



This is an electronic reprint of the original article. This reprint *may differ* from the original in pagination and typographic detail.

Author(s):	Lindström, Leena; Lehmann, Philipp
Title:	Climate Change Effects on Agricultural Insect Pests in Europe
Year:	2015

Please cite the original version:

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

All material supplied via JYX is protected by copyright and other intellectual property rights, and duplication or sale of all or part of any of the repository collections is not permitted, except that material may be duplicated by you for your research use or educational purposes in electronic or print form. You must obtain permission for any other use. Electronic or print copies may not be offered, whether for sale or otherwise to anyone who is not an authorised user.

1 C Björkman and P Niemelä (eds). 2015. Climate Change and Insect Pests, CABI

- 2 Climate Change Series.
- 3 http://www.cabi.org/bookshop/book/9781780643786

5 Chapter 8 Climate change effects on agricultural insect pests in Europe

- 7 Leena Lindström & Philipp Lehmann
- 8 Centre of Excellence in Biological Interactions Research
- 9 Department of Biological and Environmental Science
- 10 University of Jyväskylä, Finland

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

- 32 Leena Lindström & Philipp Lehmann
- 33 Centre of Excellence in Biological Interactions Research
- 34 Department of Biological and Environmental Science
- 35 University of Jyväskylä, Finland

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; Hoye 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 (Myeni 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 (Wand 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, ± 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
	$km/a \pm SE (sp)$	$km/a \pm SE (sp)$	$km/a \pm SE (sp)$	$km/a \pm SE (sp)$	$km/a \pm SE (sp)$	$km/a \pm SE (sp)$
Coleoptera	$7.61 \pm 1.87 (70)$	$12.21 \pm 4.33 (70)$	2.48 ± 0.43 (86)			
Diptera	3.11 ± 2.48 (24)	3.95 ± 6.08 (24)				
Hemiptera	6.13 ± 3.25 (47)	$13.71 \pm 5.32 (47)$				
Hymenoptera	4.60 ± 9.48 (6)	8.11 ± 11.64 (6)				
Isoptera	19.62 ± 10.83 (1)	-7.51 ± 13.89 (1)				
Lepidoptera	8.00 ± 2.71 (36)	17.78 ± 8.58 (36)	1.76 ± 0.46 (29)	7.49 ± 1.75 (48)		
Neuroptera			1.76 ± 1.16 (6)			
Odonata			4.16 ± 0.68 (20)			
Orthoptera			1.36 ± 0.32 (22)			
Thysanoptera	7.68 ± 4.36 (3)	1.06 ± 9.31 (3)				
OVERALL		$2.7 \pm 0.8 (600)$	$1.74 \pm 0.82 (329)$		0.61± 0.24 (99)	1.76 ± 0.29 (764)

^{135 1} Bebber et al. 2013, Estimates based on CABI records

131

132

133

134

139

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

^{137 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 Bebber 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 nonpest 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).

163164

165

166

167

168

169170

171

172

173

174

141

142

143

144

145

146

147

148

149

150

151

152

153

154

155

156

157

158

159

160

161

162

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.

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

210211

212

213

214

215

216217

218

219

220

221

222

223

224

225

226

227

228

229

208

209

To highlight some recent research and observations on insect pest species in Europe, we chose to investigate beetles (Coleoptera) in more detail. Beetles are among the most diverse insect taxa and several important pests are beetles, most notably in forestry, but also in agriand horticulture (Bebber et al. 2013). These include, for instance, the Colorado potato beetle Leptinotarsa decemlineata (Alyokhin 2009) and the Western Corn rootworm Diabrotica virgifera (Dupin et al. 2011). Table 2 lists some of the most important beetle pests found in agri- and horticultural systems in Europe (Bebber et al. 2013). As can be seen the best represented families are Curculionidae (true weevils or snout beetles), Cerambycidae (longhorn beetles) and Chrysomelidae (leaf beetles). Of these insects, 26 feed primarily on wood, 11 on soft plant tissue (including leaves, fruits, flowers, tubers) and 1 is carnivorous. The majority (78 %) of these beetles have a dedicated overwintering stage, which in 72 % is the adult stage. Interestingly, comparing ranges of beetle pests found in Europe with beetle pests whose ranges do not include Europe (listed in Bebber et al. 2013) reveals that pests whose range includes Europe are found over a larger latitudinal range (mean = 77.6°, SEM = 6.2) than those whose range excludes (mean = 55.0° , SEM = 4.5) Europe (two-tailed t-test: $t_{66.2} = 2.43$, P = 0.018). This could indicate a sampling bias, since European (together with North American) countries generally use more resources to track and report pest movements (e.g. EPPO, NAPPO etc.), but the involvement of some biological mechanisms cannot be ruled out.

