Once symptoms have appeared, treatment is exclusively symptomatic: oral antihistamines to control pruritus and topical corticosteroids for eczematous lesions and papular eruption. A novel treatment with topical application of potassium dobesilate 5 % cream, a specific inhibitor of fibroblast growth factor, has been useful in a case of dermatitis due to contact with pine processionary larvae (Cuevas et al. 2011).

In patients with extensive or refractory lesions, oral corticosteroids can be used. In the event of anaphylactic reactions, early diagnosis is needed, along with immediate treatment with epinephrine as well as corticosteroids and antihistamine agents. Reactions caused by oral exposure can require urgent orotracheal intubation and they should be managed by a qualified specialist.

The acute ocular itchiness can be controlled by antihistamines. However, keep in mind the possibility of more serious consequences and if the symptoms persist or if the patient refers foreign body sensation, grittiness, photophobia, or visual worsening, the patient should be managed by an ophthalmologist. On the other hand, some authors report that the removal of intracorneal hairs significantly reduces the risk of intraocular penetration. However, other authors do not advise it because they have not found any case of setae-induced intraocular penetration and because efforts to physically remove them are likely to do more harm than good (Portero et al. 2013).

General doctors and specialists should become familiar with *Thaumetopoea*-related disease. Correct diagnosis and appropriate information that emphasizes preventive measures will reduce the incidence and severity of these reactions.

Table 8.2 Recommendations for avoiding reactions to *Thaumetopoea* larvae

Avoid heavily infested areas in the months in which the larvae are urticating, especially on windy days and when the larvae descend in processions from the trees. Pets (for example dogs) should also avoid these forests at this time
If larva processions are seen, keep children away and never disturb, touch, or sweep them
Do not collect objects (pine cones, wood, etc) from infested forests or touch the larva tents
In communities located close to infested trees, during the month in which the larvae are urticating, avoid to dry the clothes outdoors. Moisten the surrounding area to ensure that the setae of the larvae remain on the ground.
In edges and clears of infested pine/oak forests avoid removing the soil
In cases of occupational exposure, precautionary measures are essential when working in infested forests. It is important to leave as small an area of skin exposed as possible and to wear appropriate clothing and footwear. If the exposure is high use protective goggles or even a mask. Patients allergic to larvae should not work in infested forests

5 The Pine Processionary Moth: Assessment of Animal Health Issues

Julie Rivière, François Moutou, and Barbara Dufour

The pine processionary moth *Thaumetopoea pityocampa* causes significant forest damages (defoliation, weakening of trees, esthetic prejudice...) but can also induce important sanitary consequences in men and animals, both in pets (dogs, cats) and also in farm animals (horses, cattle, sheep, goats). Contact with irritating hairs of larvae can provoke oral, skin and eye damages which are most of the time benign but sometimes leading to allergic reactions up to anaphylactic shock.

5.1 The Pine Processionary Moth and Its Sanitary Consequences

The procession is the most dangerous period for men and animals, when larvae release irritant hairs when they feel assaulted or stressed. Damages may therefore result either from direct contact (with larvae or their tents, as they contain hairs remaining irritating even after the departure of the colony) or from indirect contact (with stinging hairs left on pasture during the procession or carried by the wind).

Urban, peri-urban and rural sanitary nuisances are more extensive and disturbing with the gradually spread of the pine processionary moth to northern France: populations of areas newly colonized are in fact usually not informed of these sanitary consequences.

5.1.1 Symptomatology

Envenomation by processionary larvae can be observed both in domestic pets (dogs, cats) and in farm animals (horses, cattle, sheep, goats). Clinical signs appear rapidly after exposure to stinging hairs, a few minutes to a few hours later on average. Symptoms depend on the terms of contamination but are globally similar whatever the species of larva involved (pine, oak, etc). Four main routes of exposure are classically described: skin contact, eye contact, inhalation and ingestion. The preferred involvement of the face and oral cavity can be explained by the behavior of animals. Thus, dogs are often contaminated by the nose and mouth by sniffing or even chewing and eating larvae in procession, whereas ruminants are contaminated when grazing grass on which larvae have left after their procession the stinging hairs (Charmot 1987).

Symptomatology in carnivores

Various studies report that the dog is by far the species most affected by envenomation (Charmot 1987; Darrasse 1991; Gleyze 1995; Pineau and Romanoff 1995; Pineau 1999; Scheiner 2003; Turpin 2006). This can be explained by their heightened curiosity during forest walks or even in gardens (procession is a curious phenomenon!), in contrast to the cat, which is more suspicious and so enters rarely in contact with larvae (oral exploration is less developed in the feline species).

- Local symptoms

  Oral damages following ingestion of larva or a contact with them are often predominant. Lingual impairment may also result from licking itching body parts of the animal. There is a strong inflammation and a swelling of the oral mucosa of the lips and tongue. Glossitis thus induced causes discomfort swallowing and results in an abundant salivation, anorexia and watering difficulties, which can lead to kidney failure (Blanchard 1994; Poisson et al. 1994). Necrosis of the tongue can also develop after blood coagulation of lingual vessels which prevent tissue oxygenation; it can go up to a loss of substance in the few days following envenomation, especially on dogs (Blanchard 1994) (Fig. 8.20).

  Skin lesions can also be observed: an acute onset of urticaria, erythematous and itching can be found in areas where the skin is thin, such as lips, chamfer, eyelids and ears (Poisson et al. 1994).

  Respiratory impairment can also be reported when dust loaded with irritating hairs reach the respiratory tract. This results in inflammation of the nasal mucosa, rhinitis and bronchitis, coughing violently and sometimes in dyspnea and shortness of breath (Bergia and Keck 1991). Some fatal cases have been reported after angioedema and asphyxia (Darrasse 1991).

Fig. 8.20 Edema of the tongue of a dog with blister on the ventro-rostral part of the tongue after envenomation by *T. wilkinsoni* (Bruchim et al., 2005)

Ocular impairment may also be observed but is less common. It takes the form of keratoconjunctivitis, glaucoma or sometimes corneal ulceration, causing pain, photophobia and lacrimation. Hairs can be embedded in ocular structures, in particular in cornea, causing relapse with chronic conjunctivitis.

In cats, the symptoms are similar to those observed in dogs. Acute pododermatitis can also be observed. Cases of envenomation in cats are nevertheless relatively rare (Darrasse 1991; Gleyze 1995; Pineau and Romanoff 1995; Poisson et al. 1994).

- General symptoms
  General symptoms are relatively rare, occurring primarily as marked exhaustion with hyperthermia which can go up to shock. A few animals sometimes develop an anaphylactic shock. Ingestion of larvae can also cause gastritis and vomiting (Chuzel 2004; Darrasse 1991).

Symptomatology in Ruminants

Ruminants, from the grip of fodder containing stinging hairs, develop vesicles on the apex of the tongue. They are very fragile, break easily and then lead to the formation of extensive superficial ulcers (Figs. 8.21, 8.22, and 8.23). Affected animals are often exhausted, anorexic and isolated themselves from the rest of the herd.

Fig. 8.21 Envenomation by a pine processionary larva (Photo J. M. Gourreau)

Fig. 8.22 Envenomation by an oak processionary larva with large superficial ulcer on the tongue of a cow (Braque 1999)

Fig. 8.23 Oral lesions (superficial ulcers) in small ruminants following envenomation by pine processionary larvae (Gourreau et al. 2002; photo M. Cornelis)

Symptomatology in Horses

In horses, congestion of the tongue, colics and extended urticaria were reported. According to the observations of Darrasse (1991), pruritus is sometimes intense and can lead to self-mutilation: for example, to relieve hives of the flanks, a mare gave herself frequently blows of hooves on the abdomen. Sweating may also be important (Charmot 1987). Many studies have recently been conducted to explore the envenomation in horses. Indeed, twice, massive waves of abortions were observed for which no known agent (microorganism, alkaloids, toxic plants . . .) have been identified, but epidemiological studies have revealed the presence of larvae in the environment; mares have certainly consumed them inadvertently (Cawdell-Smith et al. 2009; McDowell et al. 2010; Stewart 2009; Tobin et al. 2004). Thus, some species of stinging larvae can therefore now be considered as abortifacient potential agents in mare, as well as a few microorganisms, alkaloids and toxic plants (Stewart 2009).

