A critical read of the database of the literature on climate change resulted in surprisingly few documented examples of climate change-induced range expansion. Of course, long-term trends in the distribution and abundance of insect pests are notoriously difficult to document. Thus, it is possible that more insect pests could have responded to climate change, or are likely to do so in the near future, than can be detected in our literature search. It is also possible, however, that biological systems, including insect pests, are less sensitive to direct climate effects than previously thought (due to the buffering effects of trophic interactions). Future research needs to focus more on the mechanisms of responses to changed climate in order to understand better, and predict more accurately, the likelihood that insect pests will expand their outbreak range.

1.1 Introduction

The geographical distribution of organisms is, in principle, easy to define; namely, the area under which, at any given point, population growth is positive (e.g. Gaston, 2003). Unfortunately, in practice, species distribution areas are difficult to determine in any detail; in fact, Gaston (2009) argues that for no single species do we have a complete understanding of its distribution. Despite
these obvious difficulties, there is a pressing need to understand better the dynamics of species’ distribution, in particular when it comes to predicting the outcomes of climate change-inflicted variations in range distributions.

Insects are highly sensitive to increases in temperature because of their ectothermic lifestyle, in particular species inhabiting high-latitude environments (Deutsch et al., 2008). Several life history traits, such as survival, growth rate and voltinism, are likely to change in a warmer environment. Thus, even though we are far from understanding the details in range expansion dynamics, we would still expect climate-induced changes in life history traits to result in altered range edges under certain circumstances. Research over the past three decades has shown convincingly that such range shifts have indeed occurred for a number of taxa, with respect to latitude as well as elevation (Parmesan and Yohe, 2003; Chen et al., 2011).

For many insect taxa, range expansions are not easy to detect, simply because their presence remains undetected in habitats at the range edge, where they are likely to occur at low densities. It is not surprising, therefore, that our best understanding of range expansion following warming refers to taxa that are particularly conspicuous and of special interest to collectors, such as Lepidoptera (e.g. Mair et al., 2012). Economically important species (‘pests’) is another group for which information on range expansion is beginning to accumulate, for the obvious reason that their effects on managed ecosystems often require action. Thus, managers of agriculture and forestry increasingly are concerned with the predicted range expansions of important insect pests (e.g. Weed et al., 2013). In addition, accidental introductions of insects into novel geographic areas where they subsequently acquire pest status, i.e. become invasive (Blackburn et al., 2011), have increased in numbers during the last decades, and at least partly because of changes in climate (e.g. Robinet and Roques, 2010).

This chapter offers an update on the range expansions of insect pests in agriculture and forestry, native and alien. We summarize information from the literature where climate change has been interpreted as, or predicted to become, the driver of range expansion. We discuss the type of evidence for the expansion, ongoing or predicted to occur, and aim to classify according to its empirical nature.

1.2 Concepts and Definitions

In recent decades, much has been said about climate warming and increasing threats from insect pests to forestry and agriculture. In a very general way, such claims seem to be based on good logic; weather, and in particular temperature, does have a strong impact on insect growth and survival. However, a fair amount of these claims lack scientific support. It should be remembered that almost all insect populations are part of organism communities where trophic interactions play a crucial role. This means that extrapolating from climate-induced effects on insect individuals, or populations in isolation, to real insect populations in complex food webs must be viewed with caution.

Here, we present the state-of-the-art when it comes to understanding climate change-induced range expansion; intensified dispersal to novel geographic areas is an expected consequence of climate change. It is notoriously difficult to obtain good data on the dynamics of the distribution range of insects because of the large spatial scale, the timescale over which range changes take place and the difficulty in observing insect individuals (often at low density) that have extended outside of their previous range. The complex spatio-temporal dynamics taking place at the range edge (latitudinal and elevational) in need of consideration when determining insect range expansion are outlined schematically in Fig. 1.1.

