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Assessment of the potential area for the establishment of the Colorado potato beetle in Finland and Sweden

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Summary

The Colorado potato beetle (CPB, *Leptinotarsa decemlineata*) is a protected zone quarantine pest in the southern parts of Finland and Sweden. The units responsible for pest risk assessments in Finland and Sweden were requested to identify the geographical areas likely to be suitable for establishment of the CPB given a climate change scenario that covers the years 2023–2040.

Based on previous studies, the northern limit of the potential range of the CPB appears to depend, above all, on where the summer temperatures enable the development of one complete generation. To identify such areas in Finland and Sweden, we first estimated the annual growing degree day (GDD) requirement (above 10 °C) of the CPB based on the two-decade mean annual GDD in the northernmost locations where the CPB is present in Russia. The lowest mean annual GDD among these locations was 587 which was used as the GDD requirement of the CPB in this assessment. Next, we delineated the areas in Finland and Sweden where this GDD requirement was met in a recent time period (2003–2022) and in a future time period (2031–2050) assuming an intermediate greenhouse gas emission scenario, i.e., Representative Concentration Pathway (RCP) 4.5.

The results show that the GDD requirement of 587 is met in large areas in southern Finland and Sweden, and by 2040, also in central Finland and the Baltic Sea coastline. We further assessed that there are enough hosts for the CPB to enable establishment in these areas. These areas were therefore assessed as likely to be suitable for the establishment of the CPB. Importantly, they include areas much further north than the current protected zones. This result was assessed to be rather robust since even a 20% higher GDD requirement (704) was met in a much larger area than the protected zones both in Sweden (in the recent and future climate) and in Finland (in the future climate).

The greatest sources of uncertainty in the assessment are the uncertainty of the annual GDD that the CPB needs to complete its life cycle, the future climate projections, and the abundance of hosts necessary in a landscape to enable the CPB to establish.

1 Background and scope

The Colorado potato beetle (*Leptinotarsa decemlineata*, EPPO code: LPTNDE) is a protected zone quarantine pest in parts of southern Finland and Sweden (Annex III of (EU) 2019/2072[1]). In Finland the protected zone covers seven Centres for Economic Development, Transport and the Environment (ELY) and in Sweden it covers five counties (Figure 1). Recent studies indicate, however, that the Colorado potato beetle (CPB) may be able to establish north of the protected zones (e.g. Pulatov et al. 2014; EFSA 2020). Further, with climate change it is likely that the conditions for establishment of the CPB further north will improve in the future.

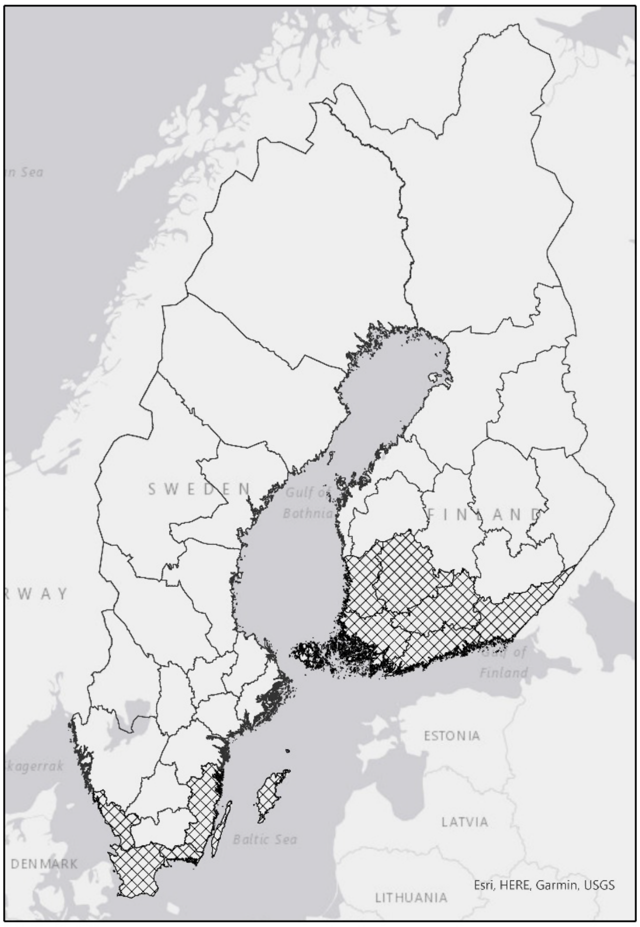

Figure 1. The protected zone for the CPB (crosshatched areas) in Sweden (five counties, i.e., Blekinge, Gotland, Halland, Kalmar and Skåne) and Finland (seven Centres for Economic Development, Transport and the Environment (ELY), i.e. Ahvenanmaa, Häme, Kaakkois-Suomi, Pirkanmaa, Satakunta, Uusimaa and Varsinais-Suomi). The borders of the Swedish counties were sourced from GADM (2020), and the borders of ELYs from Statistics Finland (2022a).

[1] Annex III of (EU) 2019/2072, Official Journal of the European Union, L 319, 1-279 https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A32019R2072

The Risk Assessment Unit of the Finnish Food Authority and SLU Risk Assessment of Plant Pests in Sweden were requested to assess the potential for establishment[2] of CPB in Finland and Sweden. Specifically, the risk assessments units were asked to specify the geographical areas in Finland and Sweden where the conditions are likely to be suitable for the CPB to establish given a climate change scenario for the years 2023–2040.

The potential area for establishment of the CPB was assessed based on the likelihood for the pest to survive and reproduce taking into account both the ecoclimatic conditions and the availability of host plants. The likelihood of entry to the country and the likelihood of transfer to suitable hosts, which may vary between different parts of the countries, were not taken into account in the assessment.

An analysis to support surveillance of the protected zone for the CPB in Sweden is presented in another report. That report deals with the adequate width of an inner band within the protected zone where surveys should be conducted more intensively following Commission delegated regulation ((EU) 2022/2404) (Björklund and Boberg 2024).

2 Distribution and range expansion

2.1 From a regional to a global distribution

The CPB is native to North America, where the Central Plains of the USA are considered its center of origin (Izzo et al. 2018). During the mid-19th century, the CPB expanded its host range from native *Solanum* species to cultivated potatoes and started to spread rapidly across the potato production areas in the USA and Canada (Alyokhin et al. 2013; Izzo et al. 2018). According to de Wilde and Hsiao (1980), the pest occurs in North America between 15 and 55° North Latitude.

In Europe, the first established population of the CPB was found in 1922 in the Bordeaux area of France (Feytaud 1950). Since then, the pest has swiftly extended its range across Western and Central Europe, reaching the eastern parts of Europe in 1949 (Alyokhin et al. 2013). Currently, the CPB is prevalent throughout Europe, with the exception of the Nordic countries, Ireland and the UK[3] (CABI 2021; IPPC 2023b; EPPO 2023a). It is also widely distributed in Russia reaching the Far East in Primorsky Krai in 2000 (Popova and Semenov 2013 and references therein; Bieńkowski and Orlova-Bienkowskaja 2018 and references therein). Beyond Russia, the CPB has also extended its range to the Middle East and Central Asia, reaching China in 1993 (Alyokhin et al. 2013; Liu et al. 2012).

[2] We here use the IPPC definition of the word, i.e. establishment (of a pest) refers to perpetuation, for the foreseeable future, of a pest within an area after entry (IPPC Secretariat. 2023).
[3] In 2023 the CPB was found in a single potato field and it is under official control (EPPO 2023d).

The spread of the CPB has been rapid, but its latitudinal spread has lately slowed down in Europe, presumably due to unsuitable climatic conditions and the northern photoperiod conditions to which the pest has only gradually adapted (Lehmann et al. 2014). For example, the pest was first found in Estonia in 1965, but it took two decades until it had successfully established in the region (Hiiesaar et al. 2006 and the references therein).

It has been suggested that the CPB has not yet reached its potential range in Russia and continues to spread both eastwards and northward, and that it should reach the White Sea coast by 2031–2050 (Popova and Semenov 2013; Popova 2014). The current northern limit of the pest's range in Russia passes through the southern and central Republic of Karelia and the Republic of Komi, as well as Arkhangelsk, Tyumen, Tomsk oblasts, and Krasnoyarsk Krai (Popova and Semenov 2013; Bieńkowski and Orlova-Bienkowskaja 2018). Boman (2008) determined the distribution of the pest around Lake Ladoga and identified a population near Petroskoi (61.47° N) as the northernmost established population in Russia at that time (Figure 2; Table 1). Bieńkowski and Orlova-Bienkowskaja (2018) reported even more northern populations from the Republic of Komi, the northernmost in the town of Yemva (62.58° N, 51.85° E).