5.1.2 Diagnosis and Differential Diagnosis

The clinical signs are generally nonspecific; the diagnosis is based on history: symptoms appearing suddenly, a few minutes to a few hours after a walk outdoor, in a forest or in a garden. Consultations are seasonal and take place mainly from February to May. Symptoms are dominated by a glosso-stomatitis which can be necrotic and ulcerative, and by an abundant salivation. Animals are often brought in emergency to the vet, because of the rapid onset of symptoms and their spectacular nature, which may suggest poisoning.

In carnivores, care must be taken not to confuse envenomation by the pine processionary moth with the ingestion of various caustics (irritating products), or with insect bites (wasps, bees, hornets) which also result in oral symptoms but rarely lead to necrosis. Ophidian envenomation may also be considered, although induced lesions are often more severe - the presence of fang can help to establish the diagnosis. Finally, the root of the tongue and the throat must systematically be inspected to eliminate any hairs which can cause inflammation and glossitis (Poisson et al. 1994).

In ruminants, oral symptoms may strongly suggest vesicular diseases such as foot-and-mouth disease (FMD) or bluetongue (BT). Epidemiological data must then be considered with interest in the differential diagnosis. Indeed, envenomations by processionary larvae are seasonal and occur mainly between January and May, as already mentioned. This affection can affect many animals grazing on the same area but the apparent contagion is less important than during outbreaks of FMD or BT. In addition, the udder and feet are not concerned in the case of envenomation by larvae (Gourreau 2002; Gourreau et al. 2002).

In the absence of specific test, diagnosis of envenomation by the pine processionary larva is primarily a diagnosis of exclusion based on clinical and epidemiological criteria, whatever the species affected. Specific tests depending on the location of symptoms (skin, eye, vascular . . .) can also be realized.

5.1.3 Treatment, Recommendations and Prognosis

The success of the treatment is related to three main factors (Demory 2004a, b):

- The precocity of the treatment: it allows limiting the consequences of envenomation (in particular lingual necrosis and loss of apical substance) and thus determines both the survival of the animal, but also the preservation of the tongue;
- The realization of a long-term treatment (during several weeks);
- The “non-breaking” of stinging hairs during treatment, so as not to facilitate the diffusion of the irritant substance.

Treatment is mainly symptomatic, with its main aims at fighting against the effects of histamine-releasing irritant substance. A corticosteroid, anti-histaminic and diuretic association is often recommended to support or restore the general condition of the animal. Antibiotics may also be prescribed if the lesions are already at an advanced stage (oral administration of amoxicillin or spiramycin). It is also important to ensure the good nutrition and good watering of the animal.

Prescription of local care is required; it should be established as soon as possible after the envenomation to limit the risk of lingual necrosis and to improve prognosis. Gentle washing should be done without rubbing the affected areas, to avoid breaking hairs and thus to prevent the release of the irritating substance. Injections of heparin in the wake of necrosis may be recommended. Lingual plasty can sometimes be considered after necrosis to restore the tongue to a form compatible with normal eating and watering (Darrasse 1991).

The prognosis of envenomation by pine processionary larvae can be severe, although many cases are mild. It depends largely on the intensity of contact with stinging hairs, the precocity and the duration of the treatment (Blanchard 1994). When the treatment is implemented early, in the first hours after envenomation, the prognosis is generally good and the animal's life is not in danger. Evolution is generally favorable and benign lesions heal in 8 to 10 days. When treatment is delayed (more than 24 h after envenomation) or if the contact with stinging hairs was intense (many bristles or long-term contact), the glosso-stomatitis evolves rapidly to necrotizing ulcerative on a large area (Blanchard 1994).

Thus, the short-term prognosis depends mostly on the severity of the systemic implications (acute renal failure, laryngeal edema ...), while the longer-term prognosis depends on the severity of the lingual lesions, loss of apical part being relatively common during envenomation (Demory 2004a). Fatal cases are fortunately rare, but sometimes euthanasia is the only possible outcome when the lingual necrosis extends to the throat (Gleyze 1995).

5.2 Importance of Clinical Cases of Envenomation in Animals in France

As part of the URTICLIM project, two retrospective epidemiological surveys (Rivière 2011; Rivière et al. 2011) were conducted among veterinary practitioners, in order to:

- Identify veterinarians confronted with cases of envenomation in livestock and pets: this allowed identifying areas that have been most affected and highlighting geographical areas at risk (detection of cases of envenomation in animals may allow alerting public health actors and population of the newly colonized areas),
- Identify the main clinical signs and lesions of envenomation,
- Highlight the main diagnostic difficulties that may be encountered by veterinarians, especially the difficulties in diagnosing an envenomation in ruminants because of potential confusion with vesicular diseases,
- Find a serological test able to distinguish envenomation by the pine processionary moth from other vesicular diseases like FMD or BT, because these diseases could have severe sanitary, social and economic consequences. Unfortunately, this part of the project has not been successful, because laboratories contacted for the development of the diagnostic tool did not respond to the request -there is in fact actually not commercial reason to develop this tool.

5.2.1 Material and Methods

The two retrospective surveys were conducted 2 years apart, the first in 2008, covering the period 2005–2008, the second in 2010, covering the period 2008–2010. An electronic questionnaire including some sixty items all closed or mixed was sent to French veterinary practices all over the country through the SNGTV,[1] an association (NGO) including more than 600 contacts (a combination of single or multi practices, meaning one or more than one practitioner, in both rural and urban areas). We also contacted some respondents by phone to gather expended information. The second survey was conducted for the purpose of comparing the results with the first survey and to assess the temporal and geographical evolution of envenomation cases, in order to follow the expanding migration of the pine processionary moth via the location of animals affected. Both surveys were administered and stripped using "Sphinx" survey software online.

Moreover, a study of a data base located in the National Center for Veterinary Toxicological Information of Lyon (CNITV), which provides assistance for advices, diagnosis, treatment or prognosis about requests concerning poisoning of wild and domestic animals, was performed from 2008 to 2010.

5.2.2 Results

Epidemiological Surveys Among Veterinary's Clinic in France

A total of 122 answers were obtained in the first survey and 49 in the second (which equals respectively a response rate of 20 and 8 %). Between 2005 and 2008, 58.2 % of respondents said that they have seen cases of envenomation (Table 8.3). By the time of the second survey, that number had climbed to 63 %: the rate of practitioners who have been confronted with cases of envenomation by pine processionary moth was however equivalent in the two surveys and concerns approximately 60 % of practitioners in each study.

Table 8.3 Number of veterinarians who have been confronted with cases of envenomation by the pine processionary moth between 2005 and 2008 and between 2008 and 2010

	No. 2005–2008	% 2005–2008	No. 2008–2010	% 2008–2010
No	51	41.8	19	38.8
Yes	71	58.2	30	61.2
Total	122		49	

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[1] Société Nationale des Groupements Techniques Vétérinaires (National Society of Veterinary Technical Groups)

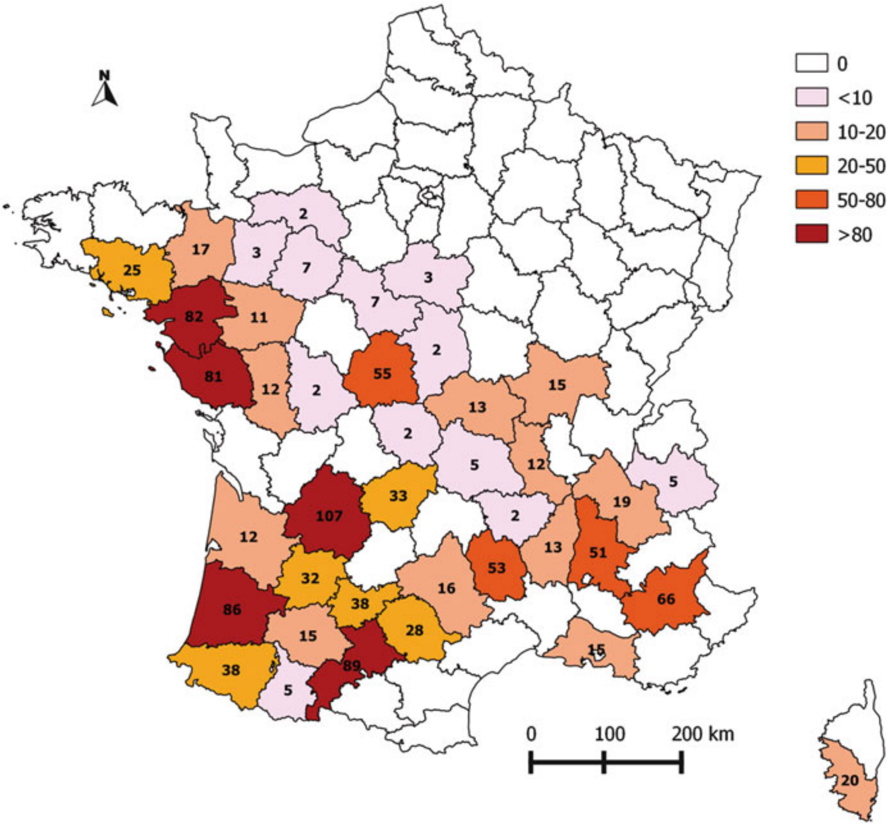


Fig. 8.24 Departmental location and number of envenomation cases by the pine processionary moth in animals

Geographical Location of Concerned Practitioners

For the geographical localization, the practitioners who have seen cases were mainly located in south and west regions of France, which corresponded to other scientific data (and especially consistent with data from the French Department of Health Forestry (DSF)) (Fig. 8.24). The number of cases of envenomation mentioned by veterinarians was higher in the south-west and north-west of France, which corresponds to endemic areas where the processionary moth has been present for several years.

