

Distribution of *Drepanaphis acerifoliae* – aphid pest of *Acer* trees – faced with global climate change

Kamila MALIK^{id}, Agnieszka BUGAJ-NAWROCKA^{id}, Karina WIECZOREK^{id}

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The genus *Drepanaphis* del Guercio currently includes 16 species, all of which are found in North America. Representatives of this genus are narrow oligophages associated mainly with plants of the genus *Acer*. Previous studies have focused only on the morphology of selected species, while not considering their geographical distribution. Among all species, the painted maple aphid *Drepanaphis acerifoliae* deserves particular attention, because it represents the broadest range in North America and is the only species of this genus to be found outside of its natural range, i.e. in Europe. Thanks to suitable niche modelling based on a maximum entropy model, we were able to present maps with the potential distribution of *D. acerifoliae* in its natural range. In North America, its distribution coincides with the natural range of the host plants (native to the eastern part), as well as the areas where they are planted (the western part). An extrapolation of these results to the area of Europe allowed for the designation of places where the aphids can find suitable climatic conditions for developing and expanding their spatial distribution. The model indicated the Mediterranean basin, almost all of Italy, excluding mountainous areas, Spain, Portugal, France, Belgium, the Netherlands, the western part of Germany, the southeast and central part of Great Britain, Hungary and the Balkan Peninsula. In a more continental view, the model pointed to areas stretching from the middle of eastern Ukraine, including Crimea, through Russia, to northern parts of Kazakhstan along the border with Russia. Additionally, the impact of climate change on the spread of the species within the next 80 years was analysed, both in North America and Europe. Models considering the potential future climate changes indicate that *D. acerifoliae* may find suitable niches further north of its current ranges. In North America, this is mostly areas of eastern Canada, while in Europe it includes the central and eastern part and the Asian part of Russia.

Key words: ecological niche modelling, climate change simulations, maple, biological control, pest risk.

Kamila MALIK, Agnieszka BUGAJ-NAWROCKA[✉], Karina WIECZOREK, Institute of Biology, Biotechnology and Environmental Protection, Faculty of Natural Sciences, University of Silesia in Katowice, Poland. E-mail: agnieszka.bugaj-nawrocka@us.edu.pl

The *Acer* genus, also known as the maple, is a diverse taxon of trees found mainly in the northern hemisphere (Grimm *et al.* 2007). Trees of this genus reach a height of 42 m and are characterised by oppositely arranged leaves, as well as open, irregular crowns, and a long or short trunk (Geyer *et al.* 2010). The ancestor of this group of plants probably came from eastern Asia, where as many as 130 out of approximately 150 known species originated (Li

et al. 2019; Areces-Berazain *et al.* 2020). Other species are present in Europe, western Asia and North America (Li *et al.* 2019). A reconstruction of the evolutionary unfolding of the *Acer* species showed that in North America, the species in the western and eastern parts probably had two independent sources of migration (Renner *et al.* 2008; Areces-Berazain *et al.* 2021). The current *Acer* classification divides the group into 18 sections, some of which are also

subdivided into series (Davis 2021). Phylogenetic analyses indicate that most sections of the *Acer* are monophyletic, but the relationship between the sections is still unclear (Li *et al.* 2019). Maples stand out owing to their variety of growth habits, cold resistance and adaptability. That is why they are often chosen for planting in urban spaces, and they sometimes do very well in such environments (i.e. Uhrin *et al.* 2018; McDermot *et al.* 2020). For example, the silver maple (*Acer saccharinum* L.), which occurs mainly in North America, is one of the fastest growing deciduous trees in the eastern and mid-western forests, it competes well with other plants and its seeds germinate rapidly (Geyer *et al.* 2010). The sugar maple (*Acer saccharum* Marsh.), which is also abundant in North America, is a source of the popular maple syrup and is one of the most important tree species in this region (Minorsky 2003).

Because of the valuable nutritional properties of the sweet phloem sap, maples are often attacked by various groups of insects, including aphids. The aphid genera that are specific to *Acer* spp. are mainly from the subfamilies Chaitophorinae and Drepanosiphinae (Blackman & Eastop 2022). The subfamily Drepanosiphinae includes five genera and 37 species related to different geographic regions (Remaudière & Remaudière 1997; Favret 2022). *Drepanaphis* del Guercio, 1909 is the most speciose genus in this subfamily, represented by 16 species that are distributed in its natural range in North and Central America. This genus consists of monoecious, holocyclic species whose sexual generations develop in the au-

tumn. All species of the genus *Drepanaphis* are associated with different *Acer* spp., except *D. monelli* (Davis, 1909) which feeds on *Aesculus* spp. (Smith & Dillery 1968; Blackman & Eastop 2022).

The most common species in this genus, the painted maple aphid *D. acerifoliae* (Thomas, 1878) (Fig. 1), has also been recorded in Europe. Its occurrence has been reported in Italy (Lozzia & Binaghi 1992; Colombo *et al.* 1996; Barbagallo *et al.* 2008; Barbagallo & Cocuzza 2014), Spain (Perez Hidalgo *et al.* 2008), Hungary (Ripka 2010) and Serbia (Petrović-Obradović *et al.* 2018, 2021). *Drepanaphis acerifoliae* is the only species to be associated with more than one species of the genus *Acer*: *A. saccharinum*, *A. saccharum* and *A. rubrum* L. (Smith & Dillery 1968; Blackman & Eastop 2022). However, in Europe, this species has been found exclusively on *A. saccharinum* (Petrović-Obradović 2021), which was introduced to the area by Sir Charles Wager in 1725. *Acer saccharinum* spread quickly as an ornamental species (Harris 1991) and was naturalised, i.e. in Belgium (Ronse 2011), France (Tison & de Foucault 2014), Germany (Aas *et al.* 2010) and the British Isles (Stace 2010).

Since maples also occur naturally in Europe, particularly from the same section as *A. saccharum*, and considering the fact that *D. acerifoliae* is an oligophagous species with the potential to change its host, we cannot exclude the risk that it may also feed on other *Acer* species. This provides an additional justification for interest in the invasive potential of this species. In its natural range, the painted maple

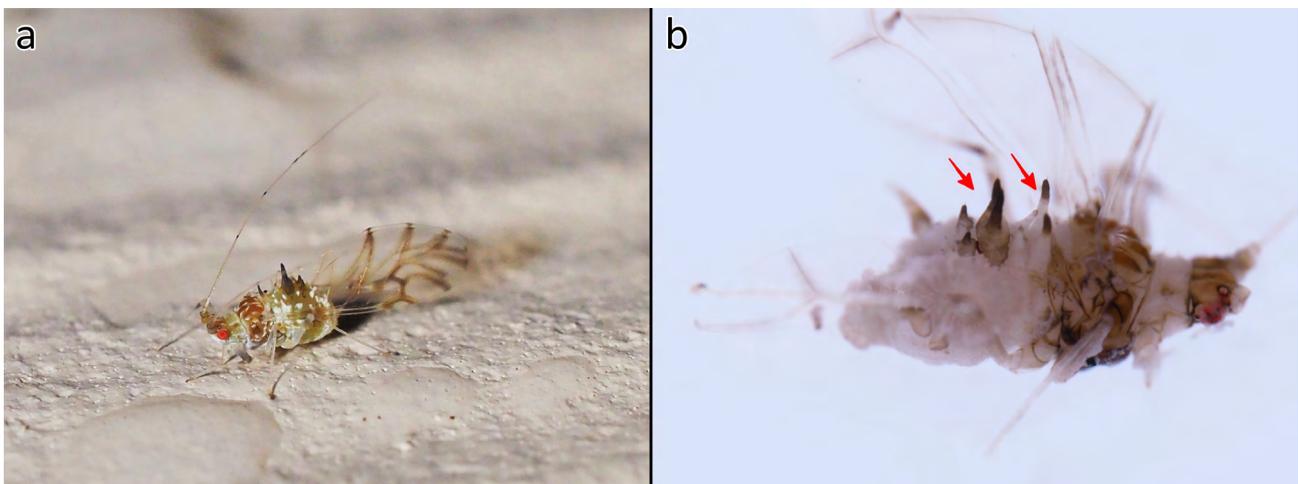


Fig. 1. *Drepanaphis acerifoliae* (Thomas, 1878). Alate viviparous ♀. (a) Live specimen. Image copyright V. Charny, under the Creative Commons 3.0 Licence; and (b) lateral general view. The lateral view reveals the long, finger-like dorsal abdominal tubercles that are characteristic of the *Drepanaphis* species (indicated by arrows).