230231

232

233

234

235

236

237

238

239

240

241

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

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

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
Acanthoscelides obtectus*	Chrysomelidae	Neotropical	A	N	G	Y?	Adult?	7.1	356
Agrilus planipennis	Buprestidae	Eastern Asia	Н	Y	S	Y	Pre-pupa	127.8	236
Anthonomus bisignifer	Curculionidae	Japan	Н	N	S	Y	Adult	28.4	0
Anthonomus pomorum	Curculionidae	Palearctis	Н	N	S	Y	Adult	35.5	35
Callidiellum rufipenne	Cerambycidae	Eastern Asia	Н	Y	G	Y	Pupa	120.7	13
Cylas formicarius	Brentidae		A	N	S	N^{C}	Adult	85.2	197
Diabrotica virgifera	Chrysomelidae	North America	A	N	S	Y	Egg	30	700
Diocalandra frumenti	Curculionidae	Australia	Н	Y	S	N		78.1	1
Gonipterus scutellatus	Curculionidae	Australia	Н	Y	S	Y	Adult	113.6	39
Harmonia axyridis	Coccinellidae	Central- and Eastern Asia	A	N	G	Y	Adult	120.7	850
Hylobius abietis	Curculionidae		Н	Y	G	Y	Larva	127.8	310
Hylotrupes bajulus	Cerambycidae	Europe	Н	Y	S	N^C	Larva	127.8	90
Hylurgus ligniperda	Curculionidae	Europe	Н	Y	S	Y	Adult	131.35	29
Hypothenemus hampei	Curculionidae	Central Africa	Н	N	S	N		78.1	293
Ips cembrae	Curculionidae	Europe	Н	Y	S	Y	Adult	134.9	24
Ips sexdentatus	Curculionidae		Н	Y	S	Y	Adult	63.9	95
Ips subelongatus	Curculionidae		Н	Y	S	Y	Adult	39.05	14

Ips typographus	Curculionidae	Europe	Н	Y	S	Y	Adult	35	787
Leptinotarsa decemlineata	Chrysomelidae	Mexico	A	N	S	Y	Adult	71	1592
Lilioceris lilii	Chrysomelidae		Н	Y	S	Y	Adult	49.7	17
Listroderes costirostris	Curculionidae	South America	A	N	G	N^C	Pre-pupa	110.05	6
Megaplatypus mutatus	Curculionidae	Neotropical	Н	Y	G	Y ?	Larva	99.4	12
Meligethes aeneus	Nitidulidae	Holarctic Region	A	N	G	Y	Adult	49.7	175
Monochamus galloprovincialis	Cerambycidae	Eurasia	Н	Y	S	Υ?	Larva	49.7	54
Monochamus sutor	Cerambycidae	Eurasia	Н	Y	G	Y	Larva and pupa	49.7	11
Phaedon brassicae*	Chrysomelidae	East and South Asia	A	N	G	Y	Adult and larva?	35.5	12
Phoracantha recurva	Cerambycidae	Southeast Asia	Н	Y	S	N?		106.5	20
Phoracantha semipunctata	Cerambycidae	Australia	Н	Y	S	N?		127.8	88
Pissodes castaneus	Curculionidae	Europe	Н	Y	G	Y	Larva, adult	49.7	22
Rhynchophorus ferrugineus	Curculionidae	Southeast Asia	Н	Y	G	N?	Adult	78.1	131
Saperda candida	Cerambycidae	Costa Rica	Н	Y	G	Y ?	Larva	35.5	0
Scolytus morawitzi	Curculionidae	Asia	Н	Y	S	Y	Larva	28.4	0
Scolytus schevyrewi	Curculionidae	Eastern Asia	Н	Y	G	Y?	Larva, adult	35.5	13
Scyphophorus acupunctatus	Dryophthoridae	New World	Н	N	S	N?		63.9	22
Sinoxylon conigerum	Bostrichidae		Н	Y	G	Y	Adult	85.2	1
Xylosandrus crassiusculus	Curculionidae	Southeast Asia	Н	Y	G	N?		78.1	26
Xylosandrus germanus	Curculionidae	East Asia	Н	Y	G	Y	Adult	85.2	37
Xylotrechus altaicus	Curculionidae	Asia	Н	Y	S	Y	Larva	21.3	0
M. AD 1.	7 10 Bxx 1 0	. O . (M. O) (4)	11	1 (1 1 1	/9.9	104 4 001 4 CM	1' 1		

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

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.

