The European Zoological Journal

ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/tizo21

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To cite this article: K. Wieczorek, A. Bugaj-Nawrocka, B. Borowiak-Sobkowiak, A. Endrestøl, H. P. Ravn, W. Solarz & R. Durak (2025) Adapting to change: exploring the distribution dynamics of the alien and potentially invasive aphid species *Cinara curvipes* (Hemiptera: Aphididae) in the context of global warming, The European Zoological Journal, 92:1, 258-279, DOI: 10.1080/24750263.2024.2449152

To link to this article: https://doi.org/10.1080/24750263.2024.2449152

The European Zoological Journal, 2025, 258–279
Vol. 92, No. 1, https://doi.org/10.1080/24750263.2024.2449152

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Adapting to change: exploring the distribution dynamics of the alien and potentially invasive aphid species *Cinara curvipes* (Hemiptera: Aphididae) in the context of global warming

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(Received 21 June 2024; accepted 22 December 2024)

Abstract
This study investigates the potential ecological niche and distribution of the Nearctic bow-legged fir aphid, *Cinara curvipes*, an alien and potentially invasive species, across Europe. Utilising climate modelling based on climatic preferences in its native range, we assess the suitability of European climates for facilitating the spread of this aphid. Coupled with the presence of suitable host plants, mostly firs (*Abies* spp.) or cedars (*Cedrus* spp.), there is potential for the bow-legged fir aphid to extend its range across most European regions, with projections suggesting potential expansion into Asia Minor. Furthermore, future climate scenarios predict a northward expansion of suitable habitats for this aphid species, confirmed by its detection in Denmark and Norway. Our research reveals that *C. curvipes* displays notably higher fecundity compared to its *Cinara* genus counterparts. Specifically, wingless viviparous females of this species achieve peak fecundity at lower temperatures (10–15°C), explaining their spring mass appearances. At 25°C, nymphs fail to moult or reach maturity, leading to summer population declines. Unique survival mechanisms, including the production of numerous winged morphs under overcrowded conditions, enable rapid dispersal facilitated by human-mediated transport, notably through the "Christmas trees" trade. Its high reproductive output allows the species to quickly colonise new habitats and exploit available resources, contributing to its potential invasiveness. We emphasise the critical need for collaborative engagement among researchers, stakeholders, and the public to bolster citizen science initiatives and reinforce environmental monitoring networks, all within the framework of an early detection and rapid response (EDRR) process. This collaborative approach is vital for effective environmental management and mitigating potential invasive threats.

Keywords: "*Christmas trees*" *trade*, *citizen science*, *demographic parameters*, *Lachninae*, *mass outbreaks*

Introduction

Abies, or fir, is a genus of about 50 conifer species in the family Pinaceae, distributed mainly in the Northern Hemisphere, particularly in North America and eastern Asia (Xiang et al. 2018). These evergreen trees dominate northern boreal forests and high-altitude southern mountain systems, playing a vital role in maintaining biodiversity and ecological balance (Farjon & Filer 2013). Firs are valued for timber and are used in construction, furniture, and pulpwood, and certain species like *A. nordmanniana* (Steven) Spach, *A. balsamea* (L.)

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Mill., and *A. koreana* E. H. Wilson are popular as 'Christmas trees' due their needle-holding qualities (Wolf 2003). While some species have restricted ranges, a few like the silver fir *A. alba* Mill. and subalpine fir *A. lasiocarpa* (Hook.) Nutt. cover larger areas. However, their populations have declined significantly due to deforestation, overexploitation, air pollution, and improper forestry practices. Fir forests are also declining due to a combination of climate change, pests, diseases, and shifting wildfire patterns (Perret et al. 2023). Global warming-induced dieback, insect infestations, and diseases like root rot and defoliation significantly impact tree health and survival, leading to widespread tree mortality and forest degradation (Darr et al. 2022).

Among hemipterans, 47 aphid species feed on firs globally, with *Adelges* Vallot, *Mindarus* Koch, and *Cinara* Curtis being the most significant pests. The balsam woolly adelgid *Adelges piceae* (Ratzeburg), invasive in North America, damages fir bark and wood, often causing tree death. Similarly, the silver fir woolly adelgid *Adelges nordmannianae* (Eckst.) harms young silver firs and Nordmann fir plantations in Europe (Newton et al. 2011; Endrestøl et al. 2023a). Woolly aphids like *Mindarus abietinus* Koch and *M. pinicola* (Thomas) damage shoots and needles, affecting natural forests, timber production, and the "Christmas trees" industry (Fondren & McCullough 2002; Doherty et al. 2017). Among species of the genus *Cinara* (Lachninae), the bow-legged fir aphid *C. curvipes* (Patch) causes similar losses on fir plantations in North America (DeFrancesko & Murray 2009). In the native range of the Nearctic region, from Canada to Mexico, *C. curvipes* is a monoecious and holocyclic species associated with various *Abies* spp. (*A. balsamea*, *A. concolor* (Gordon et Glend.) Lindl. ex Hildebr.), *A. grandis*, *A. lasiocarpa*, *A. magnifica*, *A. procera*, *A. religiosa*) and occasionally with other conifers (*Cedrus deodara* (Roxb. ex Lamb.) G.Don, *Picea glauca* (Moench) Voss, *P. pungens* Engelm., *Pinus contorta* Dougl. ex Loud, *Pseudotsuga menziesii* (Mirbel) Franco) (Voegtlin & Bridges 1988). In the early 21st century, *C. curvipes* was found in Europe, where it spread very quickly, and had mass appearances in some regions. The species was first detected in a limited location in the Royal Botanic Gardens, Kew, UK (Martin 2000), and then subsequently in locations in continental Europe: Germany (Gottschalk 2001; Scheurer et al. 2001), Serbia (Poljaković-Pajnik & Petrović-Obradović 2002), Switzerland (Angst et al. 2007), Czech Republic (Olbrechtová 2007), Slovakia (Nakládal et al. 2007), Slovenia (Jurc et al. 2009), Bulgaria (Tomov et al. 2009), Hungary (Bodor 2013), Austria (Perny 2014), Poland (Hałaj & Osiadacz 2015) and Turkey (Görür et al. 2015). Outside its native range, the bow-legged fir aphid is also not restricted to a single genus of conifers. In addition to the main host plants, which are firs (both native and alien species), it can also occur on cedar (*Cedrus* Trew), the Douglas fir (*Pseudotsuga menziesii*) and the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). In Central Europe, the annual life cycle comprises six generations with a rapid population increase during the sprouting of host trees in May/June when, in suitable conditions, aphids are able to form colonies comprising several thousand individuals inhabiting the underside of branches and the stems of their hosts. Such a phenomenon has rarely been observed in native *Cinara* species of Europe. After a decrease in population numbers in July/August, a second peak of population density in September is observed. Winter eggs are laid in November; however, in milder winters, individuals of the last generation overwinter, occupying the underside of the branches of 1.5 to 3 m high trees and also up to the upper third of the stems (Scheurer & Binazzi 2004). In particular, the flexible reproductive strategy of the bow-legged fir aphid has strongly influenced its expansion abilities, allowing for the rapid buildup of outbreak populations. During the short history of *C. curvipes*' expansion in Europe, at least two significant overpopulations of the aphid were observed. The first occurred in numerous regions of Germany (Scheurer et al. 2001), followed by another in the Czech Republic (Olbrechtová 2007). This resulted in the infestation of host plants in various settings, including botanic gardens, parks, private gardens, and commercial "Christmas trees" plantations. In response, pesticide treatments were employed to suppress this new pest (Mertelík et al. 2007).

Aphids are poikilothermic organisms, and temperature is the main factor influencing their life cycles. The observed mass appearances of *C. curvipes* have been closely linked to mild winters preceding rapid population growth of the overwintering generation in late spring, without explaining why the aphid population collapses rapidly in the summer. A similar phenomenon was encountered in the spring of 2020, when reports from concerned foresters and citizens indicated mass outbreaks of the bow-legged fir aphid on fir trees in numerous regions of Poland, where it had not been previously reported. Similarly, a mass appearance of this species was observed for the first time in Norway in 2022, with reports disseminated firstly through social media platforms. Early detection and rapid response (EDRR) are key prerequisites to solving the problem of biological invasions of alien species effectively (Reaser et al. 2020). Solutions should involve both a bottom-up approach, including citizen science, and a top-down approach in which institutional framework is engaged (Sandercock et al. 2022; Endrestøl et al. 2023b). Citizen scientists play a pivotal role in collecting valuable data and observations, contributing to the understanding of species distribution and dynamics, in particular the early detection of pest infestations (Potgieter et al. 2024). The bow-legged fir aphid is a cause for concern among foresters, as it is one of the few *Cinara* species that is polyphagous, capable of feeding on various conifer species. There is a possibility that it may switch to favour other tree species, potentially posing a threat to trees critical to local forestry or urban landscape (Jurc et al. 2009; Dransfield & Brightwell 2023).

In this study, we predict potential ecological niches and assess the impact of climate change on the distribution of *C. curvipes*, an alien and economically significant insect species, that has been rapidly spreading throughout Europe. Then, we correlate climate model outputs and variables obtained from monthly weather data with empirical observations. We test the hypothesis that temperature significantly influences the developmental rates, reproductive strategies, and overall population dynamics of *C. curvipes* under experimental conditions, noting variations across different temperature regimes. Finally, we outline our efforts in implementing elements of EDRR strategies for future crisis and risk management in forestry insect outbreaks, with a specific emphasis on understanding the role of fir plantations in facilitating the spread of *C. curvipes* and the contribution of citizen science towards its early detection and surveillance in forest and urban environments.

Material and methods

Mapping C. curvipes distribution in the context of global warming

Occurrence data. The occurrence data were obtained from specimens studied in museum collections, the scientific literature, biodiversity databases (iNaturalist 2023; Global Biodiversity Information Facility (GBIF) 2023; Data associated with the article: https://doi.org/10.15468/dl.7aks4d) and information from private persons and co-authors of this paper. Records with unspecified or unknown localities were excluded. The Geographic Distance Matrix Generator 1.2.3 was used to calculate the geographic distance between each pair of localities (Boria et al. 2014; Ersts 2016). Points close to each other (less than 10 km apart) were removed to reduce inherent geographic biases (effect of spatial autocorrelation) associated with collecting methods. Overall, 73 unique occurrence localities were compiled for representatives of *C. curvipes* in North America (Figure 1) and 74 in Europe (Figure 2). Regional species diversity and ecological specificity should be properly evaluated to enable the successful management of the local aphid species. Therefore, the existing data on the location of the bow-legged fir aphid in Poland were supplemented with new locations obtained during its mass appearance in 2020 and subsequent years (Figure 3). Similarly, new locations found in Denmark and Norway have been included in the dataset. Details of occurrences and localities used in the model are available in Supplementary material 1. All localities were georeferenced using Google Earth 9.186.0.0 (Google Inc. 2023; http://www.google.com/earth/index.html) (coordinates were collected in decimal degrees, datum: WGS84). Natural range boundaries for major host plants were taken from http://databasin.org (Conservation Biology Institute (CBI) 2023; maps are a digital representation of the tree species range maps of the Atlas of the United States Trees by Little (1971)) and https://data.mendeley.com/datasets/hr5h2hcgg4/6 (Caudullo et al. 2017; DOI : https://doi.org/10.17632/hr5h2hcgg4.17) through https://www.euforgen.org/.

Environmental and climate predictors. Nineteen current bioclimatic variables were obtained from the WorldClim 2.0 dataset (Fick & Hijmans 2017; http://www.worldclim.org). The influence of possible global climate change on the potential distribution of *C. curvipes* was estimated for four periods (2021–2040, 2041–2060, 2061–2080 and 2081–2100) and four future representative shared socioeconomic pathways (SSPs) (SSP1–2.6, SSP2–4.5, SSP3–7.0 and SSP5–8.5). The mean values of the modelling results for the three future climate scenarios came from the Coupled Model Intercomparison Project Phase 6 (CMIP6): ACCESS-ESM1-5, CNRM-ESM2-1 and MIROC-ES2L. A spatial resolution of 30 arc-seconds (~1 km^2) for the continental models and 60 arc-seconds (~2 km^2) for global models were selected (downloaded from WorldClim 2.0; 30 arc-second spatial resolution grids were interpolated to a 60 arc-second spatial resolution). All maps were prepared in QGIS 3.26.0 (QGIS Development Team 2023; http://www.qgis.org) using the WGS84 datum and EPSG: 4326 or 3857 (Web Mercator).