aphid is considered to be a common pest of maples growing in urban areas. Infestations result in dieback and aesthetic damage, i.e. leaf discoloration and premature leaf drop. Severe infestations can also lead to the production of large amounts of honeydew, which covers the leaves and the surfaces and objects (i.e. cars) beneath the trees. It also facilitates the production of sooty mould fungi, which can injure plants (Dreistadt & Flint 1995). The problems with invasive species are becoming more and more noticeable in the context of climate change. For many insect species, increased levels of atmospheric greenhouse gases and a higher temperature may increase the probability of their spreading to new habitats (i.e. Dukes & Mooney 1999; Bergant *et al.* 2005; Bale and Hayward 2010). Global climate change can significantly impact the species' survival, reproduction, spread and population dynamics. It can also modify the relationships between the environment, pests and their natural enemies (Prakash *et al.* 2014).

Due to the pest status that this aphid has in its natural range and its expansion in Europe, we decided: (I) to evaluate the range of *D. acerifoliae* in relation to the natural range of its host plants; (II) to predict the potential current distribution of *D. acerifoliae* in its natural range and additionally in Europe, from which it is already listed; (III) to predict the potential past distribution of *D. acerifoliae*, to determine where its place of origin could potentially be, and whether it is consistent with the assumption of the evolutionary unfolding of the *Acer* species; and (IV) to indicate areas potentially at risk of invasion by this species on a global scale, significantly beyond its Nearctic range, using modelling for future climate scenarios.

Materials and Methods

Occurrence data

The occurrence data was obtained from the scientific literature, as well as specimens studied in museum collections and biodiversity databases. The search was based on keywords, i.e. the name of the species and its synonyms. Museum curators were asked to provide information about their collections. Photographs of the preparations were provided from the collections in which specimens of the discussed species were identified. Some of them were also examined in the collections during a personal stay. We excluded the records with unspecified or unknown

localities. 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). To reduce the inherent geographic biases (the effect of spatial autocorrelation) associated with the collecting methods, we removed points closer to each other than 10 km. Overall, 90 unique occurrence localities were compiled for the representatives of *D. acerifoliae* in North America and 22 in Europe. All the localities were georeferenced using Google Earth 7.3.2.5776 (Google Inc. 2022; <http://www.google.com/earth/index.html>) (coordinates were collected in decimal degrees, datum: WGS84). Details of the occurrence localities used during the modelling process are available in Supplementary Material 1 (SM.01).

Environmental predictors, climate classification and terrestrial ecoregions

We used 19 current bioclimatic variables obtained from the WorldClim 2.0 dataset (SM.02) (Fick & Hijmans 2017; <http://www.worldclim.org>) and downscaled the paleoclimate data for the Last Interglacial (LIG; ~120,000–140,000 years ago), the Last Glacial Maximum (LGM; between 26,500 and 19,000–20,000 years ago) and the Mid-Holocene (about 6,000 years ago) from the WorldClim 1.4 dataset (Hijmans *et al.* 2005). The influence of possible global climate change on the potential distribution of *D. acerifoliae* was estimated for four different periods (2021–2040, 2041–2060, 2061–2080 and 2081–2100) and for 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 were obtained from the Coupled Model Intercomparison Project Phase 6 (CMIP6): ACCESS-ESM1-5, CNRM-ESM2-1 and MIROC-ES2L.

Since only climate variables were used in the modelling, to help in understanding which types of climate are most favourable for the occurrence of *D. acerifoliae*, we used the Köppen-Geiger climate classification system (Peel *et al.* 2007). The places where representatives of the species occurred were plotted on a raster with the climate classification data, and the raw data was obtained. Using SAGA GIS, the resulting rasters from MaxEnt were plotted on a raster of the Köppen-Geiger climate classification.

The natural range outlines for the major host plants were taken from <http://databasin.org> (Fig. 2) (Conservation Biology Institute (CBI) 2023; the maps are a digital

representation of the tree species range maps from the *Atlas of the United States Trees* by Little (1971).

To determine which main plant communities *D. acerifoliae* is associated with, we used terrestrial ecoregions which were based on Olson and Dinerstein (2002), Bailey (1995) and Wiken (1986), modified by The Nature Conservancy (TNC – an American charitable environmental organisation). This biogeographic regionalisation contains 814 terrestrial ecoregions classified into 14 different biomes.

We used SAGA GIS 7.8.2 (Conrad *et al.* 2015; SAGA Development Team 2022) to extract raw environmental data from all raster layers of the species occurrence records. We performed a Spearman rank correlation test in the Excel (ver. 2207) add-in program Analysis ToolPak (Microsoft Corporation 2022), to minimise the number of variables by discarding those that were highly correlated ($r \geq 0.75$) (SM.02).

Ecological niche modelling

We used MaxEnt (version 3.4.1; <http://www.cs.princeton.edu/~schapire/maxent>) to model the *D. acerifoliae* niches and distribution. MaxEnt is a machine learning software based on a maximum entropy algorithm (Phillips *et al.* 2006). 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), a different combination 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 (SM.03).

If the models resulted in biologically nonsensical curves (i.e., highly jagged or multimodal), they were removed or were ranked low. It was difficult to distinguish environmentally-unsuitable areas from those that were under-sampled. Therefore, to deal with the likelihood that certain areas had fewer records and that some places were poorly sampled, we decided to use a method that gave meaning to the records with few neighbours in the geographic space. To weigh the selection of the background points, to account for the sampling intensity and any potential sampling bias, a bias file was implemented in the MaxEnt modelling. A bias grid file was created in SAGA GIS, and all the distribution records of *D. acerifoliae* were weighted by a Gaussian kernel with a standard deviation (SD) of 200 km (using the kernel density estimation). A range of 200 km was chosen, because we assumed that this aphid could easily spread by several kilometres a year, sometimes with short periods of irregular spreads. However, tak-