271

272

254

255

256

257

258

259

260

261

262

263

264

265

266

267

268

269

270

4. Model systems in more detail

273274

4.1 The Colorado potato beetle and the Rape beetle

275276

277

278

279

280

281

282

283

284

285

286

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

290 The rapid range expansion of *L. decemlineata* across most of the northern hemisphere has 291 been very well documented (Johnson 1967; EPPO 2014). *Leptinotarsa decemlineata* 292 originally stems from northern Mexico, and has in around 200 years transformed from a low-293 density, low-latitude, non-pest species, to a high-density, high-latitude commercially 294 significant pest species (Alyokhin 2009). In this section we will briefly outline the life- and

295 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 deregulation 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 Piiroinen 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; Piiroinen 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 (Piiroinen 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 Bebber 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.

390

391

392

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

393

394

395

396

397

398

399

400

401

402

403

404

405

406

407

408

409

410

411

412

413

414

415

416

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 x 10⁶ 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).

417418

419

420

421

422

423

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 Hokkainen 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

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

References

469 470

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.

473

474 Alford, D.V. (2003). *Biocontrol of Oilseed Rape Pests*. Oxford, UK: Blackwell Publishing.

475

Altermatt, F. (2010). Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B* 277, 1281-1287.

478

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.

481

482 Ammunét, T., Kaukoranta, T., Saikkonen, K., Repo, T. and Klemola, T. (2012). Invading and 483 resident defoliators in a changing climate: cold tolerance and predictions concerning extreme 484 winter cold as a range-limiting factor. *Ecological Entomology* 37, 212-220.

485

486 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.

488

- 489 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.
- 491 Nature Climate Change 3, 244-248.

492

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.

496

- 497 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.
- 500 (2002). Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8, 1-16.

502

Bale, J.S. and Hayward, S.A.L. (2010). Insect overwintering in a changing climate. *Journal* of Experimental Biology 213, 980–94.

505

Baranchikov. Y., Mozolevskaya, E., Yurchenko, G. and Kenis, M. (2008). Occurrence of the emerald ash borer, Agrilus planipennis in Russia and its poential impact on European forestry. *EPPO Bulletin* 38, 233-238.

509

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.

513

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.

517 Boiteau, G. and Coleman, W. (1996). Cold tolerance in the Colorado potato beetle,

- 518 Leptinotarsa decemlineata (Say) (Coleoptera: Chrysomelidae). Canadian Entomology 128,
- 519 1087-1099.

520

- 521 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 522
- 523 traits. Biological Invasions 10, 1135-1145.

524

- 525 Bradshaw, W.E. and Holzapfel, C.M. (2001). Genetic shift in photoperiodic response
- 526 correlated with global warming. Proceedings of the National Acadademy of Sciences of USA
- 527 98, 14509-14511.

528

- 529 Bradshaw, W.E., Zani, P.A. and Holzapfel, C.M. (2004). Adaptation to temperate climates.
- 530 Evolution 58, 1748-1762.

531

- 532 Breed, G.A., Stichter, S. and Crone, E.E. (2014). Climate-driven changes in northeastern US
- 533 butterfly communities. *Nature Climate Change* 3, 142-145.

534

- 535 Cannon, R. (1998). The implications of predicted climate change for insect pests in the UK,
- 536 with emphasis on non-indigenous species. Global Change Biology 4, 785-796.

537

- 538 Caprio, M. and Grafius, E. (1990). Effects of light, temperature and feeding status on flight
- 539 initiation in postdiapause Colorado potato beetle. Environmental Entomology 19, 281-285.