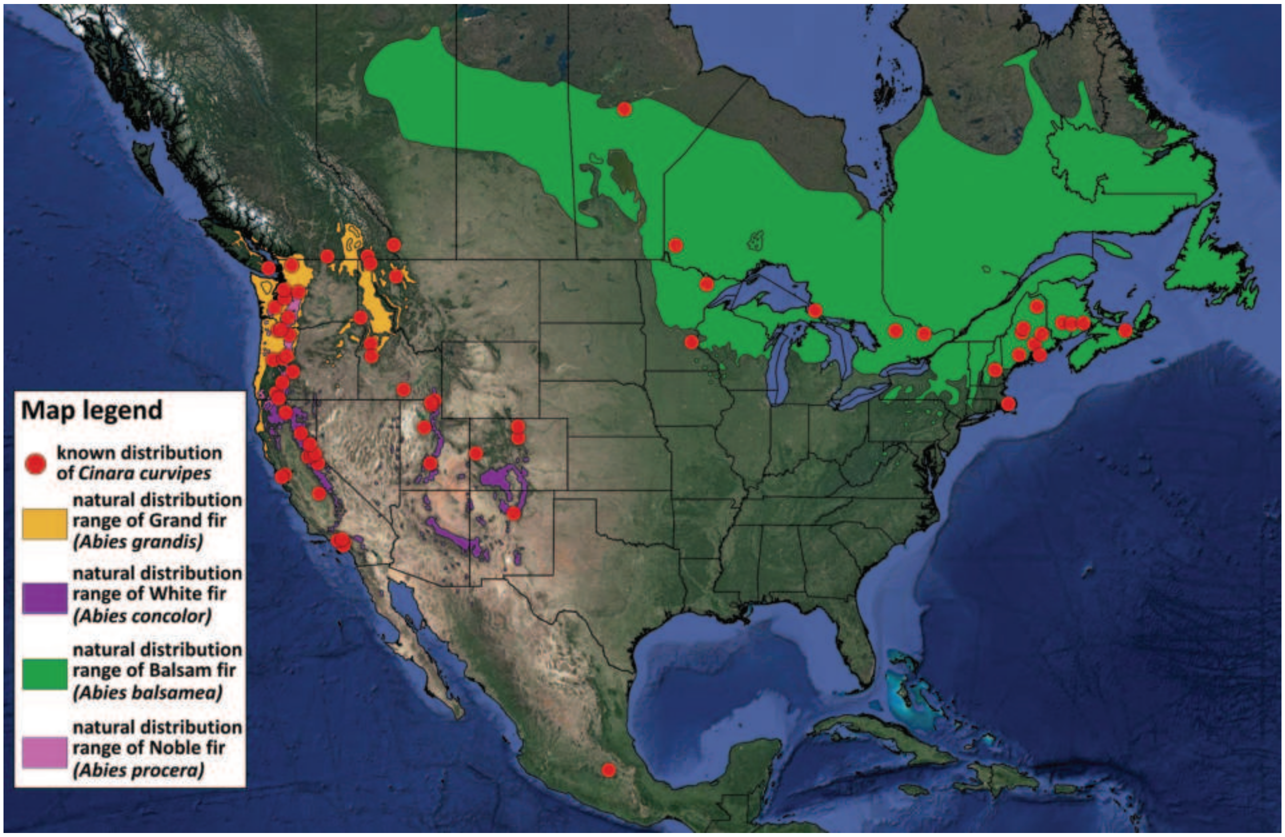

Figure 1. Known distribution of *Cinara curvipes* in North America (red dots), with the distribution ranges of its host plants.

SAGA GIS 7.8.2 (Conrad et al. 2015; SAGA Development Team 2023) was used to extract raw environmental data from all raster layers of the species occurrence records. A Spearman rank correlation test was performed in the Excel (v. 2207) add-in program Analysis ToolPak (Microsoft Corporation 2024) to minimise the number of variables by discarding those which were highly correlated ($r \geq 0.75$). Variables that did not make any significant contribution to the model were removed. Finally, five variables that did not show high correlation and had a reasonable impact on the habitat preferences of the discussed aphid were used – Bio01, Bio05, Bio09, Bio15 and Bio19 (see the Results section for expansion of abbreviations and discussion of variables).

In addition, we incorporated variables derived from monthly weather data downloaded from WorldClim spanning from 1990 to 2021. This enabled us to monitor changes in average monthly temperatures and identify patterns in the seasonal appearance of *C. curvipes* in Europe.

Ecological niche modelling. MaxEnt software (version 3.4.1; http://www.cs.princeton.edu/~schapire/maxent) was used to model the *C. curvipes* potential niches and distribution. MaxEnt is a machine learning software program based on a maximum entropy algorithm (Phillips et al. 2006). Different combinations of feature types (auto features or linear, quadratic and product features together (LQP)) and regularisation multiplier values (ranging from 0.5 to 1.75) were used, as the default settings in MaxEnt may not produce the best predictions (Merow et al. 2014; Kumar et al. 2014; Samy et al. 2016; Bugaj-Nawrocka et al. 2021) (Supplementary material 2).

A classical approach to modelling the potential niche for invasive species was followed by using data from the natural range of occurrence (North America) and its projections (in Europe). Some authors suggest using global occurrence records (Zhang et al. 2020). However, we believe that first of all, it is important to use niche conservatism to evaluate invasion hotspots.

If models produced biologically nonsensical curves (i.e. very jagged or multimodal), they were removed or given a low score. As it was difficult to distinguish environmentally unsuitable from undersampled areas, we used a method that gave weight to records with few neighbours in geographic space to deal with the likelihood that some areas had fewer records and that some places were poorly sampled.

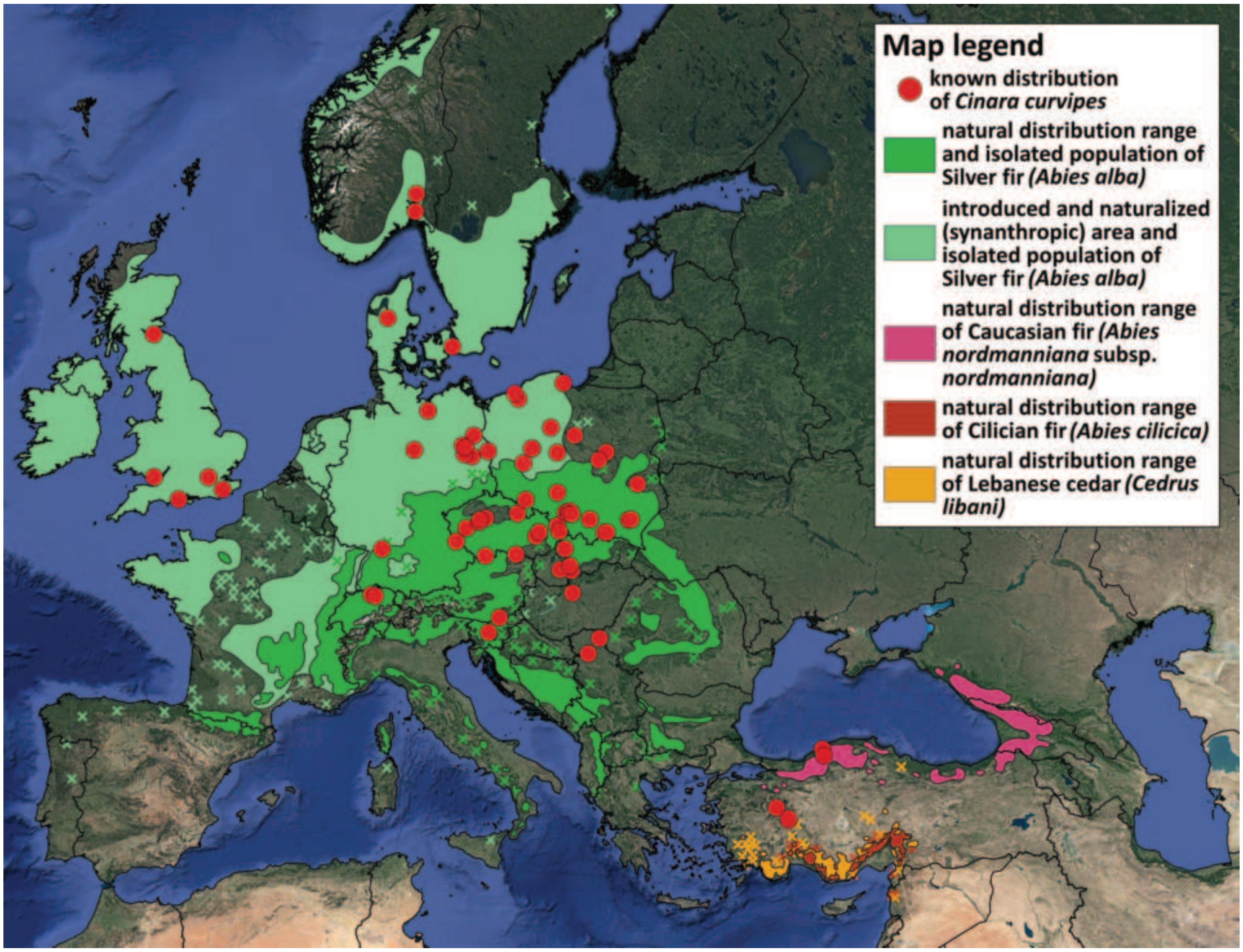

Figure 2. Known introduced distribution of *Cinara curvipes* in Europe (red dots), with the distribution ranges of its potential host plants.

A bias file is implemented in MaxEnt modelling to weigh the selection of background points to account for sampling intensity and any potential sampling bias. All distribution records of *C. curvipes* were weighted by a Gaussian kernel with a standard deviation (SD) of 200 km (using the kernel density estimation) in SAGA GIS to create a bias grid file. A range of 200 km was chosen because we assumed that in its native range, this aphid could easily spread by several kilometres a year, sometimes with short periods of irregular spreading. Considering the period from which most of these reports from North America come (1910–1990), we assumed that within 90 years, a representative of this species could have travelled 200 km or more in its natural habitat. The resulting grid was scaled to have values ranging from 1 to 20 (using grid normalisation) (see Elith et al. 2010; Syfert et al. 2013).

A ten-fold cross-validation was performed. Therefore, all of the data were used for the validation, thus making better use of small data sets (Phillips et al. 2006; Phillips & Dudík 2008). The logistic output of MaxEnt was selected with prediction values from 0 (unsuitable habitat) to 1 (optimal habitat). Sample size-corrected Akaike's information criterion (AICc and ΔAICc) (measures of the relative quality of models for a given dataset, calculated with ENMTools (Warren et al. 2010)), the area under the receiver operating characteristic (ROC) curve (AUC) (the performance of the model and the weight of omission and commission errors) and the partial area under the ROC curve (pAUC) (calculated with Niche Analyst 3.0 (Qiao et al. 2015)) were used for model evaluation (Supplementary material 2).

Empirical assessment of C. curvipes demographic parameters influenced by various temperatures

Aphids and plants. In March 2022, viviparous females of *C. curvipes* were collected from *A. concolor* in the Botanic Garden, Poznan, Poland. The collected aphids were transferred to the

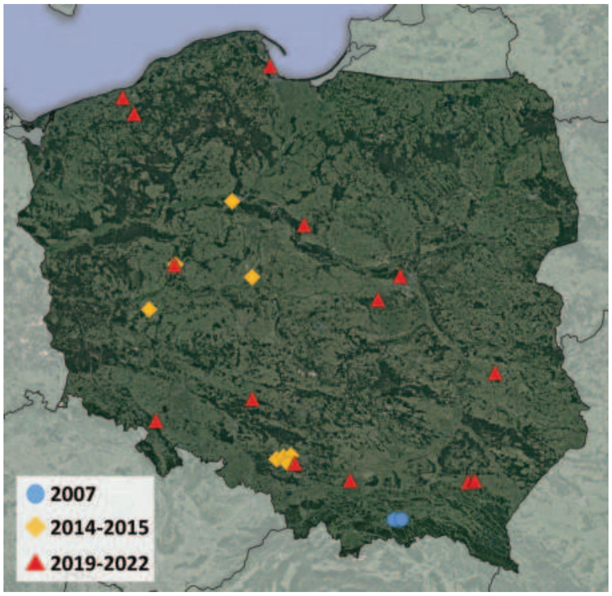

Figure 3. Known *Cinara curvipes* localities in Poland, divided into periods in which subsequent reports appeared.

laboratory and reared on 1-year-old seedlings of *A. concolor* under controlled conditions (20 ± 1°C temperature, 60 ± 5% humidity, photoperiod of L: D = 16:8) in a climatic chamber (MLR-351 h; Sanyo Corp., Japan). Plants were free of pathogens and planted in 30 × 30 × 30 cm pots. Before starting the experiments, plants were kept at 20°C for 2 weeks to acclimatise. All experiments were carried out on wingless viviparous females from March to October 2022.

Experimental procedures.

Longevity and total fecundity. The experiment was carried out at four different temperatures: 10, 15, 20, 25°C. For each experimental temperature, 20 young adult wingless viviparous females of the same age were placed on plants. The first 20 L1 born nymphs were observed and monitored until they reached maturity. Then, newborn nymphs were counted and removed once a day with a soft brush. The experiment continued until all the aphids died. The length of the following developmental stages was determined: pre-reproduction, reproduction, post-reproduction and total longevity; also, female fecundity was determined. Observations were carried out seven times per week.

