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Title: Climate Change Effects on Agricultural Insect Pests in Europe

Year: 2015

Version:

Please cite the original version:

Lindström, L., & Lehmann, P. (2015). Climate Change Effects on Agricultural Insect Pests in Europe. In C. Björkman, & P. Niemelä (Eds.), Climate Change and Insect Pests. CABI. CABI Climate Change Series, 7.
<https://doi.org/10.1079/9781780643786.0136>

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C Björkman and P Niemelä (eds). 2015. Climate Change and Insect Pests, CABI Climate Change Series.
<http://www.cabi.org/bookshop/book/9781780643786>

Chapter 8 Climate change effects on agricultural insect pests in Europe

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Abstract

In this chapter we will discuss observations of climate change effects on agricultural pests in Europe, the possible mechanisms behind these observed effects and finally delve into more detail through some, relatively well studied model species (the Colorado potato beetle and the rape beetle). Direct effects of climate change on agricultural pests in Europe are difficult to dissect from all the human induced changes that have taken place in parallel with an increased mean annual temperature. During the last decade agriculture has become more professionalized in terms of land use, crop cultivation techniques and pest management strategies. We review the effect of climate change on agricultural pest by comparing the speed of range expansion of pest species to non-pest species. It seems that the poleward range shift has been faster for pest than non-pest species. We partly attribute this to the globalization of agriculture as human assisted movement has broken many natural dispersal barriers. Since the biology of many pest species is relatively poorly studied, direct conclusions on how climate change has affected biological processes of pests are challenging to make.

Keywords: Coleoptera, range expansion, diapause

Chapter 9 Climate change effects on agricultural insect pests in Europe

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1. Introduction

While climate change scenarios for European agriculture suggest both positive and negative effects, the net effects are calculated to be negative (Hyvönen 2011; Hoyer et al. 2013; Challinor et al. 2014). The effects depend on location and future scenarios vary largely for different parts of Europe. In northern Europe mean temperatures are increasing (especially during winter and spring) and thus the immediate effects of climate change could be positive due to a prolonged growth season length (Myer et al. 1997). Similarly the predicted increase in air CO₂ and temperature can boost plant growth if necessary water, nutrients and pest control is available (Ward et al. 1999). Indeed, in many countries, such as Finland, increasingly shorter development times of various crops have been documented during the last 50 years (Peltonen-Sainio and Hakala 2014). In southern Europe, in turn, temperatures have been suggested to increase even more than the estimated average mean global temperature increase (Carraro and Sgobbi 2008; IPCC 2013). When this is accompanied with an increased frequency and severity of heat waves and decrease in precipitation, the end result may be an increase of desertification rather than an increase of agricultural productivity.

Similarly as for plants, growth season length and thermal stress are amongst the most important factors limiting ranges also in many arthropods (Addo-Bediako et al. 2002). Therefore we can ask: what are the major predictions of climate change responses of European pests. A longer, warmer growth season is expected to affect pests through increasing the time available for development and growth, provided that also hosts or prey are available, or put another way, provided that the pests have been temporally restricted previously (Bale et al. 2002). Depending on the life history strategies of the pest, signs of climate change effects could be variable (see e.g. Musolin 2007; Kingsolver et al. 2011) and expected for instance in development time (Boman et al. 2008), voltinism (the number of

annual generations) (Altermatt 2010) and the duration of the reproductive period (van Asch et al. 2013). These changes in life history traits can have population consequences and lead to increased population sizes or enlarging or alternatively, shifting, ranges (Gaston 2003; Bebber et al. 2013; Bacon et al. 2014). On the other hand increased temperatures may also allow host plants to be able to better protect themselves against herbivory (DeLucia et al. 2012), which again can reduce pest population sizes. Additionally most major agricultural pest species are under continuous surveillance and actively controlled by humans when needed and therefore might not be able to fully utilize the benefits of temperature increase and climate change.

In the present chapter we aim to summarize observed effects of climate change on important agricultural insect pests in Europe. Many pests exist in complex, often non-natural conditions in agricultural systems. Climate change is expected to influence both the agricultural systems as well as the pests in both indirect and direct ways. Therefore it can be challenging to show a causal connection between climate change and pest species biology. For the purposes of simplicity we will divide climate change into both climatic effects (e.g. temperature, humidity), and anthropogenic effects, which mainly are responses to climate change (changes in agricultural practices, land use, human population sizes, transport pressure). Of these, direct climatic effects are more studied. In this chapter we will discuss: the basis of the observation of climate effect, the possible mechanisms behind these observed changes and finally delve into more detail through some, relatively well studied model species.

2. Observed increase in pest introductions and range shifts towards the poles

Due to the negative impact pest species generally have on agriculture there is an acute interest to monitor and restrict the spread of pest species as well as to influence their population dynamics. However, although many governmental and agricultural officials keep records (e.g. Vänninen et al. 2011; Genovesi and Scalera 2011; Hyvönen 2011) of pest species in a given country and EPPO (The European and Mediterranean Plant Protection Organization) keeps a record of new introductions of many pests to Europe, systematic record keeping is fairly recent. This makes it hard to estimate the effect of climate change on European pests over long periods of time. Furthermore, the majority of existing literature on climate change effects actually consists of predictions rather than observations (Cannon

1998; Dupin et al. 2011; Aragón and Lobo 2012; Kroschel et al. 2013; Maiorano et al. 2012; Stöckli et al. 2012; Jönsson et al. 2013; Bacon et al. 2014).

At the same time as changes in climate have taken place during the last 100 years (IPCC 2013), agricultural practices have changed and become more professionalized. The productivity of agriculture has increased due to the increase in plant breeding programs, fertilizer use and organized pest management monitoring and control. In Europe there has been an organized plant protection practice since the establishment of EPPO in 1951. This means that there has been an early alert system as well as organized quarantine practices for many pest species. This might have hindered pest species to respond to changes in climate and invade new areas unnoticed. However, within the last 30 years, in parallel with temperature increase, globalization and the associated large up-scaling in trade has broken the natural dispersal barriers of many species (see e.g. Lebarbenchon et al. 2008). All these changes have happened at the same time and disentangling effects due to changes in climate from the other changes is extremely difficult.

According to the latest assessment by the IPCC, mean annual temperatures have increased by approximately 0.85°C during the last 100 years and will continue to increase under all envisioned climate change scenarios (IPCC 2013). The observed increase in temperature has resulted in range enlargements or shifting of the entire range towards higher latitudes or altitudes in many non-pest species (Parmesan et al. 1999; Walther et al. 2002; Chen et al. 2011). The speed of climate change-dependent range shifts vary depending on the species group as well as the time investigated (see Table 9.1; Hickling et al. 2006; Bebber et al. 2013). The first estimates of range shifts of several non-pest species suggested that the speed has been on average 6.1 km per decade (Parmesan and Yoche 2003) whereas recent estimates, at least for butterflies, suggest a 10 times faster speed (e.g. Pöyry et al. 2009). For non-pest butterfly species in northern Europe, dispersal ability together with habitat availability has been suggested to play major roles in the observed range expansions (Pöyry et al. 2009). This and other studies highlight that species life-history traits are imperative to consider when assessing their capacity to respond to climate change (Saikkonen et al. 2012; Breed et al. 2014; Mair et al. 2014). While most studies on responses to climate change have focused on non-pest species, these results may be used as tools to estimate effects also for the numerous pest species (Bebber et al. 2013).