Our interest here is on the range expansion of insect pests in forestry and agriculture, i.e. insect populations that occur at densities high enough to cause economic damage. This type of insect is likely to be discovered by managers, and scientifically reported by applied entomologists, at the
Fig. 1.1. Schematic representation of the dynamics of distribution range and effects of changes in climate. (a) Effects of changing climate on the distribution of organisms in the northern hemisphere (modified from Gorodkov, 1985). The horizontal axis represents the latitude and the vertical axis the elevation. The triangles along the horizontal line identify mountains occurring at different latitudes. The oblique lenses represent the potential range of the organism as determined by climate (both inclination and width of the lens may vary depending on the reaction norms of the individual species). The potential range may shift from south to north and from low to high elevation, and vice versa, depending on warming and cooling of the climate. Gorodkov exemplified different types of distribution that could be observed in relation to the position of the lens along the gradient, i.e. 2: montane local (endemic), 3: montane wide, 4: disjuncted plain–montane, 5: continuous plain–montane, 6: plain local (endemic). Types 1 and 7 drive to extinction. Types 4 and 5 are the most common and are associated with wider geographic distribution. (b) Spatial dynamics of hypothetical populations at the range edge (modified from Gorodkov, 1986). (c) Expected effects of climate change on the spatial occurrence of populations as detailed in b.
early stage of an expansion (a ‘true’ expansion, however, might have taken place earlier through the dispersal of pioneer insects that have remained undetected). Consequently, this means that the literature is likely to cover most of the insect pests that have expanded into novel areas. For the purpose of this chapter, we compiled a database on pest expansion by conducting keyword searches using Web of Science and by examining the literature-cited sections of the papers.

When putting together the database, we discovered very soon that the quality of the empirical support for range expansion varied substantially among publications. We classified publications reporting evidence of climate change-induced range expansion into three categories: (i) studies where recent expansion has been observed and documented, and where there are plausible causal explanations linking expansion to climate change; (ii) studies documenting recent changes in range distribution possibly associated with climate change, but with little or no mechanistic support; and (iii) studies reporting the outcomes of modelling attempts, most often in the form of species distribution models (also referred to as envelope models), with the primary aim of predicting future changes in species ranges but with little or no evidence of actual range change occurring.

One could perhaps argue that it is only the first category that presents evidence allowing conclusions about causal relationships between climate change and range expansion. For the other two categories of studies, firm conclusions about the role of climate change are more problematic. In particular, results from the third category, envelope modelling, have commonly been discussed despite the fact that the approach is entirely correlative, resting on past and expected future relationships between spatial variation in climate and species occurrence. Thus, envelope models allow predictions about potential future distributions, but whether or not these will be realized depends on a number of unknown conditions, in particular novel trophic interactions.

1.3 Database

The literature survey resulted in 50 species whose range have been observed to be affected by climate change, or predicted to be so in the future (Table 1.1). The number of species with observed range expansion and with a plausible causal explanation (Category 1) was, however, much smaller (eight cases). For 17 species, range expansions have been documented, but without clear empirical support for the hypothesized link to climate change (Category 2). For the remaining 25 species, range expansions were predicted based on modelling data (Category 3), either climate matching alone or climate matching combined with insect physiology data. Cases refer mainly to pests from the temperate and boreal region.

Category 1 includes seven forestry pests and only one agricultural pest. There are six native and two alien species. A latitudinal range expansion was observed in all species, while elevational and longitudinal expansions were also observed in four and one species, respectively. The most frequent mechanism of range expansion is reduced winter mortality in the novel areas. In the following, we summarize first the key findings for the Category 1 species, starting with the most known examples of native forest defoliating moths and bark beetles, and then proceed with other native and alien species in forestry and agriculture.

The pine processional moth (Thaumetopoea pityocampa) is one of the best examples of an insect responding to climate change, documented in a number of publications during recent years (e.g. Battisti et al., 2005; Buffo et al., 2007; Robinet et al., 2007, 2013). Increased winter temperature results in better performance of the winter-feeding larvae. The improved performance comes 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 made possible 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
**Table 1.1.** Range expansion of insect pests in agriculture and forestry.