Survival, average daily fecundity and demographic parameters. To determine the demographic parameters of *C. curvipes* populations, 100 individuals were observed. Ten adult wingless viviparous females were placed on a single plant at each experimental temperature and left until nymphs were born. After this, adults were removed, and 100 newborn nymphs were left on each plant ($n = 100$). The survival of the individuals was checked every day. When the females matured and started to reproduce, the nymphs were counted every day and removed. The experiment continued until the death of all individuals. Based on the collected data, the survival, average daily fecundity of females and demographic parameters of populations were calculated (intrinsic rate of increase (r_m), net reproduction rates (Ro), finite rate of increase (λ) and mean generation time (T)), according to equations (Birch 1948; Wyatt & White 1977): $r_m = (\ln Md \times 0.738)/D$, where: D is the developmental period from birth to the beginning of the first reproduction (pre-reproductive period) and Md is the number of nymphs produced by the adult in the first D days of reproduction after the adult moult; $Ro = \Sigma(lxmx)$ where: lx and mx are cumulative daily survival and fecundity, respectively; and $\lambda = er_m$ where: e is the base of natural logarithms; $T = \ln Ro/r_m$.

Statistical analyses were performed using the program Statistica (data analysis software system), v. 13 (TIBCO Software Inc. 2017, http://statistica.io.) and PAST (PAleontological STatistics v. 3.25; Hammer et al. 2001). The figures were prepared using Corel Draw v. 23 (Corel Corporation, Ottawa, Ontario, Canada), PhotoScapeX v. 4.2.1 (Mooii Tech, South Korea) and BioRender.com.

Results

From citizen science to policy and management implications

Implementation elements of the EDRR strategy for crisis and risk management in forestry in the example of C. curvipes outbreaks. The initial reports of the widespread presence of *C. curvipes* in various regions of Poland emerged in May 2020, with contributions from scientists, foresters, and citizens alike. These observations primarily documented the colonisation of various fir species (e.g. *A. concolor*, *A. siberica*, *A. alba*, *Abies* sp.) by aphids in private properties, parks, green areas, and botanical gardens. During the outbreak, aphids, initially wingless viviparous females and their nymphs followed by winged viviparous females, predominantly occupied the underside of branches and the trunk of host plants. Additionally, wingless individuals were observed on neighbouring plants, the ground, building facades, and garden arbours, eliciting some concern (Figure 4(a–c)). These reports triggered cooperation between experts studying aphids and those studying biological invasions, which resulted in communication efforts aiming at strengthening citizen science capacity. We prepared an alert notice with a picture and description of the species, the threats it poses, and a request to provide information on its findings. It was posted on the homepage of the online database Alien Species in Poland. Information on *C. curvipes* was also spread through social media networks, including Facebook groups and individual profiles of users associated with the state forest administration. In addition to promoting bottom-up data collection, we elevated the issue of *C. curvipes* presence by preparing institutional letters describing the problem and calling for the need to implement emergency measures to prevent and mitigate negative impacts caused by the species. The letter was sent to the Phytosanitary Supervision Department and International Affairs of Plant Health and Seed Inspection Service (PIORiN), the General Director of State Forests, Department of Nature Conservation and the Department of Forestry and Hunting of the Ministry of Climate and Environment, and to the General Director of the General Directorate for Environmental Protection. While some of these institutions did not react, the PIORiN raised an alert providing information on the species identification, impacts, and control measures. This information was then published in a few portals and newspapers dealing with forestry and the trade of ornamental plants. Because *C. curvipes* outbreaks were recorded near natural fir forest complexes (including protected areas) in southern Poland, the General Director of State Forests sent an alert to all forest districts about the presence of this alien and potentially invasive aphid species. As a result, the following year, we received information from Świdnica and Piskorzów Forest Inspectorates (south-west Poland) about the presence of this aphid species on silver firs. Thanks to our efforts, we also received considerable feedback on new findings of *C. curivpes* from localities scattered throughout Poland. We verified this information and included it in the dataset used in the analyses presented here. In 2014, when the bow-legged fir aphid was first observed in Poland, this species was known only in two regions (Hałaj & Osiadacz 2015). However, a detailed survey of Internet resources, including gardening forums,

Figure 4. The mass occurrence of *Cinara curvipes* (a) in the private garden near Kampinoski National Park, Poland, photo by J. Malinowska. (b,c) the use of self-adhesive tape against aphids to protect ornamental fir trees in the private garden of the vicinity of Lipno, Poland, source: https://www.instagram.com/zielone_pogotowie.

showed that as early as 2007, its outbreaks had already been observed in southern Poland, similar to what was reported at that time in the Czech Republic. This confirms how important and useful citizen science is in the EDRR process of coordinating a set of actions to find and eradicate potential invasive alien species in a specific location before they spread and cause harm. This was also confirmed by the first finding of *C. curvipes* in Norway, which is also the northernmost locality of this species (Oslo, Ankerparken, 10 October 2022, on *A. alba*). The occurrence of the species in Norway first came to our attention via a forwarded video originally posted on Instagram, where a colony of large aphids displayed anti-predator behaviour, i.e. when they were disturbed, the whole colony moved with a rocking motion. After getting more precise data on the locality, the aphids were found in the exact spot shown in the video. The locality was a small backyard with several trees and bushes within a fenced kindergarten area. There were two *A. alba* trees on the site, about 20 m in height. Colonies were found in the thousands on the underside of branches (Figure 5(a–b)). Also the Danish record was documented thanks to citizen science, in a private garden in Dragør (17 September 2018), where a large number of bow-legged fir aphid individuals were found on *A. balsamea* (Figure 5(c)).

According to our observations, the presence of one or several trees of the host plant, even in isolated locations, has facilitated the appearance of *C. curvipes*. This intricate relationship underscores the significance of citizen science in uncovering such occurrences.

The role of fir plantations in facilitating the further distribution of C. curvipes. The first information about the presence of the bow-legged fir aphid on fir trees sold as “Christmas trees” (i.e. *A. koreana*, *A. nordmanniana*) in Poland came from both commercial garden stores and specialised nurseries in the winter of 2020. At the same time, we gathered essential information from homeowners regarding the presence of these aphids on indoor “Christmas trees”. A survey conducted among owners of “Christmas trees” plantations located in northern Poland showed that in 2019 and 2020, an overpopulation of these aphids was observed on at least two large plantations. According to growers, even if the aphid appears in mass, it does not cause economic losses; moreover, irrespective of this species’ presence, the plantations are subjected to routine chemical control.

A “Christmas trees” plantation was also the first, previously unpublished, bow-legged fir aphid location in Denmark (Viborg, Mønsted, November 2002, on *A. nordmanniana* Figure 6(a)). Therefore, it is one of

Figure 5. Known *Cinara curvipes* localities in the Scandinavian countries: (a) two *Abies alba* trees in a semi-closed backyard (kindergarten) at Ankerparken in Oslo municipality representing the first locality of *C. curvipes* in Norway, photo by A. Endrestøl. (b) A branch of one of the trees from (a) infested with *C. curvipes*, photo: A. Endrestøl. (c) *Cinara curvipes* on *Abies balsamea* in Dragør (private garden), representing the second locality of this species in Denmark, 17 September 2018, photo by N. Jacobsen.

the first three localities of this aphid in continental Europe, right after its occurrence in Germany (2000) and Serbia (2001).

In November 2022, a shipment of *A. nordmanniana* and *Picea omorika* (about 2000 trees total) was imported to Norway as "Christmas trees" from Denmark where they were investigated at a plant-importer facility. Soil samples and beating samples were taken from a selection of trees (Figure 6(b-c)). Later investigations found one individual of *C. curvipes* from *A. nordmanniana*, establishing the import of "Christmas trees" as a vector for this species into Norway.

Present and future distribution of C. curvipes in the context of global warming

Evaluation of the models and the importance of environmental predictors for C. curvipes. Two types of model results were analysed: present and future (four time periods and four SSPs (SSP1–2.6, SSP2–4.5, SSP3–7.0, and SSP5–8.5)). Both training and test AUC values differed significantly from random for all models. The model's settings selection was chosen based on the results of pAUC, AICc and ΔAICc (Supplementary material 2). Higher values of pAUC, and lower values for AICc and ΔAICc, were observed when linear, quadratic and product

Figure 6. The role of fir plantations and the trade of "Christmas trees" in the dispersal of *Cinara curvipes*: (a) *C. curvipes* on *Abies nordmanniana* in Viborg, Mønsted ("Christmas tree" plantation), Denmark, 3. November 2002, photo by Ch. N. Nielsen. (b) Removing the wrapping on *A. nordmanniana* at a "Christmas trees" importer in Moss, Norway, 17 November 2022, to investigate the possible presence of *C. curvipes*, photo: A. Endrestøl. (c) Beating *A. nordmannianae* inside a plastic bag to collect specimens of *C. curvipes* and possibly other hitchhikers at a "Christmas trees" importer in Moss, Norway, 17 November 2022, photo by A. Endrestøl.

features (all together) were chosen, regardless of the number of iterations. The regularisation multiplier settings were also analysed, and a value of 0.5 worked the most effectively. For the maximum number of iterations, the best results were obtained with a value of 1000 (Supplementary material 2).

A jackknife test (see Supplementary material 3 for the details and MaxEnt outputs) showed that among all environmental variables used, annual mean temperature (Bio01) was the most informative by itself and had a significant amount of information that was not contained in the other variables. Annual mean temperature varies throughout the native range of *C. curvipes* in North America from −2.6 to 18.0°C (with a median of about 6.9°C); the lowest values were estimated for the species' location in Canada. The warmest month (Bio05) in North America and Europe was June or July. The mean temperature in June/July in places where *C. curvipes* has been found in North America is 25.9°C (min. 17.5°C in Mount Baker, Washington, USA and max. 36.4°C in Fresno, California, USA). The precipitation of the coldest quarter (Bio19) was also significant, and the average rainfall for the studied areas from December to February was 246 mm (min. 25 mm in Cerro de Guerrero, Federal District, Mexico City, Mexico (or 42 mm in Grand Junction, Colorado, USA) and max. 947 mm near Mount St. Helens in Skamania County, Washington, USA). The mean precipitation seasonality (Bio15), a measure of the variation in monthly precipitation totals over the year, fluctuated around 46.5%. The most considerable fluctuations were recorded in Los Angeles County, California, USA, and the smallest in New Brunswick, Canada. Due to the size of the analysed area, the driest quarter may cover a range of different months. However, for North America, it will be three selected months between December and May. The average temperature of the driest quarter (Bio09) in places where *C. curvipes* has been found in North America is 14.7°C (min. −19.2°C in Mystery Lake, Manitoba, Canada, and max. 25.9°C in Fresno, California, USA).

Potential distributions and localities vulnerable to possible invasion of C. curvipes

All resulting maps show the median of the output grid of 10 model replicates. For the present model in North America (Figure 7) – the native range of *C. curvipes*, modelling results show that the potential ecological niche largely coincides with the areas where the discussed aphid species has been identified so far. The most favourable climatic conditions for its occurrence are on the west coast, including California (excluding the Mojave Desert), Oregon, Washington, southern British Columbia, Graham Island, and Vancouver Island. It also includes Idaho and Nevada, and deeper into the mainland interior, western Montana (Rocky Mountains area), Wyoming, Utah, Colorado, Arizona, and New Mexico (especially the Colorado Plateau region). A potential ecological niche in Mexico is located in the Sierra Madre Occidental and the Trans-Mexican Volcanic Belt. The central part of the continent does not provide favourable climatic conditions. In turn, on the east coast, the best conditions are in Newfoundland and along the entire belt of the Appalachian Mountains (from New Brunswick, Nova Scotia, and southern Quebec in Canada through Maine, Vermont, New Hampshire, New York, Pennsylvania, Ohio, and Virginia to Tennessee and North Carolina in the United States). The conditions in the areas bordering the Great Lakes Region are also suitable.

For Europe (Figure 8), the model indicates that the potential ecological niche covers almost the entire continent. Consequently, *C. curvipes*, with favourable weather conditions and access to one of the host plants, could probably spread freely around Europe, and only high-mountainous areas would be an obstacle. According to the modelling result, the area most at risk of spreading *C. curvipes* is Western Asia, especially Turkey, Iran, the Syrian coast, Lebanon, Israel, and the western part of Jordan. The northern coast of Africa, which borders the Mediterranean Sea (in Morocco, Algeria, Tunisia, Libya, and Egypt), may also be at risk.

Models considering potential future climate changes indicate that representatives of *C. curvipes* may find suitable niches farther north of their current ranges (Supplementary material 4). The areas currently occupied in North America will remain largely stable regarding climatic conditions. However, in the eastern part of the continent, the border will move farther north to include Ontario, Quebec, and Newfoundland and Labrador, whereas the area in Mexico will become almost completely unfavourable.

Meanwhile, in the scenarios for higher CO_2 concentrations (SSP3–7.0 and SSP5–8.5), climate changes may primarily affect the occurrence of *C. curvipes* in southern and central Europe. The maps show a clear shift of a suitable niche to the territories of Scandinavian countries and northern areas of Russia to the border with the Urals. In turn, the areas covering Turkey and Iran will remain most stable and suitable.