Affected Species

In total, 94 veterinarians have seen at least one case of envenomation between 2005 and 2010 and 1,112 cases have been recorded over the 6 years period, but some respondents admitted that they have not recorded all the cases that they have seen.

Table 8.4 Number of veterinary practitioners who have observed cases of envenomation between 2005 and 2010 and number of affected animals by species

	Cattle	Cats	Horses	Dogs	Small ruminants
Animals	39	106	96	826	45
% Animal group	3.5	9.5	8.6	74.3	4.1
Practitioners	7	15	7	94	4

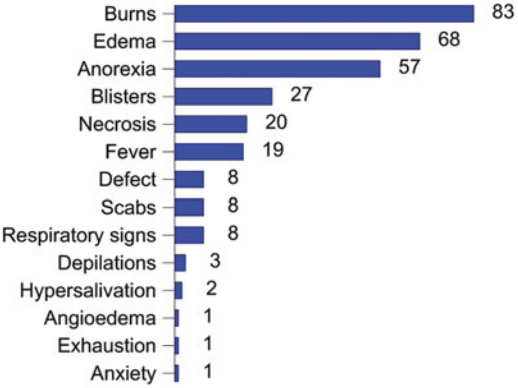


Fig. 8.25 Symptoms of envenomation by processionary larvae in dogs (number of veterinarians who observed the symptoms mentioned in dogs between 2005 and 2010)

Table 8.4 shows the number of cases mentioned in each species and the number of practitioners who have seen cases in each species. All respondents have seen at least one case in dogs, and the cases in this species represent 74 % of all cases. Only few cases have been reported in farm animals (cattle, sheep, and goats): they represent 7.5 % of the total number of cases observed between 2005 and 2010.

When comparing the number of animals affected by report number of concerned practitioners, we noticed that most cases were sporadic in dogs and cattle (about 5–10 cases by practitioner and by year), although some massive envenomation can be reported (for example a practitioner who reported 50 cases of envenomation in horses, or another who faced 30 cases in small ruminants).

Symptoms

- Dogs
  The main symptom of envenomation by the processionary larva in dogs is burning (with vesicles) in 87 % of the cases mentioned (Fig. 8.25). The swelling (edema) of the tongue, lips and sometimes of the face is also a common sign, which is accompanied in some cases, and logically, by lesions on the tongue and anorexia. Lesions could evolve into necrosis, with a possible loss of a part of the tongue. The appearance of "blisters" (term used in the questionnaire) and fever is more random, such as respiratory problems, crusts and depilation. The chamfer was also sometimes reached, with blisters and scabs. Local signs, oral signs, are predominant. No nervous disorder was observed.

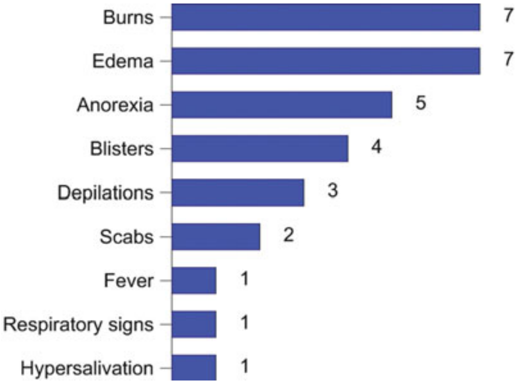


Fig. 8.26 Symptoms of envenomation by the processionary larvae in ruminants (number of veterinarians who observed symptoms mentioned in ruminants between 2005 and 2010)

Treatment must be implemented quickly. Anti-inflammatory, antihistaminic and antibiotics have been used to manage the affection and prevent the potential complications, associated with local care on oral cavity. Some veterinarians have made a fluid therapy and have fixed a nasogastric esophageal catheter to provide needed fluids and nutrition to animals.

Three practitioners have said that envenomation could be fatal for dogs: two veterinarians have notified that euthanasia was necessary and one had observed a death consecutive to the necrosis of the lips and the nose with a loss of substance, despite hospitalization and treatment implemented quickly.

- Ruminants
  The main clinical sign of an envenomation by processionary larvae in cattle is also burning and edema. Then occur other signs, more inconstant: “blisters”, edema, depilation, crusts and anorexia. Finally, non- specific signs have been mentioned: fever, respiratory disorders, salivation. As in dogs, nervous symptoms were not observed (Fig. 8.26).

  Affected animals stop eating and separate themselves from the herd. Treatment is also globally similar, and some animals could die.

Differential Diagnosis

Regarding the differential diagnosis, this survey focused only on the possible diagnostic difficulties among farm animals. Indeed, the potential confusion of envenomation with certain regulated diseases is to be considered, because confusion could have serious economic consequences (including commercial constraints, restriction on movement. . .).

Of the 10 practitioners who have seen cases in ruminants from 2005 to 2010 (39 reported cases in cattle and 45 in small-ruminants), five have actually encountered difficulties to establish the diagnosis; the main disease which can be confused with an envenomation by the processionary larvae has been BT. Then were mentioned FMD and malignant catarrhal fever (MCF). Confusion with an irritant

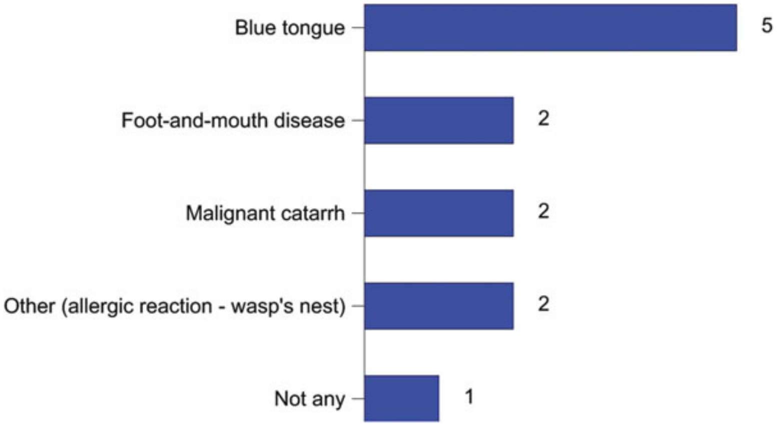


Fig. 8.27 Main diseases in the differential diagnosis of envenomation by the pine processionary moth among farm animals identified in both epidemiological surveys

or allergic reaction from an insect bite (wasp tent for example) had also been cited (named "other" in Fig. 8.27). One practitioner had no difficulty to establish the diagnosis (Fig. 8.27).

According to some practitioners contacted by telephone following investigations, cases of envenomation in ruminants are certainly under-diagnosed, and essentially based on a diagnosis of exclusion. In addition, it seems that farmers are unaware of this affection, especially because the loss of production is minimal and mortality very rare.

In endemic areas, practitioners are very aware of this affection and have no particular difficulty in establishing the diagnosis, thanks to the seasonality of envenomation to avoid confusion with other diseases.

5.3 Data of the National Center of Veterinary Toxicological Information

For the data from the CNITV, they were 116 calls concerning envenomation by larva (whatever the species of larva involved) between 2008 and 2010, including 69 cases considered as certain or probable. 65/69 calls related to dogs, 4/69 cats and 1/69 horses, no appeal having been identified for ruminants. Altogether, 72 cases of envenomation have been reported in dogs, 12 in cats and 1 in horses.

Digestive disorders are the majority, accounting for nearly 57 % of the symptoms mentioned (Fig. 8.28).