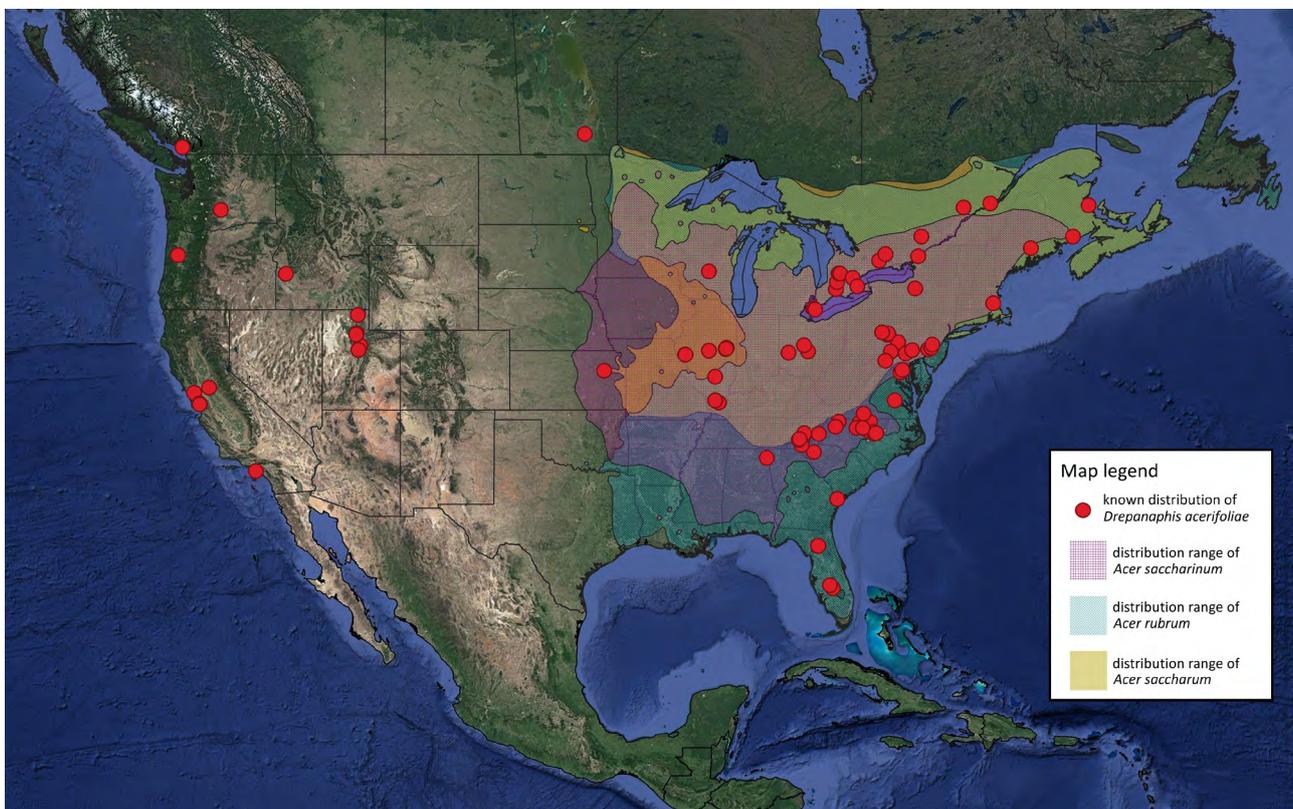


Fig. 2. Known distribution of *Drepanaphis acerifoliae* (Thomas, 1878) in North America (red dots), with the distribution ranges of its host plants.

ing into account the years from which most of that reports came from (the 1930s to 1960s), we assumed that over 60 years, a representative of this species could have travelled 200 km or more in its natural habitat. This was confirmed by the data collected in Europe, where within a few years, *D. acerifoliae* spread several hundred kilometres from the place of its first finding. The resulting grid was then scaled to have a minimum value of 1 and a maximum value of 20 (using grid normalisation) (see Elith *et al.* 2010; Syfert *et al.* 2013). A ten-fold cross-validation was performed, so all of the data was used for the validation, thus making better use of small data sets (Phillips *et al.* 2006; Phillips & Dudík 2008). The logistic output of MaxEnt with prediction values from 0 (unsuitable habitat) to 1 (optimal habitat) was selected.

We used the sample size corrected Akaike's information criterion (AICc and Δ AICc) (measures of the relative quality of models for a given dataset; calculated using ENMTools (Warren *et al.* 2010)), the area under the receiver operating characteristic (ROC) curve (AUC) (the performance of the model and the weight of the omission and commission errors) and the partial area under the ROC curve (pAUC) (calculated using Niche Analyst 3.0 (Qiao *et al.* 2015)) for the evaluation of the models (SM.03).

The models were used to predict suitable niches in present, past and future conditions. The resulting maps for the potential past and present distribution were prepared on a continental scale, where a spatial resolution of 30 arc seconds (~1 km²) was selected. A global scale was used for the potential future distribution with a spatial resolution of 60 arc seconds (~2 km²) (downloaded from WorldClim; 30 arc sec-

onds spatial resolution grids were interpolated to a 60 arc seconds spatial resolution). All of the maps were prepared in QGIS 3.26.0 (QGIS Development Team 2022; <http://www.qgis.org>) using the WGS84 datum and EPSG: 4326 or 3857 (Web Mercator).

Results

Evaluation of the models and importance of the environmental predictors

In this study, we analysed the results from three prediction periods: past (LIG, LGM and Mid-Holocene), present and future (four time periods and four SSPs (SSP1-2.6, SSP2-4.5, SSP3-7.0 and SSP5-8.5)). The training and test AUC values differed from random for all of the models. The setting selection for the model was mainly chosen based on the results of pAUC, AICc and Δ AICc (SM.03). We observed higher values of pAUC, AICc and Δ AICc when we used the auto features, regardless of the number of iterations. The regularisation multiplier settings were also analysed, and we found that a default value of 1 worked fine. For the maximum number of iterations, the best results were obtained with the value of 750 (SM.03).

A jackknife test (refer to SM.04 for more details and MaxEnt outputs) showed that the mean temperature of the warmest quarter (Bio10) was the environmental variable that was the most informative by itself, and it had a significant amount of information that was not contained in the other variables (Fig. 3). The warmest quarter in North America and Europe mostly covered June to August. For humid subtropical climates and subtropical highland climates, in the hottest months the mean temperature is about 26.5°C; while for con-

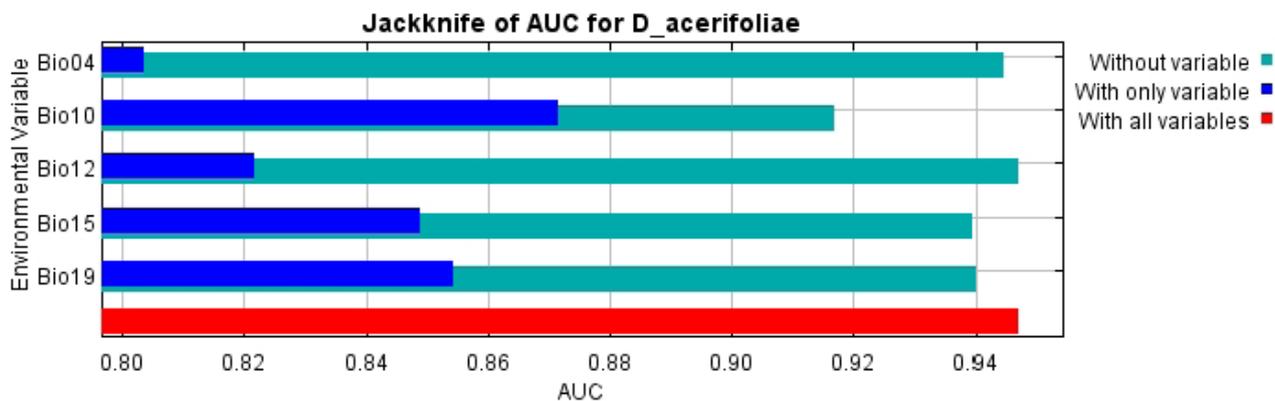


Fig. 3. Results of a jackknife test of the variable importance using AUC on the test data for *Drepanaphis acerifoliae* (Thomas, 1878). The jackknife test, in blue bars, shows the individual environmental variable importance relative to the red bar that shows all environmental variables. The light blue bar represents the Area Under the Curve (AUC) when a specific variable is excluded from the model. It demonstrates the information that the variable carries which is not present in other variables. A lower bar indicates that the variable is more informative by itself. The values shown are averages over replicate runs.

tinental climates it is about 22°C (and below). The mean temperature in the places where *D. acerifoliae* has been found is 21.8°C (min. 14.9°C in Mount Mitchell, North Carolina, USA; and max. 27.3°C in Lake Placid, Florida, USA). The precipitation during the coldest quarter (Bio19) was also significant, and the average rainfall for the studied areas from December to February was 238 mm (min. 55 mm in Winnipeg, Manitoba, Canada; and max. 540 mm in Corvallis, Oregon, USA). The mean precipitation seasonality (Bio15), a measure of the variation in the monthly precipitation totals over the year, fluctuated by around 24%. The most considerable fluctuations were recorded in Los Angeles, California, USA; and the smallest were recorded in Boston, Massachusetts, USA. The mean values for the variable annual precipitation (Bio12) were around 1040 mm/m²/year (min. 211 mm in Yakima, Washington, USA; and max. 1801 mm in Mount Mitchell, North Carolina, USA). The temperature seasonality (Bio04) had a minor significance among the selected variables, but still was important for the models. It is calculated as the standard deviation of the weekly mean temperatures and expressed as a percentage of the mean of those temperatures. In the case of our research, it fluctuated around 8.6%, which means that

the standard deviation of the weekly mean temperatures in the occurrence places was relatively small.