Table 8.1 Average range shifts of both pest and non-pest insect species collected from various meta-analyses published during the last decade. The observation time (as recorded in the given literature) and the rate of range shifts (kilometres/year, $\pm$ standard error of mean) within the observed time period. The number of species is given in the brackets.

	Pest species		Non-pest species			
Observation time	ca.1920-2010	1960-2010	ca.1965-1990	1992-2000	ca.1920-2000	Variable
	Rate ¹	Rate ¹	Rate ²	Rate ³	Rate ⁴	Rate ⁵
	km/a ± SE (sp)	km/a ± SE (sp)	km/a ± SE (sp)	km/a ± SE (sp)	km/a ± SE (sp)	km/a ± SE (sp)
Coleoptera	7.61 ± 1.87 (70)	12.21 ± 4.33 (70)	2.48 ± 0.43 (86)			
Diptera	3.11 ± 2.48 (24)	3.95 ± 6.08 (24)				
Hemiptera	6.13 ± 3.25 (47)	13.71 ± 5.32 (47)				
Hymenoptera	4.60 ± 9.48 (6)	8.11 ± 11.64 (6)				
Isoptera	19.62 ± 10.83 (1)	-7.51 ± 13.89 (1)	7.49 ± 1.75 (48)			
Lepidoptera	8.00 ± 2.71 (36)	17.78 ± 8.58 (36)				
Neuroptera						
Odonata						
Orthoptera						
Thysanoptera	7.68 ± 4.36 (3)	1.06 ± 9.31 (3)	1.76 ± 0.46 (29)			
OVERALL		2.7 ± 0.8 (600)	1.76 ± 1.16 (6)			
			4.16 ± 0.68 (20)			
			1.36 ± 0.32 (22)			

1 Bebbier et al. 2013, Estimates based on CABI records

2 Hickling et al. 2006, Estimated from different UK species, times vary

3 Pöyry et al. 2009, Estimated from Finnish butterflies

4 Parmesan & Yoche 2003, Includes also birds, herbs and butterflies

5 Chen et al. 2011, Based on several published meta-analysis

The range shifts of pest species has been recently estimated from 612 species including fungi, bacteria and viruses in addition to arthropods by Bebbber et al. (2013). This study shows a poleward shift of pests which is 27 km per decade since the 1960s and therefore it seems that range shifting has been significantly faster in pest species than for non-pest natural arthropods (Table 9.1). So can agricultural pests respond to climate change faster than non-pest species? To dissect the effect of climate change on the range expansion of many pest species from other anthropogenic effects, such as land use (Kalnay and Cai 2003) or human assisted movement (Smith et al. 2007) is, like stated, challenging. During the last 100 years, massive changes in agricultural policies and other anthropogenic factors have taken place. These include, pesticide use together with quarantine regulations (see Bacon et al. 2014), which should both hinder pest range shifts due to constant control of pest population size. On the other hand, the transport of goods in turn has increased the interconnectivity of the globe which should increase the rate of range expansion of many pathogens and pests (Lebarbenchon et al. 2008) due to enhanced propagule pressure (Mack et al. 2000; Tatem & Hay 2007). Indeed, it has been shown that the ornamental plant trade is one major contributor to the introduction of new plant pest to European countries (Smith et al. 2007). This is probably because an increase in trade elevates propagule pressure and makes introductions more frequent. In Great Britain 70 % of pest species established since 1970 have been estimated to be assisted by humans while only 30 % managed to establish on their own (Smith et al. 2007). Similarly EPPO records show that there is actually an increase of new pest records in Europe (Figure 9.1), although it is unknown whether this is related to the changes in climate or changes in human transport (EPPO 2013a).

An additional problem is that the same pest species are imported from several places at the same time. This can be illustrated with an example of a quarantine pest, the Silverleaf whitefly, *Bemisia tabaci*. In 2013 alone, a significant number of *B. tabaci* individuals were detected in imported vegetable and ornamentals shipments in the United Kingdom. These individuals were brought to the UK from 14 countries from four continents (EPPO 2013a; Figure 9.2) which could result in that the introduction site harbours higher genetic variability than any of the original or native sites (Kolbe et al. 2004). This is part of the reason why for instance tree nurseries in Europe can act as gateways for many plant pathogens in Europe (Santini et al. 2013). Seedlings are brought to nurseries from various parts of the globe together with their plant pathogens. In the nurseries it is therefore possible that different disease strains meet and hybridize, resulting in high genetic variability of the plant pathogens.

When these seedlings are then sold to various parts of Europe the pathogens are exported to large areas. Although we will observe a shift in ranges of these pathogens or pests, this is not necessarily due to climate change but rather due to the human activities in the 21st century. As an aside, forest pathologists have formulated “the Montesclaros Declaration”, which states that: “*We thus propose a phasing out of all trade in plants and plant products determined to be of high risk to forested ecosystems but low overall economic benefit*”(see Santini et al. 2013).

3. Can changes in winter biology explain changes in pest biology?

Winter temperatures are predicted to be more strongly influenced by future climate change than summer temperatures (IPCC 2013). Since winter abiotic and biotic conditions are major factors governing arthropod biology in Europe, less severe and shorter winters in the future could have a major impact on pest species population and range dynamics (Bale and Hayward 2010). In a recent study the range shifts in non-pest butterflies in Finland were found to relate to the stage in which the species overwinter (Pöyry et al. 2009). Species which overwinter as adults were found to have expanded their ranges at a higher rate than those that overwintered in other stages. This could be related to the fact that adults more easily can prepare for winter, for instance through microhabitat selection, or it is easier for adults to adapt to changes in the photoperiod (Lehmann et al. 2012; Saikkonen et al. 2012).

Although seasonal temperature averages and fluctuations are predicted to change in the future, photoperiodic cycles will remain the same. As Europe is located in the temperate, seasonal zone, any species invading to Europe or which can expand its range in Europe should also be able to adapt to the changing relationship between photoperiod and season. In temperate zones both the life-cycle of arthropods, as well as their hosts, are generally governed by large seasonal fluctuations (Tauber et al. 1986). The season can be characterized by a division into two phases, where summers constitute the active and winter the non-active phase. This means that the species, which responds to changes in temperature by invading northwards, have to be able to synchronize their life cycle with the new local seasonal cycle (Bradshaw and Holzapfel, 2001; Bradshaw et al., 2004). For arthropods the observed range shifts have been attributed to a release of thermal stress (Ammunét et al. 2012) as well as seasonal re-synchronization of life-history (Gaston 2003; Bean et al. 2012; Saikkonen et al.

208 2012). This may require adaptive changes and ultimately the range shifts are then dependent
209 on the genetic variability within the species (e.g. Piironen et al. 2011).