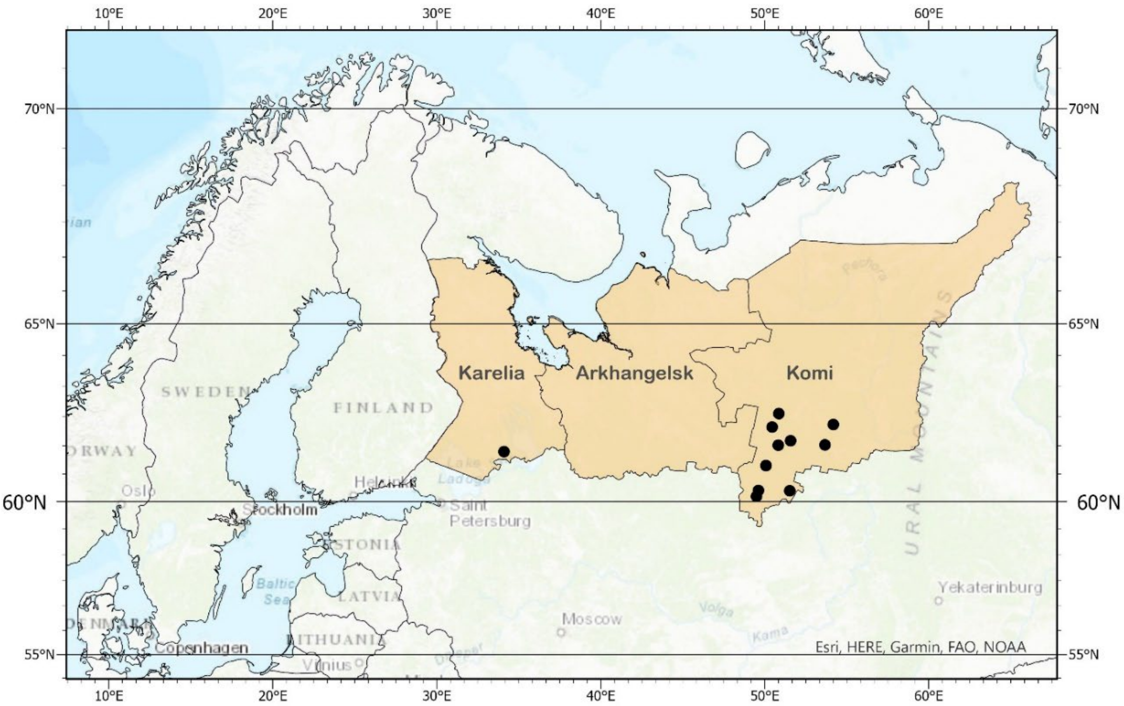

Figure 2. The northern limit of the CPB’s range in the European part of Russia passes through the southern and central Republic of Karelia and the Republic of Komi and the Arkhangelsk region). The black dots show the locations in Russia north of the 60th parallel where the CPB is known to be established. Data was obtained from Boman 2008 and Bieńkowski and Orlova-Bienkowskaja 2018. The region borders were sourced from GADM (2020).

2.2 History in the Nordic countries

In Denmark the first year of significant problems due to CPB was in 1949, the pest entered the country with imported potatoes and larvae were found up to 14 km from the German border (Hurst 1975). In 1978, there was a permanent population of the CPB in Denmark according to Hämäläinen and Markkula (1978). The same year the State Plant Pathology Institute (1978) emphasized that they had managed to decrease the population levels of the CPB, and they were convinced that, given enough resources, they would be able to eradicate it. In 1979, the population levels were lower, but the pest was still present (Bejer and Esbjerg 1980). In 1996, the CPB was listed as a Danish species (and not under the category "Accidental migrants and introduced species") in the Catalogue of the Coleoptera of Denmark (Hansen 1996). One year later, the obligation to report findings of the CPB was lifted (Landbrugsstyrelsen 2023) and presumably all attempts to eradicate the beetle were stopped. In 2004 Landbrugs- og Fiskeristyrelsen stated that the CPB had failed to establish, primarily because the Danish winter climate, with alternating cold and warm temperatures, caused a significant increase in winter mortality (Hansen et al. 2004). The winter climate combined with the control measures that were carried out in the Danish potato fields were, however, assumed to still prevent major impact of the pest (Hansen et al. 2004). In 2011, the CPB was classified as present in Denmark in the Catalogue of Palaearctic Coleoptera (Löbl and Smetana 2011). In 2017, the problem caused by the recently increased abundance of the CPB to the insecticide-free organic production of potatoes was raised (Landbrugs- og Fiskeristyrelsen 2017). In the same year, the Danish CPB population was considered stable in an evaluation for the Danish Red List by Aarhus University (2023). Currently, the CPB is well established in Denmark (Hans Peter Ravn, Københavns Universitet, pers. com. 2023). The population of the CPB in Denmark consists of a mixture of domestic beetles and beetles that fly in from countries south of Denmark (Bejer and Esbjerg 1983; Hansen et al. 2004). At present, EPPO classify the pest status as "Present, few occurrences" (EPPO 2024) but it should be noted that the CPB is reported relatively frequently (Arter.dk 2023; Beetlebase 2023; GBIF 2023; Naturbasen 2023). The degree to which the increase in frequency of observations of the CPB stems from a climate change-induced increase in suitability of the climate or to the deregulation of the CPB is unknown.

In Finland, the CPB has occasionally been found since 1948 on imported potatoes, but also on other commodities, as well as on vehicles (Hämäläinen and Markkula 1978; Ekbom 1982; Grapputo et al. 2005; EPPO 2023f). Further, the CPB has entered Finland through natural spread with air currents. In some cases, individual beetles may have been able to overwinter in the southernmost parts of Finland (Evira 2008). The most recent outbreaks were during the summer of 2021 in the municipality of Parikkala and the commune of Tuulos (EPPO 2023e; Finnish Food Authority 2023). So far, all findings have been eradicated, and consequently, the CPB is considered absent from the country (EPPO 2023f).

The CPB has been intercepted several times in Norway since 1948, but there appears to be no outbreaks in potato fields (Hofsvang, 1996; Rafoss and Saethre, 2003; EPPO 2023c). It is currently considered absent from the country (EPPO 2023c; Miljolare.no 2023).

In Sweden, the CPB was found for the first time already in 1876, when three individuals were detected by customs, presumably arriving directly from America since the CPB was not established in Europe at that time (Ahlberg 1937). After that, the CPB was not detected for a long time but since 1965 it has occasionally been reported mainly in the field but also in association with imported commodities (Gränsbo 1980; SLU 2023a). A mass invasion occurred in 1972 when enormous numbers of beetles were carried by the winds to the southern parts of Sweden in early June, mainly to the counties of Skåne and Blekinge but also to Halland (up north to the city Falkenberg) and Småland (to the city Västervik) as well as to the island Öland (Johansson 1973). The beetle was found in more than 2000 potato fields (of which almost 25% were home gardens), corresponding to 5600 ha. Massive eradication measures were undertaken in the infested areas in the following years (Johansson 1973; Gränsbo 1973, 1974, 1980). During these years, additional beetles also flew in from continental Europe (Gränsbo 1974, 1975, 1980). It was considered that unsuitable climatic conditions, in combination with the implemented eradication measures, prevented the establishment of the CPB in Sweden (Gränsbo 1975, 1980; Wiktelius 1985). The pest was reported as eradicated by the Swedish Plant Protection Service in 1978 (EPPO 1978). A smaller invasion occurred in 1983, but this time during August (Wiktelius 1985). Beetles were found along the coast of Halland and in potato fields in Skåne, Halland and Blekinge. A combination of high populations in Germany and Poland and conductive weather and wind directions is believed to have caused these mass invasions (Johansson 1973; Wiktelius 1985). The most recent outbreak in Sweden was in 2021 in Skåne (EPPO 2023g). Larvae were found in one potato field in the area around the city Kristianstad (Swedish Board of Agriculture 2021). Eradication measures were taken, and no beetles were found in subsequent surveys in 2022 and 2023. The pest status is reported as “Absent, pest eradicated” by the Swedish NPPO (EPPO 2023g).

2.3 Conclusion on the range expansion

During its remarkable range expansion, the CPB has shown extraordinary adaptability to new ecoclimatic conditions. Further, it is very likely that beetles will arrive in Finland and Sweden also in the future, both through natural spread and with human-assisted spread.