Signs could be most extensive, for example with cutaneous disorders when dogs roll in a procession. They are also respiratory difficulties or cardiovascular difficulties like hemorrhage, or anaphylactic shock. Eyes could also be affected, with burns.

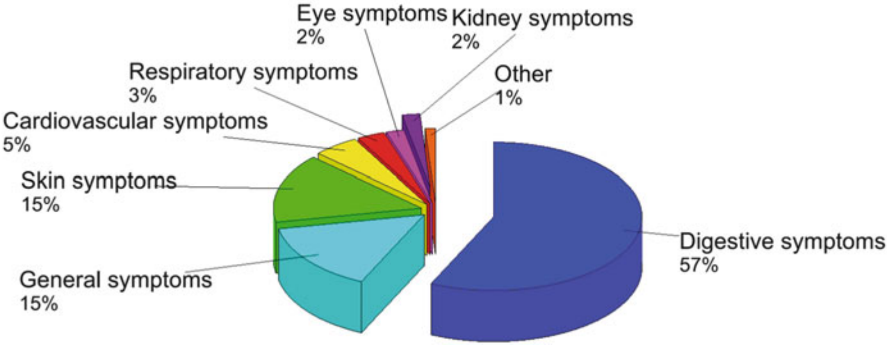


Fig. 8.28 Symptoms of envenomation by pine processionary moth notified in the CNITV between 2008 and 2010

5.4 *Discussion*

These exploratory surveys show various biases (including practitioners' selection bias because practitioners were contacted via the SNGTV, an NGO composed mainly of rural practitioners) do not allow any generalization of the results obtained at the national level. However, the results and the distribution of the cases match other results and scientific data.

Only 20 % of veterinarians contacted responded to the first survey, and 8 % to the second. If this rate of answer for an anonymous questionnaire by computer is usual (it is even rather pretty good for the first survey), it is however important to note that it is impossible to know why some veterinarians did not respond to these investigations. The assumption that they were not concerned by the problem is obviously not excluded.

Geographical maps with veterinarians who have been confronted with cases of envenomation have been established to evaluate the expansion of pine processionary moth. However, the geographical representativeness can be discussed.

We received in fact some false negative answers, because some practitioners who have observed no cases of envenomation have nevertheless seen cocoons of pine processionary moth and processions around their workplace. Furthermore, some veterinarians admitted that they are unaware of the symptoms although they have observed clinical signs like burns, vesicle, edema of the tongue… and veterinarians are the main applicants of information to the national center for toxicologic information. The main reason of calls to this center is a need of advices for the treatment and for the diagnosis, which highlights the need of information about, among others, pine processionary moth for veterinarians and owners (Fig. 8.29).

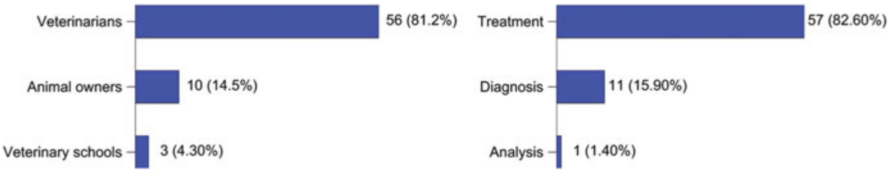
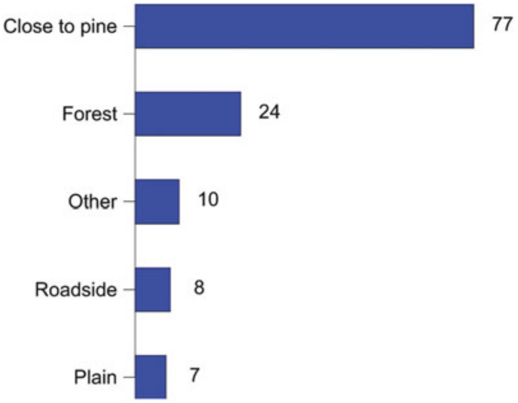


Fig. 8.29 Applicants for information regarding the processionary larvae from the CNITV and reasons calls

Fig. 8.30 Environment of affected animals



Similarly, we have also received some false positive answers: it cannot be excluded that some of the observed envenomation have been caused by the oak processionary larva (*T. processionea*), which also owns the stinging properties from May to July (however, the procession and pupation of the oak processionary are taking place on the tree, and not on the ground; so pets are significantly less frequently in contact with this insect). In fact, the majority of cases had been observed within proximity of pine trees, but some veterinarians did not specify the environment of the animal affected and the specific identification of trees, giving answer like in plain, forest and garden – and one practitioner had evoked a pear tree (Fig. 8.30).

Therefore, the geographical distribution of affected animals does not reflect accurately the geographical evolution of populations of processionary larvae.

Otherwise, the comparison between the two surveys did not highlight a significant evolution in the number of cases of envenomation, or even a particular geographic evolution. Among the 171 practitioners who participated in this study, 12 responded to both questionnaires. Only two veterinarians have reported an occurrence of cases of envenomation in animals of their clinic.

5.5 Conclusions

The pine processionary moth, which continues its geographical expansion inexorably from the south to the North of France in conjunction to climate change, caused a number of envenomation on animals; the intensity and frequency vary according to regions. A thousand cases of envenomation were recorded over the 6 years under study and this affection could also be actually considered as a real problem in animal health, especially for dogs. Envenomation is mainly benign, but the severity and outcome of infected animals may depend on the precocity and effectiveness of the treatment started by the practitioner. However, according to the investigations, some practitioners of still uncolonized areas are unaware of envenomation symptoms, which could prove problematic in the coming years, if the geographical expansion of the pine processionary moth continues at the current rate. Indeed, some mathematical models consider the presence of this insect in Paris in 2025 (Robinet et al. 2007).

We highlighted also the difficulty of diagnosing envenomation in livestock and the importance of the seasonality of the cases as a help for the diagnosis. However, some respondents have observed that this seasonality has been modified by the global warming in recent years, and this could make the diagnosis even more difficult in the future. Due to the geographical extension of the pine processionary moth, populations must be informed of health risks, especially in newly colonized areas.

The realization of two informative leaflets, one for veterinary practitioners and the second for animal owners, would be an interesting way to better promote the dissemination of information. We thus realized, in project, two informative brochures in French to explain the biology and the danger of the pine processionary moth, the clinical signs and the main recommendations to prevent and manage an envenomation for humans and animals. It could be also interesting to make more local epidemiological surveys around clinics really concerned or localized along the front of the geographic areas of the pine processionary moth distribution.

6 URTIRISK, a Software for Assessing the Allergy Risk

Lionel Roques

6.1 Objectives

The software URTIRISK allows the user to observe the evolution of the allergic risk associated with the presence of pine processionary moth, over a year and throughout the French territory. This software is mainly based on the observations of the population range carried out by INRA URZF (UR633).

6.2 Data

The software is based on the following data:

1. Position of the colonization front (observed by INRA URZF): Northern front (2010–2011) and altitudinal front in the Massif Central (2005–2006).
2. IGN map showing the location of pine trees.
3. Chart describing the life cycle of the pine processionary moth and its variations between southern France and the colonization front, as a function of latitude. This chart was obtained by adapting the observations of Huchon and Démolin (1970) to the current geographical distribution of the pine processionary moth.

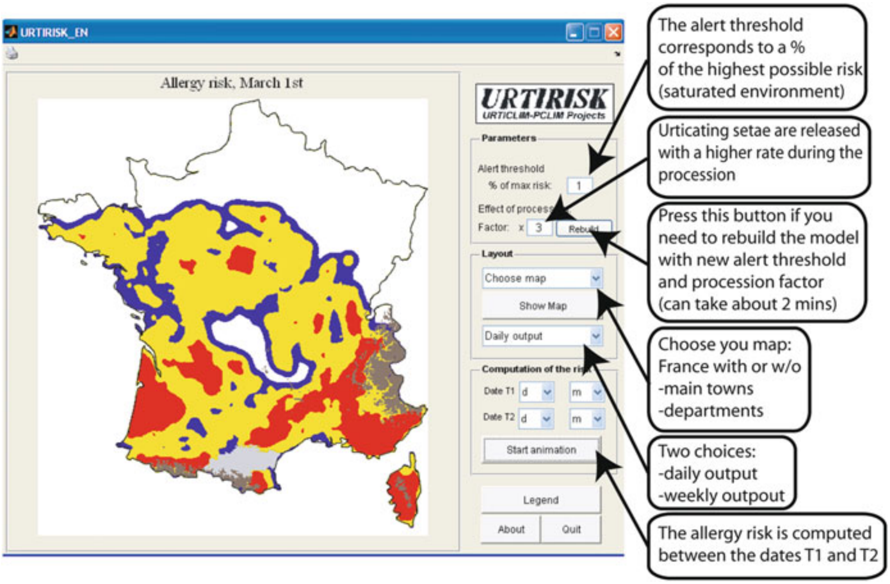
6.2.1 Computing the Allergy Risk

The allergy risk depends on the time of year, and, of course, on the presence of larvae. The production of urticating setae begins during the larval stage "L3" (Huchon and Démolin 1970). We begin by defining a potential allergy risk R_0 which depends on the latitude and on the time of year, but which is independent on the presence of pine processionary moth. The computation of this potential allergy risk is based on the following assumptions:

(i) There is a time t_0, which corresponds to the beginning of the larval stage L3 and a time t_1 which corresponds to the beginning of the procession. These times depend on the latitude only. They are computed on the basis of the chart in Huchon and Démolin (1970), adapted to the current geographical distribution of the pine processionary moth.
(ii) The duration of the procession is fixed to 30 days.
(iii) Urticating setae are released with a constant rate between t_0 and t_1, and with another (higher) rate during the procession.
(iv) The half-life of the setae is fixed to 10 days in the current version of the software.