210
211 To highlight some recent research and observations on insect pest species in Europe, we
212 chose to investigate beetles (Coleoptera) in more detail. Beetles are among the most diverse
213 insect taxa and several important pests are beetles, most notably in forestry, but also in agri-
214 and horticulture (Bebber et al. 2013). These include, for instance, the Colorado potato beetle
215 *Leptinotarsa decemlineata* (Alyokhin 2009) and the Western Corn rootworm *Diabrotica*
216 *virgifera* (Dupin et al. 2011). Table 2 lists some of the most important beetle pests found in
217 agri- and horticultural systems in Europe (Bebber et al. 2013). As can be seen the best
218 represented families are Curculionidae (true weevils or snout beetles), Cerambycidae
219 (longhorn beetles) and Chrysomelidae (leaf beetles). Of these insects, 26 feed primarily on
220 wood, 11 on soft plant tissue (including leaves, fruits, flowers, tubers) and 1 is carnivorous.
221 The majority (78 %) of these beetles have a dedicated overwintering stage, which in 72 % is
222 the adult stage. Interestingly, comparing ranges of beetle pests found in Europe with beetle
223 pests whose ranges do not include Europe (listed in Bebber et al. 2013) reveals that pests
224 whose range includes Europe are found over a larger latitudinal range (mean = 77.6°, SEM =
225 6.2) than those whose range excludes (mean = 55.0°, SEM = 4.5) Europe (two-tailed t-test:
226 $t_{66,2} = 2.43$, $P = 0.018$). This could indicate a sampling bias, since European (together with
227 North American) countries generally use more resources to track and report pest movements
228 (e.g. EPPO, NAPPO etc.), but the involvement of some biological mechanisms cannot be
229 ruled out.

230
231 While some species clearly have enlarged their ranges during the last 100 years, there are
232 several examples of beetle species which have not seemingly responded through range shifts
233 or changes in population dynamics (voltinism, population size). In fact, of the 37 beetle
234 species occurring in Europe which were studied by Bebber et al. (2013) only 2 showed a
235 significant range expansion or shift since 1960, while the absolute majority showed no
236 significant shift (Table 9.2). Since temperatures have increased, growth season become
237 longer and the winter shorter, the majority of species have likely not been restricted by
238 temperature previously, but more likely by other factors which are temperature-independent,
239 such as for instance pesticide use. Therefore it is important to consider the difference between
240 climatic unsuitability and invasion dynamics when trying to estimate whether species occur
241 where they do due to climate change. For example, as stated by Dupin et al. in their study

242 (2011): “*Only presence data (ed. of Diabrotica virgifera) were considered in Europe as the*
243 *range of the pest is still expanding and hence absences from this region may not be an*
244 *indication that the climate is unsuitable.*”
245

Table 8.2 Major coleopteran pests found in Europe with some of their important biological traits. Data was gathered from EPPO and CABI. A generalist species is defined as a beetle with over 5 host plant species. Latitudinal range was estimated based on Bebber et al. (2013). Some species are less well studied, and a question mark denotes that uncertainty exists regarding that particular trait or that references are contradictory. Two species, (*Agrilus planipennis* and *Rhynchophorus ferrugineus*), have significantly enlarged ranges due to climate change according to Bebber et al. (2013). All species occur in outdoor fields except for *Scyphophorus acupunctatus* which is limited to greenhouses, and some species which occur both in outdoor fields and greenhouses (marked with a * after the species name).

Species	Family	Origin	Horti- (H) or Agricultural (A)	Feeds on wood	Generalist (G) or specialist (S)	Overwinters in diapause	Overwintering stage	Latitudinal range (°) ^A	Number of references in WoS ^B
<i>Acanthoscelides obtectus</i> *	Chrysomelidae	Neotropical	A	N	G	Y?	Adult?	7.1	356
<i>Agrilus planipennis</i>	Buprestidae	Eastern Asia	H	Y	S	Y	Pre-pupa	127.8	236
<i>Anthonomus bisignifer</i>	Curculionidae	Japan	H	N	S	Y	Adult	28.4	0
<i>Anthonomus pomorum</i>	Curculionidae	Palearctis	H	N	S	Y	Adult	35.5	35
<i>Callidiellum rufipenne</i>	Cerambycidae	Eastern Asia	H	Y	G	Y	Pupa	120.7	13
<i>Cylas formicarius</i>	Brentidae		A	N	S	N ^C	Adult	85.2	197
<i>Diabrotica virgifera</i>	Chrysomelidae	North America	A	N	S	Y	Egg	30	700
<i>Diocalandra frumenti</i>	Curculionidae	Australia	H	Y	S	N		78.1	1
<i>Gonipterus scutellatus</i>	Curculionidae	Australia	H	Y	S	Y	Adult	113.6	39
<i>Harmonia axyridis</i>	Coccinellidae	Central- and Eastern Asia	A	N	G	Y	Adult	120.7	850
<i>Hylobius abietis</i>	Curculionidae		H	Y	G	Y	Larva	127.8	310
<i>Hylotrupes bajulus</i>	Cerambycidae	Europe	H	Y	S	N ^C	Larva	127.8	90
<i>Hylurgus ligniperda</i>	Curculionidae	Europe	H	Y	S	Y	Adult	131.35	29
<i>Hypothenemus hampei</i>	Curculionidae	Central Africa	H	N	S	N		78.1	293
<i>Ips cembrae</i>	Curculionidae	Europe	H	Y	S	Y	Adult	134.9	24
<i>Ips sexdentatus</i>	Curculionidae		H	Y	S	Y	Adult	63.9	95
<i>Ips subelongatus</i>	Curculionidae		H	Y	S	Y	Adult	39.05	14

<i>Ips typographus</i>	Curculionidae	Europe	H	Y	S	Y	Adult	35	787
<i>Leptinotarsa decemlineata</i>	Chrysomelidae	Mexico	A	N	S	Y	Adult	71	1592
<i>Lilioceris lili</i>	Chrysomelidae		H	Y	S	Y	Adult	49.7	17
<i>Listroderes costirostris</i>	Curculionidae	South America	A	N	G	N ^C	Pre-pupa	110.05	6
<i>Megaplatypus mutatus</i>	Curculionidae	Neotropical	H	Y	G	Y?	Larva	99.4	12
<i>Meligethes aeneus</i>	Nitidulidae	Holarctic Region	A	N	G	Y	Adult	49.7	175
<i>Monochamus galloprovincialis</i>	Cerambycidae	Eurasia	H	Y	S	Y?	Larva	49.7	54
<i>Monochamus sutor</i>	Cerambycidae	Eurasia	H	Y	G	Y	Larva and pupa	49.7	11
<i>Phaedon brassicae</i> *	Chrysomelidae	East and South Asia	A	N	G	Y	Adult and larva?	35.5	12
<i>Phoracantha recurva</i>	Cerambycidae	Southeast Asia	H	Y	S	N?		106.5	20
<i>Phoracantha semipunctata</i>	Cerambycidae	Australia	H	Y	S	N?		127.8	88
<i>Pissodes castaneus</i>	Curculionidae	Europe	H	Y	G	Y	Larva, adult	49.7	22
<i>Rhynchophorus ferrugineus</i>	Curculionidae	Southeast Asia	H	Y	G	N?	Adult	78.1	131
<i>Saperda candida</i>	Cerambycidae	Costa Rica	H	Y	G	Y?	Larva	35.5	0
<i>Scolytus morawitzi</i>	Curculionidae	Asia	H	Y	S	Y	Larva	28.4	0
<i>Scolytus schevyrewi</i>	Curculionidae	Eastern Asia	H	Y	G	Y?	Larva, adult	35.5	13
<i>Scyphophorus acupunctatus</i>	Dryophthoridae	New World	H	N	S	N?		63.9	22
<i>Sinoxylon conigerum</i>	Bostrichidae		H	Y	G	Y	Adult	85.2	1
<i>Xylosandrus crassiusculus</i>	Curculionidae	Southeast Asia	H	Y	G	N?		78.1	26
<i>Xylosandrus germanus</i>	Curculionidae	East Asia	H	Y	G	Y	Adult	85.2	37
<i>Xylotrechus altaicus</i>	Curculionidae	Asia	H	Y	S	Y	Larva	21.3	0

252 Notes ^A Resolution was 7.1°. ^B Web of Science (WoS): "http://apps.webofknowledge.com/" was accessed 24.4.2014. ^C Non-diapause dormancy.