Potential species distributions and localities vulnerable to potential invasion

All the resulting maps show the median of the output grid of ten model replicates. For the present period in North America (Fig. 4) – the native range of *D. acerifoliae* – the results suggest that the most suitable areas for this species are located mainly in the areas where it is already present. In the United States, these include all eastern states to the border of the eastern half of Wisconsin and Iowa, the whole of Missouri, part of Kansas, and the eastern halves of Oklahoma and Texas. Conversely, in the west of the United States there are fewer favourable areas, mainly limited to Washington without the area of the Cascade Range, the west coast of Oregon to the border with the Cascade Range, California without the Sierra Nevada and the Mojave Desert, the Snake River Plain in Idaho, regions of Great Salt Lake and the western parts of the Wasatch Mountains in Utah, and the central part of Arizona within the Arizona transition zone. In Canada, these areas are the Great Lakes regions, the most southern areas of Ontario including Ottawa, the southern regions near Montreal

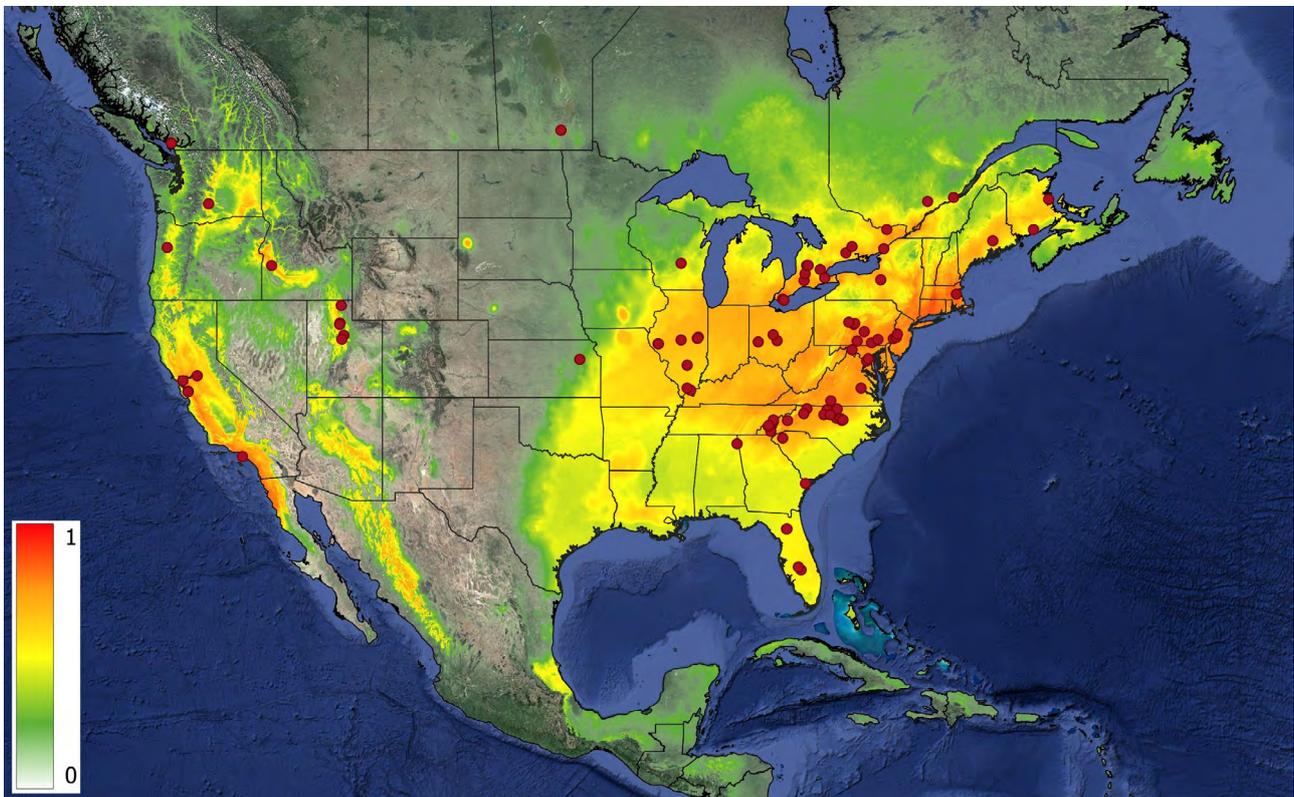


Fig. 4. Model result of a potentially suitable ecological niche for *Drepanaphis acerifoliae* (Thomas, 1878) in North America at present. Red dots represent the currently-known sites of the occurrence of the species. The colour scale shows the probability of a suitable ecological niche. Black lines represent the current national boundaries and the internal divisions into states.

in Quebec, and almost the entire area of New Brunswick. By contrast, the southernmost areas in North America are located in Mexico, along the Sierra Madre Occidental range.

In Europe (Fig. 5), the model indicated the Mediterranean basin as the main area with a suitable ecological niche. It also indicated almost all of Italy, excluding the mountainous areas in the north of the country, Spain, Portugal, France, Belgium, the Netherlands, the west part of Germany, the southeast and central parts of Great Britain, Hungary and the Balkan Peninsula. In all of the aforementioned areas, mountainous areas were shown to be unfavourable. From a more continental standpoint, the model also pointed to areas stretching from the middle of eastern Ukraine, including Crimea, through Russia (the oblasts: Belgorod, Voronezh, Rostov, Krasnodar, Volgograd, Saratov and Orenburg), to northern parts of Kazakhstan along the border with Russia. They also included the territories of Georgia and Azerbaijan.

In West Asia, the model suggested almost the entire territory of Türkiye, Iran (excluding desert areas), northern parts of Iraq, the north and west coasts of Syria, Lebanon, Israel, Palestine and western Jor-

dan. It also indicated the northern part of the African countries lying on the Mediterranean Sea – Morocco, Algeria, Tunisia, Libya and Egypt (Fig. 5).

The results obtained for the last interglacial period (~ 120,000–140,000 years ago) (Fig. 6) largely pointed to the northern part of the east coast as the area potentially most suitable for the development of aphids (based on the conditions that are favourable for these insects at present). The results for later periods showed that the conditions prevailing during the last glacial maximum may have forced the aphids to migrate south (Fig. 7). In turn, the conditions during the Mid-Holocene favoured the further spread of *D. acerifoliae* (Fig. 8).

