Research article

Aedes aegypti in the Mediterranean container ports at the time of climate change: A time bomb on the mosquito vector map of Europe

Attila J. Trájer [*]

Sustainability Solutions Research Lab, University of Pannonia, Egyetem utca 10, H-8200, Veszprém, Hungary

HIGHLIGHTS

- The former Mediterranean ecotype of *Aedes aegypti* persists in the Black Sea area.
- The current climate of the Mediterranean ecoregion is appropriate for the mosquito.
- Climate change will trigger the spread of *Aedes aegypti* in the sub-Mediterranean ecoregion.
- The Black Sea area can serve as the starting region of the expansion of *Ae. aegypti* in Europe.

GRAPHICAL ABSTRACT
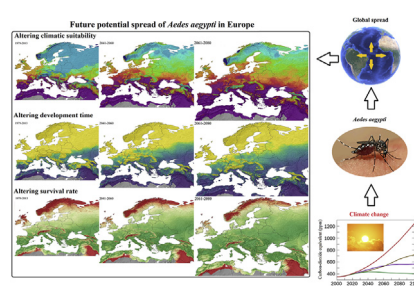
ARTICLE INFO

ABSTRACT

In the past, *Aedes aegypti* was present in Southern Europe. Although the mosquito was eradicated from the Mediterranean region, its regional ecotype survived the second half of the 20th century in the eastern Black Sea area. The aim of the study was to model the changes in the altering climatic suitability, ontogenetic development time and the survival rate of *Aedes aegypti* from first-stage larvae to adulthood in Southern Europe. The modelled present climatic suitability patterns of the mosquito show that large areas of the lower altitude Mediterranean regions, including the coastal areas of the Balkan Peninsula, South France, and large regions of the Apennines and the Iberian Peninsulas could be suitable for *Ae. aegypti*. The future (2041–2060 and 2061–2080) projections predict the potential northward shift of the northern occurrence of the species in the circum-Mediterranean and Black Sea areas. Both, the potential development time, and survival rate of *Ae. aegypti* in the late 19th and the early 20th century could be like in the present times along the Mediterranean coast. The current climatic conditions cannot explain the absence of the mosquito in wide areas of the Mediterranean and sub-Mediterranean ecoregions. The future models predict the notable increase in the development time and survival rate of the mosquito in the southern and central regions of Europe. In general, the container ports of the Alboran, Balearic, and Aegean seas seem to be the most suitable sites for the re-colonization of the mosquito, and such northern parts of the Mediterranean Sea like the Gulf of Lion, the Ligurian, and Adriatic Seas are in less extent.

1. Introduction

Aedes (*Stegomyia*) *aegypti* (Linnaeus in Hasselquist, 1762; hence: Ae aegypti), is among the most important arthropod vectors of several serious human diseases. This mosquito is the vector of yellow fever (Fontenille et al., 1997; Soper, 1967), dengue fever (Yang et al., 2014), Chikungunya fever (Vega-Rúa et al., 2014), Mayaro virus (Long et al., 2011), and Zika fever (Guerbois et al., 2016; Chouin-Carneiro et al.,

---

* Corresponding author.
  E-mail addresses: trajer.attila@mk.uni-pannon.hu, attilatrajer@gmail.com.

2016; Black et al., 2002). It is a typical container-inhabiting mosquito (Koenraadt and Harrington, 2008) like another globally important disease vector mosquito, *Aedes* (*Stegomyia*) *albopictus* (Skuse, 1894). In the tropical-subtropical areas of the Americas, it is also the vector of the emerging Mayaro virus (Wiggins et al., 2018). This mosquito has African origin (Mousson et al., 2005), but it was introduced to many parts of the world (Kraemer et al., 2015). *Aedes aegypti* was a tropical mosquito taxon that lived in the tropical forests of sub-Saharan Africa (McBride et al., 2014; Lounibos, 1981). The ancient Ae. aegypti mosquito could be a sylvatic species. It could adapt to the human environment about 400–600 years ago (Kotsakiozi et al., 2018) and started to spread around the tropical-subtropical areas of the world by ship transport about the same time (Powell and Tabachnick, 2013; Tabachnick, 1991). It is easy to notice the temporal coincidence of the time of the evolutionary event with the early modern European colonization in Africa. Powell et al. (2018) showed that Ae. aegypti was introduced to the New World about 400–550 years ago from West Africa by the European slave trade. It should also be noted that several post-classical and early modern civilizations occurred at that time in West Africa, e.g., the Mali Empire from c. 1235 to 1670 (Ly-Tall, 1984) in which civilizations the domestication of the mosquito could be started. In the mid-20th century, in some areas of the world, the range of the mosquito approached the boundaries of the temperate and continental zones. For example, sporadic occurrences of the species were already observed in the 1980–1990s in such northern cities of the United States of America like Baltimore, Maryland (Sweeney et al., 1988) or in Stirling, New Jersey (Donnelly, 1993).

In Europe, presently the mosquito occurs only along the eastern coasts of the Black Sea and some adjacent regions of the West Caucasus and Northeast Turkey (Kotsakiozi et al., 2018; Akiner et al., 2016; Schaffner and Mathis, 2014; Oter et al., 2013). This mosquito species could be introduced to the Mediterranean Basin somewhen in the mid-19th century, and up to the early-mid 20th century, it was widely distributed in the region (Kotsakiozi et al., 2018). It should be noted that time, *Ae. aegypti* had a particularly light-coloured form in the Mediterranean which in phenotypical sense could be similar to the extant Australian and Eastern African *Aedes aegypti* var. *queenslandensis* Theobald (Mattingly, 1967) (Powell and Tabachnick, 2013 (nullQ); Mattingly, 1967). However, on a phylogenetic basis, the existence of *Aedes aegypti var. queenslandensis* is questionable because a study found that the extant individuals of this pale form could not be distinguished in a genetic sense from the more common melanotic types of the mosquito (Rašić et al., 2016). In contrast, Akiner et al. (2016). Kotsakiozi et al. (2018) showed that the 'Black Sea populations' of the mosquito represent the only living, surviving Mediterranean ecotype population of *Ae. aegypti*. It is important that this ecotype was split from an American population about 100–150 years ago, Black Sea populations are highly differentiated from both New World and Asian populations in a phylogenetic sense (Kotsakiozi et al., 2018). Regardless of how genetically the Mediterranean population may have been genetically different from the mosquito populations that exist today, there was a significant epidemiological factor in the Mediterranean areas in the early 20th century. *Aedes aegypti* caused outbreaks of Dengue fever in Greece during the late summers of 1927 and 1928 (Louis, 2012; Cardamatis, 1929) causing more than 1 million cases (Akiner et al., 2016). Yellow fever epidemics were also observed in the Mediterranean region at that time (Schaffner and Mathis, 2014). However, due to the intense mosquito control campaigns with the use of DDT, the changing hygienic circumstances and maybe the cold winters of the mid-20th century (Holstein, 1967; Curtin, 1967), *Ae. agypti* became rare and only sporadic observations were reported from the Mediterranean countries (Schaffner and Mathis, 2014). Then, *Ae. aegypti* re-appeared or maybe, in the case of the eastern Black Sea region, it simply was re-observed at the start of the 21st century in certain parts of Europe again. The mosquito was reported from Georgia several times in the mid-20th century (e.g., Brooks et al., 1966; Morlan and Hayes, 1958; Smith and Love, 1958). In 2001–2015, the mosquito was reported e.g., from South Russia, Madeira (Portugal), West Georgia, and North Turkey (Akiner et al., 2016;

Ganushkina et al, 2012, 2016; Yunicheva et al., 2008; Margarita et al., 2006; Riabova et al., 2005).

According to the global occurrence-based environmental requirements of *Ae. aegypti*. Dickens et al. (2018) found that the environmental suitability of *Ae. aegypti* is low or medium-low in certain islands and the coastal areas of the Apennine Peninsula, and it is very low in the eastern Black Sea coastlines. Dickens et al. (2018) also showed that based on the global data, both the minimum temperature and absolute humidity excludes the present occurrence of the species in the eastern Black Sea coastlines. Integrating also the eastern Black Sea populations of *Ae. aegypti*, Kamal et al. (2018) returned the present eastern Black Sea coastal occurrence of the mosquito, but their model – like the model of Dickens et al. (2018) and Campbell et al. (2015) – found that *Ae. aegypti* could only occur in certain small, disperse-disjunct ranges in the coastal regions of the Mediterranean Basin. Modelling the future occurrence of the mosquito, Kamal et al. (2018) also did not predict the notable future spread of the mosquito in Southern Europe. Kraemer et al. (2020) found the increasing suitability of *Ae. aegypti* for 2050, but not in Europe or in the Middle East. Rogers et al. (2012) found that the present climatic suitability of *Aedes aegypti* in Europe can reach the 0.6–0.7 value (in the 0–1 value scale), e.g., in some coastal areas of the eastern Black Sea region and the Balkan Peninsula and other parts of the North Mediterranean coasts.

The above-described facts indicate that there is a partial discrepancy between the present/past occurrence of the species and the modelled values. The main reason for this may be that the Mediterranean ecotype has survived only in the eastern part of the Black Sea due to human interventions. In 1935, thirteen South European and Caucasian countries accepted a program to limit the spread and, if it is possible, to eliminate Dengue fever in Europe (Schaffner and Mathis, 2014). The milestone in this program was the eradication of *Ae. aegypti*. This surviving Mediterranean, currently the eastern Black Sea population, represents such a small area in a global context that it can be assumed that the models cannot take it into account at the appropriate level. In statistical terms, the problem is that the eastern Black Sea population covers such a small area that machine-based self-learning methods can greatly underestimate the true potential distribution of the ecotype in Europe now or in the future. In contrast, in North America, *Ae. aegypti* occurs in large regions where the climate is temperate, and the eastern Black Sea populations also live under humid-subtropical conditions. The observed occurrences contradict the modelled and expected occurrence areas in Europe because 1) the species currently is absent from the plausibly suitable temperate climate areas of Europe, and 2) the existing models show only a few regions where the climate could be suitable for the mosquito; however, in the past, it was relatively widespread in the Mediterranean areas near the coast. It is curious because *Ae. aegypti* occurs in several parts of, e.g., California which have a similar warm Mediterranean climate as, e.g., large areas of Greece or Italy. Comparing the Californian occurrences of the mosquito based on the occurrence data of Porse et al. (2015) and the 1-km resolution Köppen-Geiger classification of the planet at California according to Beck et al. (2018) it is hard to explain why the mosquito is absent from the climatically plausibly appropriate regions of Southern Europe. It can be assumed that 1) the existing suitability climate models generally may over-represent the tropical-subtropical climatic needs of the mosquito for spatial reasons (most of the known occurrences came from the equatorial to the subtropical regions) and 2) the models may underestimate the true climatic suitability of the mosquito species in the northern peripheral zone.

The vital biological dynamics of mosquitoes can be modelled for two subpopulations based on mosquito ontogeny: for the group of the winged and mobile imagoes and an aquatic and static stage that consists of eggs, larvae, and pupae (Yamashita et al., 2018). In the case of migration dynamic models of invasive mosquitoes, such factors also should be included in models like 1) the time between the emergence of female mosquitoes from pupae to insemination, 2) the time of host-seeking activity for a blood meal, and 3) the time of blood digestion and ovarian

development lasting to oviposition (Trájer et al., 2017). While the temporal dimension of post-emergence factors can be approximated by constant days and is relatively temperature-independent (de Lima-Camara et al, 2007, 2014; Helinski et al., 2012; Mori and Wada 1977), the duration of the ontogeny of a mosquito strongly depends on temperature. The temperature-dependence of mosquito ontogeny was showed in the case of such important human disease vector species like *Anopheles gambiae* Giles 1902 (Bayoh and Lindsay, 2004), *Ae. albopictus* (Calado and Silva, 2002; Delatte et al., 2009) and it is also true for *Ae. aegypti* (Farnesi et al., 2009). Temperature predominantly determines the development kinetics in the temperate and continental regions (Lacour, 2016). In contrast, in tropical semi-arid areas, the primarily climatic factor is less temperature, but rainfall is what determines the development time (Caminade et al., 2011). As the boundary of the northern range of the *Aedes aegypti* falls in the temperate zone, the main limiting factor for the development of the species should be temperature.

1.1. Aims

The modelling of the potential past, present, and future occurrence patterns of the existing European populations of *Ae. aegypti* would be very important because the eastern Black Sea area may be the source of the invasion of the mosquito in Europe. For this purpose, 1) the climatic suitability, 2) the potential ontogenetic development time (hence: development time) and 3) the survival rate from first-stage larvae to adulthood (hence: survival rate) of *Aedes aegypti*– the last two factors were used as indicators of the climate-based ontogeny time and population kinetics of the species – were modelled in Europe and the Mediterranean parts of North Africa and Western Asia.