253

Although the poleward range shift for Coleoptera was estimated to be 12.2 km/year in the data collected by Bebber et al. (2013), only two species showed significant, climate-change driven, enlargements of their range. These were the Emerald ash borer, *Agrilus planipennis*, and the Red palm weevil, *Rhynchophorus ferrugineus*, both serious wood-feeding forest pests (Bebber et al. 2013). *Agrilus planipennis* feeds on various *Fraxinus* species and has a distribution covering most of northern Asia including European Russia (Baranchikov et al. 2008) and North America, where it was introduced in the beginning of the 21st century (EPPO 2005). Larvae feed in the cambium of trees or in the stems of smaller woody plants and will ultimately kill attacked trees. While still absent from the EU, despite several interceptions, the likelihood the species could establish itself is considered very high (EPPO 2005; Baranchikov et al. 2008). While *A. planipennis* is native to Far East Russia and thus adapted to seasonal environments, *R. ferrugineus* is native to the tropics and has expanded its range into seasonal environments only relatively recently (EPPO 2008). As can be deduced from its common name, *R. ferrugineus* feeds on various Palm trees. Currently it is found in most of southern Europe, where palm trees are cultivated both commercially and for ornamental purposes. While a serious pest in the tropics it is less of a problem in Europe, primarily due to the relatively small scale of palm cultivation.

4. Model systems in more detail

4.1 The Colorado potato beetle and the Rape beetle

What is evident from the literature search on pest species we list in Table 9.2, is that we know very little of the basic biology on many of them. Therefore it is difficult to actually document changes that might have taken place due to climate change. We have therefore chosen two pest species that are relatively well studied and ask how climate change has affected their range expansion dynamics or general biology within ranges. The Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera:Chrysomelidae), is chosen as its range expansion is well documented over the past and it originates from low latitudes in North America and whose high latitude range expansion thus potentially has been restricted by temperature. The Rape or Pollen beetle, *Meligethes aeneus* (Fabricius) (Coleoptera:Nitidulidae), in turn is native to Europe and its expansion potential might be related to indirect effects of climate change.

4.2 The range expansion of the Colorado potato beetle across the northern hemisphere

The rapid range expansion of *L. decemlineata* across most of the northern hemisphere has been very well documented (Johnson 1967; EPPO 2014). *Leptinotarsa decemlineata* originally stems from northern Mexico, and has in around 200 years transformed from a low-density, low-latitude, non-pest species, to a high-density, high-latitude commercially significant pest species (Alyokhin 2009). In this section we will briefly outline the life- and expansion history of *L. decemlineata* and attempt to answer whether its range expansion has been driven or influenced by ongoing climate change, and how climate change is expected to affect established populations at different latitudes.

Leptinotarsa decemlineata was discovered and named by Thomas Say in the early 19th century (Say 1824). The then described leaf beetle was just one of a group of 30-odd closely related chrysomelids living in rather low density populations in Central America and the southwestern part of the United States of America. This changed dramatically when potato, *Solanum tuberosum*, was introduced into the southern states of the USA as a crop between 1840 and 1850. Soon afterwards some of the native *L. decemlineata* shifted host plants from the local potato relative Buffalo bur, *Solanum rostratum*, to potato and became invasive. The first American state where a major outbreak occurred was Colorado, which is the origin of the beetles' common name (Casagrande 1987). Today *L. decemlineata* is the most important insect pest of potato found in an area covering 16 million km² from Mexico, through North America, to most of Europe and deep into Asia (Johnson 1967, EPPO 2014, Alyokhin 2009).

The capacity of *L. decemlineata* adults to burrow into the soil for overwintering in diapause (e.g. Hsiao 1985) is probably among the most important features which has assisted its range expansion into high latitude habitats (EPPO 2014). Diapause is a deep resting stage which normally lasts one winter season, but can also be prolonged and last up to 9 years (Tauber and Tauber 2002). Another interesting characteristic is that around 20 % of all newly eclosed adults in every thus far studied population enter diapause regardless of environmental conditions (Danilevski 1965; Hsiao 1985; Tauber et al. 1986; de Kort 1990). As *L. decemlineata* is a major pest of potato, quarantine inspections and regulations has hindered its spread (first notification in Europe 1875, permanent populations 1922). It is likely that de-regulation of concerted pest management during the First World War was pivotal in allowing the beetle to establish in France. The beetle has further been heavily selected by pesticides as

chemical control of population densities has been forcefully employed throughout its range. The species is very capable of resisting pesticides, which probably is partly due to the natural toxicity of the alkaloids of the host plant, potato (see discussion in Piironen et al. 2013), and also rapid evolution of resistance against new pesticides (Alyokhin 2009). Indeed *L. decemlineata* is justifiably called a super-pest due to the many features (fecundity, dispersal, overwintering, and pesticide resistance) which have made containment and management very challenging (Hsiao 1985; Alyokhin 2009).

The annual expansion distance of *L. decemlineata* has been estimated to be between 80 - 130 km in North America and Europe (Walsh 1865; Tower 1906; Johnson 1967; EPPO 2014). The original historic spread of *L. decemlineata* across North America from relatively low latitudes in Nebraska (41°N) where the first major outbreak took place in 1859 (Tower 1906) to 50 °N in Canada 1901-1911, occurred took place during a time when little change in ambient temperature occurred (IPCC 2013). Consequently, it is likely that this spread was facilitated by habitat availability, dispersal ability, plastic life-history strategies and local adaptation to pronounced seasonality at higher latitudes (Hsiao 1985) rather than changes in climate. In Europe, in turn, the beetle has invaded northwards at a rate of approximately 28.6 km/year since the 1920s when the population was considered established in Europe in France (44 °N) to its current northernmost latitude of around 61 °N in 1970. Thus it has expanded its range at a much faster rate than non-pest species responding to climate change (Table 9.1) which suggests that human involvement has been important.

Several studies on European and North American *L. decemlineata* populations suggest rapid divergence of adaptive variation in life-history and physiological traits (e.g. Danilevskij 1965; Hsiao 1985; Boman et al. 2008; Lyytinen et al. 2012; Lehmann et al. 2012; 2014a; Izzo et al. 2014). The question is whether these changes are driving range expansion, or whether local adaptations arise secondarily after successful establishment (see Urbanski et al. 2012), which primarily occurs without adaptation, through for instance plasticity or broad general stress tolerance (Lehmann et al. 2014b). The range expansion of *L. decemlineata* in northern Europe has slowed down during the last 30 years (EPPO 2014). This could be due to many factors, including a shorter growth season, and a longer and harsher winter or due to a low genetic variability (Grapputo et al. 2005). It is unlikely that a short and cold growth season is strongly limiting expansion, since genetic variability still exists in growth related traits (Boman et al. 2008; Lyytinen et al. 2008). At northern latitudes the progressively harsher

winter is a likely expansion barrier (Valosaari et al. 2008; Piironen et al. 2011). It is possible that plasticity in avoidance behavior, which might have assisted in expansion in more benign environments, fails to provide enough thermal buffering at high latitudes, thus requiring local adaptation (Lehmann et al. 2014b). The retardation of expansion is therefore probably due to an inability to respond to selection as high-latitude populations show low amount of heritable variation in physiological traits important for winter survival (Piironen et al. 2011).