3 Life history and traits relevant for the establishment in the north

3.1 Life cycle

The development time of the CPB is temperature-dependent, and in the northern extent of its distribution, conditions typically support only one generation per year (Boiteau, G. 2001; Hansen et al. 2004; Smatas et al. 2008; Popova 2014; Hiiesaar et al. 2016; EFSA 2020; Hiiesaar et al. 2020; Naturbasen 2023). The CPB overwinters as adults[4], and in the northern part of its range beetles usually burrow down into the soil to a depth of 20–50 cm but sometimes they dig as deep as 100 cm in dry mineral soil (Johansson 1973). Studies in Sweden have shown that the

[4] According to Jernelöv (2017) and Bebber (2015) it can overwinter as a pupae but no information was provided to support that statement and it is not in agreement with information from other sources.

adults leave their winter dwelling places in May-June and walk or fly to their host plants (Gränsbo 1974; Gripwall 1993). The adults feed and mate after which each female may lay up to 2000 eggs (CABI 2021). The eggs hatch in 8–10 days (Johansson 1973), after which the larvae emerge and start feeding on leaves. After about two weeks, the CPB has completed its fourth instar stage and pupates in the soil (Johansson 1973). After another two weeks, the adults emerge and begin feeding. Depending on the conditions, i.e., temperature, quantity and quality of food sources, and daylength, the beetles either burrow down to enter diapause and overwinter or they mate and start laying eggs for a second generation (Johansson 1973). The temperature accumulation required for different developmental steps, and for the development of a complete generation, is measured as growing degree days (GDD). There are several estimates of the GDD requirements for the CPB (see Appendix 1).

3.2 Traits relevant for surviving in the north

Cool and short growing seasons and harsh winter conditions are considered the main challenges for the further northward expansion of the CPB (Boman et al. 2008). Both arguments have, however, been challenged.

It has been argued that cool and short growing seasons are unlikely to strongly limit the northward expansion of the CPB since there is genetic variability in its growth-related traits, which would facilitate adaptation to such conditions (Lindström and Lehmann 2015). In addition, there are mechanisms that may, at least theoretically, allow populations to survive over the years when the summer conditions do not allow the development of one complete generation. A small proportion of the beetles have a prolonged diapause which should enable them to survive over the years when the GDD does not allow one complete generation. For example, a prolonged diapause was observed for 2.3% of 12 607 beetles in a 10-year field study in Upstate New York (Tauber and Tauber 2002). Most beetles with prolonged dormancy emerged after two years but some emerged after 3-9 years. Further, some beetles survive a second winter and can lay fertile eggs the following spring (Campell et al. (1989) citing other sources). Finally, the CPB females may already have mated when they enter diapause (Johansson 1973; Tauber and Tauber (2002) citing another source) and therefore should get a head start the following season since they don't need to find a male.

A field study showed that major winter mortality occurred only when the air temperature dropped below -30 °C for a long period. Even in such conditions, 12% of the beetles survived in light soils, i.e., soils high in sand relative to clay (Hiiesaar et al. 2006). In field experiments in southern Sweden, only 19% of the beetles died in mineral soil whereas in more compact and water retaining soil, the mortality was approximately twice as high (Johansson 1974). The experiments were repeated the following winter, but only in light soils, and approximately 50% of the beetles survived that winter (Johansson 1975). The lowest recorded soil temperature was -4 C° the first winter and -1 C° the second winter. The author concluded that mortality due to cold temperatures was probably insignificant and that the overwintering conditions are unlikely to prevent the CPB from establishing in the dry light soils in south-eastern Sweden.

In Estonia, the survival of overwintering beetles varied from 18 to 47% during seven years (Hiiesaar et al. 2016). The conditions during hibernation, e.g. low winter temperatures, were not considered to threaten the survival of beetles in any of the years. Instead, the summer conditions, i.e. the quality and availability of food and the summer weather conditions, were considered to determine winter mortality.

Interestingly, despite the challenges that the CPB faces in its northern range, the population densities can be high, as reported in northern Russia (Boman et al. 2008).

3.3 Adaptation and variability among the CPB populations

The CPB shows remarkable adaptability (Cingel et al. 2016). For example, the populations in the northern part of its range differ from the other populations in many aspects that are relevant for its establishment potential. Northern populations require a longer daylength for diapause initiation than populations further south (Tauber et al. 1988c; Lehmann et al. 2014). Populations also differ in cold tolerance (Hiiesaar et al. (2014) and references therein). Populations far north in Russia have been shown to develop faster and have a higher survival rate in cooler conditions than populations further south (Boman et al. 2008). Also in America, the thermal development thresholds were lower and development faster for populations from cooler areas (Tauber et al. 1988b). Populations differ also with regard to behaviors, i.e. in the north, locally adapted "winter hardy" phenotypes for example dig deeper and overwinter in the warmer parts of the soil profiles (Izzo et al. 2014).

3.4 Conclusion on the traits relevant for the establishment

Based on the studies described above, we conclude that the suitability of the climate for the CPB in the northern part of its range appears to mainly depend on the summer temperatures required to complete one generation.

The CPB populations that have survived in the northern range of the current distribution differ in many aspects from the populations further south. Accordingly, further adaptations may be necessary before the CPB can survive even harsher conditions. In the current assessment, however, we do not take the possibility of future adaptations into account but instead base the assessment on information about the populations in the coldest areas where it is established.

4 Results from previous climate suitability studies

The climate suitability and potential distribution of the CPB have been estimated using different modelling approaches such as CLIMEX, Maxent and phenology models. Here we provide a brief account of those that have addressed the potential for establishment of the CPB in Finland and Sweden.

4.1 Historic, recent and future climate

The potential distribution of the CPB has been estimated in numerous studies by using the Compare Location model of the CLIMEX software (Kriticos et al. 2015) (Worner 1988; Sutherst et al. 1991; Baker et al. 1996, 1998; Rafoss and Sæthre 2003; Kocmánková et al. 2010, 2011; Svobodová et al. 2013, 2014). This model estimates the potential distribution of a species based on a set of climatic variables that reflects the seasonal growth and reduction of a species' population (Kriticos et al. 2015). The model provides a measure of the climatic suitability of a specific location for a species as an Ecoclimatic Index (EI) ranging from 0 to 100, where EI = 0 indicates unsuitable climate and EI > 0 indicates suitable climate to a varying degree (Kriticos et al. 2015).

Baker et al. (1998) analyzed the potential distribution of the CPB in Europe with CLIMEX using climate data for 1961–1990 and parameters estimated by Sutherst et al. (1991). The model predicted climate to be unsuitable in Finland while the EI was 10–20 for some parts of southern Sweden (northern limit approx. *Limes Norrlandicus*). Using a climate scenario for 2035–2065 (equivalent to a mean of 2.3°C warming of Europe), Baker et al. (1998) predicted that the area with EI values > 0 would extend to cover the southern half of Finland. The suitable area in Sweden was not predicted to reach the same latitude, although the EI values were predicted to increase to 25–35 in parts of south-western Sweden. The results based on this CLIMEX model must be used with caution since the parameters used, i.e., those from Sutherst et al. (1991) have been shown to mispredict the distribution of the CPB in China (Bebber 2015). Also, the CPB is a very adaptable species with both behavioral and physiological adaptations observed in its northern populations (Lehmann et al., 2014; 2015; Bebber 2015).

Svobodová et al. (2013) adjusted the parameters estimated by Sutherst et al. (1991), e.g., lowered the threshold temperature for development but kept the number of GDD, and used climate data for 1961–2000. Svobodová et al. (2013) suggested that the potential northern range would follow EI values of 24–27, which correspond to some coastal areas in southern Finland and Sweden. Svobodová et al. (2014) estimated the potential range of the CPB in 2055 using five global circulation models. Under a high emission scenario (SRES A2), the northern limit was predicted to move north to 64.8°N (which corresponds to the north of Skellefteå in Sweden and south of Oulu in Finland). It is unclear why an EI of 24 –27 was used as a threshold for potential establishment in Svobodová et al. (2013) and whether the same threshold was used in Svobodová et al. (2014). Thus, we could not fully evaluate these results.