2. Materials and methods

2.1. Bioclimatic data

As a reference period's georeferenced bioclimatic data, the 1970–2000 climate model of WorldClim version 2.1 was used (Fick and Hijmans, 2017). The 1960–1990 period's bioclimatic data of the database was also involved in the study to show how the climate change of the recent decades could influence the habitability of Europe related to *Ae. aegypti*. The applied spatial resolution was 2.5 min (4.5 km). The database contains the data of 19 bioclimatic variables in GeoTiff (.tif) file format. Future climatic data were gained from WordClim database Version 1.4 (Hijmans et al., 2005). The Coupled Model Intercomparison Project Phase 5 (hence: CMIP5)-based future scenarios were based on the downscaled Global Climate Model (hence: GCM) data. The predictions of all the four Representative Concentration Pathways (RCPs) were used in the modelling, namely the models based on the rcp2.6, 4.5, 6.0 and 8.5 scenarios. The future periods were 2041–2060 and 2061–2080. The used global climate models were as follows: Beijing Climate Center Climate System Model 1.1 (hence: BCC-CSM1.1; Ren et al., 2016), Community Earth System Model 4.0 (hence: CCSM4.0; Gent et al., 2011); Institut Pierre Simon Laplace Model CM5A-LR (hence: IPSL-CM5A-LR; Dufresne et al., 2013) and Meteorological Research Institute CGCM Version 3 (hence: MRI-CGCM3; Yukimoto et al., 2012). The future climatic predictions are also expressed in bioclimatic values. The Koninklijk Nederlands Meteorologisch Instituut's (hence: KNMI) Climate Explorer (Trouet and Van Oldenborgh, 2013) was the source of the site (point)-like past and the reference period's climatic data covering the eras of 1860–1939 and 1960–1990. The 1860–1939 era was divided into four subperiods: 1860–1879, 1880–1900, 1901–1919 and 1920–1939. The warmest quarter's mean temperature values of the correlated historical (1500–2002) climatic reconstructions of Luterbacher et al. (2004) and Xoplaki et al. (2005) were used as a source of the climatic conditions of the period of 1860–1939. The used value is equal to the BIO10 bioclimatic variable of WordClim database (Ramírez-Villegas and Bueno-Cabrera, 2009).

2.2. Selected ports, and sites

To quantify the result of suitability modelling, the northern Mediterranean and the sub-Mediterranean ecoregions were investigated because the highest potential changes in the suitability and seasonal activity conditions of the studied mosquito can be expected predominantly in this region (Liu-Helmersson et al., 2016). The interpretation of European ecoregions – including the Mediterranean and sub-Mediterranean ecoregions – was based on the geographical classification of Stonis et al. (2014). Because in the 19th and the early 20th century, *Ae. aegypti* was present in the Mediterranean coastal areas and – as it was already mentioned – the mosquito plausibly was introduced from the New World by ship transport to the harbours (Kotsakiozi et al., 2018), 11 major present-day ports of the Mediterranean area and 2 Black Sea port cities of the eastern Black Sea coasts, where the mosquito still occur, were selected for the sampling of the modelled values. The sampled values were as follows: the potential past warmest quarter's mean development time and the survival rate of *Ae. aegypti*. For this purpose, the following Mediterranean and Black Sea ports were selected: Algeciras (Spain), Valencia (Spain), Barcelona (Spain), Marseille-Fos (France), Genoa (Italy), La Spezia (Italy), Gioia Tauro (Italy), Marsaxlokk (Malta), Koper (Slovenia), Piraeus (Greece), Marport (Turkey), Sochi (Russia) and Batumi (Georgia). To create the basis of the reconstruction of past bioclimatic conditions in Europe and the Mediterranean region, 11 additional cities were also added to the above-mentioned Mediterranean and Black Sea port sites, namely: Algiers (Algeria), Amsterdam (The Netherlands), Berlin (Germany), Bucharest (Romania), Budapest (Hungary), Copenhagen (Denmark), Edinburgh (UK), Nicosia (Cyprus), Oviedo (Spain), Paris (France), Riga (Latvia), Sevastopol (Crimean Peninsula), Stockholm (Sweden), Tunis (Tunisia), Warsaw (Poland) (Figure 1).

2.2.1. Reconstruction of the 1880–1939 temperature conditions

To model the 1860–1939 potential warmest quarter's development time and the survival rate of *Ae. aegypti* along the northern Mediterranean coasts, the former mean temperatures of the warmest quarters were reconstructed. The steps of the reconstruction were as follows:

1) The reference period's warmest quarter's mean temperature values of the 13 ports and the 11 additional cities were determined;
2) then, the warmest quarter's mean temperatures of the 24 cities were determined for 1860–1879, 1880–1899, 1901–1919 and 1920–1939 which periods represents the pre-eradication era when *Ae. aegypti* was widespread in the Mediterranean coastal regions (Schaffner and Mathis, 2014; Louis, 2012; Cardamatis, 1929);
3) then, the differences between the reference periods and the selected past period's values were calculated;
4) then, the calculated difference values were interpolated using inverse distance weighted (IDW) interpolation method by periods;
5) and in the last step, the reference period's values were modified with the interpolated difference values.

The interpolated mean temperature values of the warmest quarter based on the climatic data of the 13 port cities and the 11 additional cities can be seen in coloured heat maps. The absolute mean annual temperature difference interval was 1.5 °C (Figure 2).

2.3. Methodological considerations and factor selection

A total of 21 present-day and recent occurrence sites of *Ae. aegypti* from the Crimean Peninsula, South Russia, Georgia, and Northeast Turkey were involved in the study. The occurrence sites of *Ae. aegypti* in the region was localized and georeferenced. Supplementary Table 1 shows the locality of the sites and the related publications. Since the climatic values were identified based on well-localizable, nearly point-like geographical data and the number of the known occurrences of the
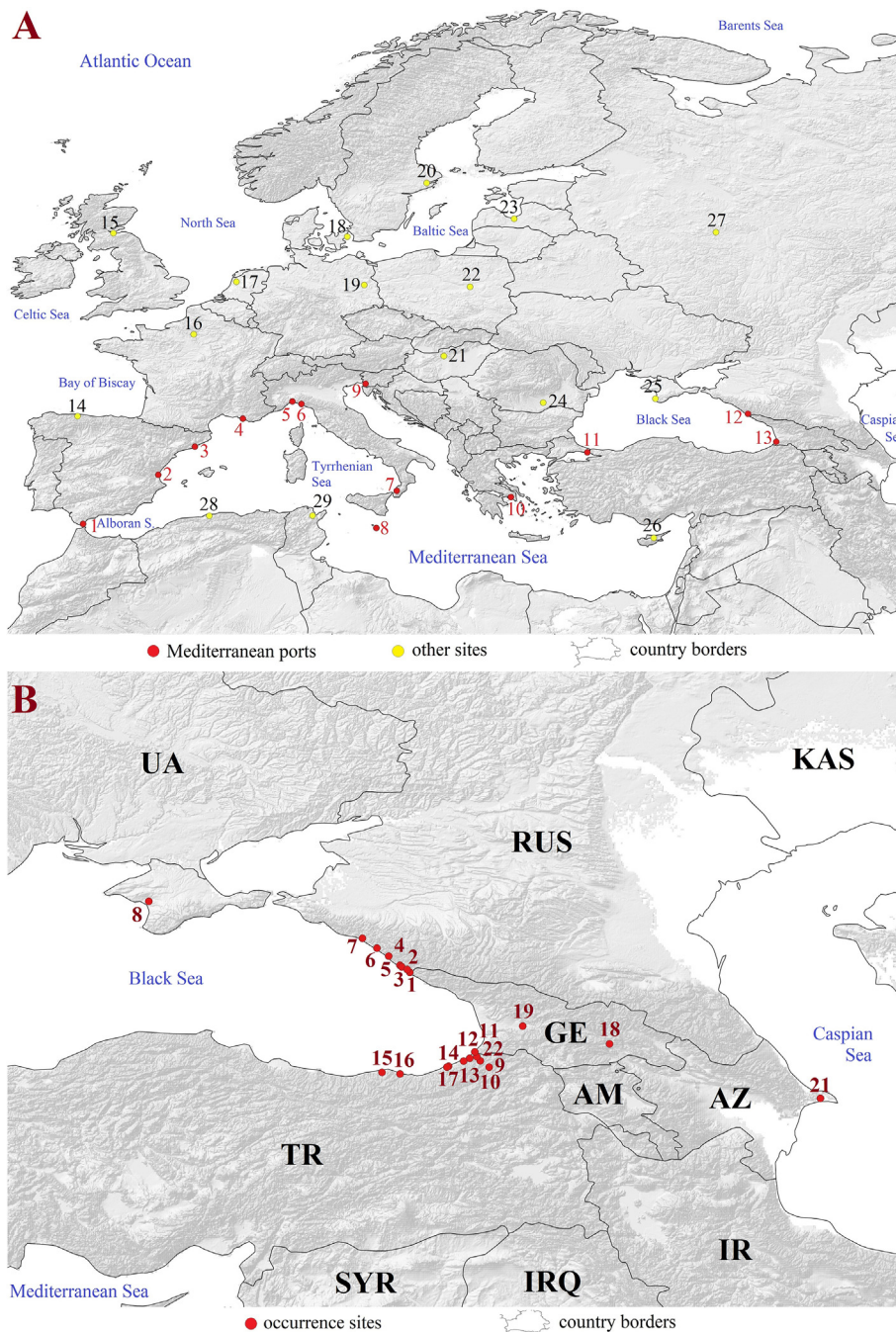
Figure 1. A: The studied area with the selected Mediterranean and Black Sea ports (red spots; 1: Algeciras, 2: Valencia, 3: Barcelona, 4: Marseille-Fos, 5: Genoa, 6: La Spezia, 7: Gioia Tauro, 8: Marsaxlokk, 9: Koper, 10: Piraeus, 11: Marport, 12: Sochi, 13: Batumi) and other cities which were selected for interpolation of bioclimatic values (yellow spots; 14: Oviedo, 15: Edinburgh, 16: Paris, 17: Amsterdam, 18: Copenhagen, 19: Berlin, 20: Stockholm, 21: Budapest, 22: Warsaw, 23: Riga, 24: Bucharest, 25: Sevastopol, 26: Nicosia, 27: Moskva, 28: Algiers, 29: Tunis). Grey areas mark the territories where bio12 < 55mm. B: The occurrence sites of *Aedes aegypti* in the Black Sea and Caucasus area. The location numbering is the same as in Table 1 (UA: Ukraine, RUS: Russia, KAS: Kazakhstan, GE: Georgia, AM: Armenia, AZ: Azerbaijan, IR: Iran, TR: Turkey, SYR: Syria, IRQ: Iraq).

mosquito in the Black Sea and Caucasus region is limited, the absolute lower or upper extremes related to the total studied occurrence sites were used in modelling. A central problem of the modelling of the eastern Black Sea populations of *Ae. aegypti* is the fact that this relatively well-demarcated area only represents a very small portion of the global distribution of the mosquito.

If extremes on both sides (the lower and upper ones) are selected for this region, then in the modelling we obtain essentially those areas whose climate is the same as the area of the eastern Black Sea coastal populations of *Ae. aegypti*.

In a methodological sense, it is fundamentally flawed because it is well known that the real distribution of the mosquito is much wider on the global level. To resolve this problem, a hybrid solution is needed, which means the selective use of the gained extrema. It is known that at the northern occurrence border of invasive Diptera species in Europe, the

lower extrema of the temperature factors and the upper extrema of the precipitation factors are the most important (Tráier et al., 2013). Bioclimatic factors were considered in the selection of the bioclimatic factors according to the following criteria:

1) *Ae. aegypti* is a cold-sensitive mosquito taxon (Montini et al., 2021);
2) this mosquito also occurs in such dry and hot countries with a relatively notable annual temperature fluctuation that is a common phenomenon in semi-arid environments (Sikka, 1997), e.g., in Eritrea, Djibouti, and Senegal (Khormi and Kumar, 2014);
3) the Black Sea area populations of Ae. aegypti form one of the most northernmost populations of the mosquito, which in fact indicates the importance of the lower temperature limits;
4) the Mediterranean and subtropical Diptera species do not prefer cold and humid conditions (Tráier and Padisák, 2019; Tráier et al., 2013).

Table 1. Occurrence sites of *Aedes aegypti* in the Black Sea and Caucasus area.

Number	Site	Area	Reference
1	Adler	Southwest Russia	Ganushkina et al. (2016)
2	Khosta	Southwest Russia	Ganushkina et al. (2016)
3	Sochi	Southwest Russia	Riabova et al. (2005); Ganushkina et al. (2016)
4	Mamayka	Southwest Russia	Ganushkina et al. (2016)
5	Lazarevskoe	Southwest Russia	Ganushkina et al. (2016)
6	Tuapse	Southwest Russia	Ganushkina et al. (2016)
7	Dzhubga	Southwest Russia	Ganushkina et al. (2016)
8	Priboy	Crimean Peninsula	Ganushkina et al. (2020)
9	Artvin	Asia Minor	Akiner et al. (2018)
10	Borçka	Asia Minor	Akiner et al. (2018)
11	Hopa	Asia Minor	Akiner et al. (2018)
12	Arhavi	Asia Minor	Akiner et al. (2018)
13	Fındıklı	Asia Minor	Akiner et al. (2018)
14	Pazar	Asia Minor	Akiner et al. (2018)
15	Vakfıkebir	Asia Minor	Akiner et al. (2018)
16	Trabzon	Asia Minor	Akiner et al. (2018)
17	Ardeşen	Asia Minor	Akiner et al. (2018)
18	Tbilisi	Caucasus	Akiner et al. (2016)
19	Kutaisi	Caucasus	Ganushkina et al. (2016)
20	Batumi	Caucasus	Ganushkina et al. (2016)
21	Baku	Caucasus-East Caspian Sea Region	Ganushkina et al. (2016)

The logic of factor selection could be summarized in the way that considering the geographical position of the studied region within the global distribution of the species (as it was mentioned, it belongs to the northernmost ranges of the mosquito), in the case of temperature kind of bioclimatic variables the minimum, in the case of the bioclimatic precipitation values, the maximum values of the bioclimatic extrema were used. In a logical sense, it can be accepted that at the northern range of mosquito species of tropical-subtropical origin, low temperatures and the high precipitation sums due to the cooling effect of notable rainfalls generally could be unfavourable and limiting factors.

Seven temperature (bio1, 5–6, 8–11) and seven precipitation-kinds of bioclimatic variables (bio12-14, 16–19) were involved in the study. The selected limits of the following temperature-like climatic variables can be seen in Table 2. This means 14 environmental limits in the model, which is an acceptable number for species range modelling purposes.