540

- 541 Carraro, C. and Sgobbi, A. (2008) Climate Change Impacts and Adaptation Strategies in
- 542 Italy. An Economic Assessment. FEEM Nota di Lavoro, Fondazione Eni Enrico Mattei,
- 543 Milan, Italy, vol. 06.08.

544

- 545 Casagrande, R.A. (1987). The Colorado potato beetle: 125 years of mismanagement. Bulletin
- 546 of the Entomological Society of America 33, 142–150.

547

- 548 Challinor, A.J., Watson, J., Lobell, D.B., Howden, S.M., Smith, D.R. and Chhetri, N. (2014).
- 549 A meta-analysis of crop yield under climate change and adaptation. Nature Climate Change 4, 287-291.
- 550

551

- 552 Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. and Thomas, C.D. (2011). Rapid range
- 553 shifts of species associated with high levels of climate warming. Science 333, 1024-1026.

554

- 555 Costanzo, J.P., Moore, J.B., Lee, R.E., Kaufman, P.E. and Wyman, J.A. (1997). Influence of
- 556 soil hydric parameters on the winter cold hardiness of a burrowing beetle, Leptinotarsa
- 557 decemlineata (Say). Journal of Comparative Physiology B 167, 169-176.

558

- 559 Costanzo, J.P., Humphreys, T.L., Lee, R.E., Moore, J.B., Lee, M.R. and Wyman, J.A. (1998).
- 560 Long-term reduction of cold hardiness following ingestion of ice-nucleating bacteria in the
- 561 Colorado potato beetle, Leptinotarsa decemlineata. Journal of Insect Physiology 44, 1173-
- 1180. 562

563

- 564 Coyette, C. (ed) (2012) Agriculture, fishery and forestry statistics. Eurostat Pocketbooks, EU,
- 565 Luxembourg.

567 Danilevskij, A.S. (1965). Photoperiodism and seasonal development of insects. Oliver and

568 Boyd, London, Great Britain.

569

- 570 DeLucia, E.H., Nabity, P.D., Zavala, J.A. and Berenbaum, M. (2012). Climate Change:
- Resetting Plant Animal Interactions. *Plant Physiology* 160, 1677-1685.

572

- 573 Dupin, M., Reynaud, P., Jarošík, V., Baker, R., Brunel, S., Eyre, D. and Pergl, J. (2011).
- 574 Effects of the Training Dataset Characteristics on the Performance of Nine Species
- 575 Distribution Models: Application to *Diabrotica virgifera virgifera*. *PLoS ONE* 6, e20957.

576

577 EPPO Bulletin (2005) Agrilus planipennis. 35, 436–438. DOI: 10.1111/j.1365-

578 2338.2005.00844.x.

579

580 EPPO Bulletin (2008) Rhynchophorus ferrugineus. 38, 55–59. DOI: 10.1111/j.1365-

581 2338.2008.01195.x.

582

- 583 EPPO 2013a. Reporting Service Pests & Diseases NO. 11 PARIS, 2013-11-01. 2013/246
- 584 EPPO report on notifications of non-compliance. pp. 11-22.

585

- 586 EPPO 2013b. Archives of the EPPO Reporting Service. Cumulative index from 1967 to
- 587 2013. URL: http://archives.eppo.int/EPPOReporting/Reporting_Archives.htm (accessed 24.
- 588 April 2014)

589

- 590 EPPO (2014) EPPO A2 List of pests recommended for regulation as quarantine pests.
- 591 Datasheet for Leptinotarsa decemlineata Available at:
- 592 http://www.eppo.int/QUARANTINE/insects/Leptinotarsa_decemlineata/LPTNDE_ds.pdf
- 593 (accessed 24 April 2014)

594

- 595 Eurostat Pocketbooks 2012. Agriculture, fishery and forestry statistics. 2012 edition. Eurostat
- 596 Pocketbooks, Cat. No KS-FK-12-001-EN-C, European Union, Luxembourg.

597

- 598 Gaston, K. (2003). The structure and dynamics of geographic ranges. Oxford Series in
- 599 Ecology and Evolution, Oxford University Press, Oxford, Great Britain.

600

- 601 Genovesi, P. and Scalera, R. (2011) Aliens: The Invasive Species Bulletin. Issue 31.
- 602 IUCN/SSC. ISPRA Rome, Italy.

603

- 604 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
- 606 Colorado potato beetle populations. *Molecular Ecology* 14, 4207-4219.