<table>
<thead>
<tr>
<th>Category</th>
<th>System</th>
<th>Origin</th>
<th>Species</th>
<th>Host</th>
<th>Expansion Area</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Range expansion observed and mechanism known</td>
<td>Forestry</td>
<td>Native</td>
<td><em>Dendroctonus frontalis</em></td>
<td>Pinus</td>
<td>LA</td>
<td>N America Ungerer <em>et al.</em>, 1999; Trần <em>et al.</em>, 2007</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Dendroctonus ponderosae</em></td>
<td>Pinus spp.</td>
<td>E, LA, LO</td>
<td>N America de la Giroday <em>et al.</em>, 2012; Raffa <em>et al.</em>, 2013</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Dendroctonus rufipennis</em></td>
<td>Picea</td>
<td>LA</td>
<td>N America Berg <em>et al.</em>, 2006; DeRose <em>et al.</em>, 2013</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Epirrita autumnata</em></td>
<td>Broadleaves</td>
<td>E, LA</td>
<td>Europe Jepsen <em>et al.</em>, 2008; Ammunét <em>et al.</em>, 2012</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Operophtera brumata</em></td>
<td>Broadleaves</td>
<td>E, LA</td>
<td>Europe Jepsen <em>et al.</em>, 2008; Ammunét <em>et al.</em>, 2012</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Thaumetopoea pityocampa</em></td>
<td>Pinus, Cedrus</td>
<td>E, LA</td>
<td>Europe Battisti <em>et al.</em>, 2005; Robinet <em>et al.</em>, 2007</td>
</tr>
<tr>
<td>2. Range expansion observed and mechanism unknown</td>
<td>Agriculture</td>
<td>Alien</td>
<td><em>Adelge tsugae</em></td>
<td>Tsuga</td>
<td>LA</td>
<td>N America Paradis <em>et al.</em>, 2008; Fitzpatrick <em>et al.</em>, 2012</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Nezara viridula</em></td>
<td>Various</td>
<td>LA</td>
<td>Japan Musolin and Saulich, 2012; Tougou <em>et al.</em>, 2009</td>
</tr>
<tr>
<td></td>
<td>Forestry</td>
<td>Native</td>
<td><em>Malacosoma disstria</em></td>
<td>Broadleaves</td>
<td>LA</td>
<td>N America Dukes <em>et al.</em>, 2009; Lapointe-Garant <em>et al.</em>, 2010</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Matsucoccus faytaudi</em></td>
<td>Pinus</td>
<td>LO</td>
<td>Europe Burban <em>et al.</em>, 1999</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Neodiprion sertifer</em></td>
<td>Pinus</td>
<td>LA</td>
<td>Europe Virtanen <em>et al.</em>, 1996; Veteli <em>et al.</em>, 2005</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Thaumetopoea processionea</em></td>
<td>Quercus</td>
<td>LA</td>
<td>Europe Groenen and Meurisse, 2012; Meurisse <em>et al.</em>, 2012</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Zeiraphera diniana</em></td>
<td>Larix, Picea</td>
<td>E</td>
<td>Europe Esper <em>et al.</em>, 2007; Johnson <em>et al.</em>, 2010</td>
</tr>
</tbody>
</table>