During the last 100 years, in parallel with the range expansion of *L. decemlineata*, climate has warmed by approximately 0.85°C (IPPC 2013). Has this increase in temperature had a meaningful impact on the range expansion propensity of the beetle? Many life-history traits have been shown to depend on temperature in *L. decemlineata*, such as development time (Boman et al. 2008), dispersal capacity (Caprio and Grafius 1990), and the decision to enter diapause (Danilevskij 1965). While most of these traits are affected positively by increased temperature, the decision to enter diapause is more complex since increased temperature decreases diapause propensity (Danilevskij 1965) thus potentially increasing the ovipositing period of beetles. Since late summers are associated with higher climatic variability, especially at high latitude, under current climate change scenarios the decision to prolong the reproductive period can have negative consequences for beetles. Furthermore, warmer winters mean less snow cover, which, combined with wetter conditions, means that low temperatures can more easily penetrate deep into the soil, potentially increasing overwintering mortality of diapausing beetles (Boiteau and Coleman 1996; Constanzo et al. 1997; 1998; Groffman et al. 2001).

Taken together, we think it is unlikely that *L. decemlineata* has been significantly affected by climate change related ambient temperature increase in its expansion thus far (see supplement in Bebbler et al. 2013). Future expansion and population dynamics in established populations might show both positive and negative associations with increased temperature (see e.g. Milner et al. 1992). In case winters become more benign (shorter, warmer) a major potential obstacle for spread to higher latitudes in Europe may disappear (Jönsson et al. 2013). Furthermore, many models predict fairly rapid responses in increased voltinism in European *L. decemlineata* populations, in case growth season, and importantly, potato growing season, increases in length significantly (Valosaari et al. 2008; Jönsson et al. 2013). Therefore we stress that care must be taken when partitioning out the effect of climate change in driving historical, current or future range expansion in pest species.

4.3 Population dynamics of the Rape beetle, *Meligethes aeneus*, at high latitudes in Europe

The rape beetle, *Meligethes aeneus* is a common beetle occurring in most of the holarctic region (Alford 2003). It feeds on a range of naturally occurring plants, especially Brassica and Sinapis species and is not considered particularly harmful when on natural plants. However, since it also uses commercially grown Rape crops as hosts, it has the potential to become a serious pest with a large economic impact. Populations of *M. aeneus* are generally univoltine, and adults overwinter as adults in woodlands. Due to their high protein content, Rape crops (*Brassica napus*, *B. rapa*) have increasingly been appreciated as animal feed, and an increasing interest in biofuel applications (Tiilikainen and Hokkanen 2008) have further increased the attractiveness of growing Rape. Indeed, Rape is one of the most important crop plants in Europe with a total production volume of 19×10^6 tonnes grown during 2010-2011 in the EU (Eurostat Pocketbooks 2012). At high latitude in Europe, such as Finland, *B. rapa*, has traditionally been favored over *B. napus*, due to shorter growth season requirements (Peltonen-Sainio et al. 2009). The increasing utilization potential of Rape has led to the development of more cold-tolerant and hardy high-latitude variants which can be found in northern Europe (Mäkelä et al. 2011). This has led to shifts in the prevalent or preferred variant of Rape in northern growing regions (*B. rapa* spp. *oleifera* becoming more common while the more traditional *B. napus* spp. *oleifera* has become less common). Shifting to a hardier variant has allowed Rape crops rearing at higher latitude and at higher areals (Peltonen-Sainio et al. 2009). Indeed, the total cultivated area of different Rape species has increased by several orders of magnitude in Finland during the last 50 years (Figure 3). The increased growing areals of Rape crops has had positive effects on *M. aeneus*, which also has increased in abundance in concert with its host plant (Tiilikainen and Hokkanen 2008) (Figure 3).

Both adult and larval *M. aeneus* can damage Rape crops. The adults can eat the flowers and supporting structures while larvae eat pollen within buds and flowers. In case populations are not controlled, yield losses in commercial rape crops can be up to 70 % (Nilsson 1987). *Meligethes aeneus* is widely controlled both through biological (Veromann et al. 2006), and more commonly, chemical means (Smatas et al. 2012). Chemical management is complicated by high levels of pesticide resistance (Tiilikainen and Hokkainen 2008; Smatas et al. 2012)

which is exacerbated by host shifts of *M. aeneus* individuals from commercially grown Rape crops to wild relatives (Hokkanen 2000). This shifting of host plants can increase spatial heterogeneity and contribute to the maintenance of large potential genetic variation in the populations.

The effect of climate change is difficult to estimate in *M. aeneus* since this univoltine species already has a more northern distribution than its crop host plants. Therefore climate change effects appear to be indirect as warming affects the range of its host plant range, Rape being cultured at higher latitudes and at larger areas. According to Bebber et al. (2013) *M. aeneus* has not shifted or enlarged its range during the last 60 years, however its severity has increased, primarily through an enlargement host plant planting areas and increasing pesticide resistance (Tiilikainen and Hokkanen 2008; Smatas et al. 2012). According to Hakala et al. (2011) climate change might make cultivation of different Rape variants possible as far north as Lapland by 2085. If this is the case, *M. aeneus* most likely will transition along with its host, and increase in severity as pest.

5. Conclusions

The fifth IPCC report (IPCC 2013) presents, clearer than any time before, evidence supporting the dynamics of ongoing climate change. Therefore the general emphasis has already shifted from merely predicting climate change, into discussing means to mitigate damage due to already occurred or currently occurring climate change (see e.g. Carraro and Sgobbi 2008). For agriculture this means that across the globe, both governmental and non-governmental groups are calling for more information for more strongly integrated pest management and discuss various adaptation strategies since climate change already is apparent in many European agricultural systems (Genovesi and Scalera 2011; Vänninen et al. 2011).

The observed climate change effect include both direct (loss of thermal constraints) or indirect (changes in habitat, species interactions, host plant ranges etc.) effects, which are often hard to dissect from other, anthropogenic, effects (pesticide usage, assisted dispersal). There is also very little systematic information on population sizes of a given pest over large areas for long periods of time, which makes it difficult to observe the changes in the first place. What is needed is a more systematic record keeping or a unifying Europe-wide

458 database, similar to what already is available for non-pest species (see e.g. Atlas of Finnish
459 Macrolepidoptera, Huldén et al. 2000). The citizen science application used for instance to
460 detect and monitor the invasion of *Harmonia axyridis* (Coleoptera:Coccinellidae) in UK
461 (<http://www.ladybird-survey.org/default.aspx>) might be a possible application beneficial also
462 for agricultural professionals. Finally, effective utilization of the internet with rigorous data
463 selection criteria also allows us to utilize available databases (EPPO, NAPPO, CABI) more
464 thoroughly, as recently seen in Bebbier et al. (2013). Taken together, these various systematic
465 approaches should provide the necessary tools to better predict likely responses of pest
466 species to climate change. The goal should be to develop means for horti- and agricultural
467 stake-holders to more effectively mitigate the negative impact which current and future
468 climate change might have through changes in pest species biology.