607

- 608 Groffman, P.M., Driscoll, C.T., Fahey, T.J., Hardy, J.P, Fitzhugh, R.D. and Tierney, G.L.
- 609 (2001). Colder soils in a warmer world: A snow manipulation study in a northern hardwood
- 610 ecosystem. *Biogeochemistry* 56, 135-150.

611

- 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.
- 614 Agricultural and Food Science 20, 3-14.

Hyvönen, T. ed. (2011). A Special Issue: Alien pest species in agriculture and horticulture in

617 Finland. Agricultural and food science 20, 1-121.

618

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.

621

Hokkanen, H. (2000). The making of a pest: recruitment of *Meligethes aeneus* onto oilseed Brassicas. *Entomologia Experimentalis et Applicata* 95, 141-149.

624

- Hoye, T.T., Post, E., Schmidt, N.M., Trojelsgaard, K. and Forchhammer, M.C. (2013).
- 626 Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic.
- 627 Nature Climate Change 3, 759-763.

628

- 629 Hsiao, T.H. (1985). Eco-physiological and genetic aspects of geographic variations of the
- 630 Colorado potato beetle. Research bulletin Massachusetts Agricultural Experiment Station
- 631 704, 63-77.

632

- Huldén, L., Albrecht, A., Itämies, J., Malinen, P. and Wettenhovi, J. (2000). Atlas of Finnish
- 634 Macrolepidoptera. Lepidopterological Society of Finland, Finnish Museum of Natural
- History, Helsinki, 328 p.

636

- 637 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
- 639 (IPCC). Cambridge University Press, Cambridge, Great Britain.

640

- 641 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.

644

Johnson, C.G. (1967). International dispersal of insects and insect-borne viruses. *European*

646 Journal of Plant Pathology 73, 21-43.

647

- 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*
- 650 *Change Biology* 19, 1043-1055.

651

Kalnay, E. and Cai, M. 2003. Impact of urbanization and land-use change on climate. *Nature* 423, 528-553.

654

- Kolbe, J.J., Glor, R.E., Schettino, L.R., Lara, A.C., Larson, A. and Losos, J.B. (2004).
- 656 Genetic variation increases during biological invasion by a Cuban lizard. Nature 431, 177-
- 657 181.

658

de Kort, C.A.D. (1990). Thirty-five years of diapause research with the Colorado potato beetle. *Entomologia Experimentalis et Applicata* 56, 1-13.

661

- 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.
- 664 Integrative and Comparative Biology, doi: 10.1093/icb/icr015.

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
- 668 tuber moth Phthorimaea operclella (Zeller) distribution and abundance using phenology
- modeling and GIS mapping. Agricultural and Forest Meteorology 170, 228-241.

670

671 Lehmann, P., Lyytinen, A., Sinisalo, T. and Lindström, L. (2012). Population dependent 672 effects of photoperiod on diapause related physiological traits in an invasive beetle 673 (Leptinotarsa decemlineata). *Journal of Insect Physiology* 58, 1146-1158.

674

Lehmann, P., Piiroinen, 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.

678

Lehmann, P., Lyytinen, A., Piiroinen, 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.

683

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.

686

687 Lyytinen, A., Lindström, L. and Mappes, J. (2008). Genetic variation in growth and development time under two selection regimes in *Leptinotarsa decemlineata*. *Entomologia* 689 *Experimentalis et Applicata* 127, 157-167.

690

691 Lyytinen, A., Mappes, J. and Lindström, L. (2012). Variation in Hsp70 levels after cold 692 shock: signs of evolutionary responses to thermal selection among *Leptinotarsa decemlineata* 693 populations. *PLoS ONE* 7, e31446.

694

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.

698

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.

702

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.

706

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.

711

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.

716 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.

718

- 719 Mäkelä, P.S.A., Tuulos, A., Turakainen, M., Santanen, A. and Stoddard, F.L. (2011).
- 720 Revitalizing the winter turnip rape crop in the northern latitudes. Acta Agricultururae
- 721 Scandinavica Section B Soil and Plant Science 61, 195 201.

722

- 723 Nilsson, C. (1987). Yield losses in summer rape caused by pollen beetles (*Meligethes* spp).
- 724 Swedish Journal of Agricultural Research 17, 105 111.