*continued*
<table>
<thead>
<tr>
<th>Category</th>
<th>System</th>
<th>Origin</th>
<th>Species</th>
<th>Host</th>
<th>Expansion</th>
<th>Area</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alien</td>
<td>Agrilus planipennis</td>
<td>LA, LO</td>
<td>Fraxinus</td>
<td>N America</td>
<td>Muirhead et al., 2006</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Andricus spp.</td>
<td>LA, LO</td>
<td>Quercus</td>
<td>Europe</td>
<td>Walker et al., 2002</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Anoplophora glabripennis</td>
<td>Broadleaves</td>
<td>LA, LO</td>
<td>China</td>
<td>Smith et al., 2001; Bancroft and Smith, 2005</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cameraria ohridella</td>
<td>Aesculus</td>
<td>LA, LO</td>
<td>Europe</td>
<td>Gilbert et al., 2005</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dryocosmus kuriphilus</td>
<td>Castanea</td>
<td>LA, LO</td>
<td>Europe</td>
<td>EFSA, 2010</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lymantria dispar</td>
<td>Broadleaves</td>
<td>E, LA</td>
<td>N America</td>
<td>Liebhold et al., 1992; Régnière et al., 2009</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Phyllocoptes platanus</td>
<td>Platanus</td>
<td>LA, LO</td>
<td>Europe</td>
<td>Sefrova, 2001 in Gilbert et al., 2005</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Thecodiplosis japonensis</td>
<td>Pinus</td>
<td>LA, LO</td>
<td>Korea</td>
<td>Lee et al., 2007</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agriculture</td>
<td>Diuraphis noxia</td>
<td>Cereals</td>
<td>E, LA</td>
<td>China, EU, USA</td>
<td>Zhang et al., 2012; Ulrichs and Hopper, 2008</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Heteroptera spp.</td>
<td>Rice</td>
<td>LA</td>
<td>Japan</td>
<td>Kiritani, 2013</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Schizaphis graminum</td>
<td>Cereals</td>
<td>LA</td>
<td>Europe</td>
<td>Harrington and Woowd, 2007</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alien</td>
<td>Liriomyza huidobrensis</td>
<td>Various</td>
<td>LA</td>
<td>Europe</td>
<td>Cannon, 1998</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. Range expansion predicted based on models</td>
<td>Choristoneura fumiferana</td>
<td>Abies, Picea</td>
<td>E, LA</td>
<td>N America</td>
<td>Candau and Fleming, 2011; Régnière et al., 2012</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dendroctonus rhyzophagus</td>
<td>Pinus</td>
<td>E, LA</td>
<td>N America</td>
<td>Smith et al., 2013</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lymantria monacha</td>
<td>Conifers</td>
<td>LA</td>
<td>Europe</td>
<td>Vanhanen et al., 2007</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tomicus destruens</td>
<td>Pinus</td>
<td>E, LA</td>
<td>Europe</td>
<td>Horn et al., 2012</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tomicus piniperda</td>
<td>Pinus</td>
<td>E, LA</td>
<td>Europe</td>
<td>Horn et al., 2012</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alien</td>
<td>Corythucha ciliata</td>
<td>Platanus</td>
<td>LA</td>
<td>China</td>
<td>Ju et al., 2013</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agriculture Native</td>
<td>Chilo suppressalis</td>
<td>Rice</td>
<td>LA</td>
<td>Japan</td>
<td>Morimoto et al., 1998</td>
<td></td>
<td></td>
</tr>
<tr>
<td>-------------------</td>
<td>-------------------</td>
<td>------</td>
<td>----</td>
<td>-------</td>
<td>----------------------</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conotrachelus nenuphar</td>
<td>Prunus</td>
<td>LA</td>
<td>USA</td>
<td>Ulrichs and Hopper, 2008</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cydia pomonella</td>
<td>Malus</td>
<td>LA</td>
<td>Europe</td>
<td>Rafoss and Saethre 2003; Svobodová et al., 2013</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Helicoverpa spp.</td>
<td>Various</td>
<td>LA, LO</td>
<td>Australia, USA</td>
<td>Zalucki and Furlong, 2005</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Helicoverpa zea</td>
<td>Various</td>
<td>LA, LO</td>
<td>USA</td>
<td>Ulrichs and Hopper, 2008</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leptinotarsa decemlineata</td>
<td>Solanaceous</td>
<td>LA</td>
<td>EU, USA</td>
<td>Ulrichs and Hopper, 2008</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lobesia botrana</td>
<td>Vitis</td>
<td>LA</td>
<td>Europe</td>
<td>Svobodová et al., 2013</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ostrinia nubilalis</td>
<td>Maize</td>
<td>LA</td>
<td>Europe, USA</td>
<td>Cannon, 1998; Svobodová et al., 2013</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plutella xylostella</td>
<td>Crucifers</td>
<td>LA</td>
<td>N America, Japan</td>
<td>Cannon, 1998; Morimoto et al., 1998</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhopalosiphum padi</td>
<td>Cereals</td>
<td>LA</td>
<td>Europe</td>
<td>Svobodová et al., 2013</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sitobion avenae</td>
<td>Cereals</td>
<td>LA</td>
<td>Europe</td>
<td>Svobodová et al., 2013</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tribolium confusum</td>
<td>Flour</td>
<td>LA</td>
<td>Japan</td>
<td>Morimoto et al., 1998</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alien Bactrocera oleae</td>
<td>Olea</td>
<td>LA</td>
<td>USA</td>
<td>Gutierrez et al., 2009</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ephesia kuhniella</td>
<td>Flour</td>
<td>LA</td>
<td>Japan</td>
<td>Morimoto et al., 1998</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oulema melanopus</td>
<td>Cereals</td>
<td>LA</td>
<td>Europe</td>
<td>Svobodová et al., 2013</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pectinophora gossypiella</td>
<td>Cotton</td>
<td>LA</td>
<td>USA</td>
<td>Gutierrez et al., 2006</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phthorimaea operculella</td>
<td>Solanaceous</td>
<td>LA</td>
<td>World</td>
<td>Kroshel et al., 2013</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Solenopsis invicta</td>
<td>Various</td>
<td>LA</td>
<td>USA</td>
<td>Ulrichs and Hopper, 2008</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tetranychus evansi</td>
<td>Solanaceous</td>
<td>LA</td>
<td>World</td>
<td>Meynard et al., 2013</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: expansion type – E = elevational; LA = latitudinal; LO = longitudinal.
resulted in a progressive colonization of areas outside of the core range. Furthermore, moth mobility has also been found to be favoured by the increase in temperature; 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 further contributed to the dispersal and has resulted in the establishment of populations outside of the historic range (Robinet et al., 2012, 2013). Novel host tree species encountered during the expansion are suitable for larval development (Stastny et al., 2006), and thus it seems likely that range expansion will continue as long as temperature will increase. At the southern edge of the distribution range, in northern Africa, *T. pityocampa* is expanding in native mountain stands of cedar (*Cedrus atlantica*), threatening these endangered ecosystems (Sbabdji and Kadik, 2011), while it remains stable in the low-elevation stands of Aleppo pine (*Pinus halepensis*) facing the Sahara desert (Zamoum and Démolin, 2005).