The results for potential future climate changes indicated that *D. acerifoliae* may find suitable niches further north of its current ranges (SM.05). In North America, areas of eastern Canada including Ontario, Quebec, New Brunswick, Nova Scotia and Newfoundland will be the most vulnerable. In the scenarios for higher CO₂ concentrations (SSP3-7.0 and SSP5-8.5), areas of British Columbia in the west of Canada will also be exposed. Climate changes may primarily affect the occurrence of *D. acerifoliae* in central and eastern Europe and in the Asian part of

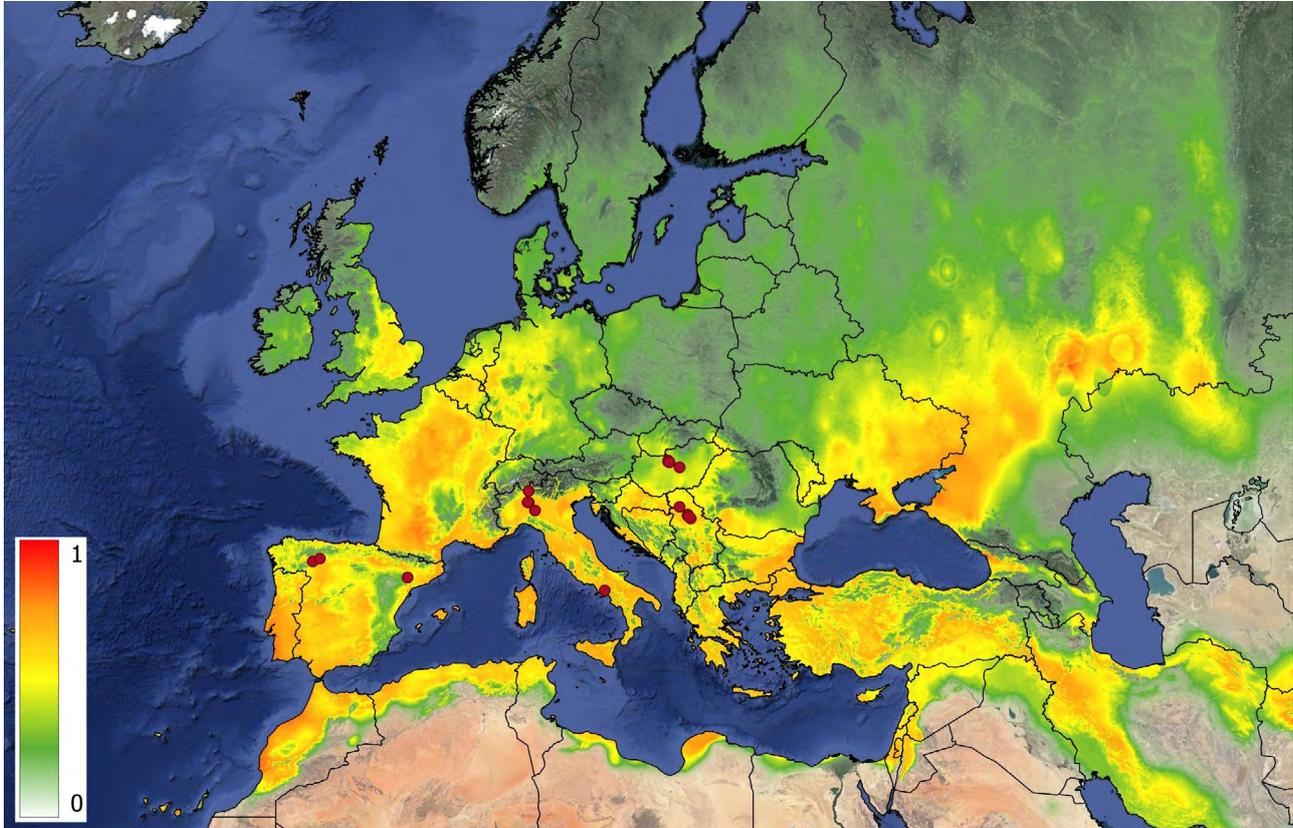


Fig. 5. Model result of a potentially suitable ecological niche for *Drepanaphis acerifoliae* (Thomas, 1878) in Europe, and partly for Africa and Asia at present. Red dots represent the currently known sites of the occurrence of the species. The colour scale shows the probability of a suitable ecological niche. Black lines represent the current national boundaries.

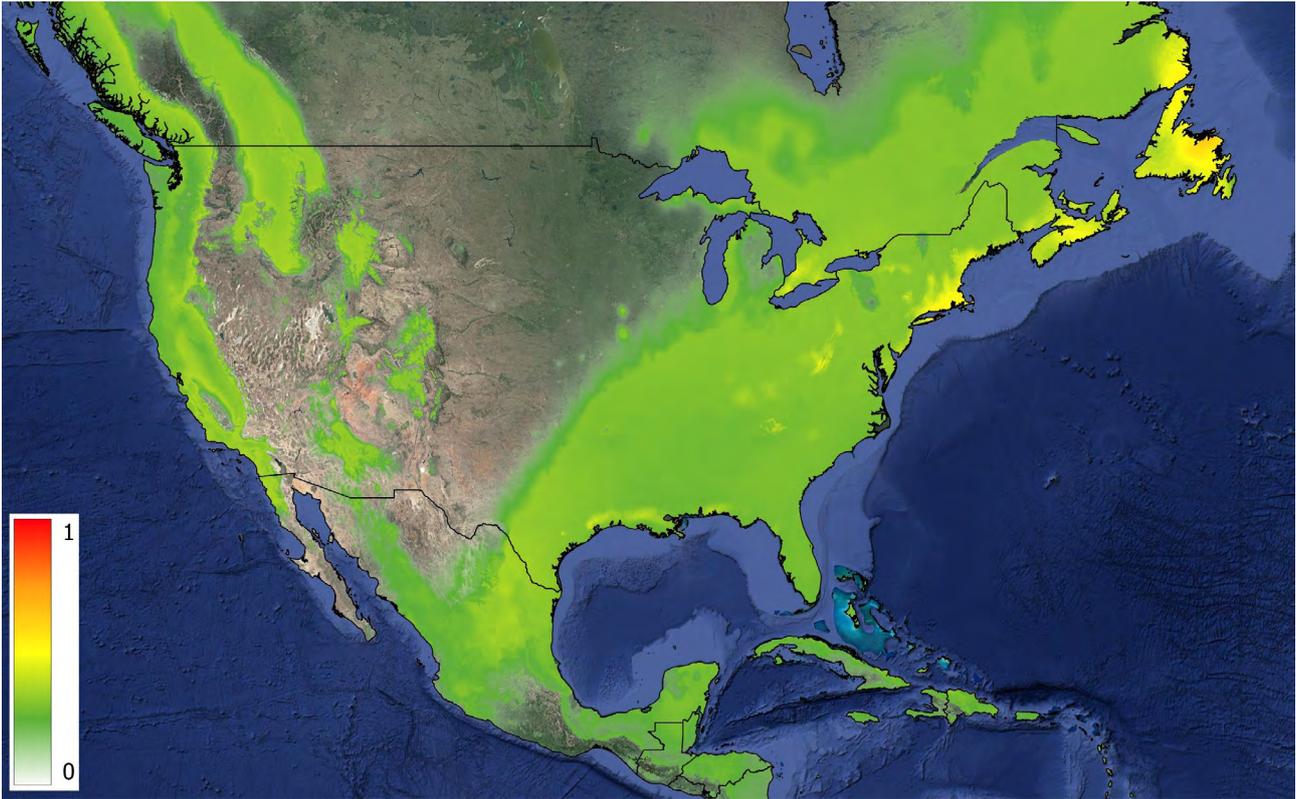


Fig. 6. Model result of the potentially suitable ecological niches for *Drepanaphis acerifoliae* (Thomas, 1878) in North America during the last interglacial period. The colour scale shows the probability of a suitable ecological niche. Black lines represent the current national boundaries.