2.4. Model identification

For the numerical modelling of the potential one-side (potentially northern occurrence border-determining) environmental requirements-based distribution areas of species, the 14 extrema of the selected bioclimatic factors described in Table 2 were used. The modelling was based on the binary logic of the Boolean algebra and formalized based on Trájer and Sebestyén (2019). That means that it indicates that the mathematical formalism of the deterministic unit step functions should also be similar (Eqs. (1) and (2)):

$$1(bioT) = \begin{cases} 0 & if \quad bioT_{min} > bioT \\ 1 & if \quad bioT_{min} \leq bioT \end{cases} \tag{1}$$

$$1(bioP) = \begin{cases} 0 & if \quad bioP > bioP_{max} \\ 1 & if \quad bioP \leq bioP_{max} \end{cases} \tag{2}$$

where $bioT$ refers to the temperature-based bioclimatic variables (bio1,5,6,8,9,10,11) and $bioP$ refers to the precipitation-based bioclimatic variables (bio12,13,14,16,17,18,19).

The potential areas allowed by the temperature factors can be determined according to the following mathematical formalism (Eq.(3)):
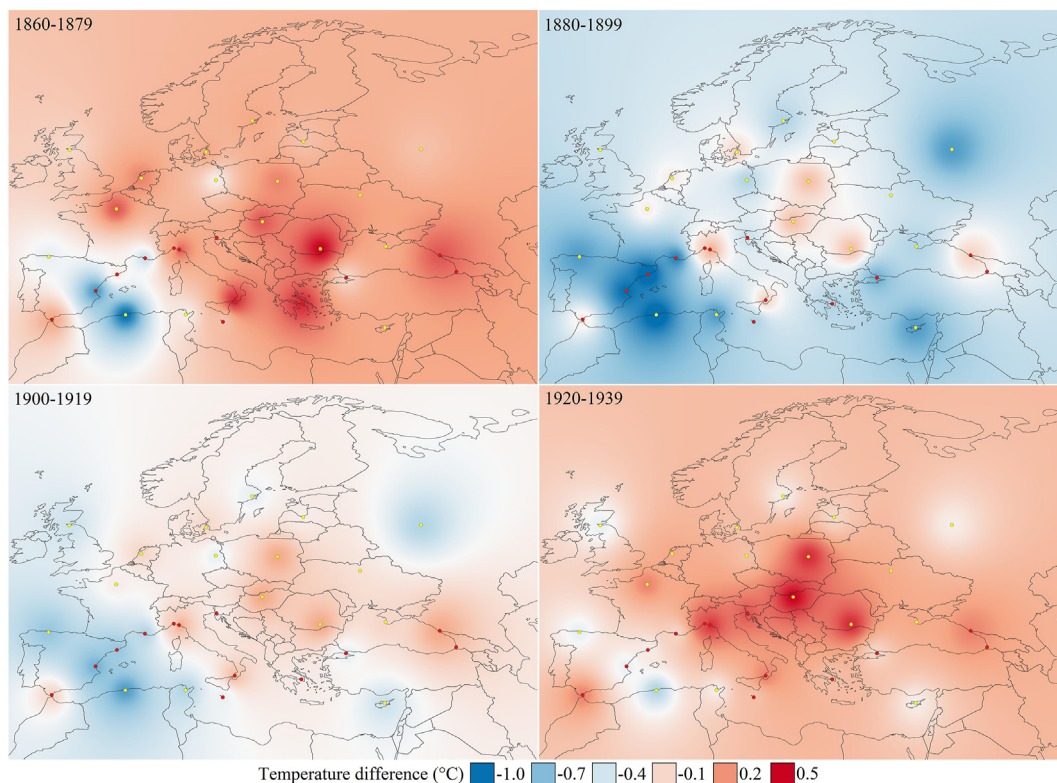

Figure 2. The modelled differences of the past period's warmest quarter's mean temperatures from the reference period's value. For the explanation of the red and yellow spots, see the legend of Figure 1. Grey areas mark the territories where bio12 < 55mm.

Table 2. The used bioclimatic variables and extrema in modelling.

Abbreviation	Bioclimatic variable	Unit	Selected extrema
bio1	annual mean temperature	°C	11.8≤
bio5	maximum temperature of warmest month	°C	24.7≤
bio6	minimum temperature of coldest month	°C	-3.8≤
bio8	mean temperature of wettest quarter	°C	4.2≤
bio9	mean temperature of driest quarter	°C	1.3≤
bio10	mean temperature of warmest quarter	°C	21.7≤
bio11	mean temperature of coldest quarter	°C	1.2≤
bio12	annual precipitation	mm	2217≥
bio13	precipitation of wettest month	mm	284 ≥
bio14	precipitation of driest month	mm	107≥
bio16	precipitation of wettest quarter	mm	823≥
bio17	precipitation of driest quarter	mm	327≥
bio18	precipitation of warmest quarter	mm	554≥
bio19	precipitation of coldest quarter	mm	556≥

$$A(bioT_{min}, P_{max}) = 1(bioT_{min}) - \sum_{i=1}^{7} 0(bioT_{min}) \cap 1(bioP_{max})$$

$$- \sum_{i=1}^{7} 0(bioP_{max}) \tag{3}$$

where $A(T_{min}, P_{max})$ shows the potential distribution area of the given species, which contains the remaining areas after taking into consideration the temperature and precipitation limitations.

The modelled number of the satisfied factors in each point was converted into percentage (%) values. Hereinafter, these values were held as the habitat-suitability factors of the mosquito. The satisfied 14-factor number means 100%, the 0 satisfied factor represents the 0% suitability value. In the depiction of the model results, the 50–100% values were visualized.

2.5. Development time and survival rate

Since mosquitoes, like other insects, are clearly poikilotherm organisms, any parts of their ontogenesis fully depend on biological and thermal factors (Damos and Savopoulou-Soultani, 2012; Davidson, 1944). It means that in the case of a mosquito species both the individual steps of the ontogenesis, including the development time of the mosquito and the survival rate depend on the ambient temperature conditions.

The correlation between the mean temperature of the warmest quarter and the development time of *Ae. aegypti* was based on the data of Tun-Lin et al. (2000) ($r^2 = 0.9792$, p = 0.0208; quadratic regression fit model; Eq. (4)):

$$t_{daq} = -381.1571 + 39.45714 \times T_{wq} - 0.8171429 \times (T_{wq}\hat{}2) \tag{4}$$

t_{daq}: development time of *Ae. aegypti* in days.
T_{wq}: mean temperature of the warmest quarter in °C.
The colour selection in the displaying of the model results was adapted to be sensible to the northern distribution area's conditions related to the development time of *Ae. aegypti*. For this purpose, the 7–17 days development time interval was selected.

The correlation between the mean temperature of the warmest quarter and the survival rate of *Ae. aegypti* was based on the data of Tun-Lin et al. (2000) ($r^2 = 0.9992$, p = 0.0412; symmetrical sigmoidal fit model; Eq. (5)):

$$R_{sa} = 7.41991 + (41345270 - 7.41991) \Big/$$

$$(1 + (T_{wq}/1.201183)\hat{}5.570304) \tag{5}$$

R_{sa}: survival rate of *Ae. aegypti* in percentage (%) value.

T_{wq}: mean temperature of the warmest quarter in °C.
Modelling results were displayed using Quantum GIS 3.4.4 (QGIS project, 2021) with GrassGis7.4.1 software. The Lambert Azimuthal Equal Area (EPSG:3035) was used as a projection system.

Because the model environment was optimized to predict the climatic suitability of the mosquito in the northern territories, it is less sensitive in the Northern Sahel zone in North Africa and Western Asia. To resolve this problem, a precipitation limit was included in the models. The 55 mm annual mean precipitation sum (identical to bio12 variable) was handled as the lower precipitation-based limit of the occurrence of *Ae. aegypti* according to Cabrera and Selvaraj (2020) (Eq. (6)):

$$1(bio12) = \begin{cases} 0 & if & 55\,mm > bio12 \\ 1 & if & 55\,mm \le bio12 \end{cases} \tag{6}$$

Areas, where the annual mean precipitation sum is lower than 55 mm, were marked with dark grey colour.

3. Results

3.1. The determined climatic suitability values

Although, the predicted potential distribution of *Ae. aegypti* for *1960–1990 and 1979–2013* are similar, some differences can be seen. In both models, the Mediterranean, most of the territories of Italy and some regions of the Balkan, and Spain characterized by Mediterranean climate are included in the potential, but not established distribution. The modelled potential suitability values seem to be higher in Western Europe and in the North Balkan, although practically the species is restricted to the Mediterranean coastlines and the lower and mid-elevations of the Mediterranean peninsulas and to the narrow eastern and southern Black Sea coastline regions and some parts of the Crimean Peninsula. For Southern France (in the Gulf of Lyon, the South Carpathian Basin, the central parts of the Iberian Peninsula, in the middle elevations of the Apennine Mts., in the central territories of Asia Minor, maximum climatic suitability values were modelled. The alteration in climatic suitability values between 1960-1990 and 1979–2013 could reach 21–29% in Vojvodina (Serbia), the Romanian Lowland and the continental areas of Croatia. In both models, the suitability values in the lower and middle altitude areas of Western Europe – including North France, the Benelux States, Ireland and in notable parts of the UK, the climatic suitability is estimated to be 79%. In Central Europe, the climatic suitability values - apart from the mountainous regions – are between 57-79% and a clear east-to-west increasing geographical trend can be seen in both the 1960–1990 and 1979–2013 models. In all the studied large Mediterranean and Black Sea ports, the climatic suitability reached the 93–100% value in 1960–1990 and by 1979–2013 there was no longer a port where this value would have been below 98%. There is no primary limiting value that could explain the difference between the observed and predicted present distribution of the species (Figure 3).

For the 2041–2060 period, expansion is predicted mainly in Southwest France, North Spain, the countries of the Carpathian Basin, South Ukraine, and the lowland part of Romania. The predicted geographical changes in the climatic suitability values in 2061–2080 are like the earlier modelled periods, although the increase in the predicted climatic suitability values in Europe are more notable in the northern regions than in the case of 2041–2060. The most excessive changes can be seen in France, the Rhine valley, Brandenburg in Northeast Germany, Lubusz in West Poland, in the low and middle elevations of the Carpathian Basin, the Balkan Peninsula – including the Romanian and Bulgarian Lowlands, along the northern coastal regions of the Black Sea and in the central and eastern regions of Asia Minor. For example, in the central parts of the Hungarian Great Plain, the alteration of the climatic suitability values is calculated to be 20–29% in the 2041–2060 models and 25–29% in the case of the 2061–2080 models comparing to the modelled values of 1960–1990 for the same area. The mean modelled climatic suitability
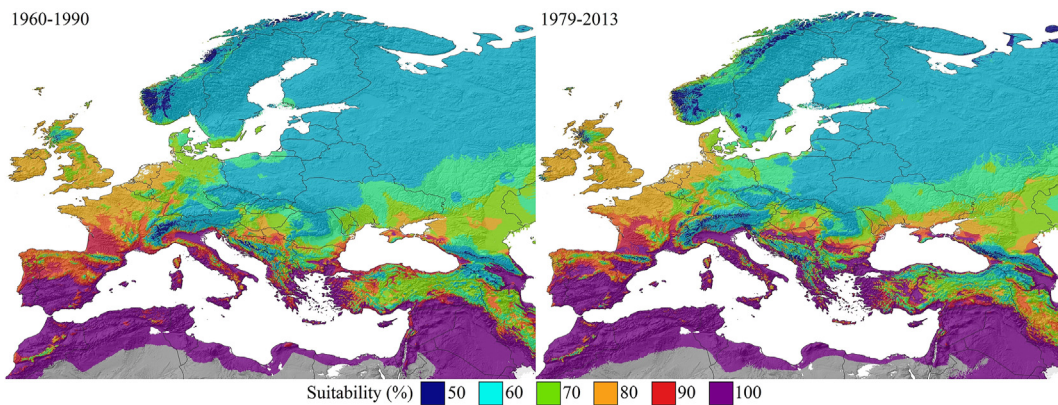
Figure 3. The suitability patterns of *Ae. aegypti* in 1960–1990 and 1979–2013 based on the one-side (northern occurrence border) environmental requirements of the eastern Black Sea Coastal populations of the mosquito. Grey areas mark the territories where bio12 < 55mm.

value of the ports is 99.6%. Although the level of the changes depends on the base climate model and scenario, it can be said that for this period, all the modelled climatic suitability values related to the studied ports are predicted to reach or overwhelm the 89% value (the mean value of the ports is 99.4%) (Figure 4).

Supplementary Table 1 shows the modelled climatic suitability values in the studied Mediterranean and Black Sea ports.

3.2. Development time

From 1860 to 1939, the shortest development times (9–10 days) are calculated to exist in the southern part of the Iberian Peninsula, the Balearic Islands, Sardinia, Sicily, in the southern coastal regions of the Apennine Peninsula, the South Balkans, in the coastal plains and valleys of West Asia Minor, Cyprus, as well as in the Mediterranean coasts of North Africa and the Middle East. Longer potential development times (11–13 days) were calculated for the coasts of the Gulf of Lyon and the Gulf of Genoa, the Poe Valley, Istria, the central plain regions of the Carpathian Basin, the Romanian and Bulgarian Lowlands, South Ukraine and for the northern foreland of the Caucasus Mts. in Southwest Russia. The average calculated development time values for the pre-mid-20th century periods related to the studied Mediterranean and Black Sea ports are calculated as between 9-13 days. The shortest development times could exist in Piraeus and Gioia Tauro and the longest ones in Genoa, La Spezia, Koper, and Sochi (Figure 5).