Wang et al. (2017) and Gao et al. (2022) used the MaxEnt software (Phillips et al. 2006) for species distribution modelling to project the potential global range of the CPB under recent and future climate. Wang et al. (2017) predicted that the northern parts of Finland and Sweden would not be suitable for the CPB in the recent climate (1950–2000). However, by 2050, both the low emission Representative Concentration Pathway (RCP) scenario (RCP2.6) and the high emission scenario (RCP8.5) indicated that even the northern regions of these countries would become suitable for the CPB. In contrast, Gao et al. (2022) predicted that most parts of Finland and Sweden are suitable for the establishment of the CPB already in the recent climate (1970–2000) and in a future climate (2021-2040) the entire countries were assessed to become suitable under all the considered Shared Socioeconomic Pathway (SSP) scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0, SSP5-8.5). Although both studies tried to eliminate biases and inaccuracies from the distribution data of the CPB used in building the MaxEnt models, the datasets still contained records from Scandinavia and northern Russia, which do not represent established populations (cf. section 3.1). Consequently, our interpretation is that these models overestimate the potential distribution towards the northern range.

The potential distribution of the CPB has also been analyzed using phenology models, which couple the developmental stages of the pest with temperature and day length (Jarvis and Baker 2001; Jönsson et al. 2013; Pulatov et al. 2014). Pulatov et al. (2014), studied the effect of climate change on the potential spread of the CPB in Scandinavia using the phenology model of Jönsson et al. (2013). Pulatov et al. (2014) used the parameters from Jönsson et al. (2013) corresponding to the fastest developing individuals with low development thresholds. Consequently, a threshold temperature of 10°C was used to calculate the GDD required for the development of the pest corresponding to 411 GDD. The model also included flight initiation (at ≥ 15°C) and the initiation of diapause (at a certain day length, which corresponds to 18 h in the Nordic region). Notably, the GDD of 411 did not include the GDD required for egg hatching or the GDD needed by the adults to prepare for overwintering. Simulations were done both using observed temperature data (1961–1990) and climate model data (1961–2050) based on the intermediate emission scenario A1b. Simulations based on observed temperature data indicated that one generation could not be completed in all years in most parts of Sweden and all of Finland. However, for the southern parts of both countries, completing one generation was predicted to be possible in most of the years. Results based on climate model data for the time period 2021–2050 did not differ to any large extent. However, the authors also show that the modelled climate data had a cold bias, i.e. were colder than the observed data (Pulatov et al. 2014). Further, results from the phenology model were also reported to be highly sensitive to biases in the climate data (Jönsson et al. 2013). In fact, established populations are found further north than indicated by the phenology model, e.g. in Estonia and Russia (Hiiesaar et al. 2001; Bieńkowski and Orlova-Bienkowskaja 2018).

Pulatov et al. (2016) studied whether any phenological mismatches between the CPB and cultivated potato would limit the northward expansion of the CPB in Europe under future climate. They used the phenology model by Jönsson et al. (2013) and bias corrected climate data for the period 1981–2099 assuming the high RCP scenario 8.5. The results indicated that in the future climate (2041–2070), at least the fastest developing individuals could complete one generation per year in large parts of southern Finland and Sweden and around the Baltic Sea. The model results further indicated that in most years, in a large part of this region, the diapause conditions are met in the autumn, preventing the initiation of a second generation, which is unlikely to be successful. However, asynchrony between the beetle's life cycle and the availability of the potato host may lead to a lack of food for up to two weeks in southern and central Sweden. In such situations, hosts other than potato may be important for the potential establishment of the CPB (see Section 6.1).

4.2 Conclusion on the previous climate suitability studies

In conclusion, several climate suitability studies, which include Finland and Sweden, have been performed previously using different modelling approaches. However, due to some of the assumptions made (as explained above) and since, in most cases, the considered time period did not correspond to the one in focus here, we did not consider any of the results directly applicable for this assessment.

5 Identifying the potential area where the climate is suitable for the establishment

Based on information in previous studies, we concluded that the suitability of the climate for the CPB in the north appears to mainly depend on the growing degree days (GDD) required to complete one generation (see Section 3.4). The GDD required was therefore used to identify the area in Finland and Sweden where the climate conditions are likely to be suitable for the establishment.

5.1 Estimating the GDD required by the CPB

While the GDD required for the development of different life-stages of the CPB has been extensively studied under both laboratory and field conditions (see Appendix 1), defining a threshold GDD required for the CPB establishment in new areas is challenging. This is because the results of studies on the GDD requirements of the CPB vary a lot, particularly concerning the GDD needed for preoviposition (Appendix 1). This variation is partly related to differences between the CPB populations (e.g. Tauber et al. 1988a; 1988b), which may for example be due to adaptations to a cool climate (Lehmann et al. 2014), as well as differences among individual beetles within populations (e.g. Lashomb et al. 1984; Mailloux et al. 1988; Tauber et al. 1988b). Moreover, differences between results from laboratory and field studies indicate that factors beyond temperature also greatly influence the CPB development (e.g. Tauber et al. 1988b). Further, for a highly adaptable species like the CPB, the use of GDD requirements of populations that are not adapted to the climatic conditions in the pest risk assessment area is likely to give misleading results (Bebber 2015).

We therefore opted for an alternative approach in which temperature data from the coldest known habitat of the pest was used to determine the minimum GDD necessary for its lifecycle completion. This approach has been recommended to determine the minimum GDD for insect species that require more than one year to develop in specific regions (Kriticos et al. 2024). It was deemed appropriate for determining the minimum GDD requirement of a species which is known to develop faster in certain regions. Thus, to estimate the GDD required for the CPB establishment at the northern front of its potential range we calculated the long-term mean annual GDD within the northernmost distribution areas of the pest in Russia, i.e. for populations adapted to cool conditions. While this approach does not provide exact information about the minimum GDD required for the establishment, it does provide an estimate of the GDD in the coolest conditions where the pest is established. The annual variation in the GDD was not considered, because the CPB populations are not expected to die out if the GDD requirement is not fulfilled every year (e.g. due to prolonged diapause; see section 3.2), and because comparing the variation between individual sites to the entire PRA area is problematic.

We calculated the two-decade mean annual GDD in locations where the CPB is known to be established in Russia, north of the 60th parallel (Figure 2; Boman 2008; Bieńkowski and Orlova-Bienkowskaja 2018). The calculation was made using daily air temperature data from 1997 to 2016 at a spatial resolution of 300 arc-seconds[5] (Karger et al. 2017; Karger et al. 2022) and Method 1 by McMaster and Wilhelm (1997), with the minimum threshold temperature for development set at 10 °C. The analysis revealed that the lowest two-decade mean annual GDD among the locations in this northern distribution area of the CPB in Russia was 587, in Karelia near the city of Petroskoi (Table 1).

Table 1. The two-decade mean annual growing degree days (GDD) above 10 °C for the most northern locations in Russia where the Colorado potato beetle is known to be established.

Region	Latitude	Longitude	GDD	References
Karelia	61.49	34.10	587	Boman 2008; Lehmann et al. 2020[1]
Komi	62.27	54.18	610	Bieńkowski and Orlova-Bienkowskaja 2018
Komi	62.58	50.85	639	Bieńkowski and Orlova-Bienkowskaja 2018
Komi	61.69	53.67	650	Bieńkowski and Orlova-Bienkowskaja 2018
Komi	62.2	50.44	672	Bieńkowski and Orlova-Bienkowskaja 2018
Komi	61.81	51.58	682	Bieńkowski and Orlova-Bienkowskaja 2018
Komi	61.68	50.83	699	Bieńkowski and Orlova-Bienkowskaja 2018
Komi	61.08	50.08	723	Bieńkowski and Orlova-Bienkowskaja 2018
Komi	60.34	49.61	744	Bieńkowski and Orlova-Bienkowskaja 2018
Komi	60.16	49.49	757	Bieńkowski and Orlova-Bienkowskaja 2018
Komi	60.33	51.53	788	Bieńkowski and Orlova-Bienkowskaja 2018

[1] Boman (2008) only provides the latitude (i.e. 61°47′N) for the findings of the CPB near Petroskoi. However, Lehmann et al. (2020) provide the full coordinates of the CPB collected near Petroskoi (61°49′N, 34°10′E) in 2006. Those coordinates were used for the calculations of the GDD.

[5] This resolution translates to a grid cell size of approximately 6 square kilometers for the most northern locations in Russia where the Colorado potato beetle is known to be established (Table 1).