Then, we define a function R_1, which depends on the position (latitude, longitude), and roughly describes the distribution of the tents of pine processionary larvae:

(i) We build a map of the potential area of distribution of the pine processionary moth, using only the northern front and the altitudinal front in the Massif Central together with the altitudinal limit of 1,400 m.
(ii) Using the IGN map showing the location of pine trees, we restrict the area of distribution of the pine processionary moth to the locations where pine trees are present.



Alert threshold % of max risk: 1

Effect of process Factor: x 3 Rebuild

Date T1 d m

Date T2 d m

The alert threshold corresponds to a % of the highest possible risk (saturated environment)

Urticating setae are released with a higher rate during the procession

Press this button if you need to rebuild the model with new alert threshold and procession factor (can take about 2 mins)

Choose you map: France with or w/o
-main towns
-departments

Two choices:
-daily output
-weekly outpout

The allergy risk is computed between the dates T1 and T2

Fig. 8.31 A screenshot from the URTIRISK software

(iii) We use a smoothing kernel to take into account the uncertainty related with the presence of unlisted isolated host trees and pine processionary tents beyond the colonization front.

By overlaying maps R_0 and R_1, we obtain a model for the risk R as a function of position (latitude, longitude) and date.

6.2.2 Outputs

The risk R is normalized (in time and space), so that the maximum risk value is $R = 1$. We define a warning threshold S in terms of the maximum risk. The URTIRISK software produces a map with four risk levels: no risk for $R < S/10$ (in white), low risk to $S/10 \leq R < S$ (blue), medium risk for $S \leq R < 10S$ (in yellow) and very high risk for $R \geq 10S$ (red) (Fig. 8.31).

6.3 Downloading the Software

The Matlab® source code (for Matlab R2011a or later) and executable versions for Windows x32 and x64 of the URTIRISK software are available on the website: http://urtirisk.biosp.org.

7 General Conclusions

Processionary moths constitute an economic problem in the affected countries, but the impact on animal and human health is becoming progressively clear. The fact that an immune response can appear after direct or indirect contact with setae and the high number of proteins present in setae makes research on new antigens/allergens mandatory. Besides IgE, other type of immune responses should be explored in sensitized people, especially cellular-mediated reactions that could explain the papular lesions frequently observed on affected patients.

Future research on animals and humans will need the development of reliable diagnostic methods. Serological approaches, such as ELISA tests could be very helpful for clinical diagnosis as well as for epidemiological studies. These epidemiological studies will show the expansion of the sensitization to moth allergens and the impact on different animal and human groups, for instance on occupationally exposed workers due to climate change. However, dealing with moth allergens has also an occupational risk for researchers, therefore the production of recombinant allergens for diagnosis should be done in the near future in order to obtain reliable and safe diagnostic tests.

These future new diagnostic methods would finally help in the follow-up of the different biocontrol methods, because a decrease of the moth population would be followed in a short time by a decrease in the number of sensitized humans and animals. Let us hope that this could be reached in a near future!

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Chapter 9
Development of Environment-Friendly Strategies in the Management of Processionary Moths

Jean-Claude Martin

1 Introduction

Although the aim of this chapter is to address all processionary moth species, the information provided is almost exclusively based on the pine processionary moth, *Thaumetopoea pityocampa*. References to other species are provided whenever available. Attempt to control the pine processionary moth quickly developed in Europe since the end of the nineteenth century because of both the risks related to the urticating larvae and the defoliation threatening pine forests and plantations. Indeed, the massive afforestation campaigns replanting Austrian black pines, *Pinus nigra*, on deforested mountains of southern Europe had led to large moth outbreaks in this region. Later, in the middle of the twentieth century, North Africa faced similar outbreaks following the plantation of pure stands of Aleppo pines to serve as a barrier to desertification. In these young plantations, control methods generally consisted in a manual removal of the larval tents. Forest General Inspector Julien Calas mentioned such removal operations carried out during winters 1894–1896 on 1,000 ha of pine forests in the French department of the Pyrénées-Orientales during which 1,275,000 winter tents of pine processionary moth were destroyed for a budget of approximately 5,000 French Francs of that period (Calas 1897, 1900). Then, spraying of large forest surfaces with DDT was commonly used until the late 1950s in Spain and France (Grison et al. 1959), being still considered by forest managers as an efficient, easy to implement and cheap control method (Dafauce 1970). However, large concerns quickly arose about the environmental impact of this pesticide as well as about the development of insect resistance. Therefore, research turned towards the possibilities of using entomopathogenic bacteria and viruses to control *T. pityocampa*, and the first studies started during the same period in France.

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Thus, the efficiency of *Smithiavirus pityocampae,* a virus specific to the moth larvae, was tested in 1958 at the Ventoux Mountain, in southeastern France, as a first alternative to chemical treatments (Grison et al. 1959). This experimentation known as the "Ventoux operation" was led on 320 ha. The viral preparation was obtained in laboratory from the breeding of ca. 200,000 processionary larvae infected by the virus. However, the unbearable working conditions necessary to breed such an amount of urticating larvae quickly led to stop the production of viruses in spite of the excellent control obtained at that time. Research then continued in France in partnership between INRA, Pasteur Institute and CNRS in order to study the control potential of an entomopathogenic bacterium, *Bacillus thuringiensis*. This work led in 1972 to the homologation of a commercial preparation based on *Bacillus thuringiensis* var. *kurstaki* 3a-3b (abbreviated in *Btk*), which appeared to be specific of lepidopteran larvae (Martin and Bonneaux 2006).

At the same period, a new chemical, Diflubenzuron, was recognized for its insecticidal properties (Démolin and Millet 1984). It was soon approved in Europe against pine processionary larvae under the commercial name of Dimilin (Démolin and Millet 1984). Its easy-to-use properties as well as its efficiency quickly led forest managers to use it massively against pine processionary larvae. At that time, a striking argument in favor of this chemical insecticide was its long persistence on foliage, higher than 1 year, thus making it possible to destroy at a stretch two generations of larvae (Démolin et al. 1993). Thus, in 1992 more than 90 % of the aerial control treatments realized in France and in Spain consisted in spraying Dimilin. Thereafter, the efficiency of the microbial formulations based on Btk increased owing to an optimization of the concentrations. Starting from 1994, microbiological air treatments using Btk sprayings then developed largely in Europe, and from 2000 to 2010 use of Btk against processionary moths became dominant. The chemical insecticides are still used in areas where a higher efficacy is requested but their use is constantly decreasing.

Recently, alternative techniques aimed at being more environmentally-friendly were developed in complement to these treatments or to replace them. They are more and more used, especially for managing processionary colonies in urban and semi-urban environments.

2 Preventing Processionary Moth Infestation Through Biodiversity Conservation and Adapted Forestry Management

In the maritime pine stands of the Landes region in southwestern France, forest health appeared to be related to biodiversity. Jactel and Brockerhoff (2007) showed there that pine trees growing in monospecific stands have a higher risk of being attacked by insect pests than those growing in mixed stands.

Indeed, forest tree diversity may limit the number and the accessibility of host trees for insect pests, for example by generating chemical barriers to colonization.