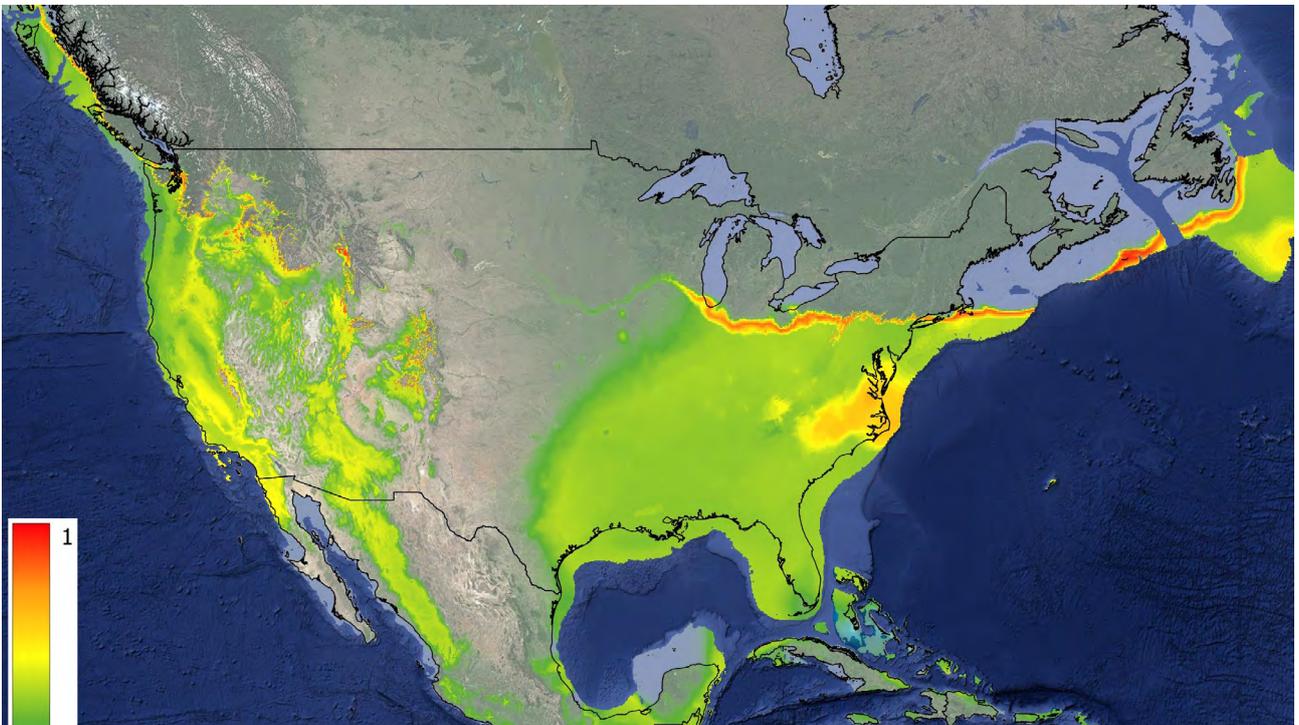


Fig. 7. Model result of the potentially suitable ecological niches for *Drepanaphis acerifoliae* (Thomas, 1878) in North America during the last glacial maximum. The colour scale shows the probability of a suitable ecological niche. Brighter areas mark the boundary of the continental land during the last glacial maximum (between 26,500 and 19,000-20,000 years ago). Black lines represent the current national boundaries.

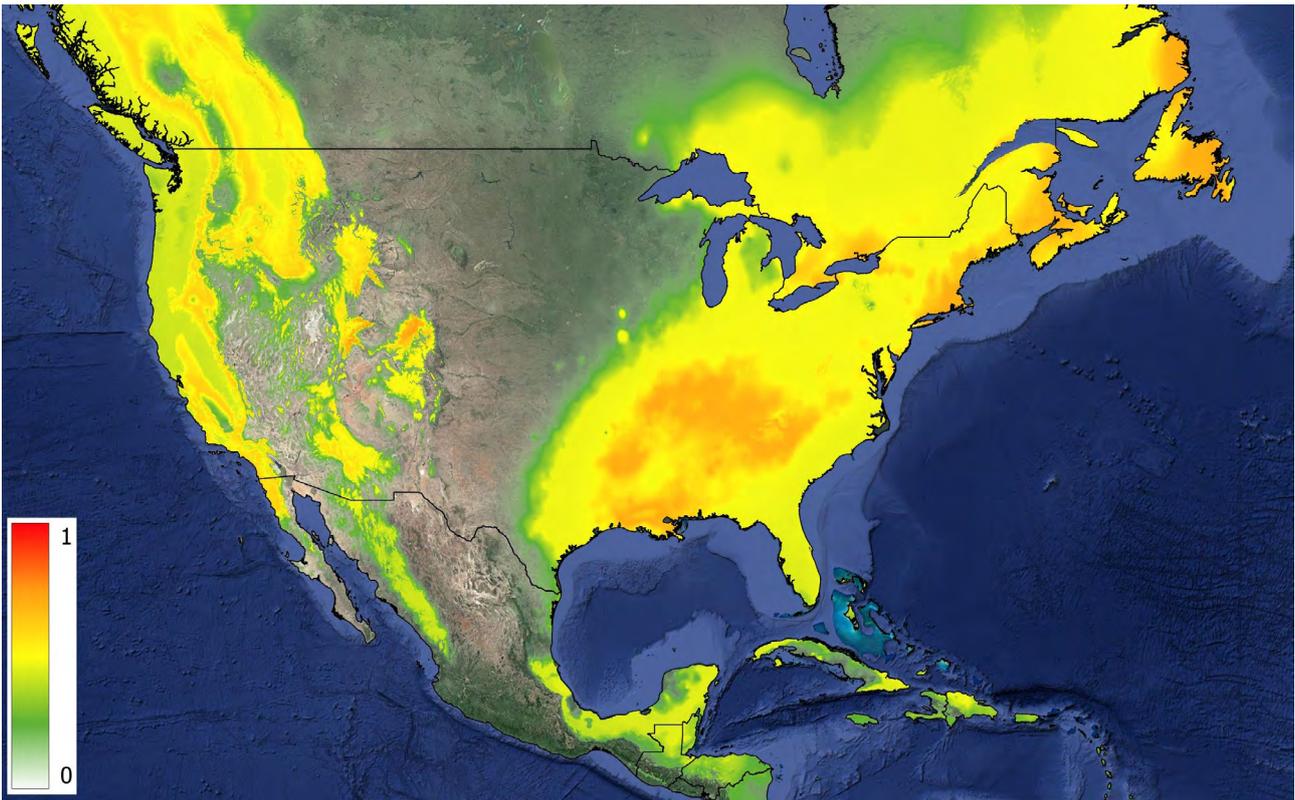


Fig. 8. Model result of the potentially suitable ecological niches for *Drepanaphis acerifoliae* (Thomas, 1878) in North America during the Mid-Holocene period. The colour scale shows the probability of a suitable ecological niche. Black lines represent the current national boundaries.

Russia. The maps also showed a clear shift in the suitable niche to the territories of Great Britain, Germany, Denmark, Poland, the Czech Republic, Slovakia, Ukraine, Belarus, Lithuania, Latvia, Estonia, Finland and the south of Sweden.

Climatic preferences and terrestrial ecoregions

The present potentially-suitable ecological niches of *D. acerifoliae* were compared with the Köppen-Geiger climate classification, to determine the possible climatic preferences of the species (SM.04 – Fig. 3). An analysis of the climate types of the known locations indicated that the representatives of *D. acerifoliae* prefer a temperate (humid subtropical) and continental climate (hot summer and warm summer humid continental). A humid subtropical climate (Cfa) is characterised by a mean temperature during the coldest month above 0°C (32°F), with at least one month when the mean temperature is above 22°C (71.6°F) and about four months above 10°C (50°F). Such climatic conditions prevail in the southeastern part of the United States.