References

- Addo-Bediako, A., Chown, S.L. and Gaston, K.J. (2002). Metabolic cold adaptation in insects: a large-scale perspective. *Functional Ecology* 16, 332-338.
- Alford, D.V. (2003). *Biocontrol of Oilseed Rape Pests*. Oxford, UK: Blackwell Publishing.
- Altermatt, F. (2010). Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B* 277, 1281-1287.
- Alyokhin, A.V. (2009). Colorado potato beetle management on potatoes: current challenges and future prospects. *Fruit, Vegetable and Cereal Science and Biotechnology* 3, 10-19.
- Ammunét, T., Kaukoranta, T., Saikkonen, K., Repo, T. and Klemola, T. (2012). Invading and resident defoliators in a changing climate: cold tolerance and predictions concerning extreme winter cold as a range-limiting factor. *Ecological Entomology* 37, 212-220.
- Aragón, P. and Lobo, J.M. (2012). Predicted effect of climate change on the invisibility and distribution of the Western corn root-worm. *Agricultural and Forest Entomology* 14, 13-18.
- van Asch, M., Salis, L., Holleman, L.J.M., van Bart, L. and Visser, M.E. (2013). Evolutionary response of the egg hatching date of a herbivorous insect under climate change. *Nature Climate Change* 3, 244-248.
- Bacon, S.J., Aebi, A., Calanca, P. and Bacher, S. (2014). Quarantine arthropod invasions in Europe: the role of climate, hosts and propagule pressure. *Diversity and Distributions* 20, 84-94.
- Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C., Bezemer, T. M. Brown, V. K., Butterfield, J., Buse, A., Coulson, J. C., Farrar, J., Good, J. E. G., Harrington, R., Hartley, S., Jones, T. H., Lindroth, R. L., Press, M. C., Symrnioudis, I., Watt, A. D. and Whittaker, J. B. (2002). Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8, 1-16.
- Bale, J.S. and Hayward, S.A.L. (2010). Insect overwintering in a changing climate. *Journal of Experimental Biology* 213, 980-994.
- Baranchikov, Y., Mozolevskaya, E., Yurchenko, G. and Kenis, M. (2008). Occurrence of the emerald ash borer, *Agrilus planipennis* in Russia and its potential impact on European forestry. *EPPO Bulletin* 38, 233-238.
- Bean, D.W., Dalin, P. and Dudley, T.L. (2012). Evolution of critical day length for diapause induction enables range expansion of *Diorhabda carinulata*, a biological control agent against tamarisk (*Tamarix* spp.). *Evolutionary Applications* 5, 511-523.
- Bebber, D.P., Ramatowski, M.A.T and Gurr, S.J. (2013). Crop pests and pathogens move polewards in a warming world. *Nature Climate Change* 3, 985-988.

- Boiteau, G. and Coleman, W. (1996). Cold tolerance in the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae). *Canadian Entomology* 128, 1087-1099.
- Boman, S., Grapputo, A., Lindström, L., Lyytinen, A. and Mappes, J. (2008). Quantitative genetic approach for assessing invasiveness: geographic and genetic variation in life-history traits. *Biological Invasions* 10, 1135-1145.
- Bradshaw, W.E. and Holzapfel, C.M. (2001). Genetic shift in photoperiodic response correlated with global warming. *Proceedings of the National Academy of Sciences of USA* 98, 14509-14511.
- Bradshaw, W.E., Zani, P.A. and Holzapfel, C.M. (2004). Adaptation to temperate climates. *Evolution* 58, 1748-1762.
- Breed, G.A., Stichter, S. and Crone, E.E. (2014). Climate-driven changes in northeastern US butterfly communities. *Nature Climate Change* 3, 142-145.
- Cannon, R. (1998). The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Global Change Biology* 4, 785-796.
- Caprio, M. and Grafius, E. (1990). Effects of light, temperature and feeding status on flight initiation in postdiapause Colorado potato beetle. *Environmental Entomology* 19, 281-285.
- Carraro, C. and Sgobbi, A. (2008) Climate Change Impacts and Adaptation Strategies in Italy. An Economic Assessment. FEEM Nota di Lavoro, Fondazione Eni Enrico Mattei, Milan, Italy, vol. 06.08.
- Casagrande, R.A. (1987). The Colorado potato beetle: 125 years of mismanagement. *Bulletin of the Entomological Society of America* 33, 142-150.
- Challinor, A.J., Watson, J., Lobell, D.B., Howden, S.M., Smith, D.R. and Chhetri, N. (2014). A meta-analysis of crop yield under climate change and adaptation. *Nature Climate Change* 4, 287-291.
- Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. and Thomas, C.D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science* 333, 1024-1026.
- Costanzo, J.P., Moore, J.B., Lee, R.E., Kaufman, P.E. and Wyman, J.A. (1997). Influence of soil hydric parameters on the winter cold hardiness of a burrowing beetle, *Leptinotarsa decemlineata* (Say). *Journal of Comparative Physiology B* 167, 169-176.
- Costanzo, J.P., Humphreys, T.L., Lee, R.E., Moore, J.B., Lee, M.R. and Wyman, J.A. (1998). Long-term reduction of cold hardiness following ingestion of ice-nucleating bacteria in the Colorado potato beetle, *Leptinotarsa decemlineata*. *Journal of Insect Physiology* 44, 1173-1180.
- Coyette, C. (ed) (2012) Agriculture, fishery and forestry statistics. Eurostat Pocketbooks, EU, Luxembourg.

- Danilevskij, A.S. (1965). *Photoperiodism and seasonal development of insects*. Oliver and Boyd, London, Great Britain.
- DeLucia, E.H., Nabity, P.D., Zavala, J.A. and Berenbaum, M. (2012). Climate Change: Resetting Plant Animal Interactions. *Plant Physiology* 160, 1677-1685.
- Dupin, M., Reynaud, P., Jarošík, V., Baker, R., Brunel, S., Eyre, D. and Pergl, J. (2011). Effects of the Training Dataset Characteristics on the Performance of Nine Species Distribution Models: Application to *Diabrotica virgifera virgifera*. *PLoS ONE* 6, e20957.
- EPPO Bulletin (2005) *Agrilus planipennis*. 35, 436–438. DOI: 10.1111/j.1365-2338.2005.00844.x.
- EPPO Bulletin (2008) *Rhynchophorus ferrugineus*. 38, 55–59. DOI: 10.1111/j.1365-2338.2008.01195.x.
- EPPO 2013a. Reporting Service – Pests & Diseases NO. 11 PARIS, 2013-11-01. 2013/246 EPPO report on notifications of non-compliance. pp. 11-22.
- EPPO 2013b. Archives of the EPPO Reporting Service. Cumulative index from 1967 to 2013. URL: http://archives.eppo.int/EPPOReporting/Reporting_Archives.htm (accessed 24. April 2014)
- EPPO (2014) EPPO A2 List of pests recommended for regulation as quarantine pests. Datasheet for *Leptinotarsa decemlineata* Available at: http://www.eppo.int/QUARANTINE/insects/Leptinotarsa_decemlineata/LPTNDE_ds.pdf (accessed 24 April 2014)
- Eurostat Pocketbooks 2012. Agriculture, fishery and forestry statistics. 2012 edition. Eurostat Pocketbooks, Cat. No KS-FK-12-001-EN-C, European Union, Luxembourg.
- Gaston, K. (2003). The structure and dynamics of geographic ranges. Oxford Series in Ecology and Evolution, Oxford University Press, Oxford, Great Britain.
- Genovesi, P. and Scalera, R. (2011) Aliens: The Invasive Species Bulletin. Issue 31. IUCN/SSC. ISPRA - Rome, Italy.
- Grapputo, A., Boman, S., Lindström, L., Lyytinen, A. and Mappes, J. (2005). The voyage of an invasive species across continents: genetic diversity of North American and European Colorado potato beetle populations. *Molecular Ecology* 14, 4207-4219.
- Groffman, P.M., Driscoll, C.T., Fahey, T.J., Hardy, J.P., Fitzhugh, R.D. and Tierney, G.L. (2001). Colder soils in a warmer world: A snow manipulation study in a northern hardwood ecosystem. *Biogeochemistry* 56, 135-150.
- Hakala, K., Hannukkala, A.O., Huusela-Veistola, E., Jalli, M. and Peltonen-Sainio, P. (2011). Pests and diseases in a changing climate: a major challenge for Finnish crop production. *Agricultural and Food Science* 20, 3-14.