Actually, many species of forest insects use olfactory cues to locate their host trees. An increase in vegetal diversity, including non-host tree species, is susceptible to result in masking attractive signals or generating repellent compounds (Dulaurent 2010). Diversity may also increase the effectiveness of the natural enemies of the pests through eg., the supply of alternate preys, complementary food resources, egg-laying sites or shelters (Dulaurent 2010). The presence of tree species more sensitive to the considered pest also makes it possible in certain cases to constitute a sink for this pest, offering thus the possibility to concentrate the control efforts.

An outer hedge of broadleaved trees has been shown to decrease processionary moth infestation in pure stands of maritime pine when this edge has an equal height or is taller than the pine trees (Jactel et al. 2012). The proximity of broadleaved trees can limit the access of female processionary moths to the pines located at the edge of plantations, which are the most often exposed to the pest attacks. Broadleaved afforestations are also susceptible to constitute refuges for the natural enemies, especially the insectivorous birds such as the specialist Eurasian hoopoe, *Upupa epops*, which may find more nesting sites in the mature oaks (see Barbaro et al. 2014, Chap. 7, this volume).

When planting new conifer plantations, a preventive management strategy for pine processionary moth would consist in surrounding these plantations by a belt of broadleaved trees at the edge in order to slow down pest dispersal which is generally more abundant at the edge, and simultaneously to support natural enemies' activity.

The sensitivity of maritime pine stands to pine processionary is thus not only related to forest management but also to the composition of the surrounding environment. The management of a forest "mosaic", including that of the distribution in space and time of the component plots which may present different tree specific composition, is thus likely to exert a noticeable influence on the population dynamics of the pest insect.

Therefore, the maintenance or the plantation of hedges of broadleaved trees can be recommended for managing pine processionary moth. In order to obtain a physical barrier to moth colonization, it would then be advisable to privilege the use of tree species with rapid growth, like birch, *Betula* spp., or honeylocust, *Robinia pseudoacacia*.

Scientists therefore recommend to restore/enhance biodiversity in forest plantations by the creation of small "islets" composed of a mixture of forest tree species, thus providing habitats favorable to the maintenance of communities of auxiliary species, without upsetting the management practices. This strategy would constitute a novel type of forestry management, developing an integrated control of forest pests based on the conservation or the restoration of the biodiversity. It could first apply to the large monospecific forest of maritime pine located in the Landes of Gascogne, which is the largest wood production area in France but also a place where insecticidal treatments are the most frequent in forest environment.

Both methods (i.e. broadleaved tree species at stand edge and islets of mixed tree species) are intended to act in a preventive way against the rise of high population density. The general idea is to create all those conditions which make the habitat less suitable to the outbreak or which is able to delay the natural increase of the density associated with the periodic fluctuations. It has not been tested whether the approach works for other processionary moth species as well.

Removing host trees susceptible to pine processionary infestation is another technique, but it's radical. It is used in locations at too strong risks for public health such as schools, and small parks within estates. It more frequently concerns isolated, introduced pine trees, and more especially those of black pine (*Pinus nigra*) which are most attractive for females of pine processionary moth.

3 Curative Methods

3.1 Removal of Egg Masses and Larval Colonies

The massive collection of egg masses as well as that of larval tents at early (autumn) or late (winter) stage are the oldest techniques used by man to manage pine processionary moths. To be efficient, taking away egg masses has to be realized before egg hatching into first instar larvae (Fig. 9.1).

Similarly, the winter tents must be removed when the larvae are still present inside. Removal of egg masses has been applied at large scale in the young afforestations of the Green Belt (Barrage Vert) in Algeria during the 1980s. This method has the disadvantage of not being exhaustive because of difficulty of visualizing the egg masses in the foliage, and it is also highly time- consuming and involving large manpower.

Removal of the early-stage tents during autumn offers the possibility of manipulating larval colonies when they are not yet urticating but spotting all colonies may

Fig. 9.1 Manual collection of egg masses of pine processionary moth (Credit: A. Leblond)

Fig. 9.2 Individual protective equipment to be worn when manipulating processionary winter tents (Credit: A. Leblond)

also be difficult. Conversely, the winter tents are easy to observe but often difficult to access when located on tree tops. Managers in urban and semi-urban areas usually use telescopic ladders and lifting nacelles to remove larval tents during winter on tall trees. This method is generally reserved for the zones at high risk for the population (schoolyards, kindergardens, children playgrounds, ...). Because of the urticating properties of the larvae at this moment, it absolutely requires an individual protective equipment for the manipulators (gloves, gas mask, glasses, bodysuits; Fig. 9.2). The same approach has been attempted for the tents of the oak processionary moth.

3.2 Trapping of Larvae

A trap model to collect larvae, Ecopiège®, was developed by the firm "La Mésange Verte" (France). This trap is made of an adjustable flange surrounding the tree trunk and of a collecting bag filled with soil, connected beforehand to the flange by a tubular pipe. The trap is set on the trunk at a sufficient height to prevent any human contact with the larvae (Fig. 9.3).

The larvae are trapped during the period when their urticating properties are the most important for human and animal health. By its principle, this control technique

Fig. 9.3 Ecopiège® designed to trap larvae of pine processionary moth on a pine trunk

is original since it directly uses a behavioral sequence of the insect. Indeed, at maturity fifth instar larvae gather along the trunk to process down in Indian file to the ground where they pupate. As they arrive in the flange, they are stopped and directed into the bag filled with soil in which they dig and finally transform into pupae (Fig. 9.4). At the end of the processions, the user takes down the plastic bag containing the pupae and can incinerate or destroy it without taking any risks.

This trap must be installed on the trunk of conifers showing fully-developed winter tents in which larvae are still present and alive. Such tents show up in pure white color because the larvae are still taking care of it. This control method is particularly interesting in private gardens, public parks, and more generally for isolated trees in the areas attended by the public. Tests carried out on 22 trees on which it were installed Ecopiège® showed an effectiveness of 96.5 % in capturing larvae (Martin et al. 2012a; Fig. 9.5). Additionally, a differed mortality was observed due to the non- viability of the small- sized processions collected at tree basis (average of 4.3 larvae per procession). The method can be combined with both pheromone trapping of adults (see below) and the installation of nest boxes for tits. Indeed, after having used the other alternative methods, if there remains processionary larval tents on pines, the installation of an Ecopiège® on each tree

Fig. 9.4 Larvae of pine processionary moth going down the pine trunk at procession time and stopped at the flange of an Ecopiège®

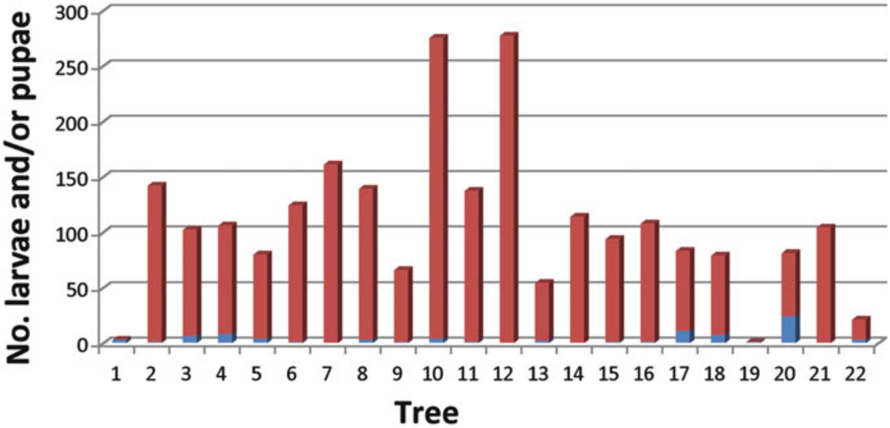

Fig. 9.5 Efficiency of the larval trapping carried out with Ecopiège® on 22 pine trees at Sarrians, Southeastern France (44,08N; 4,97E) during spring 2010. In *red*: larvae trapped per tree (2,269 in total); in *blue*: larvae having escaped from the trap (82 in total)

showing tents will make it possible to obtain a total effectiveness and thus to remove the risk related to urticating larvae.

The trapping of the processionary larvae by the Ecopiège® technique is a powerful concept for use on individual pines in parks and gardens. It has neither an environmental impact, nor a human health impact. Nevertheless, its effectiveness depends on the installation conditions. First, the trap has to be closely adjusted to the trunk surface. Slits between bark and trap must be scrupulously clogged in order to prevent larvae to escape towards the ground. Second, the Ecopièges® must be installed before the first departures in larval processions for pupation and be removed after the last processions, thus usually covering a period from January to May. In the case of areas with early processions (oceanic climate- see Battisti et al. 2014, Chap. 7, this volume), the installation of Ecopiège® must be done by mid-October and the traps must remain in place until April of the following year.