A hot summer humid continental climate (Dfa) has the coldest month with temperatures below 0°C (32°F), but at least one month with the mean tem-

perature above 22°C (71.6°F) and about four months above 10°C (50°F). Within North America, this climate includes the central and eastern United States. In the warm summer subtype (Dfb), the average temperatures in the warmest month are below 22°C (71°F), and the winters are cold, with temperatures usually well below -3°C (27°F). This subtype covers areas from about 42°N to 50°N latitude in North America, but it can be found further west in the Canadian Prairie Provinces and below 40°N in the high Appalachians. It is also found in much of Central and Eastern Europe, southern and central parts of Scandinavia, all the Baltic States, and parts of Romania, Bosnia and Herzegovina, and Türkiye. For all the climate types mentioned above, there is no significant precipitation difference between the seasons.

Among all the individuals of *D. acerifoliae* we examined, 69% inhabited a temperate broadleaf and mixed biome. Other inhabited areas include temperate coniferous forests (10%), temperate grasslands, savannas and shrublands (10%), Mediterranean forests, woodlands and scrub (6%), and last of all deserts and xeric shrublands (3%) as well as boreal forests/taiga (2%) (SM.04 – Fig. 4). As can be seen, this

species is strongly associated with temperate forest areas where, above all, the *Acer* species with which this species is associated occur in their natural state.

Discussion

In our study, we predicted possible suitable ecological niches and the climate change impact on the global distribution of *D. acerifoliae*. We managed to obtain 90 occurrence points for this purpose. On the scale on which the modelling was carried out (continents and the whole world), this amount may be insufficient to consider these results as final. Nevertheless, the research conducted on the impact of the number of samples on the quality of models shows that when using the algorithm implemented in MaxEnt (which uses regularisation to avoid over-fitting), such research attempts should not be rejected. Research also shows that the data quality is often more important than the quantity (Wisz *et al.* 2008; Mateo *et al.* 2010; Støa *et al.* 2019). In order to conduct our research as well as possible, we additionally used a bias file and tested various settings of the MaxEnt software, as recommended by the authors of other studies (Elith *et al.* 2010; Merow *et al.* 2013; Morales *et al.* 2017). Because many species are known from relatively few records, our results highlight the need to develop databases of specimen occurrences in museums or herbaria, and to raise awareness among field researchers of the importance of sharing data in open repositories.

In North America, the distribution of *D. acerifoliae* coincides with the natural range of the host plants (which are native to the eastern part of the continent; Fig. 2) and the areas where they are planted (like the western part; Fig. 2). As the pest is directly dependent on its host, the model's prediction of a potential ecological niche also implies favourable climatic conditions for the host plants (Fig. 4). In Europe, the climatic conditions seem very suitable, and the settleable area is extensive. Europe has been a place where trade exchanges have taken place for centuries, and as a result, it has been exposed to the introduction of alien species that would not normally have had such an opportunity without human participation (DAISIE 2009; Keller *et al.* 2011). For example, the introduced *A. saccharinum* has become a plant host for the parasitic European mistletoe *Viscum album* L., contributing to the spread of this species throughout Europe (Kołodziejek *et al.* 2013; Varga *et al.* 2014). The spread of this species outside cities and parks entails, among other things, the threat of new pests. There are already reports

about the presence of the gall mite species *Vasates quadripedes* Shimer, 1869, which is native to North America and forms pouch galls on maple leaves. It has spread across Europe and attacks only *A. saccharinum* (Bruun & Soika 2013). The same scenario is possible for *D. acerifoliae*, as has been shown by the introduction of other American aphids – *Prociphilus fraxinifolii* (Riley, 1879), a pest of ash trees (*Fraxinus* spp.); *Myzocallis (Lineomyzocallis) walshii* (Monell, 1879), associated with the red oak *Quercus rubra* (L.); and *Appendiseta robiniae* (Gillette, 1907), a pest of *Robinia pseudoacacia* L. Those are examples of alien species that have been able to occupy the whole of Europe in less than two decades, after the first record of their presence in the continent (Mier Durante & Nieto Nafría 1997; Petrović 1998; Ripka *et al.* 1998; Osiadacz & Wieczorek 2006; Havelka & Starý 2007; Barbagallo *et al.* 2008; Borowiak-Sobkowiak, Durak & Wilkaniec 2008; Tasheva-Terzieva 2008; Piron 2009; Modic 2010; Petrović-Obradović *et al.* 2010; Çalıřkan *et al.* 2012; Hałaj *et al.* 2016; Wojciechowski *et al.* 2016; Orlova-Bienkowskaja & Bieńkowski 2021). Their spread is especially likely when the foreign host plant is expansive, as in the case of the red oak, which is treated as one of the most frequent invasive trees from North America in temperate European forests (Chmura 2020). We described a similar scenario for species representing the genus *Eulachnus*, except that these taxa are native to Europe and are invasive in North America and Africa (Kanturski *et al.* 2016).

Since all the *Acer* species that are host plants for *D. acerifoliae* are native to eastern North America (*A. saccharinum*, *A. saccharum* and *A. rubrum*), the model obtained for the last interglacial period seems to be consistent with our assumption that the place of origin for this species may be in the region of the northeast United States, or around the Great Lakes. However, a question remains about whether the presence of this species in the west of North America is the result of its independent migration or the effect of human interference, as in the case of its presence in Europe. We are inclined to suspect the latter, as the natural range of the host plants does not extend to western areas. Instead, they are plantings, and because the local climatic conditions in the west are similar to those in the east of North America, there was no problem with adapting for both plants and aphids. From the history of *Acer* spreading around the world, it can be concluded that there are two groups of *D. acerifoliae* host plants. Renner *et al.* (2008) tried to reconstruct the evolutionary unfolding of the *Acer* species (North American/Asian disjunctions) based on combined data from up to seven

chloroplast loci and relaxed-clock rooting. They established that the North American taxa probably started to split from their Asian sister taxa at about 40 Ma, and kept up the rate of this speciation about once per 5 Ma. *Areces-Berazain et al.* (2021) estimated the divergence times between the New World and Old World lineages to be 15 Ma earlier. *Acer* species appeared first on the west coast of North America, and migrations from the Eastern Palearctic region to the Nearctic have occurred at least seven times – starting from the early Eocene (*A. glabrum* Torr. lineage) to the early Miocene (*A. rubrum* L. + *A. saccharinum* L.). The ancestor of the sugar maple species (series *Saccharodendron*) known from eastern North America probably reached from Europe via Iceland-Greenland by the beginning of the Miocene (*Areces-Berazain et al.* 2021). Therefore, *A. rubrum* and *A. saccharinum* represent the *Rubra* section, and *A. saccharum* with its subspecies represent the *Acer* section. In Europe, the *Acer* section is represented by *A. garnatense*, *A. monspessulanum*, *A. opalus*, *A. pseudoplatanus* and *A. sempervirens*. If *D. acerifoliae* has evolved along with the host plant, there may be biological indications for it to adapt to feeding on other species of the *Acer* section in Europe.

Our model for the current period indicates areas where *D. acerifoliae* has already been recorded, such as Milan, Nola, Caldasco, Como and Carlazzo in Italy (*Lozzia & Binaghi* 1992; *Colombo et al.* 1996; *Barbagallo et al.* 2008; *Barbagallo & Cocuzza* 2014), Lleida and León in Spain (*Perez Hidalgo et al.* 2008), Budapest and Cegléd in Hungary (*Ripka* 2010), and Novi Sad and Belgrade in Serbia (*Petrović-Obradović et al.* 2018, 2021). However, the introduction in Italy and Spain could have occurred in two independent ways, as the map clearly shows that mountainous areas may constitute a natural barrier to species dispersion (Fig. 9). France is a potential area where the species can be expected to be present already, or will occur soon. The presence of mountainous areas limits both of the roads from Italy and Spain. Nevertheless, both now and in the future, the area of France is one of the most favourable for the occurrence of the aphid. We therefore recommend that appropriate French institutions and researchers scan planted *A. saccharinum* for the presence of *D. acerifoliae*.