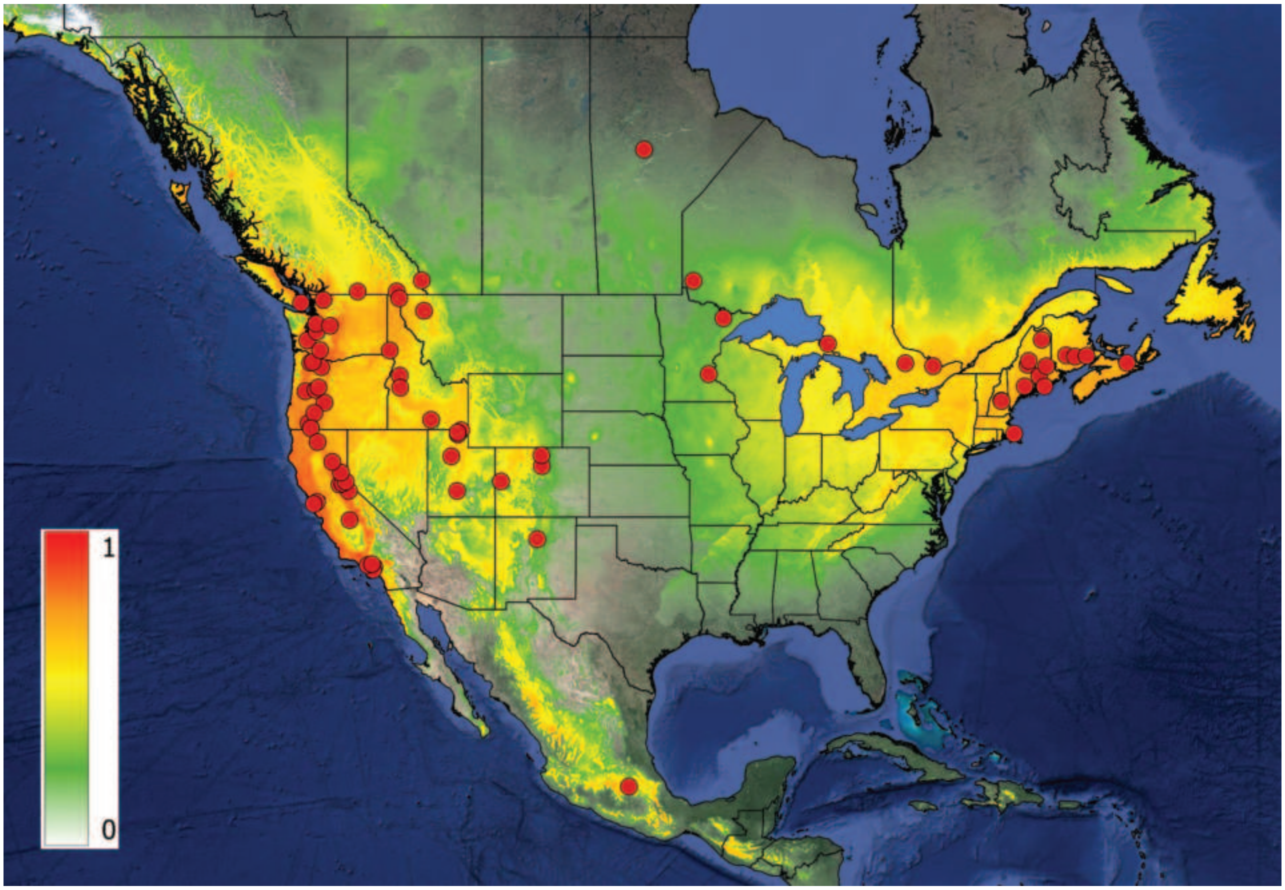

Figure 7. Model result of a potentially suitable ecological niche for *Cinara curvipes* in North America at present. Red dots represent the currently-known sites of the occurrence of the species. The colour scale shows the probability of a suitable ecological niche. Black lines represent national boundaries and the internal divisions into states/provinces.

Survival, longevity, fecundity and demographic parameters of C. curvipes under different temperatures

The development of six successive parthenogenetic generations of *C. curvipes* was studied (F1–F6). The F1 generation was observed from the moment of emergence on the host plants as adults at the end of March. We observed both wingless and winged females in the F3 generation. The last F6 generation was observed only in the pre-reproductive phase. At the tested temperatures (10, 15, and 20°C), nymphs of this generation were characterised by increased mobility and migration. Initially, they colonised the trunk of the host plant close to the ground and then went underground (Figure 9(a-b)). This migration process was observed from late September to mid-October. In spring, predation by a syrphid larva, *Episyrphus balteatus* (De Geer) (Diptera: Syrphidae), in an aphid colony was observed (Figure 9(c)).The survival of the *C. curvipes* population was strongly dependent on the temperature and was highest at 10 and 15°C. At 25°C, the nymphs did not moult properly or reach maturity. Only 20% of the nymphs reached maturity at 20°C, while at 15°C it was 80%, and at 10°C, it was as high as 100% of nymphs (Figure 10). Females had their highest daily average fecundities at 15 and 10°C, with 17.5 and 16 nymphs, respectively (Figure 10(a)). The daily fecundity of females living at lower temperatures (10 and 15°C) was higher than at higher temperatures (20°C), and females gave birth to the most nymphs at the end of the reproductive period, unlike those living at 20°C (Figure 10(b)).

The calculated demographic parameters for the population of *C. curvipes* showed that the intrinsic rate of increase (r_m) reached the minimum (0.074) at 20°C and the maximum (0.094) at 15°C (Table I).

The length of development of aphids depended on the generation and temperature at which they were reared ($F_{(10,\ 162)} = 578.6$; $p < .001$). It was observed that the length of the pre-reproduction period shortens with increasing temperature. The longest period of pre-reproduction was found at 10°C in the F6 generation (average of 42 days),

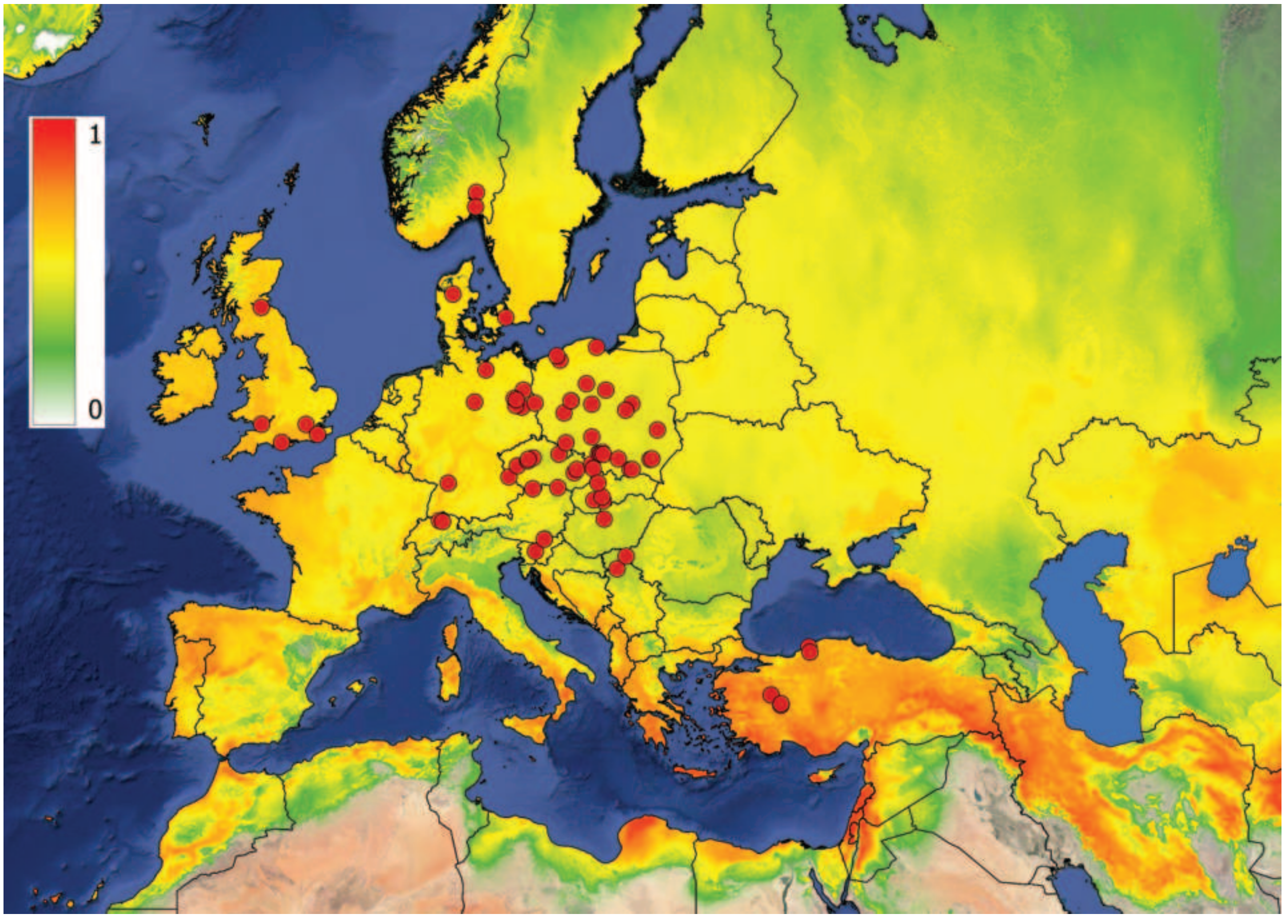

Figure 8. Model result of a potentially suitable ecological niche for *Cinara curvipes* in Europe and partly for Africa and Asia at present. Red dots represent the currently known sites of the occurrence of the species. The colour scale shows the probability of a suitable ecological niche. Black lines represent the current national boundaries.

while the shortest was found in the F3 and F4 generations at 20°C (average of 14 days) (Figure 11(a)).

The period of reproduction of aphids depended on both factors: generation and temperature ($F_{(8,\ 135)} = 723.4$; $p < .001$). The longest period of reproduction was found in females of the F3 (53 days) and F4 (64 days) generations at 10°C, while the shortest was in females of the F2 generation at 20°C, where it was 14.5 days. Interestingly, at higher temperatures, the reproduction period was significantly shorter than at low temperatures (Figure 11(b)).

Also, the period of aphid post-reproduction significantly depended on generation and temperature ($F_{(8,\ 135)} = 78.7$; $p < .001$). No post-reproduction was observed in the F1 and F2 generations, in which the aphids died immediately after the reproductive period. In subsequent generations, this period ranged from about 5 days in the F3 generation at 10°C to about 1 day in the F3 generation at 20°C (Figure 11(c)).

The total longevity of aphids differed significantly between generations and, similarly to the previous analysed parameters, was dependent on temperature ($F_{(6,\ 108)} = 662.2$; $p < .001$). Females of the F4 generation lived the longest at 10°C (98 days on average), and females of the F2 generation lived the shortest at 20°C (about 30 days) (Figure 11(d)).

The fecundity of *C. curvipes* females was dependent on temperature and generation ($F_{(8,\ 135)} = 5971.2$; $p < .001$). The highest fecundity was found in females feeding at a temperature of 10°C in the F3 and F5 generations, with an average of 255 and 274 nymphs, respectively. However, the lowest fecundity was shown by females living at 20°C in the F2 generation, with about 51 nymphs (Figure 11(e)).

Monthly temperature variations: key determinants of mass occurrence of C. curvipes

A comparison of average temperatures in places where the aphid occurred over the last 25 years

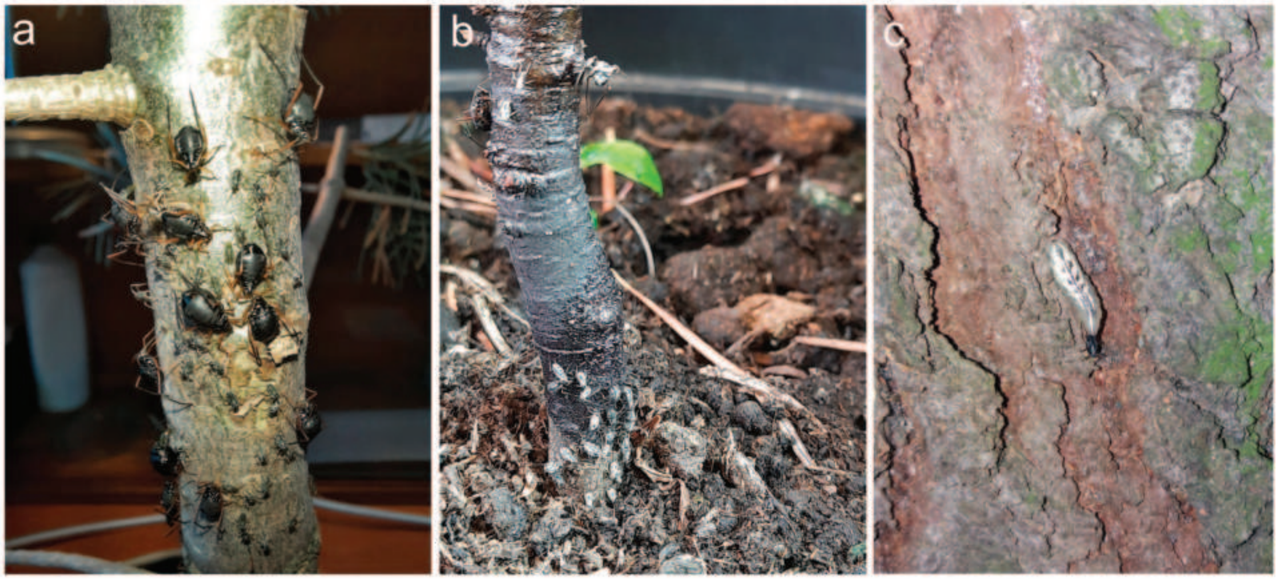

Figure 9. The movement of the last F6 generation of *Cinara curvipes* (a) adults and nymphs, down the trunk and (b) nymphs, to the root of the host plant *Abies concolor* observed during the laboratory experiment, photo by R. Durak. (c) Predation of a syrphid *Episyrphus balteatus* larva in an aphid colony, observed in the Botanic Garden Poznań, Poland, photo by B. Borowiak-Sobkowiak.