In 1960–1990 and 1979–2013, the modelled development times for *Ae. aegypti* based on the warmest quarter's mean temperatures are calculated as 9–18 days in the studied ports with a mean value of 11 days in both periods. The geographical patterns of the modelled development time values are highly similar between 1960-1990 and 1979–2013, which justifies the joint presentation of the model results for these periods. The lowest potential development durations in the warmest quarter (9–10 days) can be seen along the Mediterranean coastline, including the southern half of the Iberian Peninsula, the Balearic Islands, the southern coastal regions of the Apennine Peninsula, Sardinia, Sicily, the coastal plains of the South Balkan, the Aegean islands, western Anatolia, in the lowland areas of Azerbaijan, in the Levant and the non-hyperarid and non-high elevation regions of North Africa. Medium-long development times (11–14 days) can be seen in the Northern Meseta of Spain, in Gascogne in France, the Poe Valley in Italy, in the Carpathian Basin, in the Romanian Lowland and Moldova, in South and East Ukraine including the Dnieper Lowland, in the Southwest parts of Russia, along the Black Sea coasts of Georgia and Turkey. In the central part of Anatolia, in the middle elevations of the Mediterranean mountains and in the high mountainous regions of the Atlas Mts. in Morocco and Algeria also medium-long development times were modelled (Figure 6).

For 2041–2060, regions with equal or less than 11 days development duration values will cover a major part of the Iberian Peninsula, the low

and middle elevation regions of the Apennine Peninsula, and this short development time value will appear also in Southwest France, the Carpathian Basin, in the Bulgarian and Romanian lowlands, in the southern parts of Ukraine, South Russia, Central Anatolia, along the coasts of the Black Sea in Georgia and Turkey. Medium-high development time regions (11–15 days) can become characteristic of vast regions of the Eastern European plains and hill lands, the valley of Rhein, and certain northern parts of Central and East-Central Europe, including West Poland. The average development time of *Ae. aegypti* in 2041–2060, based on the warmest quarter's mean temperatures, the mean days are predicted to be 8–13 days in the Mediterranean ports with a mean of 10 days. The development time of *Ae. aegypti* in 2061–2080, based on the warmest quarter's mean temperatures are predicted to be 8–13 with 9 days average value in the Mediterranean ports (Figure 6). In the sub-Mediterranean ecoregion, including the lowlands and middle elevations of the Iberian Peninsula, South France, Italy, the Carpathian Basin, and the southern parts of the East European territories, the modelled length of the development of *Ae. aegypti* can drop below the 9–10 days value. Regions with medium-long development duration will be characteristic of France, excluding the northernmost and higher elevation areas of the country-, to the lowlands of Poland, and in Eastern Europe, the medium-long development time regions can reach the 56°N latitude (Figure 7).

Supplementary Table 2 shows the modelled development time values in the studied Mediterranean and Black Sea ports.

3.3. Survival rate

From 1860 to 1939, the survival rates are estimated to be 90–94% in the Mediterranean regions. In the plains of Southeast Europe, this value could be 82–86%. In the Atlantic climate regions of France, the Benelux States and in the continental, but non-mountainous regions of Central Europe, the survival rate values could be between 75-33%. In the British Isles, the highest survival rate values could occur in Southeast England with 46–50% values. The estimated average survival rates in the case of the pre-mid-20th century models related to are studied Mediterranean and Black Sea ports are 88.0% (1880–1899, 1900–1919) and 88.9% (1860–1879; 1920–1939). Between 1860 and 1939, the highest survival rate values (85%<) could exist in the southern part of the Iberian Peninsula, the middle and lower elevations of the Apennine Peninsula, along the coastlines of the Balkans, the Black Sea's coastline regions, in the lower elevation regions of Asia Minor, North Africa and the Middle East. The geographical patterns of the modelled survival rates in 1860–1939 are very similar to the calculated values of 1960–1990 (Figure 8).

In 1960–1990, the average survival rate in the studied Mediterranean and Black Sea ports is calculated as 88.4%. In the case of 1979–2013, this value is very similar, it is estimated as 92.3%. While in 1960–1990, the
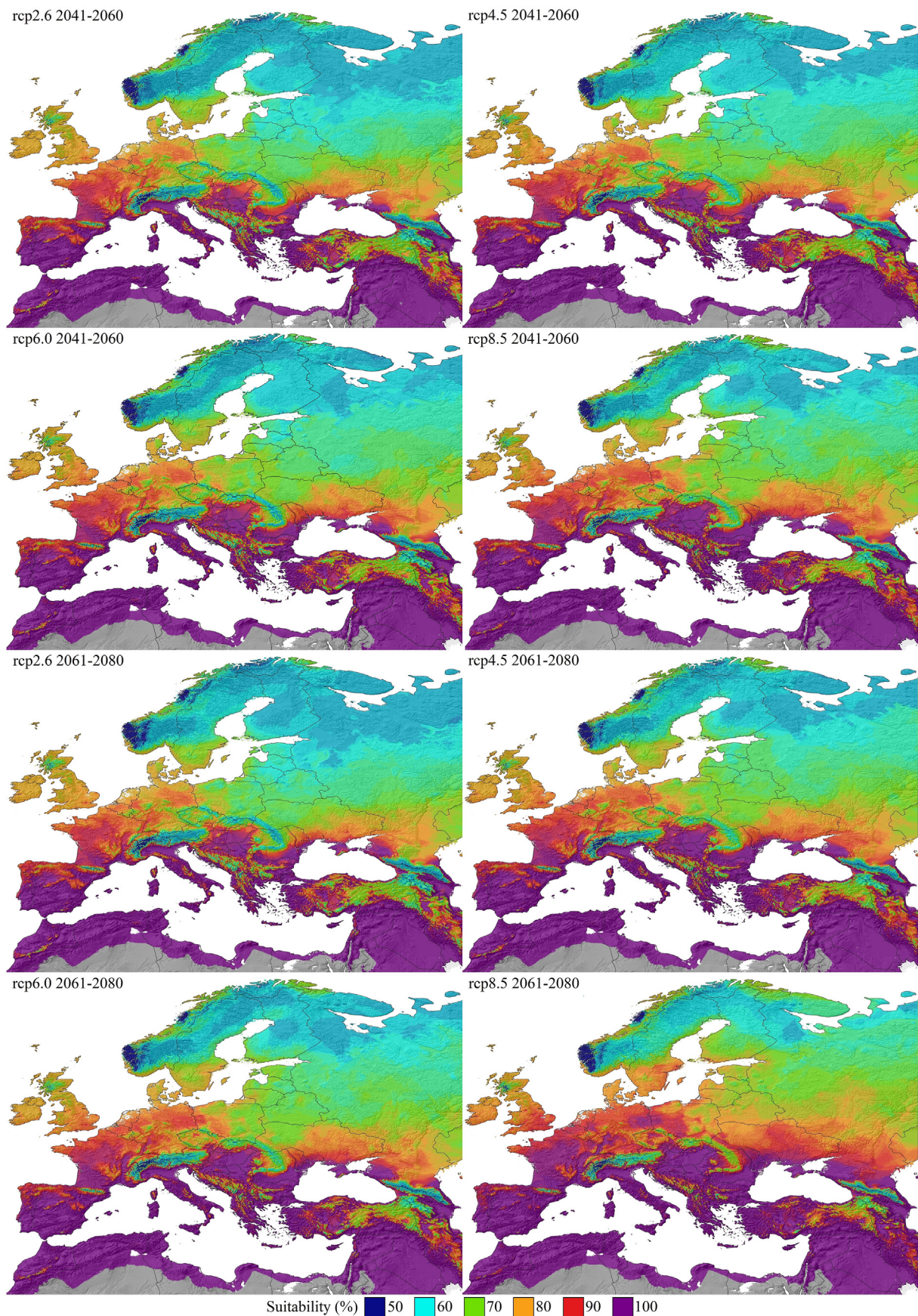
rcp2.6 2041–2060

rcp4.5 2041–2060

rcp6.0 2041–2060

rcp8.5 2041–2060

rcp2.6 2061–2080

rcp4.5 2061–2080

rcp6.0 2061–2080

rcp8.5 2061–2080

Suitability (%) ■ 50 ■ 60 ■ 70 ■ 80 ■ 90 ■ 100

Figure 4. The averaged potential future suitability patterns of the *Ae. aegypti* for 2041–2060 and 2061–2080 according to the four RCP scenarios of the climate models BCC-CSM1.1, CCSM4.0, IPSL-CM5A-LR and MRI-CGCM3, based on the one-side (northern occurrence border) environmental requirements of the eastern Black Sea Coastal populations of the mosquito. Grey areas mark the territories where bio12 < 55mm.
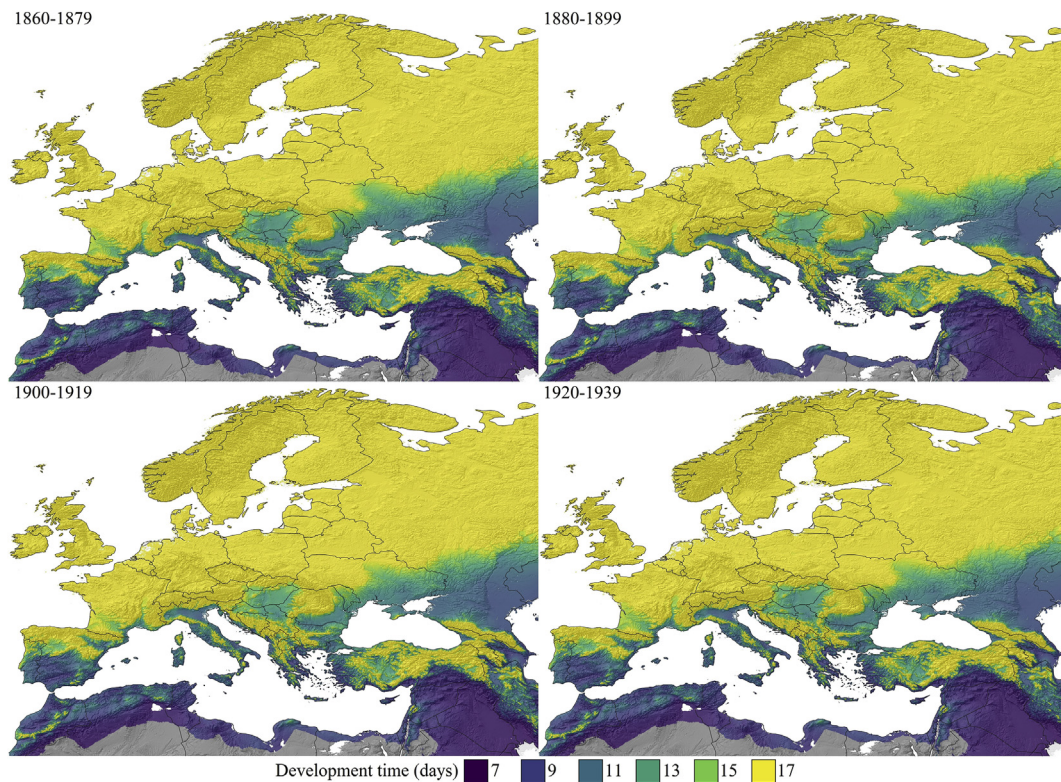
Figure 5. The past (1860–1879, 1880–1899, 1900–1919 and 1920–1939) calculated development times of *Ae. aegypti* mosquitoes according to the warmest quarter's mean temperatures and based on the historical climatic reconstructions of Luterbacher et al. (2004) and Xoplaki et al. (2005). Grey areas mark the territories where bio12 < 55mm.
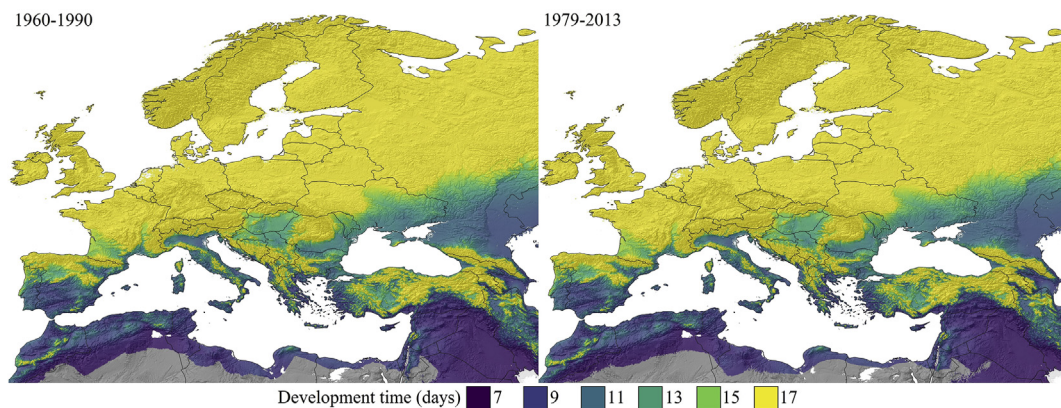

Figure 6. The modelled development times of *Ae. aegypti* in 1960–1990 and 1979–2013 according to the warmest quarter's mean temperatures. Grey areas mark the territories where bio12 < 55mm.

highest (85%<) values could occur only along the Mediterranean, the Black Sea and Caspian coastlines, for 1979–2001, areas with high potential survival rates also appeared, e.g., in Southwest France and the lowlands of East-Central and Southeast Europe. The changes between the two periods are also notable in the comparison of West and Central Europe, where the earlier 20–40% survival rates were replaced with 40–60% values in large areas. However, parallel to these changes, the survival rate could decrease in North Africa and the Middle East due to warming. The future models predict a notable increase in the extension of areas with high survival values in Europe compared to the period 1979–2013 (Figure 9).