- Hyvönen, T. ed. (2011). A Special Issue: Alien pest species in agriculture and horticulture in Finland. *Agricultural and food science* 20, 1-121.
- Hickling, R., Roy, D.B., Hill, J.K., Fox, R. and Thomas, C.D. (2006). The distribution of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* 12, 1-6.
- Hokkanen, H. (2000). The making of a pest: recruitment of *Meligethes aeneus* onto oilseed Brassicas. *Entomologia Experimentalis et Applicata* 95, 141-149.
- Hoye, T.T., Post, E., Schmidt, N.M., Trojelsgaard, K. and Forchhammer, M.C. (2013). Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. *Nature Climate Change* 3, 759-763.
- Hsiao, T.H. (1985). Eco-physiological and genetic aspects of geographic variations of the Colorado potato beetle. *Research bulletin - Massachusetts Agricultural Experiment Station* 704, 63-77.
- Huldén, L., Albrecht, A., Itämies, J., Malinen, P. and Wettenhovi, J. (2000). *Atlas of Finnish Macrolepidoptera*. Lepidopterological Society of Finland, Finnish Museum of Natural History, Helsinki, 328 p.
- IPCC (2013). *Climate change 2013 - The Physical Science Basis*. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change (IPCC). Cambridge University Press, Cambridge, Great Britain.
- Izzo, V.M., Hawthorne, D.J. and Chen, Y.H. (2014). Geographic variation in winter hardiness of a common agricultural pest, *Leptinotarsa decemlineata*, the Colorado potato beetle. *Evolutionary Ecology* 28, 505-520.
- Johnson, C.G. (1967). International dispersal of insects and insect-borne viruses. *European Journal of Plant Pathology* 73, 21-43.
- Jönsson, A.M., Pulatov, B., Linderson, M. and Hall, K. (2013). Modelling as a tool for analyzing the temperature-dependent future of the Colorado potato beetle in Europe. *Global Change Biology* 19, 1043-1055.
- Kalnay, E. and Cai, M. 2003. Impact of urbanization and land-use change on climate. *Nature* 423, 528-553.
- Kolbe, J.J., Glor, R.E., Schettino, L.R., Lara, A.C., Larson, A. and Losos, J.B. (2004). Genetic variation increases during biological invasion by a Cuban lizard. *Nature* 431, 177-181.
- de Kort, C.A.D. (1990). Thirty-five years of diapause research with the Colorado potato beetle. *Entomologia Experimentalis et Applicata* 56, 1-13.
- Kingsolver, J.G., Arthur Woods, H., Buckley, L.B., Potter, K.A., MacLean, H.J. and Higgins, J.K. (2011). Complex Life Cycles and the Responses of Insects to Climate Change. *Integrative and Comparative Biology*, doi: 10.1093/icb/ucr015.

- Kroschel, J., Sporleder, M., Tonnang, H.E.Z., Juarez, H., Carhuapoma, P., Gonzales, J.C. and Simon, R. (2013). Predicting climate-change-caused changes in global temperature on potato tuber moth *Phthorimaea operclella* (Zeller) distribution and abundance using phenology modeling and GIS mapping. *Agricultural and Forest Meteorology* 170, 228-241.
- Lehmann, P., Lyytinen, A., Sinisalo, T. and Lindström, L. (2012). Population dependent effects of photoperiod on diapause related physiological traits in an invasive beetle (*Leptinotarsa decemlineata*). *Journal of Insect Physiology* 58, 1146-1158.
- Lehmann, P., Piironen, S., Kankare, M., Lyytinen, A., Paljakka, M. and Lindström, L. (2014a). Photoperiodic effects on diapause-associated gene expression trajectories in European *Leptinotarsa decemlineata* populations. *Insect Molecular Biology* 23, 566-578.
- Lehmann, P., Lyytinen, A., Piironen, S., and Lindström, L. (2014b). Northward range expansion requires synchronization of both overwintering behaviour and physiology with photoperiod in the invasive Colorado potato beetle (*Leptinotarsa decemlineata*). *Oecologia* 176, 575-68.
- Lebarbenchon, C., Brown, S.P., Poulin, R., Gauthier-Clerc, M. and Thomas, F. (2008). Evolution of pathogens in a man-made world. *Molecular Ecology* 17, 475-484.
- Lyytinen, A., Lindström, L. and Mappes, J. (2008). Genetic variation in growth and development time under two selection regimes in *Leptinotarsa decemlineata*. *Entomologia Experimentalis et Applicata* 127, 157-167.
- Lyytinen, A., Mappes, J. and Lindström, L. (2012). Variation in Hsp70 levels after cold shock: signs of evolutionary responses to thermal selection among *Leptinotarsa decemlineata* populations. *PLoS ONE* 7, e31446.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., et al. (2000). Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10, 689-710.
- Maiorano, A., Bregaglio, S., Donatelli, M., Fumagalli, D. and Zucchini, A. (2012). Comparison of modelling approaches to simulate the phenology of the European corn borer under future climate scenarios. *Ecological Modelling* 245, 65-74.
- Mair, L., Hill, J.K., Fox, R., Botham, M., Brereton, T. and Thomas, C.D. (2014). Abundance changes and habitat availability drive species' responses to climate change. *Nature Climate Change* 4, 127-131.
- Milner, M., Kung, K.J.S., Wyman, J.A., Feldman, J. and Nordheim, E. (1992). Enhancing overwintering mortality of Colorado potato beetle (Coleoptera: Chrysomelidae) by manipulation the temperature of its diapause habitat. *Journal of Economic Entomology* 85, 1701-1708.
- Musolin, D.L. (2007). Insects in a warmer world: ecological, physiological and life-history responses of true bugs (Heteroptera) to climate change. *Global Change Biology* 13, 1565-1685.