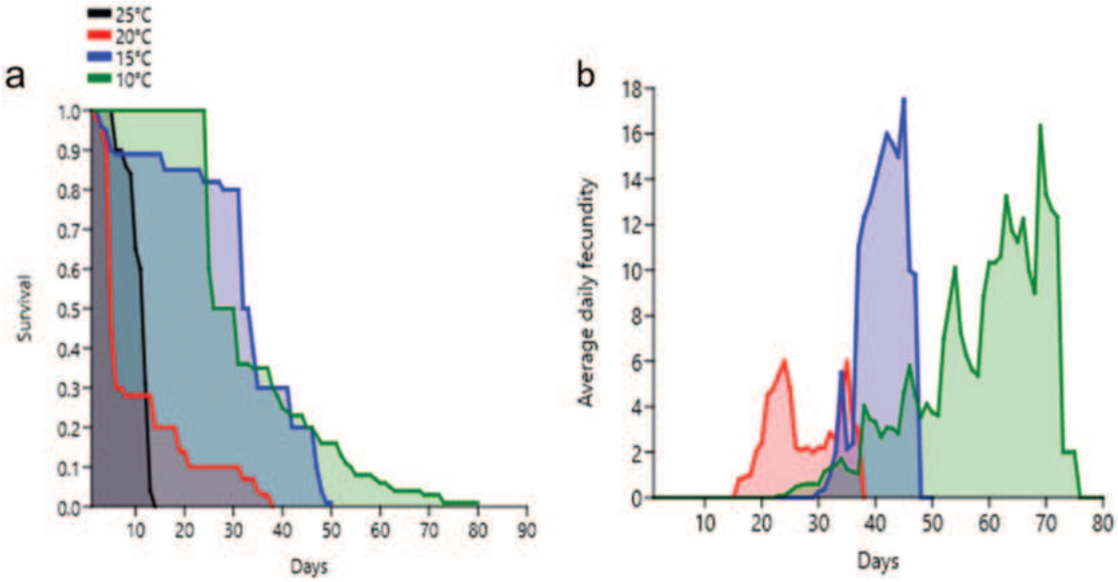

Figure 10. Survival rates (a) and daily fecundity (b) of viviparous females *Cinara curvipes* at different temperatures: 10, 15, and 20°C (n = 100 at each temperature). Significant differences between pairs of survival curves for 10 and 15°C: log-rank test chi^2 = 9.606, $p > .05$; for 10 and 20°C: log-rank test chi^2 = 6.38, $p < .01$; for 10 and 25°C: log-rank test chi^2 = 2.53, $p < .01$; for 15 and 20°C: log-rank test chi^2 = 13.17, $p < .001$; for 20 and 25°C: log-rank test chi^2 = 14.42, $p < .001$.

shows a repeatable pattern. This is particularly clear in continental Europe, where mass outbreaks of the bow-legged fir aphid were preceded by mild winters. Figure 12 shows each year's first (blue) and second (green) quarters. These are the key months for the development of the studied species. The results indicate that in the years when their mass occurrence was most common (2007, 2014, 2015, 2020), average temperatures in winter (January–March) did not drop below zero degrees. Moreover, in spring (April–June), average temperatures did not exceed 15°C in May and 20°C in June, further confirming laboratory test observations indicating that elevated temperatures are limiting for survival of *C. curvipes*.

Table I. Demographic parameters of the *Cinara curvipes* population in the experimental conditions. Ro - net reproductive rate; rm - intrinsic rate of population increase; λ - finite rate of population increase; T - mean generation time; DT - time for doubling the population.

	Parameter				
Temperature (°C)	R_o	r_m	λ	T	DT
10	27.614	0.076	1.079	43.662	9.12
15	40.952	0.094	1.099	39.494	7.374
20	6.11	0.074	1.077	24.46	9.367
25	0	0	0	-	-

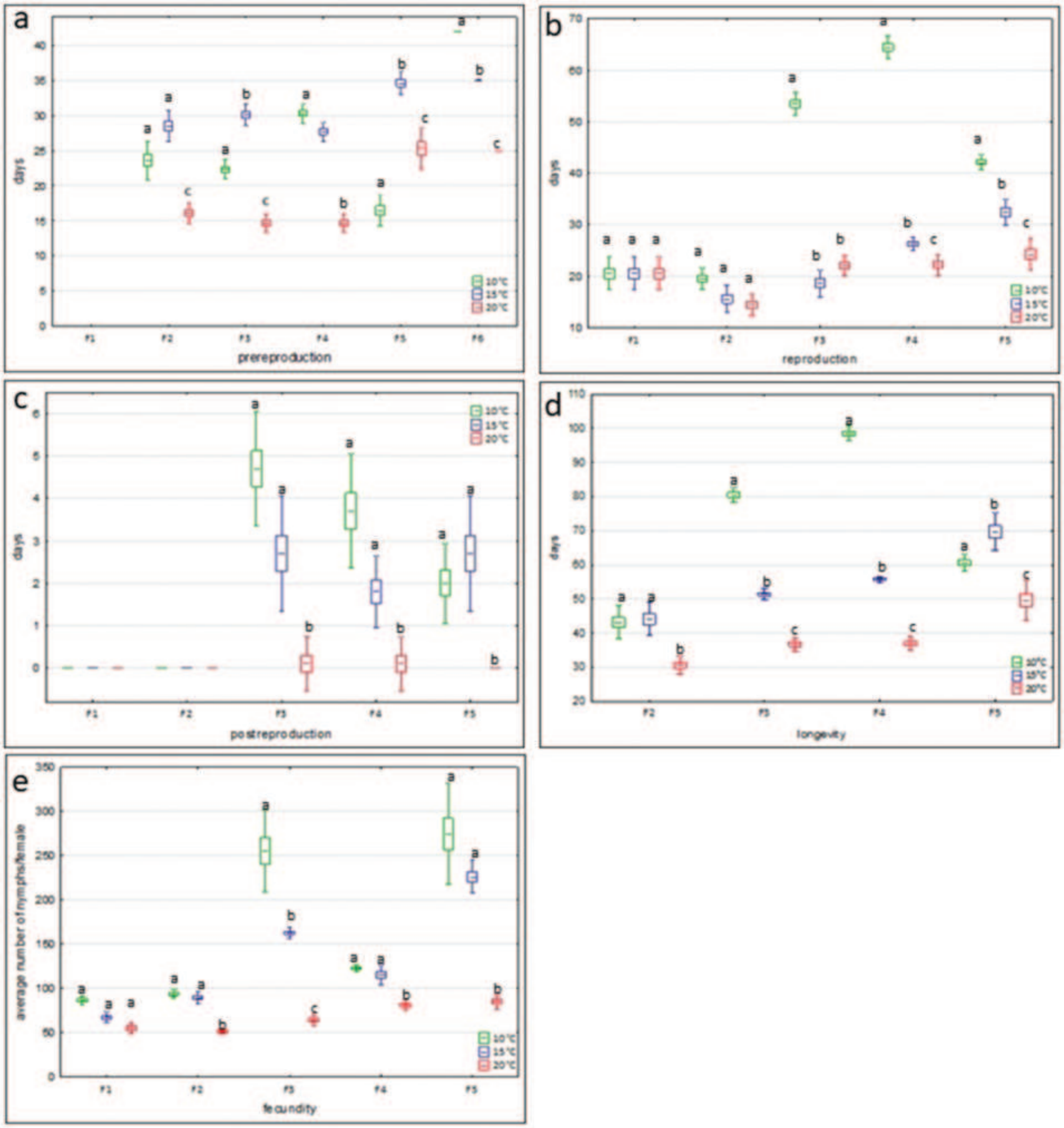

Figure 11. Developmental time and fecundity of subsequent generations of *Cinara curvipes* (F1–F6). Duration of development phases: pre-reproduction, reproduction, post-reproduction, longevity (a-d) and fecundity (e) at different temperatures. Values marked with different letters differ significantly at $p < .05$ for each generation (Tukey test).

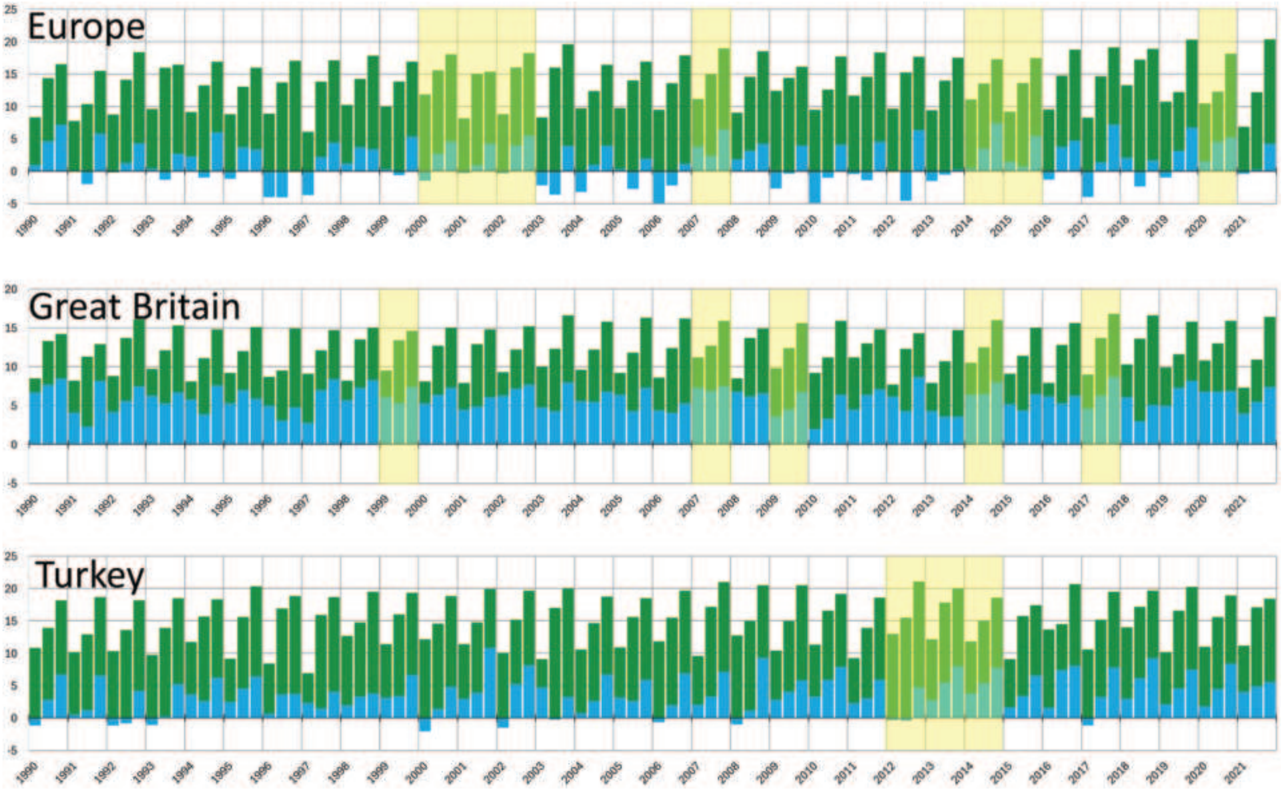

Figure 12. Average monthly temperatures from winter (January–March, in blue) and spring (April–June, in green), averaged for places where *Cinara curvipes* was detected. The periods when aphids were found in larger numbers (Europe) or at all (Great Britain, Turkey) are highlighted.

It is noteworthy that the winter season of 2019–2020 was the warmest ever measured in Oslo (Norway), while 2020–2021 was normal, and 2021–2022 was milder than normal (but not extreme), coinciding with the first record of this species in Norway (Norsk Klimaservicesenter 2023).