Bark beetles (*Dendroctonus spp.*) in North America have been discussed extensively in relation to climate change (e.g. Weed et al., 2013). Several *Dendroctonus* species have been proposed to be potential threats to forestry in novel areas (Bentz et al., 2010), but the mountain pine beetle, *Dendroctonus ponderosae*, is by far the best-studied one for which there is evidence of an ongoing expansion. It seems clear that increased temperatures have made it possible for the beetle to survive winter in geographical areas previously unsuitable; for example, expansion has been documented to occur in Canada, both northwards in British Columbia and westwards into Alberta (Carroll et al., 2006). The mountain pine beetle has also dispersed into higher mountainous areas not previously inhabited (Raffa et al., 2013). The expansions have been possible because potential host trees grow outside its historic range (Bentz et al., 2010). Outbreaks of the mountain pine beetle result in extensive tree mortality; the latest outbreak in central Canada has been of a magnitude not previously recorded, affecting more than 15 million hectares (Mha) of pine forests (mainly lodgepole pine, *Pinus contorta*) (Kurz et al., 2008). Predicted increased temperatures, leading to higher winter survival of larvae, are expected to enable expansion into areas historically not occupied, including boreal Canada, where a host shift to Jack pine, *Pinus banksiana*, seems likely to occur (Erbilgin et al., 2014). However, it is essential for the mountain pine beetle, and many other bark beetle species, to achieve synchronized population emergence in order to mass attack host trees successfully; modelling results indicate that as summer temperatures increase in potential novel areas (e.g. eastern USA), the timing of emergence could be disrupted, and thus affect population growth negatively and decrease the risk of outbreaks (Bentz et al., 2010).