- Myeni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G. and Nemani, R.R. (1997). Increased growth in the northern high latitudes from 1981 to 1991. *Nature* 386, 698-702.
- Mäkelä, P.S.A., Tuulos, A., Turakainen, M., Santanen, A. and Stoddard, F.L. (2011). Revitalizing the winter turnip rape crop in the northern latitudes. *Acta Agriculturae Scandinavica Section B - Soil and Plant Science* 61, 195 - 201.
- Nilsson, C. (1987). Yield losses in summer rape caused by pollen beetles (*Meligethes* spp). *Swedish Journal of Agricultural Research* 17, 105 - 111.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tamaru, T., Tennent, W.J., Thomas, J.A, and Warren, M. (1999). Poleward shift on geographical ranges of butterfly species associated with regional warming. *Nature* 399, 579-483.
- Parmesan, C. and Yoche, G. (2003). A globally coherent fingerprint of climate change impact across natural systems. *Nature* 421, 37-42.
- Peltonen-Sainio, P., Hakala, K., Jauhiainen, L. and Ruosteenoja, K. (2009). Comparing regional risks in producing turnip rape and oilseed rape Impacts of climate change and breeding. *Acta Agriculturae Scandinavica, Section B Soil and Plant Science* 59, 129-138.
- Peltonen-Sainio, P. and Hakala, K. (2014) Viljely muuttuvassa ilmastossa – miten peltoviljely sopeutetaan onnistuneesti. TEHO Plus - hankkeen raportti 4 (in Finnish). Varsinais-Suomen ELY-keskus, Finland.
- Piironen, S., Ketola, T., Lyytinen, A. and Lindström, L. (2011). Energy use, diapause behaviour and northern range expansion potential in the invasive Colorado potato beetle. *Functional Ecology* 25, 527-536.
- Piironen, S., Lindström, L., Lyytinen, A., Mappes, J., Chen, Y.H., Izzo, V. and Grapputo, A. (2013). Pre-invasion history and demography shape the genetic variation in the insecticide resistance related acetylcholinesterase 2 gene in the invasive Colorado potato beetle. *BMC Evolutionary Biology* 13, 13.
- Pöyry, J., Luoto, M., Heikkinen, R.K., Kuussaari, M. and Saarinen, K. (2009). Species traits explain recent shifts of Finnish butterflies. *Global Change Biology* 15, 732-743.
- Saikkonen, K., Taulavuori, K., Hyvönen, T., Gundel, P.E., Hamilton, C.E., Vänninen, I., Nissinen, A. and Helander, M. (2012). Climate change-driven species' range shifts filtered by photoperiodism. *Nature Climate Change* 2, 239-242.
- Santini, A., Ghelardini, L., De Pace, C., Desprez-Loustau, M.L., Capretti, P., Chandelier, A., Cech, T., Chira, D., Diamandis, S., Gaitniekis, T., Hantula, J., Holdenrieder, O., Jankovsky, L., Jung, T., Jurc, D., Kirisits, T., Kunca, A., Lygis, V., Malecka, M., Marcais, B., Schmitz, S., Schumacher, J., Solheim, H., Solla, A., Szabò, I., Tsopelas, P., Vannini, A., Vettraino, A.M., Webber, J., Woodward, S. and Stenlid, J. (2013) Biogeographical patterns and determinants of invasion by forest pathogens in Europe. *New Phytologist* 197, 238-250.

- Say, T. (1824). Descriptions of coleopterous insects collected in the late expedition to the Rocky Mountains, performed by order of Mr. Calhoun, Secretary of War, under the command of Major Long. *Journal of the Academy of Natural Sciences of Philadelphia* 3, 303-462.
- Smatas, R. Makunas, V., Brazauskiene, I. and Petraitiene, E. (2012). Sensitivity of pollen beetle (*Meligethes aeneus* F.) to insecticides with different modes of action and their efficacy in the field conditions. *Zemdirbyste-Agriculture* 99, 197-202.
- Smith, R.M., Baker, R.H.A., Malumphy, C.P., Hockland, S., Hammon, R.P., Ostojá-Starzewski, J.C. and Collins, D.W. (2007). Recent non-native invertebrate plant pest establishments in Great Britain: origins, pathways, and trends. *Agricultural and Forest Entomology* 9, 307–326.
- Stöckli, S., Hirschi, M., Spirig, C., Calanca, P., Rotach, M.W. and Samietz, J. (2012). Impact of Climate Change on voltinism and prospective diapause induction of a global pest insect - *Cydia pomonella* (L.). *PLoS ONE* 7, e35723.
- Tatem, A.J. and Hay, S.I. (2007). Climatic similarity and biological exchange in the worldwide airline transportation network. *Proceedings of the Royal Society B* 274, 1489-1496.
- Tauber, M.J., Tauber, C.A. and Masaki, S. (1986). *Seasonal adaptations of insects*. Oxford University Press, New York, USA.
- Tauber, M.J. and Tauber, C.A. (2002). Prolonged dormancy in *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae): a ten-year field study with implications for crop rotation. *Environmental Entomology* 31, 499–504.
- Tiilikainen, T.M. and Hokkanen, H.M.T. (2008). Pyrethroid resistance in Finnish pollen beetle (*Meligethes aeneus*) populations - is it around the corner? *EPPO Bulletin* 38, 99-103.
- Tower, W.L. (1906). *Evolution in chrysomelid beetles*. Carnegie Institution, Washington, USA.
- Urbanski, J., Mogi, M., O'Donnell, D., DeCotiis, M., Toma, T. and Armbruster, P. (2012). Rapid adaptive evolution of photoperiodic response during invasion and range expansion across a climatic gradient. *The American Naturalist* 179, 490-500.
- Valosaari, K.-R., Aikio, S. and Kaitala, V. (2008). Spatial simulation model to predict the Colorado potato beetle invasion under different management strategies. *Annales Zoologici Fennici* 45, 1-14.
- Veromann, E., Tarang, T., Kevvää, R., Luik, A., and Williams, I. (2006). Insect pest and their natural enemies on spring oilseed rape in Estonia: impact of cropping systems. *Agricultural and Food Science* 15, 61 - 72.
- Vänninen, I., Worner, S., Huusela-Veistola, E., Tuovinen, T., Nissinen, A. and Saikkonen, K. (2011). Recorded and potential alien invertebrate pests in Finnish agriculture and horticulture. *Agricultural and Food Science* 20, 96-114.

815

816 Walsh, B.D. (1865). The new potato-bug, and its natural history. *The Practical Entomologist*
817 1, 1-4.

818

819 Wand, S.J.E., Midgley, G.F., Jones, M.H. and Curtis, P.S. (1999). Responses of wild C4 and
820 C3 grass (Poaceae) species to elevated atmospheric CO2 concentration: a meta-analytic test
821 of current theories and perceptions. *Global Change Biology* 5, 723-741.

822

823 Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin,
824 J.-M., Hoegh-Guldberg, O. and Bairlein, F. (2002). Ecological responses to recent climate
825 change. *Nature* 416, 389-395.

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827 Figure legends

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829 Figure 8.1 Cumulative number of new records of pests in six western European countries
830 (data from EPPO website 2013b).

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Figure 8.2 Proportion of *Bemisia tabaci* individuals found on ornamentals and vegetables from the UK divided according to country of origin (EPPO 2013a, NO 11, N = 76).

Figure 8.3 The solid line shows areas of rape grown in Finland, 1950-2010. During 1950-1970 the predominant rape variant was Winter turnip rape (*Brassica napus* spp. *oleifera*), while the increase after 1970 up till present day primarily constitutes Spring turnip rape (*Brassica rapa* spp. *oleifera*) substituting Winter turnip rape. The dashed line shows the severity index of *Meligethes aeneus* attacks estimated in southwestern Finland between 1977 and 1992. Data is from Mäkelä et al. 2011 and Hokkanen 2000.