Discussion

In this study, we predicted potential ecological niches and assessed the impact of climate change on the distribution of *C. curvipes*, an alien and potentially invasive aphid species that has been rapidly spreading throughout Europe. Drawing primarily from the climatic preferences observed in North America, which encompasses the native range of the bow-legged fir aphid, our objective was to investigate whether climatic conditions in Europe could facilitate further spread of this aphid species. The modelling results indicate that the majority of European regions exhibit favourable conditions for the spread of *C. curvipes*. Coupled with the presence of suitable host plants, there is the potential for this aphid species to extend its range throughout Europe and into Asia Minor. Additionally, our models suggest that under future climate conditions, suitable habitats for *C. curvipes* in the Northern Hemisphere are projected to expand northward. Several studies demonstrated the tendency of insects to follow expansion of suitable habitats in Europe and/or North America by progressively expanding their range northward (e.g. Régnière et al. 2012; Delava et al. 2014; Klementová & Svitok 2014; Kistner 2017; Fält-Nardmann et al. 2018; Endrestøl & Roth 2020; Rimšaitė et al. 2022). Interestingly, the area of Asia Minor is projected to remain climatically favourable, even in the face of climate change, making it a potential permanent occurrence area for this aphid species. Moreover, Asia Minor hosts natural ranges of *Abies nordmanniana*, *A. cilicica*, and *Cedrus libani*, which have already been reported as suitable host plants for *C. curvipes* (Görür et al. 2015).

On a regional scale, based on our research in Poland, it is evident that mild winters promote population growth, mass appearances and establishment of this species. Our research indicates that the aphid not only appeared in Poland 7 years before the publication of data on its appearance (Hałaj & Osiadacz 2015) but also spread across almost the entire country in the subsequent 7 years. An analysis of average temperatures in regions where the aphid has been recorded over the past 25 years unveils a recurring trend. This trend is particularly pronounced in continental Europe, where mass outbreaks of *C. curvipes* have consistently occurred following periods of mild winters. This correlation suggests a strong link between winter temperatures and the population dynamics of this aphid species, highlighting the importance of climatic factors in its proliferation and spread across the continent.

However, it appears that we may be dealing with additional factors in the case of the Scandinavian countries. The Danish first record was identified from a "Christmas trees" plantation, around the same time as the locations in Germany and Serbia, signaling the beginning of the species' expansion in continental Europe. Subsequently, the next Danish record emerged 16 years later. It is somewhat surprising that there are no more records from Denmark, considering the abundance of fir plantations in the region, which offers a highly suitable habitat for the species. It is also challenging to speculate how long *C. curvipes* has been present in its current location in Norway. With only one known locality and limited historical data available, we cannot definitively conclude that it has become established in Norway. Considering that the bow-legged fir aphid can potentially go unnoticed for years, there is a fair possibility that this species might be established in other locations in both Denmark and Norway without being detected. This is despite the fact that it is a relatively large and conspicuous species, especially during its mass outbreaks. As we have documented *C. curvipes* on "Christmas trees" imported to Norway from Denmark, it is highly plausible that this aphid species has been imported to Norway on "Christmas trees" for some years and may possibly be the vector causing the foundation of the population found in Oslo. Another supporting argument for this scenario is the relatively low number of fir trees registered in the urban centre of Oslo, making it unlikely that the recorded specimens have expanded from other planted individuals of *Abies*. This is in strong contrast to the large number of "Christmas trees", mostly various species of firs, brought into the city each year to pop-up sales stands in December, traded, and spread out around the city to be used both indoors and outdoors in backyards. These trees are discarded in January and could be left outside until spring. Throughout this process, aphids could escape and settle on locally planted trees, particularly during milder winters (Figure 13).

Denmark is one of the major exporters of *Abies* as "Christmas trees" in Europe, producing about 11 million trees annually (www.christmastree.dk). In 2021, 40% of their production was exported to Germany and only 3% to Norway (Statista 2022). Still, since 2000, almost 7 million "Christmas trees" have been imported to Norway, peaking in 2003 with 438,400 trees (Statistics Norway 2022). These large volumes of *Abies* trees imported to Norway as "Christmas trees" annually are not monitored as vectors for alien species, mainly as they are imported during winter and regulated legally as "cut flowers". Thus, we suggest that "Christmas trees" plantations serve as important reservoir for *C. curvipes*, and that its range expansion could be facilitated by the self-accelerating process of the bridgehead effect (Bertelsmeier & Keller 2018). This is probably most important in Northern Europe, outside the natural distribution of *Abies*. "Christmas trees" are not included in the "Regulations related to plants and measures against pests" and are thus not monitored by the Norwegian Food Safety Authority either.

Similar conclusions arise from surveys conducted among Polish "Christmas tree" plantations. The presence of infected firs in garden centres and, consequently, in private houses during the festive season confirms our assumption regarding the significant role of the trade of "Christmas trees" in the spread of this particular aphid species. This assertion is further supported by previous research conducted in Austria (Perny 2014), as well as photos of "Christmas trees" infected by aphids, shared on social media platforms in both the United States and Europe. The role of citizen science, i.e. platforms like iNaturalist, should be emphasised as an invaluable tool in monitoring and documenting ecological phenomena. However, it is crucial that such data should be verified to ensure accuracy and reliability. It is essential to take particular care, in the case of *C. curvipes*, to prevent confusion with similar species, e.g. *C. confinis* (Koch), native in Europe. These two species have similar biology and are both often found in large numbers on firs growing in urban areas (Blackman & Eastop 2024).

Aphids are poikilothermic insects, meaning their body temperature is regulated by the environment. Changes in temperature can significantly impact their physiology, development, and reproductive rates. With global warming, there is a potential for altered temperature patterns that may influence aphid populations. The life cycle of *C. curvipes* appears to be unique. Viviparous females of all

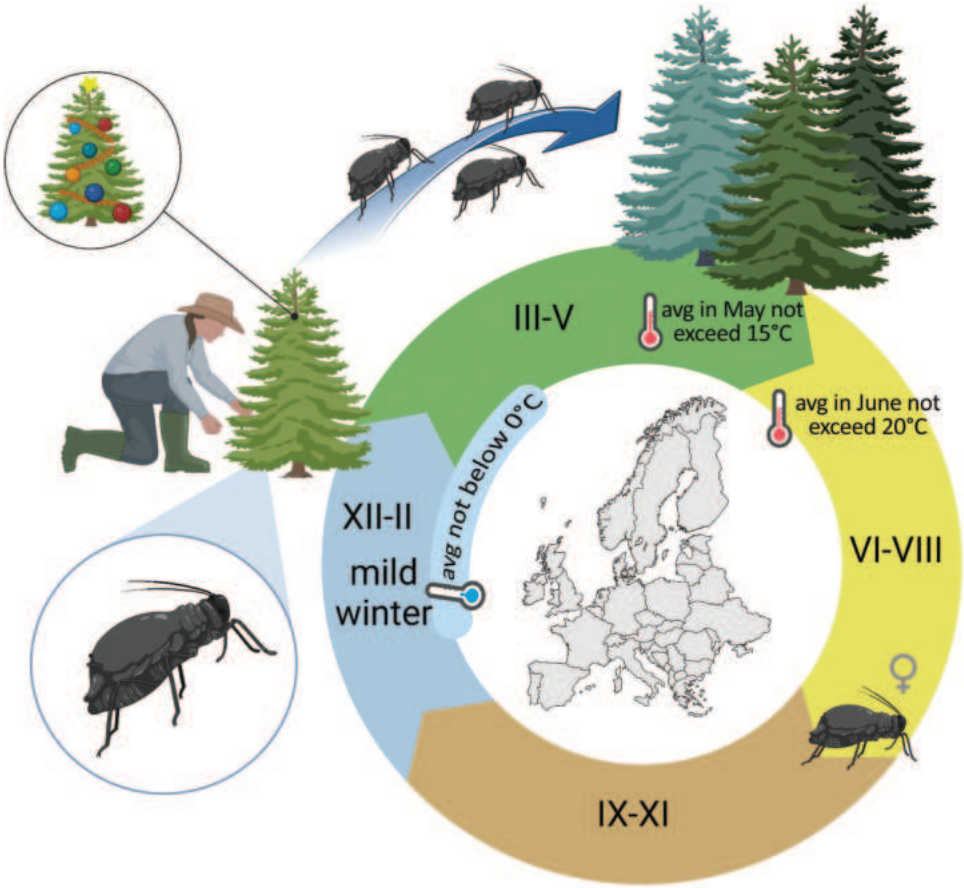

Figure 13. Mild winters promote the survival, population growth, mass appearances and establishment of *Cinara curvipes*, whereas the trade in “Christmas trees” significantly contributes to the dispersal of the species. This image was created with BioRender.com.

generations are characterised by very high fecundity, which makes them similar to aphid species considered serious pests, such as *Rhopalosiphum padi* (L.) or *Acyrthosiphum pisum* Harris (Park et al. 2017; Ahn et al. 2020). Within the subfamily Lachninae, high viviparous female fecundity was also observed in *Tuberolachnus salignus* (Gmelin) at 20°C (Collins & Leather 2001). However, our previous studies showed that in the genus *Cinara*, the average female fecundity ranged from 22–25 nymphs for *C. juniperi* (De Geer) and *C. mordvilkoi* (Pašek) to 40–45 nymphs for *C. tujafilina* (Del Guercio) and *C. cupressi* (Buckton) (Durak et al. 2007, 2016; Durak & Borowiak-Sobkowiak 2013; Durak 2014a, 2014b), whereas in this study we demonstrated that the fecundity of *C. curvipes* is more than 5 times higher. Additionally, the *C. curvipes* viviparous generation shows a different life strategy because females achieve the highest fecundity at lower temperatures (10–15°C), while for *C. juniperi* the optimal temperature is 20°C, and for *C. tujafilina* it is 25°C. Moreover, while most viviparous females of aphids produce the highest number of nymphs at the beginning of their reproductive period, the highest daily fecundity of the bow-legged fir aphid is exhibited by females at the end of this period. This may indicate that low temperatures prolong the embryonic development of parthenogenetic embryos and, consequently, they need more time to develop fully (Miura et al. 2003). This may result in high daily fecundity of viviparous females at the end of their reproductive period. All these features of *C. curvipes* may cause the observed mass appearances of this species on host plants. This strategy differs from other species belonging to the genus *Cinara*, whose survival and fecundity increase with increasing temperature, e.g. *C. tujafilina* (Durak & Borowiak-Sobkowiak 2013). The overcrowding of the colony results in large numbers of winged morphs, which is unique compared to other Lachninae (Jousselin et al. 2013). Consequently, spreading as aerial plankton, alongside transportation through plant material, i.e. the trade of “Christmas trees”, becomes a significant factor facilitating the dispersion of the species. Moreover, in the case of alien species, the lack of natural predators or parasites in their new environment allows them to proliferate without being limited and thus cause ecological imbalances. In Europe, the only known predator of *C. curvipes* appears to be the syrphid *Episyrphus balteatus* (Scheurer & Binazzi 2004), a finding also supported by our observations in Poland. Among predators, the invasive alien harlequin ladybug *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) was observed at the Norwegian locality, as was also reported in Turkey (Görür et al. 2015) and Poland (Hałaj & Osiadacz 2015).

Previous research (Jurc et al. 2009) and our observations indicate that the bow-legged fir aphid, being a polyphagous species, also exhibits a preference for European native silver fir as a host plant. Therefore, it cannot be ruled out that it may become a pest, especially considering that changing climatic conditions and the increasingly frequent mild winters in Europe appear to favour this species. The pest status of *C. curvipes* in the invaded area remains unclear. According to the European and Mediterranean Plant Protection Organization EPPO (2008), the species is considered to be a minor pest of firs; however, direct damage to trees is usually not significant and is rarely reported (Poljaković-Pajnik & Petrović-Obradović 2002; Bodor 2013). So far, alerts regarding forest protection have been issued sporadically (the Czech Republic Knížek 2010; Poland; PIORiN 2020; Alert of the General Director of State Forests; present study). However, the studied aphid species can pose a significant problem in regions where fir trees are grown commercially, such as "Christmas trees" or timber plantations. These pests excrete large amounts of honeydew, a sticky substance that can cause aesthetic damage to trees. The accumulation of honeydew not only affects the appearance of the trees but also promotes the development of sooty moulds, further compromising their visual appeal. This aesthetic degradation can diminish the value of "Christmas trees", impacting their marketability and economic revenue. Therefore, while the pest status of *C. curvipes* remains unclear, the aesthetic damage caused by aphids' honeydew secretion underscores the importance of addressing their presence in "Christmas trees" plantations. Despite the use of chemical pest control, reports of the presence of these aphids on "Christmas trees" appear every year, contributing to the further spread of the species. Thus, more effective control strategies are needed to mitigate their impact on tree health and ecosystem balance.