The northward expansion of the southern pine beetle, *Dendroctonus frontalis*, has been linked to improved conditions for overwintering beetles, either larvae or adults, based on physiological threshold (lower lethal temperature) and climate predictions (Ungerer et al., 1999; Williams and Liebhold, 2002). The link between increased temperature and damage has been explored by Trân et al. (2007), resulting in a positive effect mainly in the northern expansion area, while the core populations do not seem to respond strongly to temperature variation. Waring et al. (2009) have developed a phenological model predicting more generations per year as a consequence of temperature increase, although it is not clear whether the change has resulted in more expansion or pestilence. Recently, Weed et al. (2013) reported range expansion in New Jersey, which is associated with the overcoming of thermal thresholds and with large damage to forest stands.

An elevational shift of the spruce bark beetle, *Dendroctonus ruficollis*, has been hypothesized in Engelmann spruce (*Picea engelmannii*) forests of north-central USA, based on a bioclimatic model (DeRose et al., 2013). Both winter and summer temperature increases seem able to promote population growth and expansion outside of the
core range, although stand traits such as stand basal area and frequency of spruce trees can be as important as abiotic factors in affecting beetle performance. Berg et al. (2006) have shown that high summer temperatures are responsible for the outbreak range expansion of this species in Alaska and Yukon.

The autumnal moth (Epirrita autumnata) and the winter moth (Operophtera brumata) feeding on mountain birch (Betula pubescens), at the northern edge of their ranges in Scandinavia, have recently been reported to be affected by climate change (Jepsen et al., 2008). For both species, it has been shown that the outbreak range has shifted. O. brumata has experienced a pronounced north-eastern expansion into areas previously dominated by E. autumnata outbreaks, whereas the latter has expanded into the coldest, most continental areas. The hypothesized mechanism involves the increase in winter temperature, leading to higher survival of overwintering eggs (Jepsen et al., 2008).

There are two examples of climate change-induced range shifts among sucking insects. The hemlock woolly adelgid (Adelges tsugae) has extended its distribution range into north-eastern USA from the site of introduction in Virginia (Evans and Gregoire, 2007; Paradis et al., 2008). The limiting factor is winter temperature, which can be lethal for the overwintering stages (Paradis et al., 2008). With the increase in mean minimum winter temperature, the aphid has expanded progressively to the north and simultaneously built up high density in the already colonized areas, contributing greatly to hemlock dieback (Fitzpatrick et al., 2012). In this case, the temperature-dependent spreading occurs from the south to the north, leaving behind dead trees on which the insect cannot persist. The green stink bug (Nezara viridula) in Japan is progressively occupying areas located outside the historic northern edge of the range, because of more favourable winter temperature for the adults (Musolin and Saulich, 2012). Interestingly, the expansion has resulted in a displacement of a native bug of the same genus (Nezara antennata) (Tougou et al., 2009).

In Category 2, the forest pests are also predominant (13 species out of 17). Eight species are native and nine alien. Again, the latitudinal range expansion is the most common (15 species), alone or combined with elevational and longitudinal expansion. The most commonly suggested mechanisms refer to the effect of increased temperature on insect physiology. In several native species of defoliating and sap-sucking insects, an outbreak range expansion has been observed at the northern edge, whereas in other species, such as the larch bud moth, Zeiraphera diniana (Johnson et al., 2010), and the gypsy moth, Lymantria dispar (Liebholt et al., 1992; Régnière et al., 2009), the outbreak area has shifted to higher elevation. For alien species, a faster developmental rate has been observed in the emerald ash borer, Agrilus planipennis (Muirhead et al., 2006), a faster dispersal in the gall wasps (Walker et al., 2002; Gilioli et al., 2013) and in the Asian longhorn beetle, Anoplophora glabripennis (Smith et al., 2001; Bancroft and Smith, 2005), increased volitism in leaf miners (Cannon, 1998; Gilbert et al., 2005) and better winter survival in pine gall midges (Lee et al., 2007).