5.2 Delineating the areas in Finland and Sweden where the GDD requirement is met

To study if and where in Sweden and Finland the GDD exceed 587 in the recent climate, we calculated the two-decade mean annual GDD across Sweden and Finland using daily air temperature data from 2003–2022 at a resolution of 4 x 4 km for Sweden (SMHI 2023a) and 10 x 10 km for Finland (Aalto et al., 2016). The calculations were done using Method 1 by McMaster and Wilhelm (1997), with the minimum threshold temperature for development set at 10 °C.

To assess where the mean annual GDD of 587 above 10 °C is met in the future, we made two projections for 2040 under the intermediate RCP4.5 emission scenario. These projections were based on two separate datasets of running 20-year mean daily air temperatures centered on 2040. The first dataset (SMHI 2023b) was based on the mean values of an ensemble of 22 simulations with regional climate models at horizontal resolution of 12.5 x 12.5 km from the CORDEX program (Vautard et al. 2020; Coppola et al. 2021). These simulations were then bias adjusted to minimize systematic errors in the simulations over a region covering Scandinavia (Berg et al. 2022; SMHI 2024). The dataset covers Sweden and Finland, except the eastern part of North Karelia in Finland. The second dataset, provided by the Finnish Meteorological Institute (FMI), covered the entire Finland at a resolution of 10 x 10 km. The methodology used to project the future daily temperatures using this dataset is explained in Appendix 2. The two-decade mean annual GDD centered on 2040 was calculated using the same method used for the recent climate.

The results show that the two-decade mean annual GDD exceeds 587 in southern parts of Finland and Sweden (Figure 3). The results for the future climate indicate that by 2040 the mean annual GDD exceeds 587 also in the central parts of Finland and the coastline areas around the Baltic Sea. The results of the two future climate projections are clearly different (Figure 3). The projections differ because they are computed using different methods and climate models.

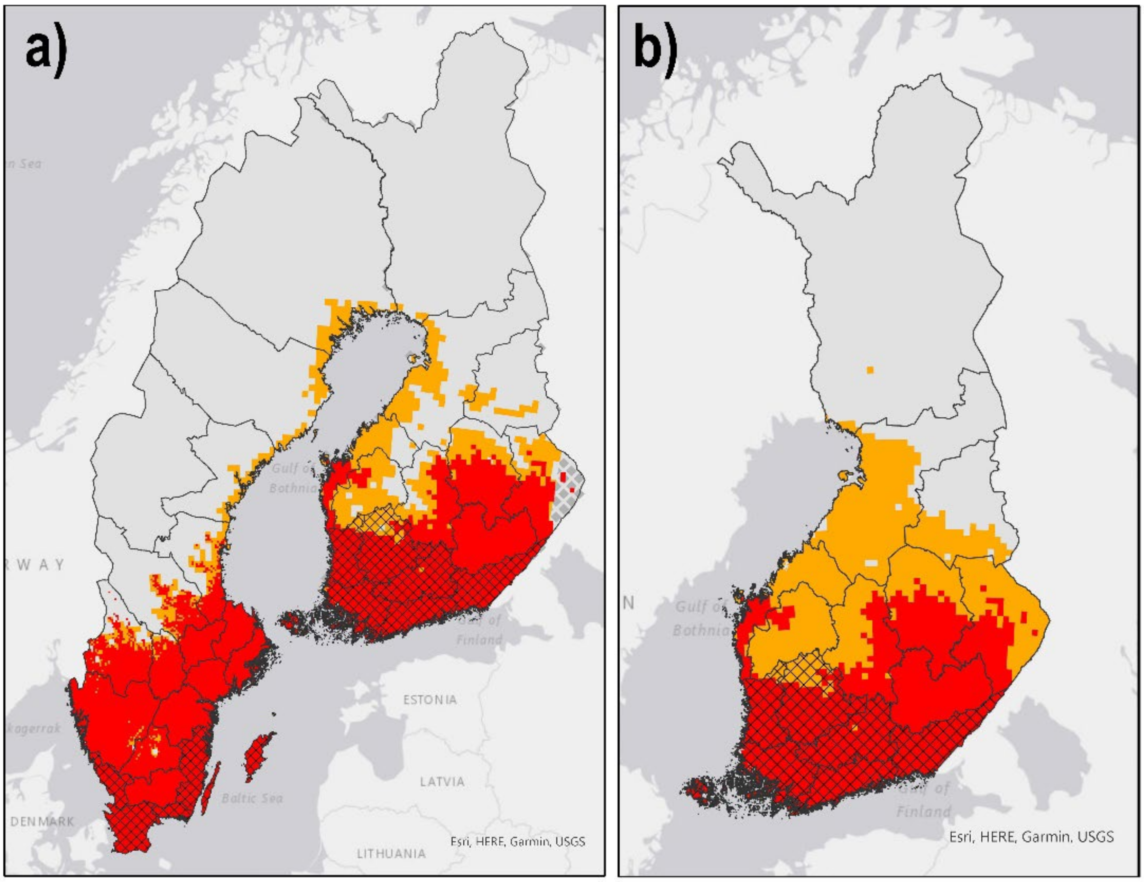

Figure 3. Areas where the requirement of 587 GDD above 10°C is met in the recent climate (2003–2022) and in a future climate (2031–2050) using data from a) SMHI and b) FMI. Red shading indicates areas where the GDD requirement is met in the recent climate, while orange shading indicates the additional areas where the requirement is met also in the future climate (virtually all areas that are suitable in the recent are also suitable in the future climate). Crosshatched pattern denotes protected zones, and diamond-filled areas (only in the eastern part of North Karelia in Finland) (in a)) are not covered by the future climate dataset from SMHI. The borders of the Swedish counties were sourced from GADM (2020) and the borders of ELYs from Statistics Finland (2022a). Explore the data in an interactive map here.

When interpreting the results, it is important to consider the impact of the GDD value that was used. Since the CPB populations vary in their GDD requirements (see 5.1 and Appendix 1), the potentially suitable area for establishment might differ depending on the origin of the population. Therefore, if the invading CPB population originates from warmer climatic conditions, such as Denmark, Northern Germany, Northern Poland, Estonia, Leningrad oblast or the southern parts of Russian Karelia, the suitable area for establishment may be smaller than predicted above. The GDD requirements of these other populations was not considered because comprehensive data was not available (see Appendix 1). Nor could the GDD requirements be obtained using a similar approach as we used for the most northern population since populations further south may not need all the available GDD or may have several generations per year. Moreover, even if data on the GDD requirements of southern CPB populations were available, using it to define the potential area for establishment would not be appropriate. This is because assessments should consider the entire known variation within the target organism.

Consequently, populations adapted to northern conditions typically define the northern limit of the potential range of the organism in the PRA area. Furthermore, the likelihood of different CPB populations entering Finland and Sweden is unknown. Given these circumstances, our assessment was based on a scenario where the threshold GDD for the establishment was determined by the conditions endured by probably one of the most cold-adapted populations of the CPB. It is worth noting, that there is also a possibility that we have underestimated the potential area of establishment since the populations in the most northern locations in Russia may fulfil their life cycle with fewer GDD than indicated by the value obtained in our estimation and there could be CPB populations even further north than the most northern locations in Russia we are aware of. In order to investigate how sensitive the results are to the GDD requirement used, we mapped the areas where GDD was 10% and 20% higher than the used GDD requirement (equivalent to 646 and 704 GDD respectively; Figure 4). A 10% increase in GDD requirement did not result in a major decrease in the area where the requirement is met in either recent or future climate. Increasing the GDD requirement by 20% had a much larger effect. However, the area where the requirement is met would still be much larger than the protected zone both in Sweden (in the recent and future climate) and in Finland (in the future climate).