725

- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley,
- 727 B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A, and Warren, M. (1999).
- Poleward shift on geographical ranges of butterfly species associated with regional warming.
- 729 Nature 399, 579-483.

730

- Parmesan, C. and Yoche, G. (2003). A globally coherent fingerprint of climate change impact
- across natural systems. *Nature* 421, 37-42.

733

- Peltonen-Sainio, P., Hakala, K., Jauhiainen, L. and Ruosteenoja, K. (2009). Comparing
- 735 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.

737

- 738 Peltonen-Sainio, P. and Hakala, K. (2014) Viljely muuttuvassa ilmastossa miten
- 739 peltoviljely sopeutetaan onnistuneesti. TEHO Plus hankkeen raportti 4 (in Finnish).
- 740 Varsinais-Suomen ELY-keskus, Finland.

741

- 742 Piiroinen, S., Ketola, T., Lyytinen, A. and Lindström, L. (2011). Energy use, diapause
- behaviour and northern range expansion potential in the invasive Colorado potato beetle.
- 744 Functional Ecology 25, 527-536.

745

- Piiroinen, S., Lindström, L., Lyytinen, A., Mappes, J., Chen, Y.H., Izzo, V. and Grapputo, A.
- 747 (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
- 749 Evolutionary Biology 13, 13.

750

- 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.

753

- 754 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
- 756 photoperiodism. *Nature Climate Change* 2, 239-242.

757

- Santini, A., Ghelardini, L., De Pace, C., Desprez-Loustau, M.L., Capretti, P., Chandelier, A.,
- 759 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,
- 761 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.

765 Say, T. (1824). Descriptions of coloepterous insects collected in the late expedition to the

- 766 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, 767
- 768 303-462.

769

770 Smatas, R. Makunas, V., Brazauskiene, I. and Petraitiene, E. (2012). Sensitivity of pollen 771 beetle (Meligethes aeneus F.) to insecticides with different modes of action and their efficacy in the field conditions. Zemdirbyste-Agriculture 99, 197-202.

772

773 Smith, R.M., Baker, R.H.A., Malumphy, C.P., Hockland, S., Hammon, R.P., Ostojá-

774

775 Starzewski, J.C. and Collins, D.W. (2007). Recent non-native invertebrate plant pest 776 establishments in Great Britain: origins, pathways, and trends. Agricultural and Forest 777 Entomology 9, 307–326.

778

779 Stöckli, S., Hirschi, M., Spirig, C., Calanca, P., Rotach, M.W. and Samietz, J. (2012). Impact 780 of Climate Change on voltinism and prospective diapause induction of a global pest insect -781 Cydia pomonella (L.). PLoS ONE 7, e35723.

782

783 Tatem, A.J. and Hay, S.I. (2007). Climatic similarity and biological exchange in the 784 worldwide airline transportation network. Proceedings of the Royal Society B 274, 1489-785 1496.

786

787 Tauber, M.J., Tauber, C.A. and Masaki, S. (1986). Seasonal adaptations of insects. Oxford 788 University Press, New York, USA.

789

790 Tauber, M.J. and Tauber, C.A. (2002). Prolonged dormancy in Leptinotarsa decemlineata 791 (Coleoptera: Chrysomelidae): a ten-year field study with implications for crop rotation. 792 Environmental Entomology 31, 499–504.

793

794 Tiilikainen, T.M. and Hokkanen, H.M.T. (2008). Pyrethroid resistance in Finnish pollen 795 beetle (Meligethes aeneus) populations - is it around the corner? EPPO Bulletin 38, 99-103.

796

797 Tower, W.L. (1906). Evolution in chrysomelid beetles. Carnagie Institution, Washington, 798 USA.

799

800 Urbanski, J., Mogi, M., O'Donnell, D., DeCotiis, M., Toma, T. and Armbruster, P. (2012). 801 Rapid adaptive evolution of photoperiodic response during invasion and range expansion 802 across a climatic gradient. The American Naturalist 179, 490-500.

803

804 Valosaari, K.-R., Aikio, S. and Kaitala, V. (2008). Spatial simulation model to predict the 805 Colorado potato beetle invasion under different management strategies. Annales Zoologici 806 Fennici 45, 1-14.

807

808 Veromann, E., Tarang, T., Kevväi, R., Luik, A., and Williams, I. (2006). Insect pest and their 809 natural enemies on spring oilseed rape in Estonia: impact of cropping systems. Agricultural 810 and Food Science 15, 61 - 72.