In Category 3, the agricultural pests are more frequent (19 species out of 25). Seventeen species are native and eight are alien. Latitudinal range expansion is predicted for all species, and for some of them is combined with elevational and longitudinal expansion. All cases are based on the envelope model, but in three species there is a plausible link with insect physiology. Specifically, Régnière et al. (2012) predict a northern and upward shift of the outbreak area of the spruce budworm Choristoneura fumiferana, in North America, because of improved overwintering conditions for the larvae and the suitability of susceptible host plants. Gutierrez et al. (2006) predict that, with winter warming, the cumulative negative effect of low temperature on the diapausing larvae of the cotton bollworm would be lower, allowing a faster colonization of the Central Valley in California. Gutierrez et al. (2009), however, suggest that the range of the olive fly, Bactrocera oleae, will retracted in the south and expand in the north part of
the range, both in North America and in Europe, due to the effect on the adult flies of high temperature during summer and a milder winter, respectively. Based on the response of native *E. autumnata* and invasive *O. brumata* to winter temperature, Ammuntet *et al.* (2012) predict the likely expansion of another birch geometrid species, *Agriontis aurantiaria*, which is currently more limited by temperature than the other geometrid species but could become invasive if conditions become more permissive. The sycamore lace bug, *Corythucha ciliata*, an invasive species in southern China, does not seem to be limited in its expansion to the south as long as the temperature is lower than 43°C, as shown by heat-shock treatments carried out in the laboratory on local genotypes (Ju *et al.*, 2013). Finally, both cosmopolitan (*Helicoverpa armigera*) and local (*Helicoverpa punctigera*) corn earworms do respond well to weather fluctuations in Australia. Zalucki and Furlong (2005) relate the pheromone-trap catch with rainfall pattern in the area of origin, indicating that a change in climate associated with a change in the precipitation regime may affect the range occupied by migratory moths, although this can have a limited effect in time.

**1.4 Discussion and Conclusions**

The range edge is characterized by strong dynamics, as illustrated in Fig. 1.1. An expansion of the distribution range of an insect pest thus needs to be manifested as the permanent establishment outside of the area of historic distribution. It is not possible to come to any firm conclusions about permanent occupancy, unless the expansion of the range edge is sufficiently large. The cases that we list as evidence of real expansions (Category 1) seem to meet such a criterion. It might come as a surprise that we have not considered more than eight species to show climate change-induced range expansion. It has been implied that many more insect pests have expanded their range (referred to as Categories 2 and 3). It is possible that these species will indeed expand in the future, as predicted, but there is presently insufficient empirical support for this yet to have occurred. It is interesting that there are almost no signs of retraction of the distribution range of insect pests (at low latitudes and elevations), seemingly in contrast with other insect groups such as certain Lepidoptera (Thomas *et al.*, 2006). Whether or not this is a real difference, and if so for what reason, is difficult to determine because little is known about retraction dynamics. We note, however, that the host plants of insect pests are managed by humans, sometimes intensively, and this could result in insect pests having a better chance to tolerate suboptimal weather conditions in the putative retraction area; for example, due to a surplus of habitats offering a variety of microclimates. A possible example is *T. pityocampa*, which is well established at its southern range in the large afforestation belt in front of the Sahara desert in southern Algeria (Zamoum and Déomlin, 2005).

From a management point of view, it is of utmost importance to understand whether or not a range expansion of a particular insect pest will also lead to this insect becoming a pest in the novel area, and if so, whether the dynamics will be similar to that in the historic range (e.g. with respect to outbreak frequencies and magnitudes). Very little is known about this. Climate-induced range expansion in *T. pityocampa* is indeed associated with outbreaks in the newly colonized areas; however, the population dynamics seem to be determined more by endogenous than by exogenous (i.e. weather) factors (Tamburini *et al.*, 2013). In spite of the evidence of outbreak range expansion by *O. brumata* at high latitudes (Jepsen *et al.*, 2008), Tenow *et al.* (2013) have not found evidence of changed population dynamics (periodicity of travelling waves) of this geometrid across Europe during the past 60 years, a period with documented increases in temperature. The expansion of tree-killing insect species (e.g. mountain pine beetle) is an interesting special case because their activity often results in large areas of dead trees (Raff a *et al.*, 2013), thus offering unsuitable habitats for future generations;
this can result in a further expansion simply because of lack of suitable resources.