So far, the occurrence of *C. curvipes* has not been reported to significantly affect natural fir forests, either in its native range in North America or after introduction to Europe. However, given the unpredictability of biological invasion processes, this risk cannot be completely ruled out. Fir species play a very important role in maintaining high biodiversity (Mauri et al. 2016) and at the same time the area of fir forests has substantially decreased within its natural range over the past few decades due to human-induced impacts (Wolf 2003), which caused the need for their protection. In Europe, silver fir is the key species in several forest habitats protected by the Habitats Directive (Council Directive 1992). One of these habitats, namely Holy Cross fir forests, is endemic to Poland. Moreover, at least 40 nature reserves in Poland were established specifically to protect silver fir (GDOŚ 2024). Invasion of *C. curvipes* in natural fir forest stands would therefore pose a very serious threat to Polish biodiversity. We expect that the efforts that we undertook immediately after detection of the mass outbreaks of *C. curvipes* in 2020 contributed to raising awareness of this problem among decision makers responsible for forest management in Poland, thus increasing the level of preparedness of forest services for this new potential threat. In contrast, outside the natural range of firs, e.g. in Northern Europe, different species of *Abies* are expanding their range and to some extent are considered alien. In e.g. Norway and Denmark, *Abies alba* was planted for the first time in the 1700s (Ridbäck 2018). In Norway, *A. alba* is regarded as a problematic species, spreading fast and becoming an unwanted element in forest, especially in broadleaf forests (Ridbäck 2018; Solstad et al. 2021). As several of the *Abies* species have a high invasive potential (Sandvik 2012), we would expect that the habitat availability for *C. curvipes* would also increase outside its current potential range based on host plant availability, facilitating its range expansion further north. Thus, it is important to monitor such range expansions and their ecological impacts to better understand and manage these changing ecosystems.

Conclusion

Our study sheds light on the potential ecological impact of *C. curvipes*, an alien aphid species that has rapidly spread throughout Europe. Through predictive modelling, we have identified favourable climatic conditions across European regions, coupled with the presence of suitable host plants, which could facilitate the further spread of this species. The correlation between mild winters and mass outbreaks of *C. curvipes* in continental Europe underscores the significance of climatic factors in its proliferation. By clearly defining the aim and objectives of modelling aphid species distribution under future climate scenarios, the research contributes to our understanding of how these insects may respond to ongoing environmental changes, facilitating informed decision-making for sustainable ecological management. We also identified the bionomic features of this species, thanks to which it has the ability to disperse and colonise new host plants. Addressing the dispersion of *C. curvipes* through the "Christmas trees" trade requires coordinated EDRR efforts among stakeholders, including "Christmas tree" growers, regulatory agencies, and consumers. Strategies could include implementing quarantine measures, promoting awareness among consumers about the risks associated with infested trees, and adopting integrated pest management practices to minimise the spread of this species.

Highlights

- Future climate scenarios predict a northward expansion of *C. curvipes.*
- Fecundity of *C. curvipes* is more than five times higher than that of other *Cinara* species.
- Mild winters and lower spring temperatures (10–15°C) cause mass outbreaks of *C. curvipes.*
- Temperatures above 25°C are detrimental to the development of *C. curvipes*, leading to summer population declines.
- The trade of "Christmas trees" significantly contributes to the dispersal of *C. curvipes.*

Acknowledgments

We thank Christian Nørgård Nielsen and Niels Jacobsen for sharing details and photos of their observations of *C. curvipes* in Denmark. Further, we thank Eva Johanne Westlund (Eventyrbrua Steinerbarnehage) for recording the colony of *C. curvipes* from Norway and sharing additional information on the observation and locality. Thanks to Anders Often for joining the search for *C. curvipes* on *Abies* stands both in Oslo and Ås municipalities, and for joining in investigating imported "Christmas trees" in November 2022. We thank Joanna Malinowska, Małgorzata Czyżewska, Katarzyna Nowik and Robert Rozwałka for sharing details and photos of their observations of *C. curvipes* in Poland, fir plantations's "Perfect Green" and Choinki.pl owners for valuable comments on *C. curvipes* presence and "https://www.instagram.com/zielone_pogotowie/" for sharing a video of mass occurrence of *C. curvipes* in the private garden in the vicinity of Lipno. We thank Kamila Malik (University of Silesia in Katowice, Katowice, Poland) for collecting aphid location data from North America.

Funding

The Norwegian part of this project was financed by The Research Council of Norway, project no. [61528 NINA] basic funding.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Author contributions

Wieczorek, Karina: Conceptualisation, formal analysis, investigation; methodology, supervision; validation; visualisation; writing – original draft; and writing – review & editing.

Bugaj-Nawrocka, Agnieszka: Methodology; validation; visualisation; writing – original draft; and writing – review & editing.

Borowiak-Sobkowiak, Beata: Investigation; methodology; resources; visualisation; writing – original draft; and writing – review & editing.

Endrestøl, Anders: Investigation; writing – original draft.

Ravn, Hans Peter: Investigation; writing – review & editing.

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Data availability statement

Data will be made available on request.

Supplementary material

Supplemental data for this article can be accessed online at https://doi.org/10.1080/24750263.2024.2449152

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References

Ahn JJ, Cho JR, Kim J-H, Seo BY. 2020. Thermal effects on the population parameters and growth of *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae). Insects 11(8):481. DOI: 10.3390/insects11080481.

Angst A, Scheurer S, Forster B. 2007. Schweizer Erstfund der Rindenlaus *Cinara curvipe*s (Patch) (Homoptera, Aphidina, Lachnidae) an der Coloradotanne. Mitteilungen Der Schweizerischen Entomologischen Gesellschaft 80:247–252.

Bertelsmeier C, Keller L. 2018. Bridgehead effects and role of adaptive evolution in invasive populations. Trends in Ecology & Evolution 33(7):527–534. DOI: 10.1016/j.tree.2018.04.014.

Birch LC. 1948. The intrinsic rate of natural increase of an insect population. The Journal of Animal Ecology 17(1):15–26. DOI: 10.2307/1605.

Blackman RL, Eastop VF. 2024. Aphids of the World's plants: An online identification and information guide. http://www.aphidsonworldsplants.info. Accessed Jan 23 2024.

Bodor J. 2013. Damage of bow-legged fir aphid (*Cinara curvipes* Patch, 1912) in Hungary. Növényvédelem 49:273–275.

Boria RA, Olson LE, Goodman SM, Anderson RP. 2014. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. Ecological Modelling 275:73–77. DOI: 10.1016/j.ecolmodel.2013.12.012.

Bugaj-Nawrocka A, Taszakowski A, Gierlasiński G. 2021. From Asia to Europe? Where could the geographical place of origin of *Polymerus* (*Pachycentrum*) *carpathicus* (Horváth, 1882) (Hemiptera: Miridae) Be? Zoological Studies 60:1–13. DOI: 10.6620/ZS.2021.60-42.

Caudullo G, Welk E, San-Miguel-Ayanz J. 2017. Chorological maps for the main European woody species. Data in Brief 12:662–666. DOI: 10.1016/j.dib.2017.05.007.

Collins CM, Leather SR. 2001. Effect of temperature on fecundity and development of the giant willow aphid, *Tuberolachnus salignus* (Sternorrhyncha: Aphididae). European Journal of Entomology 98(2):177–182. DOI: 10.14411/eje.2001.033.

Conrad O, Bechtel B, Bock M, Dietrich H, Fischer E, Gerlitz L, Wehberg J, Wichmann V, Böhner J. 2015. System for automated geoscientific analyses (SAGA) version 7.3.0. Geoscientific Model Development 8(7):1991–2007. DOI: 10.5194/gmd-8-1991-2015.

Conservation Biology Institute (CBI). 2023. Data Basin Conservation Biology Institute 136 SW Washington Ave. Ste. 202 Corvallis, OR 97333. http://databasin.org. Accessed Apr 2023 21.

Council Directive. 1992. Council directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A01992L0043-20130701.

Darr MN, Coyle D, Jetton R. 2022. Arthropod and disease management in fraser fir (Pinales: Pinaceae) Christmas trees in the Southeastern United States. Journal of Integrated Pest Management 13(1):8. DOI: 10.1093/jipm/pmac001.

DeFrancesko J, Murray K. 2009. Pest management strategic plan for Christmas trees in Oregon, Washington, and Idaho. Summary of workshop held on 2–3 February 2009, Aurora Oregon USA. 104 pp.

Delava E, Allemand R, Léger L, Fleury F, Gibert P, Whittaker R. 2014. The rapid northward shift of the range margin of a Mediterranean parasitoid insect (Hymenoptera) associated with regional climate warming. Journal of Biogeography 41 (7):1379–1389. DOI: 10.1111/jbi.12314.

Doherty J-F, Guay J-F, Cloutier C. 2017. Temperature-manipulated dynamics and phenology of *Mindarus abietinus* (Hemiptera: Aphididae) in commercial Christmas tree plantations in Québec, Canada. The Canadian Entomologist 149 (6):801–812. DOI: 10.4039/tce.2017.41.

Dransfield RD, Brightwell R. 2023. InfluentialPoints. *Cinara curvipes*. https://influentialpoints.com/Gallery/Cinara_curvipes_bow-legged_fir_aphid.htm. Accessed Dec 2 2023.

Durak R. 2014a. Life cycle, seasonal and interannual polymorphism in a monoecious aphid *Cinara mordvilkoi* (Hemiptera: Aphidoidea: Lachnidae). European Journal of Entomology 111(3):357–362. DOI: 10.14411/eje.2014.051.

Durak R. 2014b. The overwintering strategy of the anholocyclic aphid *Cinara tujafilina*. Physiological Entomology 39 (4):313–321. DOI: 10.1111/phen.12077.

Durak R, Borowiak-Sobkowiak B. 2013. Influence of temperature on the biological parameters of the anholocyclic species *Cinara tujafilina* (Hemiptera: Aphidoidea). Central European Journal of Biology 8(6):570–577. DOI: 10.2478/s11535-013-0161-x.

Durak R, Borowiak-Sobkowiak B, Socha M. 2007. Bionomy and ecology of *Cinara cupressi* (Buckton, 1881) (Hemiptera, Aphidoidea). Polish Journal of Entomology 76:107–113.

Durak R, Węgrzyn E, Leniowski K. 2016. Do all aphids benefit from climate warming? An effect of temperature increase on a native species of temperate climatic zone *Cinara juniperi*. Ethology Ecology & Evolution 28:108–201. DOI: 10.1080/03949370.2015.1034785.

Elith J, Kearney M, Phillips S. 2010. The art of modelling range-shifting species. Methods in Ecology and Evolution 1 (4):330–342. DOI: 10.1111/j.2041-210X.2010.00036.x.

Endrestøl A, Andreasen M, Davey M, Fossøy F, Jacobsen RM, Åström J. 2023b. Early detection of new terrestrial alien species. NINA report 2197. Norwegian Institute for Nature Research 44 pp. https://hdl.handle.net/11250/3057350.

Endrestøl A, Gammelmo Ø, Hatteland BA, Laugsand AE, Olberg S, Slagsvold PK, Staverløkk A, Åström S. 2023a. Nebbmunner: Vurdering av *Dreyfusia nordmannianae* for Fastlands-Norge med havområder. Fremmedartslista 2023. Artsdatabanken.

Endrestøl A, Roth S. 2020. The firebug *Pyrrhocoris apterus* (Linnaeus, 1758) (Hemiptera, Heteroptera) new to the Norwegian fauna – with an explosive expansion in Northern Europe. Norwegian Journal of Entomology 67:81–90.

EPPO (European and Mediterranean Plant Protection Organization). 2008. First report of *Cinara curvipes* (Homoptera: Aphididae) in the Czech Republic EPPO reporting service no. 03 – 2008 num. article: 2008/053 https://gd.eppo.int/reporting/article-573.

Ersts PJ. 2016. Geographic distance matrix generator, version 1.2.3. American Museum of Natural History. Center for Biodiversity and Conservation. https://biodiversityinformatics.amnh.org/open_source/gdmg. Accessed Mar 23 2023.

Fält-Nardmann J, Tikkanen OP, Ruohomäki K, Otto LF, Leinonen R, Pöyry J, Saikkonen K, Neuvonen S. 2018. The recent northward expansion of *Lymantria monacha* in relation to realised changes in temperatures of different seasons. Forest Ecology & Management 427:96–105. DOI: 10.1016/j.foreco.2018.05.053.

Farjon A, Filer D. 2013. An atlas of the world's conifers: An analysis of their distribution, biogeography, diversity and conservation status. Leiden: Brill. p. 512 pp.

Fick SE, Hijmans RJ. 2017. Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37(12):4302–4315. DOI: 10.1002/joc.5086.

Fondren KM, McCullough DG. 2002. Biology and management of balsam twig aphid. Extension Bulletin E-2813. East Lansing, MI: Michigan State University. p. 6.

GDOŚ. 2024. Centralny Rejestr Form Ochrony Przyrody. Generalna Dyrekcja Ochrony Środowiska. https://crfop.gdos.gov.pl/CRFOP/.

Global Biodiversity Information Facility. 2023. Gbif.Org (06 March 2023). Data associated with the article. DOI: 10.15468/dl.7aks4d.