- 812 Vänninen, I., Worner, S., Huusela-Veistola, E., Tuovinen, T., Nissinen, A. and Saikkonen, K.
- 813 (2011). Recorded and potential alien invertebrate pests in Finnish agriculture and
- 814 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

Wand, S.J.E., Midgley, G.F., Jones, M.H. and Curtis, P.S. (1999). Responses of wild C4 and C3 grass (Poaceae) species to elevated atmospheric CO2 concentration: a meta-analytic test

of current theories and perceptions. Global Change Biology 5, 723-741.

821

822

826

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

Figure legends

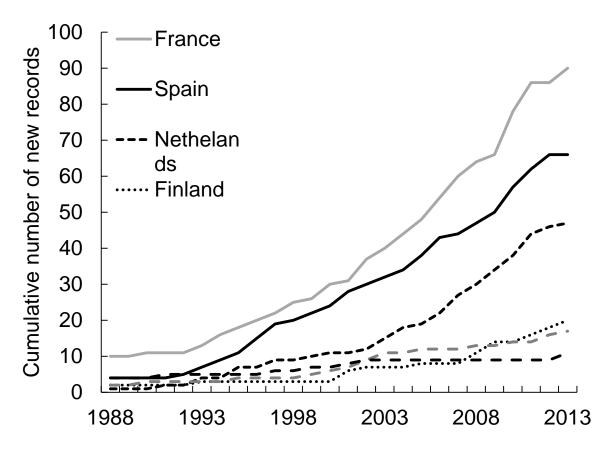


Figure 8.1 Cumulative number of new records of pests in six western European countries (data from EPPO website 2013b).

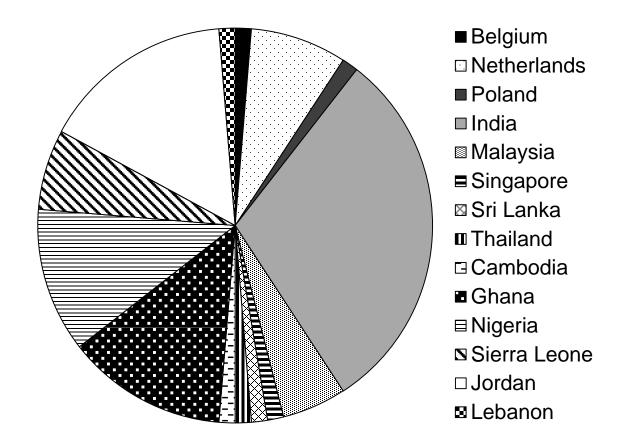


Figure 8.2 Proportion of *Bemicia tabaci* individuals found on ornamentals and vegetables from the UK divided according to country of origin (EPPO 2013a, NO 11, N = 76).

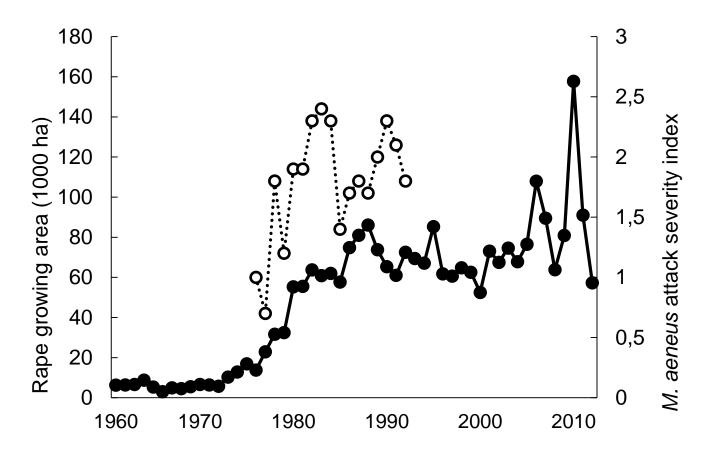


Figure 8.3 The solid line shows areas of rape grown in Finland, 1950-2010. During 1950-1970 the predominant rape variant was Winter turnip rape (*Brassica napus* spp. *oleifera*), while the increase after 1970 up till present day primarily constitutes Spring turnip rape (*Brassica rapa* spp. *oleifera*) 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.