In general, the coastal region of the entire Mediterranean Sea seems to have favourable climatic conditions for *D. acerifoliae*, which means that when

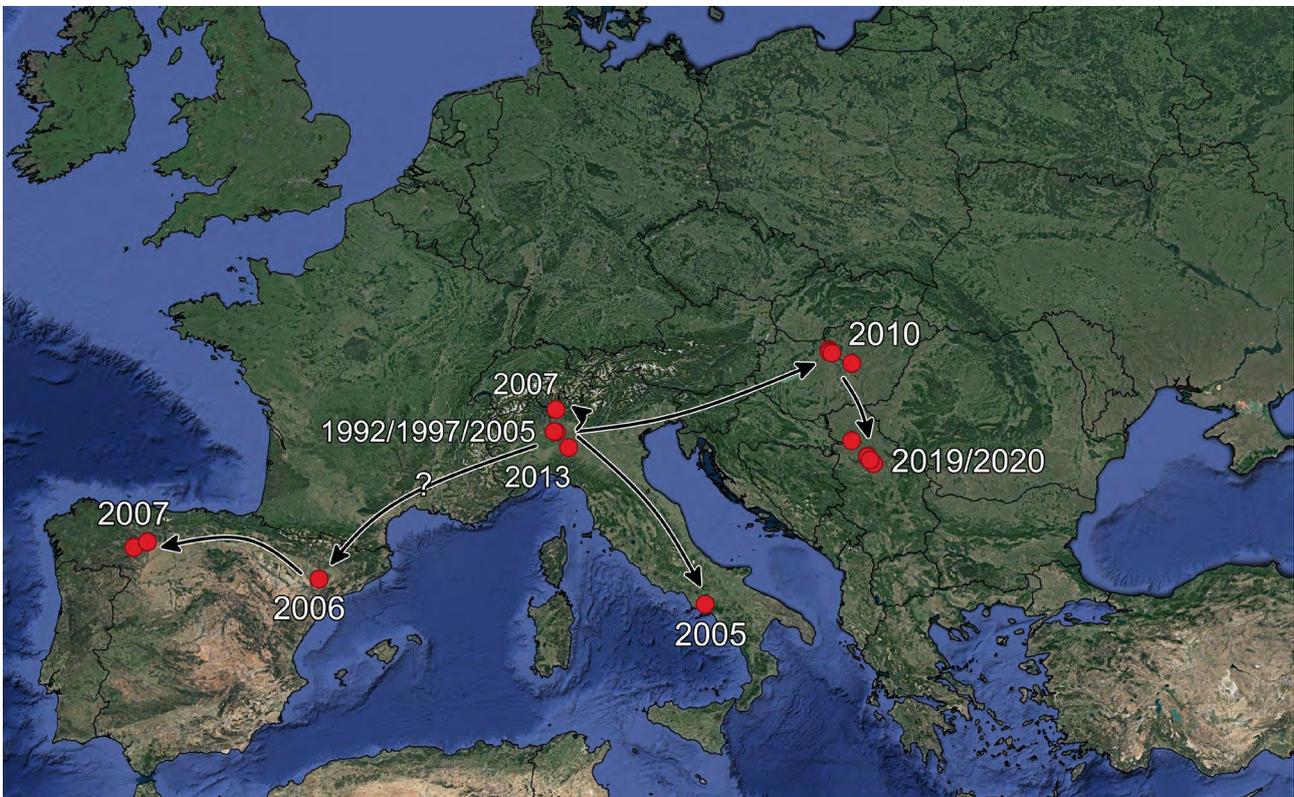


Fig. 9. Known places of the occurrence of *Drepanaphis acerifoliae* (Thomas, 1878) in Europe (red dots) with the year of its identification. The arrows indicate the possible directions of the spread of the species in Europe. The direction from Italy to Spain is marked with a question mark, because the mountainous areas present on the path may have constituted a geographical barrier. Black lines represent the current national boundaries.

a host plant is found, the species may be present not only in Europe but also in northern Morocco, Algeria, Tunisia, Libya and Egypt. In addition, the model shows suitable climatic conditions in the Middle East, particularly in Israel, Palestine, Lebanon, Syria and Türkiye. It is also highly recommended to monitor the presence of *D. acerifoliae* throughout the Balkan Peninsula, because the model shows the most suitable climatic conditions there – the presence of the host plants there may guarantee the dispersion in this part of Europe and will also open the way east to Türkiye. Moreover, this species is already present in Serbia (Petrović-Obradović *et al.* 2018, 2021). Interestingly, the best climatic conditions extend from the middle of eastern Ukraine through Russia to Kazakhstan. They also include the territories of Georgia, Azerbaijan, and Iran. It is therefore worthwhile for local biodiversity control services to pay attention to the planting of *A. saccharinum*, because it may introduce the aphid and lead to its rapid dispersion. This is perhaps not the most realistic scenario due to the presence of the Ural range, which is a good geographical barrier, but the future introduction to this area could also present a threat of the spread of this species to East Asia.

Our models under future climate conditions indicated that suitable areas for *D. acerifoliae* in the northern hemisphere can be projected to expand northward. This phenomenon appears to be common for many other insect species – not only introduced ones. Many studies have shown that over the past decades, species inhabiting Europe and/or North America are increasingly moving northward, expanding their range in that direction (e.g. Régnière *et al.* 2012; Delava *et al.* 2014; Klementová & Svitok 2014; Kistner 2017; Fält-Nardmann *et al.* 2018; Rimšaitė *et al.* 2022). On the other hand, *A. saccharinum* is also grown in temperate parts of the southern hemisphere such as Argentina, Brazil and Uruguay (Di Iorio & Farina 2009; www.gbif.org). Our results of the impact of climate change on the spread of *D. acerifoliae* show the results for South America and include the abovenamed countries and Paraguay. Thus, those countries should also control the condition of aphid species and react to the possible introduction of *D. acerifoliae*, even if it seems that the current conditions in the southern hemisphere may be too demanding.

The spreading of *D. acerifoliae* in future may be limited by the lack of planting *A. saccharinum* in Europe and Asia. However, there is a risk that this aphid will change or expand its host plants over time. Due to the climatic conditions, there is also a chance of phenological asynchrony between the host and the

insect (van Asch & Visser 2007). Another worrying phenomenon is that many invasive insects have a wider range of thermal tolerance, beyond their natural niche (Jarošík *et al.* 2015). Natural methods of biological control by using predators may also be a solution, but unfortunately, only a few are known for *D. acerifoliae*. Pérez Hidalgo *et al.* (2008) mentioned predation by *Adalia bipunctata* (Linnaeus, 1758), *Anthocoris pilosus* (Jakovlev, 1877) and *Passer domesticus* (Linnaeus, 1758). As previous authors have also mentioned, we still need to gain a better understanding of the biology of *D. acerifoliae* and the factors influencing the dynamics of its population. Additionally, as many indigenous natural enemies as possible should be identified in order to implement a sustainable conservation scenario. Nevertheless, prevention is crucial, as global trade presents the main risk of introducing and spreading this invasive insect species.

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Author Contributions

Research concept and design: K.M., A.B.-N.; Collection and/or assembly of data: K.M.; Data analysis and interpretation: A.B.-N.; Writing the article: K.M., A.B.-N., K.W.; Critical revision of the article: K.W.; Final approval of article: K.M., A.B.-N., K.W.

Conflicts of Interest

The authors declare no conflict of interest.

Supplementary Material

Supplementary Materials to this article can be found online at: <http://www.isez.pan.krakow.pl/en/fofia-biologica.html>

Supplementary files:

SM.01. Details of all of the occurrence sites used in the MaxEnt model.

SM.02. The list of bioclimatic variables considered as predictors with a correlation coefficient.

SM.03. The results of the evaluation methods for the different MaxEnt settings.

SM.04. MaxEnt model outputs and climatic diagrams.

SM.05. Modelling results for future climate scenarios.

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