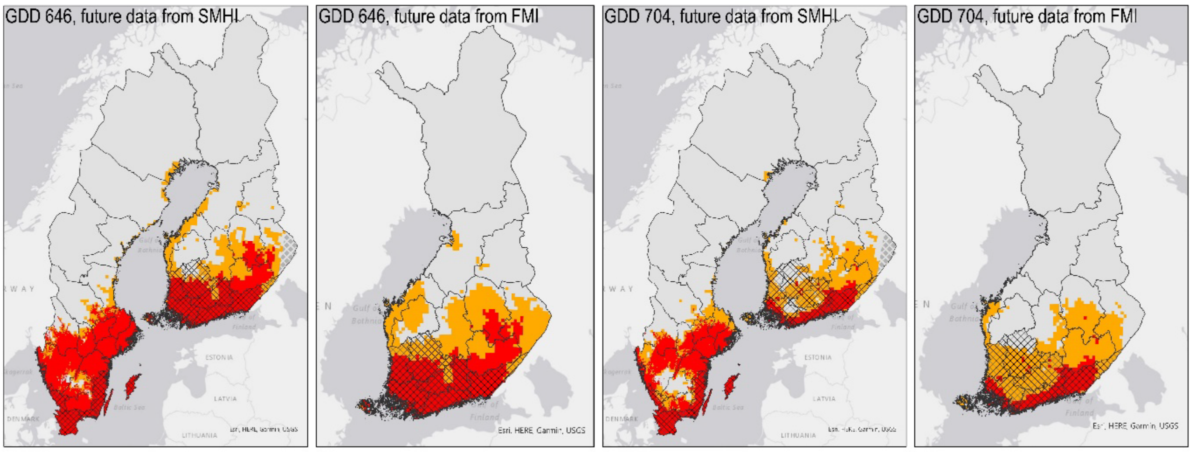

Figure 4. Areas where a GDD-requirement increased by 10% (GDD = 646 above 10°C) and 20% (GDD = 704 above 10°C) is met in the recent climate (2003–2022) and in a future climate (2031–2050) using data from SMHI and FMI. Red shading indicates areas where the GDD requirement is met in the recent climate, while orange shading indicates the additional areas where the requirement is also met in the future climate (virtually all areas that are suitable in the recent climate are also suitable in the future climate). Crosshatched pattern denotes protected zones, and diamond-filled areas are not covered by the future climate dataset from SMHI (only in the eastern part of North Karelia in Finland). The borders of the Swedish counties were sourced from GADM (2020) and the borders of ELYs from Statistics Finland (2022a). Explore the data in an interactive map here.

5.3 Conclusion on the GDD analysis

In conclusion, we assessed that the recent climate is suitable for the establishment of the CPB in large areas in the southern parts of Finland and Sweden, and by 2040, also in central Finland and the Baltic Sea coastline (Figure 3).

6 Hosts and dispersal

6.1 Host availability in Finland and Sweden

Potato (*Solanum tuberosum*) is the major host of the CPB (EPPO 2023h). The pest is also reported to feed on other Solanaceous plant species. EPPO (2023h) lists the following species as hosts; *S. melongena*, *S. lycopersicum*, *S. elaeagnifolium*, *S. rostratum*, *S. dulcamara*, *S. nigrum*, *S. sarrachoides* and *Hyoscyamus niger*. Examples of other hosts mentioned in the literature include *S. carolinense* (Hare and Kennedy 1986), *S. angustifolium* (Lu and Logan 1993), *S. nitidibaccatum* (Crossley and Schoville 2019), *S. laciniatum* (Bieńkowski and Orlova-Bienkowskaja 2018 and the references therein) and *S. villosum* as well as *Nicotiana alata* (Hiiesaar et al. 2020) and *Atropa belladonna* (Bieńkowski and Orlova-Bienkowskaja 2018 and the references therein). *Solanum rostratum* and *S. angustifolium* are considered to be the original hosts (Lu and Logan 1993; Alyokhin et al. 2013).

The degree to which the CPB feeds on the reported hosts appears to differ depending on the population and location, and adaptation to new hosts appears to be required in some cases (Hare and Kennedy 1986; Lu and Logan 1994; Hiiesaar et al. 2020 and references therein). Hiiesaar et al. (2020) investigated the potential of different Solanaceae plants as hosts for Estonian populations of CPB. Newly hatched larvae were able to complete their development on *S. melongena*, *S. dulcamara*, *N. alata*, and *S. lycopersicum*, but development was delayed, adult mortality after emergence was higher and adults underweight on the latter three hosts. Further, adult beetles only feed on *S. nigrum* and *S. villosum* if starved.

The availability of suitable hosts varies across Finland and Sweden (Table 2 and Figure 5, 6). In 2022, potato was cultivated commercially on 19 600 ha and 23 400 ha in Finland and Sweden, respectively (Swedish Board of Agriculture 2022; OSF 2023a). Potato is cultivated in large parts of the countries but is aggregated in western Finland and southern Sweden (Figure 5). Potato is also commonly grown in private gardens and allotments (Swedish Board of Agriculture 2014).

In Sweden, both *S. melongena* and *S. lycopersicum* are commercially cultivated in greenhouses (Swedish Board of Agriculture 2020). In Finland, *S. lycopersicum* is commercially cultivated in greenhouses while *S. melongena* is not (OSF 2023b). Although both species occur outdoors in private gardens, we assume that they would not be of importance for establishment of the CPB in Finland or Sweden.

Table 2. Reported hosts of the Colorado potato beetle and their presence in Finland and Sweden.

Scientific name	Common names (Finnish / Swedish)	Presence in Finland	Presence in Sweden	References
Atropa bella-donna	belladonna / belladonna	Wild, very rare	Rarely naturalized, perennial	Mossberg and Stenberg 2018; FinBIF 2023; Lampinen and Lahti 2023
Hyoscyamus niger	hullukaali / bolmört	Archaeophyte, near threatened	Wild, rare, annual/biennial	Mossberg and Stenberg 2018; FinBIF 2023; Lampinen and Lahti 2023
Nicotiana alata	valkotupakka/ stor blomstertobak	Wild, very rare	Ornamental, annual, Rarely naturalized	Mossberg and Stenberg 2018; FinBIF 2023; Lampinen and Lahti 2023
Solanum angustifolium		Not reported	Not reported	SLU 2023b; FinBIF 2023; Lampinen and Lahti 2023
Solanum carolinense	carolinankoiso / stickskatta	Wild, very rare	Not reported	SLU 2023b; FinBIF 2023; Lampinen and Lahti 2023
Solanum dulcamara	punakoiso/ besksöta	Native, common in South and Central Finland	Wild, rather common, perennial	Mossberg and Stenberg 2018; FinBIF 2023; Lampinen and Lahti 2023
Solanum elaeagnifolium	kilsekoiso / silverskatta	Wild, very rare	Urban environments, very rare (?)	SLU 2023b; FinBIF 2023; Lampinen and Lahti 2023
Solanum laciniatum	-/ känguruäpple	Not reported	Ornamental, very rarely naturalized	Mossberg and Stenberg 2018; FinBIF 2023; Lampinen and Lahti 2023
Solanum lycopersicum	tomaatti / tomat	Cultivation, in greenhouse	Cultivation, mainly in greenhouse	Swedish Board of Agriculture 2020
Solanum melongena	munakoiso / aubergin	No commercial cultivation	Restricted cultivation, mainly in greenhouse	Swedish Board of Agriculture 2020

Solanum nigrum	mustakoiso / nattskatta	Archaeophyte, common as a weed in fields	Wild, rather common to rare, also a weed, annual	Mossberg and Stenberg 2018; Weidow et al. 2020; Jauni et al. 2021; FinBIF 2023; Lampinen and Lahti 2023
Solanum nitidibaccatum (syn. *S. physalifolium* var. *nitidibaccatum)*	kehtokoiso/ bägarnattskatta	Wild, rare, except common as a weed in fields	Wild, rare, but common as a weed in southern Sweden, annual	Mossberg and Stenberg 2018; Weidow et al. 2020; Jauni et al. 2021; FinBIF 2023; Lampinen and Lahti 2023
Solanum rostratum	kärsäkoiso /taggborre	Wild, very rare	Wild, rare, annual	Mossberg and Stenberg 2018; FinBIF 2023; Lampinen and Lahti 2023
Solanum saccharoides	brasiliankoiso / klibbnattskatta	Wild, very rare	Wild, very rare	Mossberg and Stenberg 2018; FinBIF 2023; Lampinen and Lahti 2023
Solanum tuberosum	peruna / potatis	Cultivation, open field	Cultivation, open field	OSF 2023a; Swedish Board of Agriculture 2023
Solanum villosum	myskikoiso/ gul/röd nattskatta	Wild, very rare	Wild, rare, annual	Mossberg and Stenberg 2018; FinBIF 2023; Lampinen and Lahti 2023