Users should be aware that the method does not limit the tree defoliation of that year or the possibility of re-infestation in the following year, in the case there are female moths flying in from the surrounding areas or emerging from the soil after prolonged diapause.

Another possible trapping method for processionary larvae consists in circling the trunk with glued bands. This technique has often been recommended to trap the larvae during the moving down along the trunk for pupal processions. However, INRA tests revealed it completely ineffective because the larvae have the ability to cross the glued band without remaining stuck.

3.3 Spraying Microbial Insecticides

Insecticidal formulations based on Btk contain an active matter made up of protein crystals as well as spores (Martin and Bonneaux 2006). In case of liquid suspensions, the support is either oily or aqueous. The effectiveness of such microbiological products is expressed most of the time in International Biological Units (UBI) per millilitre or milligram of product, which are calculated starting from the lethal dose (DL 50) obtained on a reference insect (*Trichoplusia ni*) compared to the already known DL 50 of a standard product.

The spraying of tree foliage using this Btk formulation (Fig. 9.6) aims at making larvae ingest the protein crystal when feeding on needles. Due to the action of a pH close to 10 in the gut, the crystal dissolves there, its crystalline envelope being destroyed and protoxines released. Then, these protoxines are lysed under the action of the gut proteases to a protein fragment called toxin which fixes itself on specific receptors of the intestinal wall of the insect. The subsequent perforation of the membrane wall causes a flow of electrolytes and water in the epithelial cells, finally leading to the lysis of these cells. The larva ceases feeding since the toxin starts to lyse the gut cells, and death occurs from a few to ten days later, depending on the larval stage (Fig. 9.6).

Fig. 9.6 Spraying of pine tree foliage with BtK using a pick-up truck equipped with a turbine (**a**); Dead larvae of pine processionary moth following spraying of BtK (**b**)

Degradation of Btk microbiological insecticides by UVs occurs quickly after spreading, the action only persisting for 8–12 days. Such formulations are efficient on the first four larval stages of practically all lepidopteran species, but have virtually no incidence on natural enemies. Applications against larvae feeding in spring may have a negative impact on non-target Lepidoptera, while those against the larvae of pine processionary moth in the autumn have a reduced impact.

Control sprayings using Btk should not be systematic but programmed annually as a control measure whenever the population escapes the normal limiting factors. Indeed, the opportunity of setting up other strategies of regulation will have to be considered before the decision of applying such microbial treatment, taking into account the levels of risk and damage.

3.4 Adult Trappings

In pine processionary moth, adult females attract the males by emitting a sex pheromone, called *pityolure*, which gathers several chemical compounds (for more details, see Battisti et al. 2014, Chap. 7, this volume). Trappings using a synthetic blend of this pheromone have been used since the 1980s to monitor the populations of processionary moths (Jactel et al. 2006). However, it did not bring satisfaction as a control technique at a period when public concern was looking for a maximal control efficiency whatever the means used (Démolin et al. 1993). Since a few years the environmental requirements became taken into account by large parts of the public and research could thus be redirected towards the optimization of trapping as an environment-friendly technique for the regulation of the populations of pine processionary moth.

At present, the use of large capacity traps blended with synthetic sex pheromones presently constitutes a control technique aimed at capturing massive numbers of male moths in order to significantly decrease mating probability, and thus to maintain the pest populations at a low level.

Fig. 9.7 Different types of traps used for trapping adult males of pine processionary moths using female sex pheromone

All the traps and marketed pheromones do not have the same efficiency in capturing male moths. A comparative study is in hand within the framework of the Ecophyto 2018 program in France (Fig. 9.7) (Martin et al. 2012a, b). To date, the most powerful trap in terms of captures appears to be the Procerex® trap when it is used with 1 l of water in the moth tank. Because of this constraint, this trap model is recommended for use in parks and gardens or in forests with points of water supply.

Some simple rules must be respected during trap installation in order to optimize the captures. Indeed, the location of the trap is important in order to let the pheromone diffuse and to allow flying moths first to land on the outer surface, and then penetrate into the trap tank. A trap installed within a shrub or on a tree with too abundant foliage is likely to capture much less moths. In the same way, setting up a single trap within a garden will probably have no effect on the decrease of the number of larval tents on pines located in the surroundings. A minimum of 4 traps is necessary to result in any effect even for a small surface, or 6 traps per hectare for a larger area. For trees in rows, it is recommended to install a trap every 25 m with a trap at each extremity of the row. The efficiency of the trapping design has to be surveyed by an annual counting of winter tents, making it possible to adjust the trapping device to the spatial distribution of winter tents (Martin et al. 2013).

Under these conditions, mass trapping of male moths may gradually reduce the number of pine processionary colonies through an ecological control of mating. It is still unclear, however, the cost-effectiveness of the methods especially because males can fly long distances. Very limited information is available on the use of pheromones for the monitoring and control of other species of processionary moths.

3.5 Behavioral Methods

3.5.1 Mating Disruption

Mating disruption consists in saturating the air with a large concentration in specific, synthetic female sex pheromone during male flight period in order to decrease the probability for a male to encounter any female, thus reducing the proportion of mated females and, subsequently, egg- layings.

Preliminary experiments carried out against the pine processionary moth during 2004 and 2005 were promising (Martin and Frérot 2006). Other tests were carried out in June 2008 in pine stands of Pointe d'Arçay, Western France. The treated plots were located along the seashore in order to prevent fecundated females to re-invade the treated stands. Two types of treatments were applied each on 2 plots of 10 ha. The first treatment consisted in the spraying by hydroseeding of micro-flakes impregnated with female sex pheromone at a 18 % concentration on pine trees. The other one used SPLAT technology, a gel impregnated with sex pheromone being propelled on tree trunk using paintball guns. The treatments corresponded to a total of 22.5–45 g of pheromone sprayed per hectare. Male captures by classical pheromone traps were then significantly decreased during summer in all the treated plots with regard to untreated areas. In December, the resulting number of winter tents was decreased by 2 in the plots treated with flakes with regard to untreated control but not in these treated with SPLAT (Goussard, unpublished observations). Unfortunately, Klaus storm completely destroyed the stand before it was possible to assess the final damage by processionary moths.

However, the producing companies did not develop any commercial products because of the non-carrying market at that time. Very recently, new experiments of mating disruption were led again with excellent results in terms of effectiveness. To date, public concern for control methods alternative to chemicals makes it possible to consider that this technique may emerge again as complementary control methods, respectful of the environment. Nevertheless, mating disruption requires to treat surfaces large enough to support air saturation in sex pheromone. In the small city parks as well as in the gardens, this efficiency of this technique must be evaluated and adapted if necessary.

3.5.2 Adult Repellency

A repulsive effect of the branches of birch branches and foliage on pine processionary moth infestation has been experimentally shown (see Jactel et al. 2014, Chap. 6, this volume). Methyl salicylate (MeSa), a volatile organic compound, has been isolated from plant material and proved to be active in repelling adult moths from egg-laying (Jactel et al. 2011a, b). This molecule being marketed, it was incorporated in dispensers to test the effectiveness under natural conditions. An application of 3 mg of MeSa per meter of hedge and per day made it possible to reduce by 80 % the density of larval tents in the treated hedges of maritime pine in the Landes forest (Jactel et al. 2011a, b). Tests of formulations to be used in parks and gardens of urban areas are in progress with INRA.

3.6 Biocontrol Methods

3.6.1 Favoring the Nesting of the Predatory Avifauna (*Parus* sp.)

Tits are insectivorous birds known for their important rate of predation of mature processionary larvae at fourth and fifth instars. This bird takes its food inside the tent by perforating silk with a characteristic opening of approximately 30 mm. In a few days, the tent is thus emptied of its larval content and the silk, which is not more maintained by larvae, very quickly degrades. A major advantage of these sedentary birds lies in their opportunism for food as well as for nesting sites. However, the lack of natural cavities can prevent them to establish on a site. Therefore, the offering of artificial nesting boxes adapted to this kind of bird may support nesting and thus the predation of the larvae present on the site (Fig. 9.8).