The average predicted future survival rates for 2041–2060 and 2061–2080 are between 88.7-90.4% and 84.2–90.5%. For 2041–2060, the zone of the areas with more than 70–80% survival rates can reach South Finland, and for 2061–2080, in Estonia, Latvia and Lithuania, this value may exceed the 85% value. In South England, wherein 1960–1990 and 1979–2013, the survival rate is estimated as 50%, for 2041–2060 and 2061–2080, this value can reach 65–80%. Based on the model results, relatively high survival rates (70–85%) will characterize the lowland regions of continental Western Europe, Central Europe, and the southern areas of Eastern Europe for 2061–2080. It should be noted, that in contrast to the general increase in the survival rate values in the major parts of Europe, warming also could result in the notable, about -15 to -30% alteration of this value for 2041–2060 and 2061–2080 in the southern regions of the Iberian Peninsula, North Africa, the Greek coastal plains, and the Middle East (Figure 10).

Considering the ports-related values, while between 1860-2013, the lowest modelled potential survival values were calculated for Genoa, in
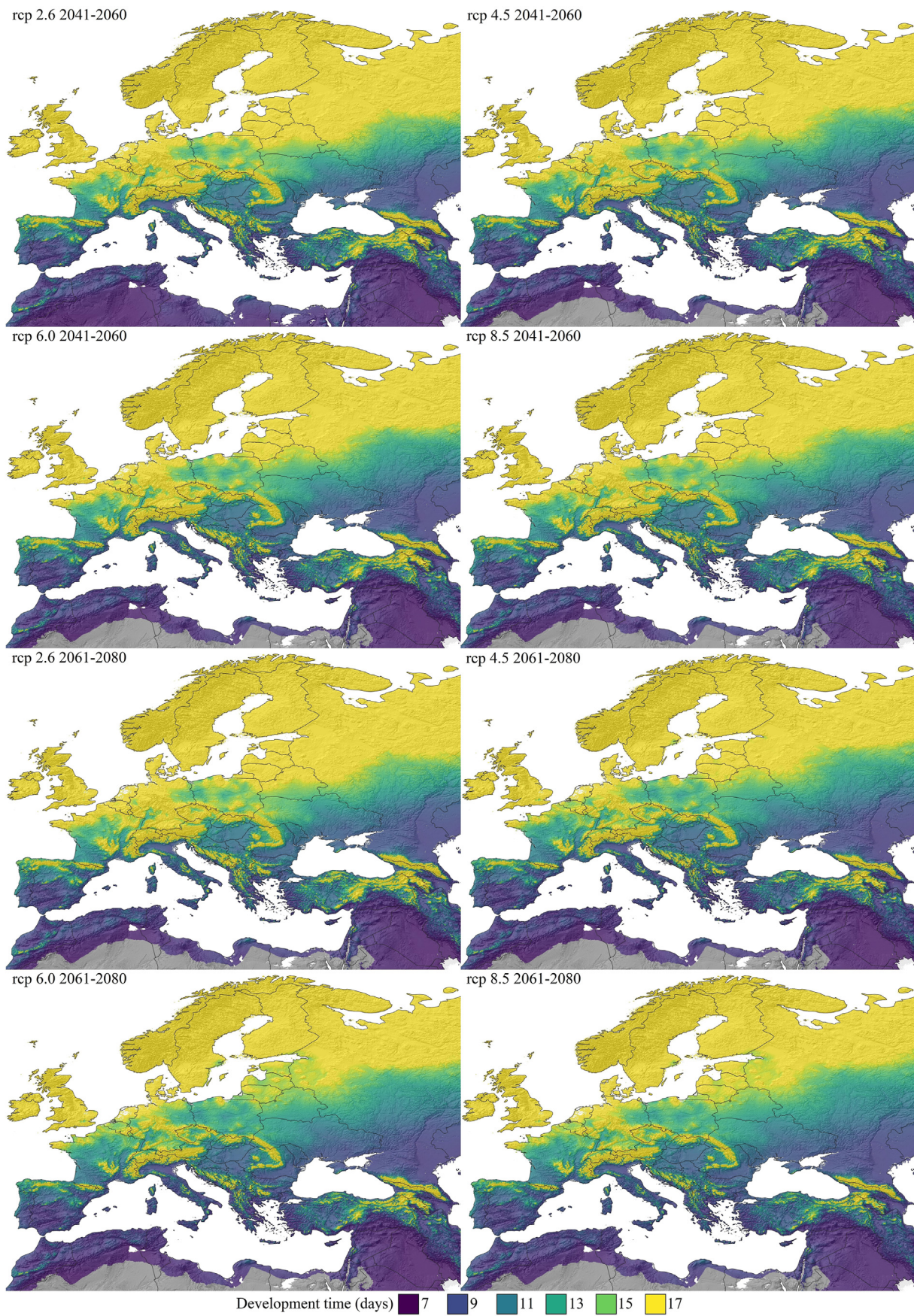
Figure 7. The averaged potential future (2041–2060 and 2061–2080) development times of *Ae. aegypti* according to the warmest quarter's mean temperatures and based on the BCC-CSM1.1, CCSM4.0, IPSL-CM5A-LR and MRI-CGCM3 climate models. Grey areas mark the territories where bio12 < 55mm.
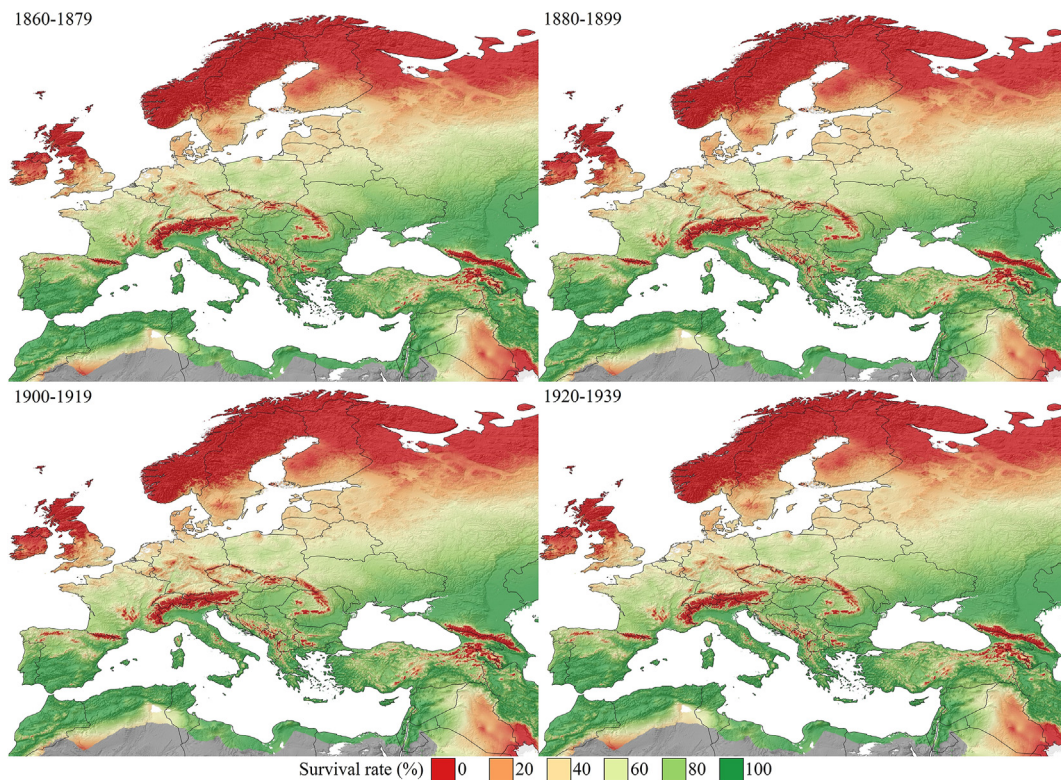
Figure 8. The past (1860–1879, 1880–1899, 1900–1919 and 1920–1939) calculated survival rates of *Ae. aegypti* mosquitoes according to the warmest quarter's mean temperatures and based on the historical climatic reconstructions of Luterbacher et al. (2004) and Xoplaki et al. (2005). Grey areas mark the territories where bio12 < 55mm.
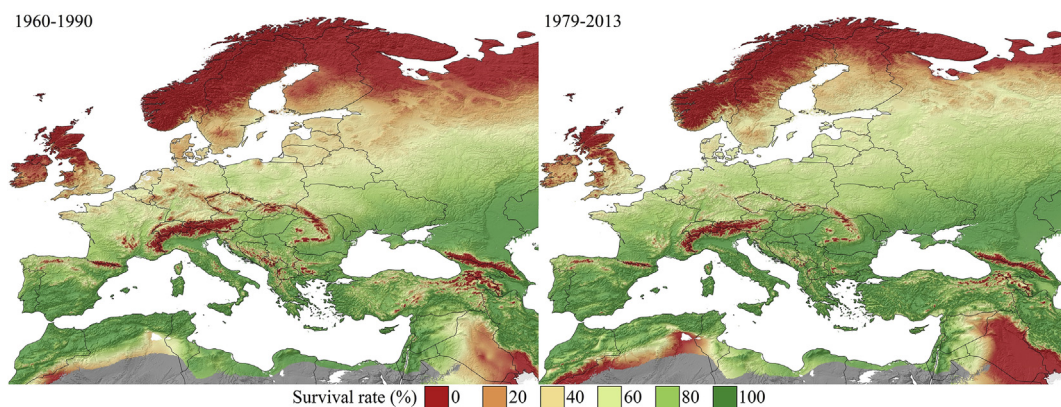

Figure 9. The modelled survival rates of *Ae. aegypti* in 1960–1990 and 1979–2013 according to the warmest quarter's mean temperatures. Grey areas mark the territories where bio12 < 55mm.

the case of the future periods, the lowest values were modelled for Piraeus. The alteration of the highest survival rates shows a more heterogeneous picture. Between 1860-1990, the highest survival rate values were modelled for Valencia, Gioia Tauro and Marsaxlokk. In 1979–2013, the maximum values could exist in Barcelona, Marseille-Fos, Genoa and Marport. In the future models, in most of the modelled ports, the predicted survival rate values show a decreasing trend between 2041-2060 and 2061–2080, and along with the increasing level of warming between rcp2.6 and rcp8.5. For example, while the highest survival rate values in the rcp2.6 2041–2060 scenario-based model can be seen in Barcelona, Marseille-Fos, Genoa and Marport ports, in the case of the rcp8.5 2061–2080 scenario-based model, the maximum values can be seen in La Spezia, Sochi and Batumi ports. The model results indicate the future shift of the survival rate values along a south to north or southwest to a northeast axis in the wider Mediterranean area.

Supplementary Table 3 shows the modelled survival rate values in the studied Mediterranean and Black Sea ports.

4. Discussion

In general, *Ae. aegypti* is thought to be a less hazardous mosquito species in Europe compared to *Aedes albopictus* (Skuse, 1894) based on its estimated lower invasion capacity and environmental suitability in the Old continent (e.g., Alaniz et al., 2017; Cunze et al., 2016). This is manifested by the fact that *Ae. aegypti* seems to have a permanently narrower range in Europe in the same model environments as those of the Asian tiger mosquito (e.g., Leta et al., 2018). The modelled potential ranges of *Ae. aegypti* is in sharp contrast to past observations, which show that the climate in southern Europe was appropriate for the mosquito in the 19th and early to mid-20th centuries. The observed disjunct-disperse

rcp 2.6 2041-2060

rcp 4.5 2041-2060

rcp 6.0 2041-2060

rcp 8.5 2041-2060

rcp 2.6 2061-2080

rcp 4.5 2061-2080

rcp 6.0 2061-2080

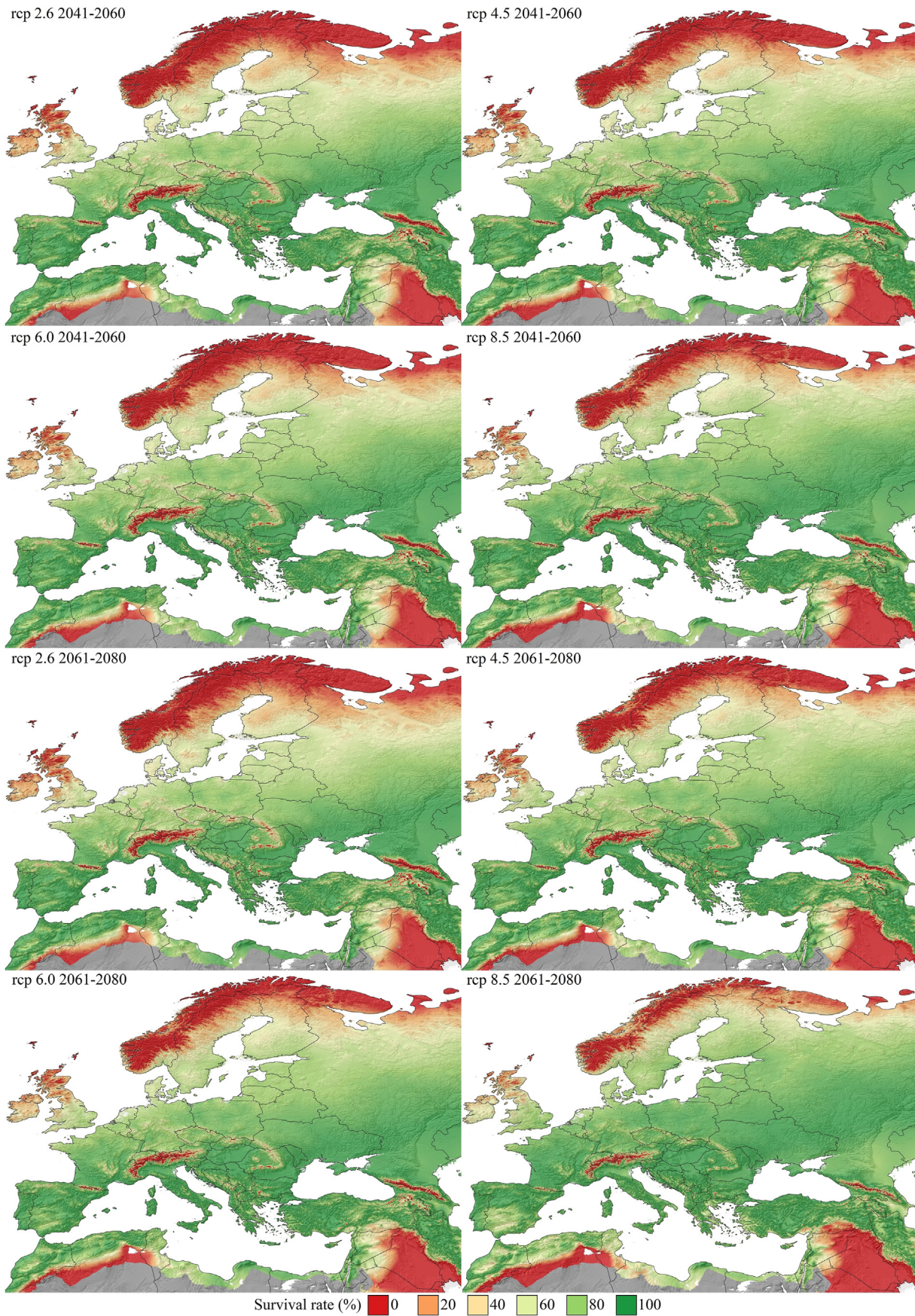rcp 8.5 2061-2080

Survival rate (%) 0 20 40 60 80 100

Figure 10. The averaged potential future (2041–2060 and 2061–2080) survival rates of *Ae. aegypti* according to the warmest quarter's mean temperatures and based on the BCC-CSM1.1, CCSM4.0, IPSL-CM5A-LR and MRI-CGCM3 climate models. Grey areas mark the territories where bio12 < 55mm.