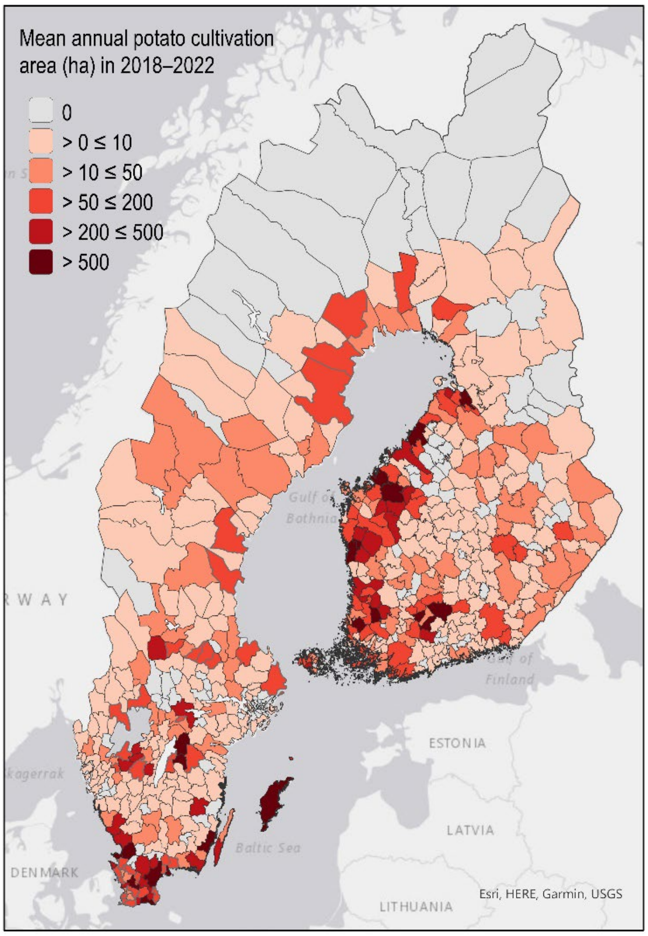

Figure 5. Mean annual commercial potato cultivation area (ha) in the Finnish and Swedish municipalities in 2018–2022 (Swedish Board of Agriculture 2022; OSF 2023a). Note that the category 0 also includes the municipalities for which information was not available. The borders of the municipalities in Sweden were sourced from SCB (2021) and in Finland from Statistics Finland (2022b). Explore the data in an interactive map here.

Of the other hosts, we only consider *S. dulcamara, S. nigrum* and *S. nitidibaccatum* to be of any potential importance for the CPB in Finland and Sweden. Although studies suggest that *S. dulcamara* is a lower quality host than potato, Hiiesaar et al. (2020), suggested that it could serve as an important food source for CPB during the early season when potato plants have not yet emerged and in the late season when potatoes have been harvested or their leaves destroyed by late blight. Both *S. nigrum* and *S. nitidibaccatum* appear to be consumed mainly when potato is not available and beetles experience starvation (Crossley and Schoville 2019; Hiiesaar et al. 2019). However, both species may be common weeds in potato fields (Jauni et al. 2021) and could potentially provide an important food source when potato is not available.

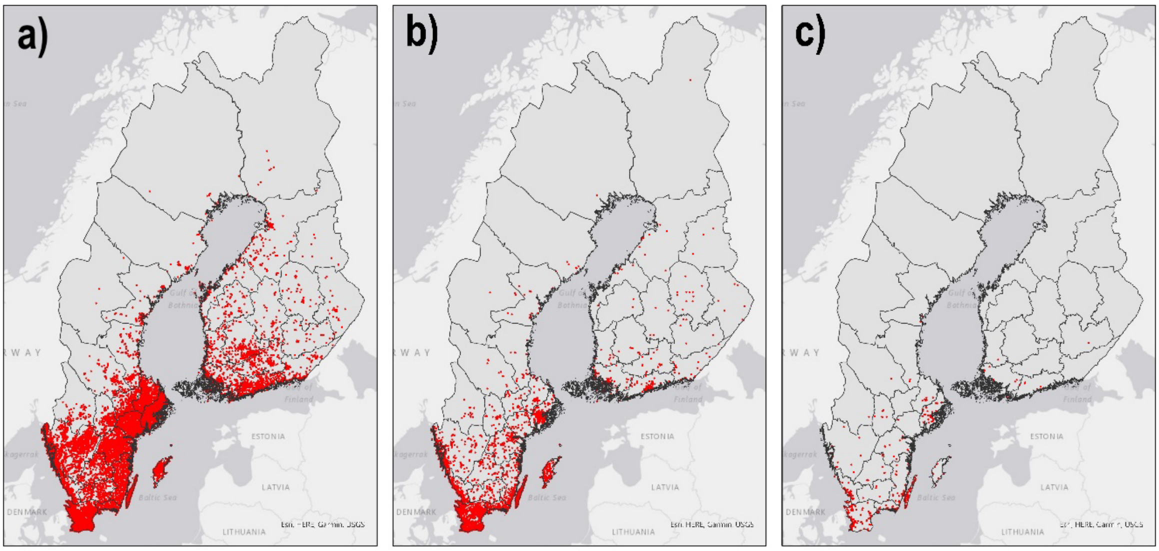

Figure 6. The observations of a) *S. dulcamara*, b) *S. nigrum* and c) *S. nitidibaccatum* in Finland and Sweden (GBIF 2023). The observations include both inventory data as well as reports from the general public. Note that these observations neither cover the entire distribution nor correctly represent the density of the species since some spatial bias in reporting is expected in this type of data and due to the problem of too big and overlapping dots. The borders of the Swedish counties were sourced from GADM (2020) and the borders of ELYs from Statistics Finland (2022a). Explore the data in an interactive map here.

6.2 Dispersal and host finding

The CPB finds its hosts using both visual and olfactory cues (Alyokhin et al. 2013 and references therein). It is however uncertain how well the beetles can locate hosts over long distances (Boiteau et al. 2003).

Migration is facultative and during suitable conditions the beetles often spend their entire lives in the vicinity of the place of eclosion (Grafius 1995; Alyokhin et al. 2013). Different factors such as unfavourable environmental conditions, low food availability and reproductive status can induce dispersal (Boiteau et al. 2003; Alyokhin et al. 2013). Three types of flight are observed; i) short distance low-altitude flight with frequent turning within fields to mate, lay eggs, and find new hosts, ii) long distance migratory flight, generally downwind for several hundred meters or more to colonize new areas, and iii) diapause flight to nearby tall vegetation surrounding fields (Boiteau et al. 2003; Alyokhin et al. 2013). The beetles also move by walking (Boiteau et al. 2003).

During one season mean distance by walking and flying for the adult beetles is 1.5-2 km, with a maximum of 5 km (Boiteau and Heikkilä 2013 and references therein). Only a small part of the population disperses long distances. Very long dispersal distances are associated with strong air currents, e.g. > 100 km as observed from mainland Europe to southern Sweden (Wiktelius 1981).

6.3 Conclusion on the host availability

Potato is cultivated in large parts of the countries, except in the most northern parts. In some municipalities the area with cultivated potato is however very small (≤ 10 ha) (Figure 5). Municipalities with such limited commercial potato cultivation may be less likely to sustain a viable population of the CPB. Since the wild *Solanum* hosts may provide a food source for the beetles before and after the potato crop is available, establishment may be more likely where these occur. The three species *S. dulcamara, S. nigra* and *S. nitidibaccatum* are mainly reported from the southern parts of the countries (Figure 6). It is uncertain to what extent the generally rather short dispersal distances of the CPB affect the capacity of the beetles to establish in landscapes with a low density of hosts. In conclusion, it was assessed that at a regional scale the availability of host plants would not prevent the establishment of the CPB where the climate was assessed to be suitable now or in the future (Figure 2).

7 Conclusion of the assessment

The aim of this assessment was to identify the areas in Finland and Sweden where the climate and host availability are likely to allow the establishment of the CPB at present and in the near future. To achieve this, we calculated the long-term mean annual growing degree days (GDD) in the coldest area in Russia where the CPB is established, and identified the areas in Sweden and Finland with similar or warmer conditions, based on the climate of the past two-decades and two estimates of the climate in 2040 assuming an intermediate emission scenario RCP4.5. These areas were assessed as likely to be suitable for establishment of the CPB at present and in the near future (red and orange area in Figure 2 respectively). We assessed that availability of host plants would not prevent the establishment of the CPB within these areas.

The main uncertainties of the assessment are, ranked by their assumed impact, the GDD requirement used for the analysis, the future climate projections and the abundance of hosts necessary in a landscape to enable the CPB to establish.