Accidental introductions of non-native organisms (alien species) do not always lead to them being invasive (Tobin et al., 2011), i.e. becoming established as economically important pests (Blackburn et al., 2011). In cases where alien species do expand their distribution range from the point of introduction, their successful establishment is assumed to be favoured by changes in climate (e.g. Robinet and Roques, 2010). There are good reasons to suspect that climate change has contributed to insect species becoming invasive, although our database does not give unequivocal support for this suggestion; for example, we found no more than two species in Category 1. It will be interesting to see if alien species already established might colonize the colder parts of the potential habitat at the same rate, assuming that temperature might limit their performance. Because expansion rates associated with climate change are in the lower part of the interval available for accidentally introduced aliens (Liebhold and Tobin, 2008) and aliens released for weed control (Paynter and Bellgard, 2011), it seems likely that temperature is still limiting the expansion potential. We may thus predict that climate change will facilitate the further establishment of alien species in the potential habitat.

The range expansion of insect pests, and their associated outbreaks, includes two main features – population growth and dispersal. Thus, the source population in the historic range needs to have a density high enough in order for enough dispersing insects to leave the core area successfully, a recent example being the mountain pine beetle dispersing eastwards and northwards from its outbreak in central British Columbia (de la Giroday et al., 2012). Furthermore, the successful dispersal hinges on the organism's dispersal capacity and the suitability of habitats beyond its historical range, e.g. T. pityocampa in the Italian Alps (Battisti et al., 2006). Finally, given that newcomers successfully arrive at the novel location, they must occur in enough numbers to establish a reproducing population there (Allee effect; Tobin et al., 2011). Although these three processes are likely to be identical for most insect species, the nature of the establishment of a reproducing population is particularly interesting for the present discussion; the environmental factors prevailing in the novel locations will determine whether or not the pest in the historical range will also reach pest status in the new location. Obviously, all the species in Category 1 are examples of this. For species in the other two categories, this is much more difficult to know. In particular, because predictions from envelope models are based entirely on climatic correlations in present ranges, it is virtually impossible to know whether or not populations in the new range will reach pest status (for example, due to biotic resistance in the new habitat). It should be noted also that new host plants can be encountered during the expansion, and sometimes result in host shifts (Clark et al., 2014), and this may affect both the insect pest and its natural enemies, with population consequences difficult to foresee (e.g. Raffa et al., 2013).

To conclude, as has been suggested repeatedly in the literature, because of their ectothermic lifestyle, it is reasonable to assume that a changed climate will have consequences for insect pest distribution and abundance. A critical read of the scientific literature, however, results in surprisingly few documented examples of climate change-induced range expansion. It should be remembered that long-term trends in the distribution and abundance of insect pests is notoriously difficult to document. Thus, it is possible that many more insect pests could have responded to climate change, or are likely to do so in the near future, than can be detected in the databases presently available. It is also possible, however, that biological systems, including insect pests, are less sensitive to direct climate effect than previously thought (due to the buffering effects of trophic interactions). We believe that both explanations apply. It is also likely that pest responses to climate change are individualistic (Lawton, 2000). Thus, future research needs to focus more on developing process-based understanding of
responses to changed climate (Schurr et al., 2012) in order to understand better, and predict more accurately, the likelihood that insect pests will expand their outbreak range.

Acknowledgements

We warmly thank Jorge M. Lobo and Dmitri Musolin for providing literature items. The manuscript benefited from comments by two anonymous reviewers. The work was supported by the EU Seventh Research Framework Program (FP7) project BAC-CARA (Biodiversity and Climate Change – A Risk Analysis. Grant No 226299).

References


Climate Change and Insect Pest Distribution Range