This method of biological regulation is presently tested in several French locations, which involve both urban and forest areas. Thus, in the Nature Reserve of the Sainte Victoire mountain (southeastern France), 815 tit nesting boxes were installed in 2007 on a surface of 51 ha, i.e., ca. 16 nesting boxes per hectare. The nesting boxes are controlled annually and the number of broods noted. Simultaneously, pine processionary dynamics is annually followed by estimating the number of larval tents in the plots with nesting boxes with regard to control plots without nest boxes. This site has not been treated by Btk since 2007 whereas it had been annually treated before by air sprayings for about 20 years. On this same site, pine processionary moth showed lower density than in the control area without nesting boxes. Conversely, the rate of colonization of the nesting boxes by the tits, although slow, follows a linear progression year by year since their installation during autumn 2007.

A comparison of the spatial dynamics of the pest and these of its bird predator showed that tent density of pine processionary decreased in the areas where the tits

Fig. 9.8 Promoting tit predation on pine processionary moth. (**a**) tit feeding on a processionary tent (Credit: R. Bigel). (**b**) Tit on artificial nesting boxes put on tree to support nesting

Table 9.1 Annual changes in infestation level of pine processionary moths (expressed in number of tents per hectare) from 2007 to 2013 in stands equipped with tit nesting boxes compared to control stands without nesting boxes in three locations of Southeastern France (Ventoux Mountain- 84, Sainte Victoire Mountain- 13, and Arbois- 13) (n.m.: data not recorded)

	Ventoux Mt.	Ventoux Mt.	Sainte Victoire	Sainte Victoire	Arbois	Arbois
Years	Control	Nesting boxes enriched	Control	Nesting boxes enriched	Control	Nesting boxes enriched
2007	n.m.	n.m.	n.m.	21.8	16.7	103.2
2008	n.m.	n.m.	n.m.	0.2	3.3	4.0
2009	65.2	48.6	4.2	11.4	3.3	27.2
2010	249.1	164.9	11.8	15.4	6.0	12.8
2011	31.1	21.1	2.7	2.3	6.0	8.4
2012	39.5	36.8	3.2	0.9	1.3	11.6
2013	117.5	28.1	1.7	4.1	3.3	15.2

nested and remained more or less stable in the zones where bird broods were scarce (Table 9.1). Several more years of survey will be necessary to conclude about the efficiency of the regulating effect of promoting tit predation on pine processionary infestations. In the sites attended by the public, it is important to combine this method of biological regulation with other alternative methods to reduce the risk related to the urticating larvae.

3.6.2 Massive Release of Egg Parasitoids

Egg parasitoids play a significant role in the natural regulation of processionary moth populations (Tiberi et al. 1991). Nevertheless, biocontrol using these natural enemies have been attempted but showed to be no cost-effective (Masutti et al. 1993).

At present, studies are looking at the possibility of applying egg parasitoids of processionary moth at low density of the host in order to delay the probability of outbreak, especially in high risk area or whenever the egg parasitoid populations are missing or scarce. Attention should be paid to use the local strains of parasitoids and to avoid negative impacts on non-target species. All related measures to increase the performance of parasitoids should be taken together with the introduction in order to maximize the performance (Dulaurent et al. 2011).

4 Processionary Moth Management Strategy Taking into Account Geographical Characteristics and Risks

Precise knowledge of the insect and its phenology is a *sine qua non* condition for the success of integrated strategies of biological control. Installation of larval as well as of adult traps may provide specific information which is essential for the management of each surveyed area. Although schematic, Fig. 9.9 gives an

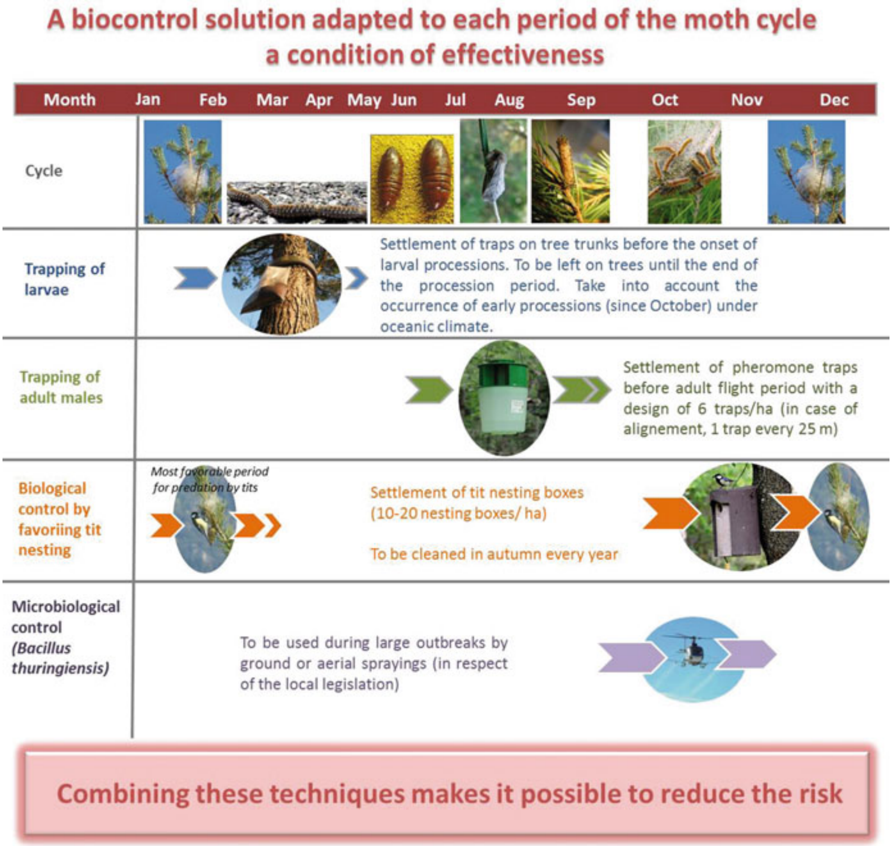

Fig. 9.9 Diagram of the management techniques to be applied at different periods of the year for an integrated control of pine processionary moths (Crédit Martin J.-C. INRA)

indication on the periods to be considered for applying control techniques with regard to the pine processionary moth life cycle according to climate.

4.1 Definition of a Risk or Tolerance Level

The tolerance level is of zero tent per tree when children are present such as in the yards of kindergardens, schools and public parks. In the same way, it is very close to zero in the semi-urban parks with high public frequentation. In such cases, a combination of several methods will be proposed.

In forests or in areas with large human frequentations for business or leisure purposes, the tolerance level is also very low; nevertheless the presence of some tents is tolerated. Alternative methods such as mass trappings of male moths can be considered when moth populations are not too large. However, aerial or ground sprayings of Btk seem the more suitable solution.

Conversely, in forests with limited human frequentation where the presence of larvae is not important, the tolerance level is much higher. In this case the management should take into account all those methods which may help the natural regulation factors to be in action.

4.2 A Reasoned Protection

Controlling pine processionary moth and/or protect humans and animals from its impact is an increasing necessity in urban areas because of the associated health problems. Conversely, humans as well as trees can usually cohabit with the insect in forests. Forest managers will have nevertheless to assess precisely the risks for the one as for the other.

A preventive management strategy applied in the urban parks and alignment trees or when settling plantations in forests can be determining to reduce the risk resulting from the presence of larval colonies. The new regulating tools for pine processionary moth using larva trapping and mass-trapping of adult moths were put at the disposal of managers as methods alternative or complementary to biopesticide (Btk) treatments. Mass-trapping of adult males can be a promising tool under certain conditions, especially when integrated with other methods. Larva trapping with Ecopiège® is a novel response to a strong demand for urban trees. However, the effectiveness of the device is directly related to the quality of its installation. These two techniques of trapping can be combined for a better effectiveness in the sectors with large public attendance, and thus of high-risk for human and pet health. Thus, in these sectors, after a moth trapping campaign during summer, it is strongly recommended to install larva traps on the trees having residual tents.

In case of very large infestations, and if adult trapping does not make it possible any more to reduce the subsequent larval populations of processionary moth, spraying formulations containing Btk will be the solution most adapted to reduce population level. The following years, trapping will maintain the populations on a tolerable level.

The installation of tit nesting boxes will facilitate the establishment of these birds and will contribute to the ecological control of moth populations. This biological control by conservation could also be combined with the trapping techniques to reduce the processionary risk.

Finally, managers of forests or parks and gardens must first evaluate the risk in order to guide the decision. The latter must be reasoned and adapted to each situation for a durable management of the forests and the protection of the humans and animals (Gatto et al. 2009). At the same time, attention has to be paid in spreading the appropriate information at all levels of stakeholders and end-users of the area subjected to control. This is an essential step for the success of any operation and for promoting the social acceptance of the proposed methods.

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