range of *Ae. aegypti* in the Crimean Peninsula, Southwest Russia, West Georgia, and Northeast Turkey contradicts the perceptions about the occurrence patterns of the Mediterranean mosquito species which generally has a wide and continuous distribution area in South Europe (Trájer and Padisák, 2019). There are also exotic, invasive aedine mosquito species, like *Ae. albopictus* that have a wide range extending from Spain to Greece in the northern Mediterranean region (Brugman, 2016). Both the modelled suitability and development time values showed that the climate of the Iberian ports of the Balearic and Alboran Seas is more favourable for *Ae. aegypti* than, e.g., the ports of the Ligurian Sea. This finding is in accordance with the results of Da Re et al. (2021) who suggested that Algeciras and Barcelona are more suitable areas for the species establishment than, e.g., Genoa. Considering the modelled highest (93% ≤) suitability value areas of *Ae. aegypti* in the present study, it can be found that it follows the range of the Mediterranean mosquito fauna modelled by Trájer (2021). It can be stated that the current European climate can support the invasion of *Ae. aegypti* in South Europe. However, in contrast to the findings of Liu-Helmersson et al. (2019), it is not limited to only small coastal areas, but it has a wider potential range including, e.g., large regions in the Southern Iberian Peninsula, in the lowlands of the Apennine Peninsula and even in the northern regions of the Balkans.

In other words, it is very plausible that *Ae. aegypti* could be present in the low and mid-elevation level areas of the Mediterranean countries. The survival rate of the mosquito to adulthood indicates that this factor may have a distribution limiting role in the more continental and Atlantic climate regions of Europe. The effect of future warming seems to be not generally favourable for *Ae. aegypti* because the future hot summer conditions may have a negative impact on the survival rate of the mosquito in the southernmost areas of Europe. It is not known how the presence of *Ae. albopictus* can modify the present and the potential future occurrence of *Ae. aegypti* in the Mediterranean Basin. Evidence suggests that the Asian tiger mosquito is among the notable competitors of *Ae. aegypti* (Juliano et al., 2004). In South Florida, Juliano et al. (2004) found that interspecific competition among the larvae of the two congeneric mosquito species seems to be a viable explanation for exclusion or reduction of *Ae. aegypti*. However, it cannot be the cause of the presently observed differences in the European distributions of the two mosquitos because *Ae. aegypti* disappeared earlier from southern Europe in the mid-20th century (Schaffner and Mathis, 2014) whereas *Ae. albopictus* started to spread in the same area in the second half of the 20th century (Scholte and Schaffner, 2007). A study showed that the presence of other aedine mosquito species has a significant positive effect on mortality of the immature stages of *Ae. albopictus*, but not *Ae. aegypti* (Farjana et al., 2012). Lounibos et al. (2002) also found that the larvae of *Ae. albopictus* are more sensitive to species/density variables than the ontogeny stages of *Ae. aegypti*. In addition, they found that the high larval density of its own species notably decreases the rate of the development of *Ae. aegypti* females which can be a self-control mechanism preventing the breeding waters from overpopulation. In contrast, Reiskind and Lounibos (2009) found significant negative effects of competition on adult longevity in the case of *Ae. aegypti*, but not in the Asian tiger mosquito. These observations suggest that the interspecific competition between the two species exists, but interspecific competition cannot explain the current absence of *Ae. aegypti* in southern Europe.

In fact, the present, partly overlapping global occurrences of *Ae. aegypti* and *Ae. albopictus* (Kraemer et al., 2015) confirm that the presence of one species does not preclude the other. Indeed, the comparison of the estimated potential range of *Ae. aegypti* and *Ae. albopictus* in the United States in 2017 (CDC, 2018) suggests that *Ae. aegypti* is more sensitive to low winter temperatures than the Asian tiger mosquito. This presumption is supported by field experiments. Chang et al. (2007) found that *Ae. aegypti* larvae had a significantly higher mortality rate which can be observed in the case of *Ae. albopictus* during winter cold fronts. However, a contradictory observation also exists related to the winter cold sensitivity of *Ae. aegypti*. Kraemer et al. (2020) showed that cold winter may

not be the preventing factor for the re-establishment of the dengue vector *Ae. aegypti* in southern Europe because e.g., *Ae. aegypti* eggs can survive at -6 °C for up to 2 days. It should be emphasized, that this value may suggest a better ecological (not physiological) cold adaptation that at first consideration would be hypothesized. For example, in Sochi where *Ae. aegypti* is present (Ganushkina et al., 2016), the daily minimum temperatures dropped below 4 times under -8.1 °C and 19 times under -5.3 °C in 2000–2012 (KNMI Climate Explorer data; Trouet and Van Oldenborgh, 2013). It should also be mentioned that Sochi can be found directly at the Black Sea coast, which geographical position indicates relatively balanced local climatic conditions. However, in the pre-DDT era, *Ae. aegypti* was reported from many more continental cities of the Caucasus like Kutaisi (Imereti region, West Georgia) and Tbilisi (Capital region, Southeast Georgia) (Ganushkina et al., 2016).

Both the modelled future potential suitability patterns and the development time of the mosquito shows notable future changes in the models. In agreement with the results of Liu-Helmersson et al. (2019), the future European infestation of Ae. aegypti depends on the level of global warming, which is clearly seen when comparing model results based on the rcp2.6 and rcp8.5 scenarios-based model results or the model outcomes of the 2041–2060 and 2061–2080 periods based on the same kind of emission scenarios. What is an important finding, the development time of the mosquito based on the indicator value could not deviate notably from the present-day conditions in 1880–1934 when the mosquito was present along the Mediterranean coasts (Schaffner and Mathis, 2014). However, it should be noted that the development time showed an elongation trend between 1860-1879 and 1920–1934 which may contribute to the easier eradication of the mosquito in the 1930s–1940s. The results of (Kotsakiozi et al., 2018) are related to the phylogeny of the eastern Black Sea populations of *Ae. aegypti* requires the reinterpretation of the modelling of the possible future distribution of the species in Europe. This is because the eastern Black Sea populations of the mosquito species represent not only a local strain within the global population of the species but also the survivors of the former Mediterranean ecotype which has previously adapted to the climate of the northern part of the Mediterranean Basin. Another warning sign is that, due to the geographical features of the site, the Black Sea areas of the species are located very close to each other in temperate and continental climates. This may allow the species to adapt to more extreme climatic conditions.

The applied approach was somewhat like that was applied by Da Re et al. (2021) who investigated the adult female abundance of *Ae. aegypti* in ports, namely in Algeciras, Barcelona, Venice, Genoa, and Rotterdam. The utilization of container ports as study sites can be justified by the fact that these ports are the hotspots for propagules of invasive, alien species (Da Re et al., 2021). It should not be forgotten, that a few centuries ago, the species evolved from a human-avoiding mosquito to one of the most important, globally significant vector species (Powell and Tabachnick, 2013), and on the other hand, it moved from its original tropical habitat to the temperate belt with human assistance and adapted to the cooler and sometimes drier environments with great success. It follows that — based on the presumed tropical African distribution of the mosquito 500 years ago — the model results plausibly would not be able to display the current occurrence of the species in the temperate belt. However, the recent findings suggest that the environmental adaptation capacity of the species is greater than previously assumed. For example, in 2016, August, *Ae. aegypti* was also recorded at the southern coast of the Crimean Peninsula after a 50-year long absence (Ganushkina et al., 2020). In the case of the Black Sea coastal areas, the mitigating role of the seawater in temperature variability is an important climatic factor. Investigating the 34-year period (1982–2015) surface seawater temperatures of the Black Sea, Sakalli and Başusta (2018) found that this value is the highest at the eastern coastal areas of the Black Sea (mean annual temperature is 16.0–16.5 °C) where the mosquito presently occurs. The authors predict that surface seawater temperatures will overwhelm the 16 °C value almost in the entire Black Sea for the period 2031–2060 (except for the

Sea of Azov and the Gulf of Odessa) and in the entire area of the sea for 2071–2100. These predicted changes are in good agreement with the modelled increases in the suitability and the completion of embryogenesis time values in the north Black Sea regions.

It should also be noted that the climate adaptability of *Ae. aegypti* can also be influenced by the anthropogenic environmental changes-triggered alteration of their beneficial microbiota because the change of the microbial midgut communities can substantially alter both the physiology and the vector competence of mosquitoes (Onyango et al., 2020). Similar observations were made in the case of *Ae. albopictus* and *Aedes (Hulecoeteomyia) koreicus* (Edwards, 1917) (Alfano et al., 2019; Guégan et al., 2018). Midgut bacterial symbionts influence such substantial metabolic, physiological, and reproductive factors as folate biosynthesis and energy storage, the modulation of immune responses, protection from parasites, and the transmission of pathogens and mating (Romoli et al., 2020; Hegde et al., 2020; Möhlmann et al., 2020; Novakova et al., 2017; Engel and Moran, 2013). Temperature plays a very important role in shaping mosquito-borne arbovirus transmission (Bellone and Failloux, 2020). Due to their specific and different thermal sensitivity, midgut microbial symbionts play important role in thermal adaptation and consequently, role in the survival and the adaptation of insects against environmental fluctuations (Wernegreen, 2012; Zilberrosenberg and Rosenberg, E, 2008; Dillon and Dillon, 2004; Breznak, 1982). These facts indicate that further studies are needed to predict the expected occurrence of vector species in the future based on the integration of the potential impact of climatic alterations on mosquito microbiota.

5. Conclusion

The geographical patterns of climatic suitability, development time, and survival rate values modelled for the second half of the 19th century, the early 20th century, 1960–1990 and 1979–2013 do not differ notably in the Mediterranean area. It is paradoxical situation that while currently *Ae. aegypti* do not occur in the Mediterranean but persist in the Black Sea region, the climatic conditions along the Black Sea coasts are less suitable for this mosquito than in several coastal areas of southern Europe. These results suggest that the current absence of *Ae. aegypti* in the Mediterranean is primarily due to non-climatic reasons. The present-day Mediterranean ports could also serve as sites with appropriate climates to become the source of the future spread of the mosquito. The Black Sea populations should be surveyed to observe in time the starting westward spread of the species because this ecotype – as the survivor of the former pan-Mediterranean populations – was adapted to the Mediterranean conditions better than any other populations of *Ae. aegypti* in the world.

The main outcomes of the study can be summarized as follows:

- There is no climatic reason for the present lack of *Ae. aegypti* in the Mediterranean.
- Apart from the southernmost areas of the Mediterranean region, all the modelled factors predict the increasing suitability of Southern Europe, especially of the sub-Mediterranean ecoregion for *Ae. aegypti* in the 21st century.
- The coasts of the Black Sea can serve as a starting area for the spread of *Ae. aegypti* in the future.

Declarations

Author contribution statement

Attila J. Trájer: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Data availability statement

Data included in article/supplementary material/referenced in article.

Declaration of interests statement

The authors declare no conflict of interest.

Additional information

Supplementary content related to this article has been published online at https://doi.org/10.1016/j.heliyon.2021.e07981.

References

Akiner, M.M., Demirci, B., Giorgi Babuadze, V.R., Schaffner, F., 2016. Spread of the invasive mosquitoes *Aedes aegypti* and *Aedes albopictus* in the Black Sea region increases risk of chikungunya, dengue, and Zika outbreaks in Europe. PLoS Neglected Trop. Dis. 10, e0004664.

Akiner, M.M., Demirci, B., Bedir, H., Öztürk, M., Demirtaş, R., Doğan, A.F., Gökdemir, A., Topluoğlu, S., Altuğ, Ü., Kurtcebe, Z.Ö., Irmak, H., 2018. Surveillance and control of invasive *Aedes* species in the Eastern Black Sea area of Turkey. Turk Hij. Ve Deney. Biyol. Derg., Turk. Bull. Hyg. Exp. Biol. 75, 225–238.

Alaniz, A.J., Bacigalupo, A., Cattan, P.E., 2017. Spatial quantification of the world population potentially exposed to Zika virus. Int. J. Epidemiol. 46, 966–975.