8 Other factors hindering establishment in Finland and Sweden

Our results suggest that the conditions have been suitable for the CPB in large parts of the countries during the past 20 years, but it has not established. We assume that this is at least partly due to that the likelihood of establishment in Finland and Sweden may have been reduced during this time due to a combination of 1) that introductions have been restricted to sporadic incidences with small founder populations, 2) the official mitigation measures, such as eradicating detected outbreaks, and 3) the use of insecticides to control other pests in potato fields[6]. Another factor that reduces the likelihood of establishment is the tendency for the beetles arriving in Finland and Sweden through natural spread to mainly be limited to areas closest to the source. For example, data from previous outbreaks in Sweden show that the

[6] In Sweden for example, 35% of the potato cultivation area was treated in 2021 with insecticides (SCB 2022)

likelihood of a field being infested decreased exponentially with increasing distance from the southern coastline of Sweden (Björklund and Boberg 2024). Furthermore, we assumed that the area of potential establishment of the CPB in Finland and Sweden is mainly limited by the temperature conditions during the growing season. However, we acknowledge that there might be factors beyond those evaluated here that might restrict the potential distribution of the CPB.

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Appendix 1. Growing degree days (GDD) requirements reported in the literature

Table 1. Assessments of the growing degree days (GDD) required for the development of life-stages of the CPB.

Development stages	GDD	Base temperature (°C)	Origin of the CPB population	Type of study[5]	References
One generation					
From egg to adult	540–590	6	Illinois, USA	Field	Girault and Zetek 1911
From egg to adult	470 ± 22.1 (SE)	9.1	New York, USA	Laboratory	Tauber et al. 1988a
From egg to adult	463 ± 19.9 (SE)	9.8	New York, USA	Laboratory	Tauber et al. 1988a
From egg to adult	440	10	Denmark	Field	Hansen et al. 2004
From egg to adult	690	10	Belarus, former USSR	NA	Hurst 1975 citing Arapova 1996
From egg to adult	542.6 ± 21.9 (SE)	10.9	China (?)	Laboratory	Zhou et al. 2010
From egg to adult	406	11	Bulgaria	NA	Hurst 1975 citing Savescu 1963
From egg to adult	275–504	11	Wisconsin, USA	Laboratory	Walgenbach and Wyman 1984
From egg to adult	243–335	11.5	Former Soviet Union	NA	Hurst 1975 citing Chigarev 1967
From 1 April to adult	61 (± 9.8 SE) – 744 (± 10.7 SE)[2]	10	Quebec, Canada	Field	Mailloux et al. 1988
From 1 April to adult	387	11.5	Former Czechoslovakia	NA	Hurst 1975 citing Neubauer 1958
From spring emergence to adult	280–375	11.5	Poland	NA	Hurst 1975 citing Łarczenko 1958
From spring emergence to adult	390	11.5	Poland	NA	Wegorek 1959
Preoviposition					
From overwintering to emergence	181 ± 8.8 (SE)	10	Massachusetts, USA	Laboratory	Ferro et al. 1991
From overwintering to emergence	1–507[1]	12	New York, USA	Field	Tauber et al. 1988b
From overwintering to emergence	60–90	NA	Massachusetts, USA	Laboratory	Ferro et al. 1999

From 1 March to emergence	50–370[3]	9.9	New Jersey, USA	Field	Lashomb et al. 1984
From 1 April to emergence	123 (± 11.9 SE) – 288 (± 22.5 SE)[2]	10	Quebec, Canada	Field	Mailloux et al. 1988
From overwintering to egg-laying	213	12	New York, USA	Laboratory	Tauber et al. 1988b
From overwintering to egg-laying	135	12.5	New York, USA	Laboratory	Tauber et al. 1988b
From 1 March to egg-laying	120–285	10	New York, USA	Field	Tauber et al. 1988a
From 1 April to egg laying	60	11.5	Former Czechoslovakia	NA	Hurst 1975 citing Neubauer 1958
From emerge to egg-laying	51–85[4]	10	Massachusetts, USA	Laboratory	Alyokhin and Ferro 1991
From emerge to egg-laying	30	11.5	Poland	NA	Hurst 1975 citing Łarczenko 1958
From emerge to egg-laying	60	11.5	Poland	Field	Wegorek 1959
From emerge to egg-laying	80 ± 9.3 (SE)	14.2	New York, USA	Laboratory	Tauber et al. 1988a
From emerge to egg-laying	60 ± 3.5 (SE)	17.2	New York, USA	Laboratory	Tauber et al. 1988a
From emerge to first flying individuals	60 ± 9.6 (SE)	10	Massachusetts, USA	Laboratory	Ferro et al. 1991
From emerge to first egg-laying	73 ± 5 (SE)	10	Massachusetts, USA	Laboratory	Ferro et al. 1991
Oviposition					
	90–110	6	Illinois, USA	Field	Girault and Zetek 1911
	88.9 ± 5.6 (SE)	8.2	New York, USA	Laboratory	Tauber et al. 1988a
	86.8 ± 10 (SE)	8.3	New York, USA	Laboratory	Tauber et al. 1988a
	73.3 ± 6.79 (SE)	9.1	China (?)	Laboratory	Zhou et al. 2010
	52–75	11	Wisconsin, USA	Laboratory	Walgenbach and Wyman 1984
	45	11.5	Former Czechoslovakia	NA	Hurst 1975 citing Neubauer 1958
	46–56	11.5	Poland	NA	Hurst 1975 citing Łarczenko 1958
Larval development					
1st instar	43.2 ± 5.6 (SE)	10.5	China (?)	Laboratory	Zhou et al. 2010
1st instar	26–53	11	Wisconsin, USA	Laboratory	Walgenbach and Wyman 1984
2nd instar	39.2 ± 2.3 (SE)	8.2	China (?)	Laboratory	Zhou et al. 2010

2nd instar	18–53	11	Wisconsin, USA	Laboratory	Walgenbach and Wyman 1984
3rd instar	34 ± 0.8 (SE)	10.3	China (?)	Laboratory	Zhou et al. 2010
3rd instar	18–45	NA	Wisconsin, USA	Laboratory	Walgenbach and Wyman 1984
4th instar	162 ± 17.9 (SE)	9	China?	Laboratory	Zhou et al. 2010
4th instar	39–91	NA	Wisconsin, USA	Laboratory	Walgenbach and Wyman 1984
Prepupae	53–88	11	Wisconsin, USA	Laboratory	Walgenbach and Wyman 1984
Whole larval development	160–250	6	Illinois, USA	Field	Girault and Zetek 1911
Whole larval development	273 ± 28.8 (SE)	9.6	China?	Laboratory	Zhou et al. 2010
Whole larval development	204–405	11	Wisconsin, USA	Laboratory	Walgenbach and Wyman 1984
Whole larval development	180	11.5	Poland	NA	Hurst 1975 citing Łarczenko 1958
Pupation					
	170–250	6	Illinois, USA	Field	Girault and Zetek 1911
	98 ± 5.3 (SE)	10.1	New York, USA	Laboratory	Tauber et al. 1988a
	94 ± 4.9 (SE)	10.2	New York, USA	Laboratory	Tauber et al. 1988a
	100.4 ± 13.8 (SE)	10.2	China (?)	Laboratory	Zhou et al. 2010
	70–99	11	Wisconsin, USA	Laboratory	Walgenbach and Wyman 1984
	100	11.5	Poland	NA	Wegorek 1959 citing Łarczenko, 1958

[1] The cumulative GDD until emergence based on data from two populations during two different years, using soil temperature at 12-15 cm.
[2] The cumulative GDD until emergence (the range represents from 20 to 90% emergence).
[3] The cumulative GDD until emergence (the range represents from 1 to 80% emergence).
[4] The cumulative emergence in different fields and years, using soil temperature at the depth of 10.2 cm. The range limits were estimated from a figure.
[5] NA = information not available

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Appendix 2. Methodology for projecting future daily temperatures in Finland

This appendix outlines the methodology employed to project the mean annual growing degree days (GDD) in Finland centered around the year 2040 under the RCP4.5 emission scenario. The projection was made with the delta-change methodology, which involves using observed historical climate data as a baseline, upon which projected future changes are added.

The baseline data consisted of daily air temperatures for 2003–2022, which has been derived from the Finnish climate station observations and interpolated over the whole country at a 10 × 10 km resolution (Aalto et al. 2016). Future climate projections were based on monthly air temperature increases under the RCP4.5 scenario, derived from simulations of 28 Coupled Model Intercomparison Project Phase 5 (CMIP5) global climate models (Ruosteenoja et al. 2016). This data was represented on the same 10 × 10 km grid as the data for the baseline data.

First, projections were computed for monthly temperature increases as running 30-year means centered around 2040, relative to the baseline data centered on 2013. Then, the projections of daily temperatures for 2031–2050 were computed by adding the monthly-mean temperature increases to the observational daily-mean temperatures of the period 2003–2022.

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