Google Inc. 2023. Google earth, version 7.3.3. Mountain View, CA, USA http://www.google.com/earth/index.html. Accessed Apr 2023 21.

Görür G, Toper Kaygin A, Şeno Ö, Akyildirim Beğen H. 2015. *Cinara curvipes* (Patch, 1912) (Hemiptera; Aphididae) as new aphid species for Turkish aphidofauna. Artvin Çoruh Üniversitesi Orman Fakültesi Dergisi 16(1):37–39. DOI: 10.17474/acuofd.75484.

Gottschalk HJ. 2001. *Cinara curvipes* (Patch), Erstfund in Mecklenburg – Vorpommern, ein potentieller Forstschädling. Mitteilungsblatt des Entomologischen Vereins Mecklenburg 1:36. DOI: 10.1111/jse.12458.

Hałaj R, Osiadacz B. 2015. On foreign land: The conquest of Europe by *Cinara curvipes* (Patch, 1912). Deutsche Entomologische Zeitschrift 62(2):261–265. DOI: 10.3897/dez.62.6457.

Hammer Ø, Harper DAT, Ryan PD. 2001. Past: Paleontological statistics software package for education and data analysis. Palaeontologia electronica 4:1–9.

iNaturalist. 2023. https://www.inaturalist.org. Accessed Dec 2023 18.

Jousselin E, Cruaud A, Genson G, Chevenet F, Foottit RG. 2013. Coeur d'acier a (2013) is ecological speciation a major trend in aphids? Insights from a molecular phylogeny of the conifer-feeding genus *Cinara*. Frontiers in Zoology 10(1):56. DOI: 10.1186/1742-9994-10-56.

Jurc M, Poljakovic-Pajnik L, Jurc D. 2009. The first record of *Cinara curvipes* (Patch, 1912) (Homoptera, Aphididae) in Slovenia and its possible economic impact. Zbornik Gozdarstva in Lesarstva 88:21–29.

Kistner EJ. 2017. Climate change impacts on the potential distribution and abundance of the brown marmorated stink bug (Hemiptera: Pentatomidae) with special reference to North America and Europe. Environmental Entomology 46 (6):1212–1224. DOI: 10.1093/ee/nvx157.

Klementová B, Svitok M. 2014. *Anisops sardeus* (Heteroptera): A new expansive species in Central Europe. Biologia 69 (5):676–680. DOI: 10.2478/s11756-014-0354-z.

Knížek M (2010) Occurrence of forest damaging agents in 2009 and forecast for 2010, TISKCENTRUM, s. r. o. Brno. 75 pp.

Kumar S, Neven LG, Yee WL. 2014. Evaluating correlative and mechanistic niche models for assessing the risk of pest establishment. Ecosphere 5(7):1–23. DOI: 10.1890/ES14-00050.1.

Little EL Jr. 1971. Atlas of United States trees. Volume 1. Conifers and important hardwoods. Miscellaneous publication 1146. Washington, DC: U.S. Department of Agriculture, Forest Service 9 p illus. [313 maps, folio].

Martin JH. 2000. Two new British aphid introductions in 1999, in the context of other additions over the preceding thirty years (Sternorrhyncha: Aphidoidea). Entomologist's Gazette 51:97–105.

Mauri A, de Rigo D, Caudullo G. 2016. *Abies alba* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A, editors. European Atlas of Forest Tree Species. Publ. Off. Luxembourg: EU. p. 01493b+. DOI: 10.2760/776635.

Merow C, Smith MJ, Edwards TC, Guisan A, McMahon SM, Normand S, Thuiller W, Wüest RO, Zimmermann NE, Elith J. 2014. What do we gain from simplicity versus complexity in species distribution models? Holarctic Ecology 37 (12):1267–1281. DOI: 10.1111/ecog.00845.

Mertelík J, Kloudová K, Havelka J, Starý P. 2007. Overpopulation of the aphid *Cinara curvipes* on *Abies concolor* in the CR. (in Czech). Rostlinolékař 18:38.

Microsoft Corporation. 2024. Microsoft Excel. Available: https://office.microsoft.com/excel. Accessed Dec 2024 15.

Miura T, Braendle C, Shingleton A, Sisk G, Kambhampati S, Stern DL. 2003. A comparison of parthenogenetic and sexual embryogenesis of the pea aphid *Acyrthosiphon pisum* (Hemiptera: Aphidoidea). The Journal of Experimental Zoology 295B(1):59–81. DOI: 10.1002/jez.b.3.

Nakládal O, Turčáni M, Šrůtka P. 2007. First record of *Cinara curvipes* (Hemiptera: Aphididae) from Slovakia. Klapalekiana 43:201–202.

Newton L, Frampton J, Monahan J, Goldfarb B, Hain F. 2011. Two novel techniques to screen *Abies* seedlings for resistance to the balsam woolly adelgid, *Adelges piceae*. Journal of Insect Science 11(158):1–16. insectscience.org/11.158.

Norsk Klimaservicesenter (2023) Observasjoner og værstatistikk. https://seklima.met.no/observations/. Accessed Feb 2024 22.

Olbrechtová J. 2007. First occurrence of *Cinara curvipes* Patch 1912 on white fir (*Abies concolor* (Gordon et Glendenning) Hildebrand 1861) in the Czech Republic. Aphids and Other Hemipterous Insects 13:43–49.

Park CG, Choi BR, Cho JR, Kim JH, Ahn JJ. 2017. Thermal effects on the development, fecundity and life table parameters of *Rhopalosiphum padi* (Linnaeus) (Hemiptera: Aphididae) on barley. Journal of Asia-Pacific Entomology 20 (3):767–775. DOI: 10.1016/j.aspen.2017.05.004.

Perny B. 2014. Die Coloradotannen-Rindenlaus, *Cinara curvipes* – Ein harmloser inwanderer aus Nordamerika in Österreichs Christbaumkulturen und Gärten? Forstschutz Aktuell 60 (61):28–30.

Perret DL, Bell DM, Gray AN, Shaw JD, Zald HSJ. 2023. Range-wide population assessments for subalpine fir indicate widespread disturbance-driven decline. Forest Ecology & Management 542:121128. DOI: 10.1016/j.foreco.2023.121128.

Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190(3–4):231–259. DOI: 10.1016/j.ecolmodel.2005.03.026.

Phillips SJ, Dudík M. 2008. Modelling of species distributions with maxent: New extensions and a comprehensive evaluation. Holarctic Ecology 31(2):161–175. DOI: 10.1111/j.0906-7590.2008.5203.x.

PIORiN. 2020. *Cinara curvipes* szkodnik stwarzający zagrożenie dla drzew iglastych w Polsce. https://piorin.gov.pl/files/userfiles/wnf/nowe_zagrozenia/cinara_curvipes.pdf.

Poljaković-Pajnik L, Petrović-Obradović O. 2002. Bow-legged fir aphid *Cinara curvipes* (Patch) (Aphididae, Homoptera) new pest of *Abies concolor* in Serbia. Acta Entomol Serbica 7:147–150.

Potgieter LJ, Cadotte MW, Roets F, Richardson DM. 2024. Monitoring urban biological invasions using citizen science: The polyphagous shot hole borer (*Euwallacea fornicatus*). Journal of Pest Science 97(4):2073–2085. DOI: 10.1007/s10340-024-01744-7

QGIS Development Team. 2023. QGIS geographic information system. Open-source geospatial foundation project. http://qgis.osgeo.org. Accessed Apr 2023 21.

Qiao H, Escobar LE, Peterson AT, Ji L, Soberón J, Campbell LP. 2015. NicheA: Creating virtual species and ecological niches in multivariate environmental scenarios. Holarctic Ecology 39(8):805–813. DOI: 10.1111/ecog.01961.

Reaser JK, Burgiel SW, Kirkey J, Brantley KA, Veatch SD, Burgos-Rodríguez J. 2020. The early detection of and rapid response (EDRR) to invasive species: A conceptual framework and federal capacities assessment. Biological Invasions 22(1):1–19. DOI: 10.1007/s10530-019-02156-w.

Régnière J, St-Amant R, Duval P. 2012. Predicting insect distributions under climate change from physiological responses: Spruce budworm as an example. Biological Invasions 14 (8):1571–1586. DOI: 10.1007/s10530-010-9918-1.

Ridbäck U. 2018. On the complexity of dealing with introduced plants as cultural heritage. A historical multidisciplinary study of plants introduced to Norway from 1750 to 1900, exemplified with *Abies alba* Mill. (European silver fir) as a case species. Philosophiae Doctor (PhD) Thesis. Norwegian University of Life Sciences.

Rimšaitė J, Ivinskis P, Bartkevičienė G, Bernotienė R. 2022. The northward spread of the European mantis, *Mantis religiosa* (Mantodea: Mantidae): Data from Lithuania. European Journal of Entomology 119:318–326. DOI: 10.14411/eje.2022.033.

SAGA Development Team. 2023. System for automated geoscientific analyses (SAGA) version 9.0.1. Germany: Institute of Geography at the University of Hamburg. http://www.saga-gis.org. Accessed Apr 2023 21.

Samy AM, Elaagip AH, Kenawy MA, Ayres CFJ, Peterson AT, Soliman DE. 2016. Climate change influences on the global potential distribution of the mosquito *Culex quinquefasciatus*, vector of West Nile Virus and lymphatic filariasis. PLOS ONE 11:e0163863. DOI: 10.1371/journal.pone.0163863.

Sandercock BK, Davey ML, Endrestøl A, Blaalid R, Fossøy F, Hegre H, Majaneva MAM, Often A, J Å, Jacobsen RM. 2022. Designing a surveillance program for early detection of alien plants and insects in Norway. Biological Invasions 25 (3):917–936. DOI: 10.1007/s10530-022-02957-6.

Sandvik H. 2012. Kunnskapsstatus for spredning og effekter av fremmede bartrær på biologisk mangfold. DN-utredning 8-2012. 44pp.

Scheurer S, Binazzi A. 2004. Notes on bio-ecology and ethology of *Cinara curvipes* (patch), a newly introduced species into Europe (Aphididae Lachninae). Redia 87:61–65.

Scheurer S, Binazzi A, Funke M, Voegtlin DJ. 2001. *Cinara curvipes* (Patch) a recently introduced species to Germany – studies of its morphs, host plants and biology. Sixth International Symposium on Aphids, Rennes (France) 3-7 Sept. 2001, Rennes.

Solstad H, Elven R, Arnesen G, Eidesen PB, Gaarder G, Hegre H, Høitomt T, Mjelde M, Pedersen O. 2021. Karplanter: Vurdering av edelgran *Abies alba* for Norge. Rødlista for arter 2021. Artsdatabanken. http://www.artsdatabanken.no/lister/rodlisteforarter/2021/12203

Statista. 2022. Share of Christmas tree exports from Denmark in 2021, by country. https://www.statista.com/statistics/1070539/share-of-christmas-tree-exports-from-denmark-by-country/. Accessed May 16 2023.

Statistics Norway. 2022. Fakta om jul. Fakta om jul - Statistisk sentralbyrå (ssb.no). Accessed Oct 2023 12.

Syfert MM, Smith MJ, Coomes DA. 2013. The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. PLOS ONE 8(2):e55158. DOI: 10.1371/journal.pone.0055158.

TIBCO Software Inc. 2017. Statistica (data analysis software system), version 13. http://statistica.io

Tomov R, Trencheva K, Trenchev G, E Ç, Ramadhi A, Ivanov B, Naceski S, Papazova-Anakieva I, Kenis M. 2009. Non-indigenous insects and their threat to biodiversity and economy in Albania, Bulgaria and Republic of Macedonia. Sofia–Moscow, Bulgaria: Pensoft. p. 114.

Voegtlin DJ, Bridges CA. 1988. Catalogue of the *Cinara* species of North America (Homoptera: Aphididae). Illinois Natural History Survey, Special Publication 8:55. https://www.biodiversitylibrary.org/bibliography/181776.

Warren DL, Glor RE, Turelli M. 2010. Enmtools: A toolbox for comparative studies of environmental niche models. Holarctic Ecology 33(3):607–611. DOI: 10.1111/j.1600-0587.2009.06142.x.

Wolf H. 2003. EUFORGEN technical guidelines for genetic conservation and use for silver fir (*Abies alba*). Rome, Italy: International Plant Genetic Resources Institute. p. 6.

Wyatt IJ, White PF. 1977. Simple estimation of intrinsic rates for aphids and tetranychid mites. The Journal of Applied Ecology 14(3):757–766. DOI: 10.2307/2402807.

Xiang Q-P, Wei R, Zhu Y-M, Harris AJ, Zhank X-C. 2018. New infrageneric classification of *Abies* in light of molecular phylogeny and high diversity in western North America. Journal of Systematics and Evolution 56(5):562–572. DOI: 10.1111/jse.12458.

Zhang Z, Mammola S, McLay CL, Capinha C, Yokota M. 2020. To invade or not to invade? Exploring the niche-based processes underlying the failure of a biological invasion using the invasive Chinese mitten crab. Science of the Total Environment 728:138815. DOI: 10.1016/j.scitotenv.2020.138815.