Alfano, N., Tagliapietra, V., Rosso, F., Manica, M., Arnoldi, D., Pindo, M., Rizzoli, A., 2019. Changes in microbiota across developmental stages of *Aedes koreicus*, an invasive mosquito vector in Europe: indications for microbiota-based control strategies. Front. Microbiol. 10, 2832.

Bayoh, M.N., Lindsay, S.W., 2004. Temperature-related duration of aquatic stages of the Afrotropical malaria vector mosquito *Anopheles gambiae* in the laboratory. Med. Vet. Entomol. 18, 174–179.

Beck, H.E., Zimmermann, N.E., McVicar, T.R., Vergopolan, N., Berg, A., Wood, E.F., 2018. Present and future Köppen-Geiger climate classification maps at 1-km resolution. Sci. Data 5, 1–12.

Black IV, W.C., Bennett, K.E., Gorrochótegui-Escalante, N., Barillas-Mury, C.V., Fernández-Salas, I., de Lourdes Muñoz, M., Farfán-Alé, J.A., Olson, K.E., Beaty, B.J., 2002. Flavivirus susceptibility in *Aedes aegypti*. Arch. Med. Res. 33, 379–388.

Breznak, J.A., 1982. Intestinal microbiota of termites and other xylophagous insects. Annu. Rev. Microbiol. 36, 323–343.

Brooks, G.D., Shoof, H.F., Smith, E.A., 1966. Evaluation of five formulations of abate against *Aedes aegypti*, Savannah, Georgia, 1965. Mosq. News 26, 580–582.

Brugman, V., 2016. Host Selection and Feeding Preferences of Farm-Associated Mosquitoes (Diptera: Culicidae) in the United Kingdom. Doctoral dissertation. London School of Hygiene & Tropical Medicine.

Cabrera, C.V.P., Selvaraj, J.J., 2020. Geographic shifts in the bioclimatic suitability for *Aedes aegypti* under climate change scenarios in Colombia. Heliyon 6, e03101.

Calado, D.C., da Silva, M.A., 2002. Evaluation of the temperature influence on the development of *Aedes albopictus*. Rev. Saude Publica 36, 173–179.

Caminade, C., Ndione, J.A., Kebe, C.M.F., Jones, A.E., Danuor, S., Tay, S., Tourre, Y.M., Lacaux, J.-P., Vignolles, C., Duchemin, J.B., Jeanne, I., Morse, A.P., 2011. Mapping Rift Valley fever and malaria risk over West Africa using climatic indicators. Atmos. Sci. Lett. 12, 96–103.

Campbell, L.P., Luther, C., Moo-Llanes, D., Ramsey, J.M., Danis-Lozano, R., Peterson, A.T., 2015. Climate change influences on global distributions of dengue and chikungunya virus vectors. Philos. Trans. R. Soc. Lond. B Biol. Sci. 370, 20140135.

Cardamatis, J.P., 1929. La dengue en Grèce. Bull. Soc. Pathol. Exot. 22, 272–292.

CDC, 2018. Centers for Disease Control and Prevention. (2018). ESTIMATED Potential Range of *Aedes aegypti* and *Aedes albopictus* in the United States, 2017. URL: https://www.cdc.gov/zika/pdfs/zika-mosquito-maps.pdf. (Accessed 6 August 2021).

Chang, L.H., Hsu, E.L., Teng, H.J., Ho, C.M., 2007. Differential survival of *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae) larvae exposed to low temperatures in Taiwan. J. Med. Entomol. 44, 205–210.

Chouin-Carneiro, T., Vega-Rua, A., Vazeille, M., Yebakima, A., Girod, R., Goindin, D., Dupont-Rouzeyrol, M., Lourenço-de-Oliveira, R., Failloux, A.B., 2016. Differential susceptibilities of *Aedes aegypti* and *Aedes albopictus* from the Americas to Zika virus. PLoS Neglected Trop. Dis. 10, e0004543.

Cunze, S., Koch, L.K., Kochmann, J., Klimpel, S., 2016. *Aedes albopictus* and *Aedes japonicus*-two invasive mosquito species with different temperature niches in Europe. Parasites Vectors 9, 1–12.

Curtin, T.J., 1967. Status of *Aedes aegypti* in the eastern mediterranean. J. Med. Entomol. 4, 48–50.

Da Re, D., Montecino-Latorre, D., Vanwambeke, S.O., Marcantonio, M., 2021. Will the yellow fever mosquito colonise Europe? Assessing the re-introduction of *Aedes aegypti* using a process-based population dynamical model. Ecol. Inf. 61, 101180.

Damos, P., Savopoulou-Soultani, M., 2012. Temperature-driven Models for Insect Development and Vital thermal Requirements. Psyche 2012.

Davidson, J., 1944. On the relationship between temperature and rate of development of insects at constant temperatures. J. Anim. Ecol. 13, 26–38.

de Lima-Camara, T.N., Honório, N.A., Lourenço-de-Oliveira, R., 2007. Parity and ovarian development of *Aedes aegypti* and *Ae. albopictus* (Diptera: Culicidae) in metropolitan Rio de Janeiro. J. Vector Ecol. 32, 34–40.

de Lima-Camara, T.N., Lima, J.B.P., Bruno, R.V., Peixoto, A.A., 2014. Effects of insemination and blood-feeding on locomotor activity of *Aedes albopictus* and *Aedes aegypti* (Diptera: Culicidae) females under laboratory conditions. Parasites Vectors 7, 304.

Delatte, H., Gimonneau, G., Triboire, A., Fontenille, D., 2009. Influence of temperature on immature development, survival, longevity, fecundity, and gonotrophic cycles of *Aedes albopictus*, vector of chikungunya and dengue in the Indian Ocean. J. Med. Entomol. 46, 33–41.

Dickens, B.L., Sun, H., Jit, M., Cook, A.R., Carrasco, L.R., 2018. Determining environmental and anthropogenic factors which explain the global distribution of *Aedes aegypti* and *Ae. albopictus*. BMJ Glob. Health 3, e000801.

Dillon, R.J., Dillon, V.M., 2004. The gut bacteria of insects: nonpathogenic interactions. Annu. Rev. Entomol. 49, 71–92.

Donnelly, J.W., 1993. *Aedes aegypti* in New Jersey. J. Am. Mosq. Contr. Assoc. 9, 238-238.

Dufresne, J.L., Foujols, M.-A., Denvil, S., Caubel, A., Marti, O., Aumont, O., Balkanski, Y., Bekki, S., Bellenger, H., Benshila, R., Bony, S., Bopp, L., Braconnot, P., Brockmann, P., Cadule, P., Cheruy, F., Codron, F., Cozic, A., Cugnet, D., de Noblet, N., Duval, J.-P., Ethé, C., Fairhead, L., Fichefet, T., Flavoni, S., Friedlingstein, P., Grandpeix, J.-Y., Guez, L., Guilyardi, E., Hauglustaine, D., Hourdin, F., Idelkadi, A., Ghattas, J., Joussaume, S., Kageyama, M., Krinner, G., Labetoulle, S., Lahellec, A., Lefebvre, M.-P., Lefevre, F., Levy, C., Li, Z.X., Lloyd, J., Lott, F., Madec, G., Mancip, M., Marchand, M., Masson, S., Meurdesoif, Y., Mignot, J., Musat, I., Parouty, S., Polcher, J., Rio, C., Schulz, M., Swingedouw, D., Szopa, S., Talandier, C., Terray, P., Viovy, N., Vuichard -Show, N., 2013. Climate change projections using the IPSL-CM5 Earth system model: from CMIP3 to CMIP5. Clim. Dynam. 40, 2123–2165.

Engel, P., Moran, N.A., 2013. The gut microbiota of insects–diversity in structure and function. FEMS Microbiol. Rev. 37, 699–735.

Farjana, T., Tuno, N., Higa, Y., 2012. Effects of temperature and diet on development and interspecies competition in *Aedes aegypti* and *Aedes albopictus*. Med. Vet. Entomol. 26, 210–217.

Farnesi, L.C., Martins, A.J., Valle, D., Rezende, G.L., 2009. Embryonic development of *Aedes aegypti* (Diptera: Culicidae): influence of different constant temperatures. Mem. Inst. Oswaldo Cruz 104, 124–126.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315.

Fontenille, D., Diallo, M., Mondo, M., Ndiaye, M., Thonnon, J., 1997. First evidence of natural vertical transmission of yellow fever virus in *Aedes aegypti*, its epidemic vector. Trans. R. Soc. Trop. Med. Hyg. T. Roy. Soc. Trop. Med. H. 91, 533–535.

Ganushkina, L.A., Tanygina, E., Bezzhonova, O.V., Sergiev, V.P., 2012. Detection of *Aedes (Stegomyia) albopictus* skus. Mosquitoes in the Russian federation. Meditsinskaia Parazitologiia i Parazitarnye Bolezni 2012, 3–4.

Ganushkina, L.A., Patraman, I.V., Rezza, G., Migliorini, L., Litvinov, S.K., Sergiev, V.P., 2016. Detection of *Aedes aegypti, Aedes albopictus,* and *Aedes koreicus* in the area of Sochi, Russia. Vector Borne Zoonotic Dis. 16, 58–60.

Ganushkina, L., Lukashev, A., Patraman, I., Razumeyko, V., Shaikevich, E., 2020. Detection of the invasive mosquito species *Aedes (Stegomyia) aegypti* and *Aedes (Hulecoeteomyia) koreicus* on the southern coast of the Crimean peninsula. J. Arthropod Borne Dis. 14, 270–276.

Gent, P.R., Danabasoglu, G., Donner, L.J., Holland, M.M., Hunke, E.C., Jayne, S.R., Lawrence, D.M., Neale, R.B., Rasch, P.J., Vertenstein, M., Worley, P.H., Yang, Z.-L., Minghua Zhang, M., 2011. The community climate system model version 4. J. Clim. 24, 4973–4991.

Guégan, M., Minard, G., Tran, F.H., Tran Van, V., Dubost, A., Valiente Moro, C., 2018. Short-term impacts of anthropogenic stressors on *Aedes albopictus* mosquito vector microbiota. FEMS Microbiol. Ecol. 94, fiy188.

Guerbois, M., Fernandez-Salas, I., Azar, S.R., Danis-Lozano, R., Alpuche-Aranda, C.M., Leal, G., Garcia-Malo, I.R., Diaz-Gonzalez, E.E., Casas-Martinez, C., Rossi, S.L., Del Río-Galván, S.L., Sanchez-Casas, R.M., Roundy, C.M., Wood, T.G., Widen, S.G., Vasilakis, N., Weaver, S.C., 2016. Outbreak of Zika virus infection, Chiapas State, Mexico, 2015, and first confirmed transmission by *Aedes aegypti* mosquitoes in the Americas. J. Infect. Dis. 214, 1349–1356.

Hegde, S., Voronin, D., Casas-Sanchez, A., Saldaña, M.A., Heinz, E., Acosta-Serrano, A., Popov, V.L., Chopra, A.K., Hughes, G.L., 2020. Gut-associated bacteria invade the midgut epithelium of Aedes aegypti and stimulate innate immunity and suppress Zika virus infection in cells. bioRxiv 866897.

Helinski, M.E., Valerio, L., Facchinelli, L., Scott, T.W., Ramsey, J., Harrington, L.C., 2012. Evidence of polyandry for *Aedes aegypti* in semifield enclosures. Am. J. Trop. Med. Hyg. 86, 635–641.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.

Holstein, M., 1967. Dynamics of *Aedes aegypti* distribution, density and seasonal prevalence in the Mediterranean area. Bull. World Health Organ. 36, 541.

Juliano, S.A., Lounibos, L.P., O'Meara, G.F., 2004. A field test for competitive effects of *Aedes albopictus* on *A. aegypti* in South Florida: differences between sites of coexistence and exclusion? Oecologia 139, 583–593.

Kamal, M., Kenawy, M.A., Rady, M.H., Khaled, A.S., Samy, A.M., 2018. Mapping the global potential distributions of two arboviral vectors *Aedes aegypti* and *Ae. albopictus* under changing climate. PloS One 13, e0210122.

Khormi, H.M., Kumar, L., 2014. Climate change and the potential global distribution of *Aedes aegypti*: spatial modelling using geographical information system and CLIMEX. Geospat. Health 405–415.

Koenraadt, C.J.M., Harrington, L.C., 2008. Flushing effect of rain on container-inhabiting mosquitoes *Aedes aegypti* and *Culex pipiens* (Diptera: Culicidae). J. Med. Entomol. 45, 28–35.

Kotsakiozi, P., Gloria-Soria, A., Schaffner, F., Robert, V., Powell, J.R., 2018. *Aedes aegypti* in the Black Sea: recent introduction or ancient remnant? Parasites Vectors 11, 1–13.

Kraemer, M.U., Sinka, M.E., Duda, K.A., Mylne, A.Q., Shearer, F.M., Barker, C.M., Moore, C.G., Carvalho, R.G., Coelho, G.E., Van Bortel, W., Hendrickx, G., Schaffner, F., Elyazar, I.R.F., Teng, H.-J., Brady, O.J., Messina, J.P., Pigott, D.M., Scott, T.W., Smith, D.L., Wint, G.R.W., Golding, N., Hay, S.I., 2015. The global distribution of the arbovirus vectors *Aedes aegypti* and *Ae. albopictus*. elife 4, e08347.

Kraemer, I.M., Kreß, A., Klingelhöfer, D., Scherer, C., Phuyal, P., Kuch, U., Ahrens, B., Groneberg, D.A., Dhimal, M., Müller, R., 2020. Does winter cold really limit the dengue vector *Aedes aegypti* in Europe? Parasites Vectors 13, 1–13.

Lacour, G., 2016. Eco-physiological mechanisms and adaptive value of egg diapause in the invasive mosquito *Aedes albopictus* (Diptera: Culicidae). Belgium. Royal Belg. Inst. Nat. Sci. Dissertation, Prom.: Hance, Thierry http://hdl.handle.net/2078.1/175328.

Leta, S., Beyene, T.J., De Clercq, E.M., Amenu, K., Kraemer, M.U., Revie, C.W., 2018. Global risk mapping for major diseases transmitted by *Aedes aegypti* and *Aedes albopictus*. Int. J. Infect. Dis. 67, 25–35.

Liu-Helmersson, J., Quam, M., Wilder-Smith, A., Stenlund, H., Ebi, K., Massad, E., Rocklöv, J., 2016. Climate change and *Aedes vectors*: 21st century projections for dengue transmission in Europe. EBioMedicine 7, 267–277.

Long, K.C., Ziegler, S.A., Thangamani, S., Hausser, N.L., Kochel, T.J., Higgs, S., Tesh, R.B., 2011. Experimental transmission of Mayaro virus by *Aedes aegypti*. Am. J. Trop. Med. Hyg. 85, 750–757.

Louis, C., 2012. Daily newspaper view of dengue fever epidemic, Athens, Greece, 1927–1931. Emerg. Infect. Dis. 18, 78–82.

Lounibos, L.P., 1981. Habitat segregation among African treehole mosquitoes. Ecol. Entomol. 6, 129–154.

Lounibos, L.P., Suárez, S., Menéndez, Z., Nishimura, N., Escher, R.L., O Connell, S.M., Rey, J.R., 2002. Does temperature affect the outcome of larval competition between *Aedes aegypti* and *Aedes albopictus*? J. Vector Ecol. 27, 86–95.

Luterbacher, J., Dietrich, D., Xoplaki, E., Grosjean, M., Wanner, H., 2004. European seasonal and annual temperature variability, trends, and extremes since 1500. Science 303, 1499–1503.

Ly-Tall, M., 1984. The Decline of the Mali empire. Niane 172–186.

Margarita, Y.S.G.A., Grácio, A.J., Lencastre, I., Silva, A.C., Novo, M.T., Sousa, C.A., 2006. First record of *Aedes (Stegomyia) aegypti* (Linnaeus, 1762) (Diptera, Culicidae) in Madeira island-Portugal. Acta Parasitol. 13, 59–61.

Mattingly, P.F., 1967. Taxonomy of *Aedes aegypti* and related species. Bull. World Health Organ. 36, 552–554.

McBride, C.S., Baier, F., Omondi, A.B., Spitzer, S.A., Lutomiah, J., Sang, R., Ignell, R., Vosshall, L.B., 2014. Evolution of mosquito preference for humans linked to an odorant receptor. Nature 515, 222–227.

Möhlmann, T.W., Vogels, C.B., Göertz, G.P., Pijlman, G.P., Ter Braak, C.J., Te Beest, D.E., Hendriks, M., Nijhuis, E.H., Warris, S., Drolet, B.S., van Overbeek, L., Koenraadt, C.J.M., 2020. Impact of gut bacteria on the infection and transmission of pathogenic arboviruses by biting midges and mosquitoes. Microb. Ecol. 80, 703–717.

Montini, P., De Majo, M.S., Fischer, S., 2021. Delayed mortality effects of cold fronts during the winter season on *Aedes aegypti* in a temperate region. J. Therm. Biol. 95, 102808.

Mori, A., Wada, Y., 1977. The gonotrophic cycle *of Aedes albopictus* in the field. Trop. Med. 19, 141–146.

Morlan, H.B., Hayes, R.O., 1958. Urban dispersal and activity of *Aedes aegypti*. Mosq. News 18, 137–144.

Mousson, L., Dauga, C., Garrigues, T., Schaffner, F., Vazeille, M., Failloux, A.B., 2005. Phylogeography of *Aedes (Stegomyia) aegypti* (L.) and *Aedes (Stegomyia) albopictus* (Skuse) (Diptera: Culicidae) based on mitochondrial DNA variations. Genet. Res. 86, 1–11.

Novakova, E., Woodhams, D.C., Rodríguez-Ruano, S.M., Brucker, R.M., Leff, J.W., Maharaj, A., Amir, A., Knight, R., Scott, J., 2017. Mosquito microbiome dynamics, a background for prevalence and seasonality of West Nile virus. Front. Microbiol. 8, 526.

Onyango, G.M., Bialosuknia, M.S., Payne, F.A., Mathias, N., Ciota, T.A., Kramer, D.L., 2020. Increase in temperature enriches heat tolerant taxa in *Aedes aegypti* midguts. Sci. Rep. 10, 1–12.

Oter, K., Gunay, F., Tuzer, E., Linton, Y.M., Bellini, R., Alten, B., 2013. First record of *Stegomyia albopicta* in Turkey determined by active ovitrap surveillance and DNA barcoding. Vector Borne Zoonotic Dis. 13, 753–761.

Porse, C.C., Kramer, V., Yoshimizu, M.H., Metzger, M., Hu, R., Padgett, K., Vugia, D.J., 2015. Public health response to *Aedes aegypti* and *Ae. albopictus* mosquitoes invading California, USA. Emerg. Infect. Dis. 21, 1827–1829.

Powell, J.R., Tabachnick, W.J., 2013. History of domestication and spread of *Aedes aegypti*-a review. Mem. Inst. Oswaldo Cruz 108, 11–17.

Powell, J.R., Gloria-Soria, A., Kotsakiozi, P., 2018. Recent history of *Aedes aegypti*: vector genomics and epidemiology records. Bioscience 68, 854–860.

QGIS project, 2021. QGIS A Free and Open Source Geographic Information System. URL: QGIS project 2021.

Ramírez-Villegas, J., Bueno-Cabrera, A., 2009. Working with climate data and niche modeling: creation of bioclimatic variables. Int. Cent. Trop. Agricult. (CIAT), Cali, Columbia.

Rašić, G., Filipović, I., Callahan, A.G., Stanford, D., Chan, A., Lam-Phua, S.G., Huat Tan, C., Hoffmann, A.A., 2016. The queenslandensis and the type form of the dengue fever mosquito (*Aedes aegypti* L.) are genomically indistinguishable. PLoS Neglected Trop. Dis. 10, e0005096.

Reiskind, M.H., Lounibos, L.P., 2009. Effects of intraspecific larval competition on adult longevity in the mosquitoes *Aedes aegypti* and *Aedes albopictus*. Med. Vet. Entomol. 23, 62–68.

Ren, H.L., Wu, J., Zhao, C.B., Cheng, Y.J., Liu, X.W., 2016. MJO ensemble prediction in BCC-CSM1. 1 (m) using different initialization schemes. Atmos. Sci. Lett. 9, 60–65.

Riabova, T.E., Iunicheva, I., Markovich, N., Ganushkina, L.A., Orabeǐ, V.G., Sergiev, V.P., 2005. Detection of *Aedes* (*Stegomyia*) *aegypti* L. mosquitoes in Sochi city. Meditsinskaia Parazitologiia i Parazitarnye Bolezni 2005, 3–5.

Rogers, D.J., Hay, S.I., Suk, J., Semenza, J., Zeller, H., 2012. The climatic suitability for dengue transmission in continental Europe. Europ. Cent. Dise. Prevent. Cont. Techn. Rep. Stockholm Sweden iv–22.

Romoli, O., Schönbeck, J.C., Hapfelmeier, S., Gendrin, M., 2020. Bacteria contribute to mosquito development via folate biosynthesis and energy storage. bioRxiv 2019, 12.

Sakalli, A., Başusta, N., 2018. Sea surface temperature change in the Black Sea under climate change: a simulation of the sea surface temperature up to 2100. Int. J. Climatol. 38, 4687–4698.

Schaffner, F., Mathis, A., 2014. Dengue and dengue vectors in the WHO European region: past, present, and scenarios for the future. Lancet Infect. Dis. 14, 1271–1280.

Scholte, E.J., Schaffner, F., 2007. Waiting for the tiger: establishment and spread of the *Aedes albopictus* mosquito in Europe. In: Takken, W., Knols, B.G.J. (Eds.), Emerging Pests and Vector-Borne Diseases in Europe, 1. Wageningen Academic Publishers, pp. 1–241. Edition: 1, Chapter: 14.

Sikka, D.R., 1997. Desert climate and its dynamics. Curr. Sci. 72, 35–46.

Smith, W.W., Love, G.J., 1958. Winter and spring survival of *Aedes aegypti* in southwestern Georgia. Am. J. Trop. Med. Hyg. 7, 309–311.

Soper, F.L., 1967. *Aedes aegypti* and yellow fever. Bull. World Health Organ. 36, 521–527.

Stonis, J.R., Hill, S.R., Diškus, A., Auškalnis, T., 2014. What is new and most interesting about the Nepticulidae of the Crimea and Lithuania. In: Navickaitė, A., Diškus, A., Stonis, J.R.2014. (Eds.), Selected Abstracts and Papers of the First Baltic International Conference on Field Entomology and Faunistics. Edukologija Publishers, Vilnius, pp. 96–117.

Sweeney, K.J., Cantwell, M.A., Dorothy, J., 1988. Collection of *Aedes aegypti* and *A. albopictus* from Baltimore, Maryland. J. Am. Mosq. Contr. Assoc. 4, 381–382.

Tabachnick, W.J., 1991. Evolutionary genetics and arthropod-borne disease: the yellow fever mosquito. Am. Entomol. 37, 14–26.

Trájer, A.J., 2021. The potential persistence of ancient malaria through the Quaternary period in Europe. Quat. Int. 586, 1–13.

Trájer, A.J., Padisák, J., 2019. Exploration of the main types of biome-scale culicid entomofauna (Diptera: Culicidae) in Europe and its relationship to the occurrence of mosquito-borne arboviruses. Acta zool. Acad. Sci. Hung. 65, 299–322.

Trájer, A.J., Sebestyén, V., 2019. The changing distribution of *Leishmania infantum* Nicolle, 1908 and its Mediterranean sandfly vectors in the last 140 kys. Sci. Rep. 9, 1–15.

Trájer, A.J., Bede-Fazekas, Á., Hufnagel, L., Horváth, L., Bobvos, J., 2013. The effect of climate change on the potential distribution of the European *Phlebotomus* species. Appl. Ecol. Environ. Res. 11, 189–208.

Trájer, A., Hammer, T., Kacsala, I., Tánczos, B., Bagi, N., Padisák, J., 2017. Decoupling of active and passive reasons for the invasion dynamics of *Aedes albopictus* Skuse (Diptera: Culicidae): comparisons of dispersal history in the Apennine and Florida peninsulas. J. Vector Ecol. 42, 233–242.

Trouet, V., Van Oldenborgh, G.J., 2013. KNMI Climate Explorer: a web-based research tool for high-resolution paleoclimatology. Tree-Ring Res. 69, 3–13.

Tun-Lin, W., Burkot, T.R., Kay, B.H., 2000. Effects of temperature and larval diet on development rates and survival of the dengue vector *Aedes aegypti* in north Queensland, Australia. Med. Vet. Entomol. 14, 31–37.

Vega-Rúa, A., Zouache, K., Girod, R., Failloux, A.B., Lourenço-de-Oliveira, R., 2014. High level of vector competence of *Aedes aegypti* and *Aedes albopictus* from ten American countries as a crucial factor in the spread of Chikungunya virus. J. Virol. 88, 6294–6306. https://www.arca.fiocruz.br/handle/icict/11067.

Wernegreen, J.J., 2012. Mutualism meltdown in insects: bacteria constrain thermal adaptation. Curr. Opin. Microbiol. 15, 255–262.

Wiggins, K., Eastmond, B., Alto, B.W., 2018. Transmission potential of Mayaro virus in Florida *Aedes aegypti* and *Aedes albopictus* mosquitoes. Med. Vet. Entomol. 32, 436–442.

Xoplaki, E., Luterbacher, J., Paeth, H., Dietrich, D., Steiner, N., Grosjean, M., Wanner, H., 2005. European spring and autumn temperature variability and change of extremes over the last half millennium. Geophys. Res. Lett. 32, 4.

Yamashita, W.M., Das, S.S., Chapiro, G., 2018. Numerical modeling of mosquito population dynamics of *Aedes aegypti*. Parasites Vectors 11, 1–14.

Yang, C.F., Hou, J.N., Chen, T.H., Chen, W.J., 2014. Discriminable roles of *Aedes aegypti* and *Aedes albopictus* in establishment of dengue outbreaks in Taiwan. Acta Trop. 130, 17–23.

Yukimoto, S., Adachi, Y., Hosaka, M., Sakami, T., Yoshimura, H., Hirabara, M., Tanaka, T.Y., Shindo, E., Tsujino, H., Deushi, M., Mizuta, R., Yabu, S., Obata, A., Nakano, H., Koshiro, T., Ose, T., Kitoh, A., 2012. A new global climate model of the Meteorological Research Institute: MRI-CGCM3—model description and basic performance. J. Meteor. Soc. Japan. Ser. II 90, 23–64.

Yunicheva, Y.U., Ryabova, T.E., Markovich, N.Y., Bezzhonova, O.V., Ganushkina, L.A., Semenov, V.B., Tarkhov, G.A., Vasilenko, L.E., Guzeeva, T.M., Shevereva, T.V., Sergiev, V.P., 2008. First data on the presence of breeding populations of the *Aedes aegypti* L. mosquito in Greater Sochi and various cities of Abkhazia. Meditsinskaia Parazitologiia I Parazitarnye Bolezni 3, 40–43.

Zilber-Rosenberg, I., Rosenberg, E., 2008. Role of microorganisms in the evolution of animals and plants: the hologenome theory of evolution. FEMS Microbiol. Rev. 32, 723–735.