

EXPLORATION OF THE MAIN TYPES OF BIOME-SCALE
CULICID ENTOMOFAUNA (DIPTERA: CULICIDAE) IN EUROPE
AND ITS RELATIONSHIP TO THE OCCURRENCE
OF MOSQUITO-BORNE ARBOVIRUSES

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The investigation of the zoogeographical patterns of mosquito faunae and the transmitted arboviruses is an important task in the time of climate change. We aimed to characterize the possibly existing large-scale mosquito faunae in Europe and compare to the occurrence of mosquito-borne arboviruses. The zoogeography of 100 mosquito taxa was investigated in a country and territory-level distribution. Based on the result of hierarchical clustering, four main large-scale faunae were found in Europe: a Mediterranean, a transitional-insular, a continental and a boreal. Significant differences were found between the taxonomic compositions of the faunae in genus level. Climatic classes have no significant influence on the number of mosquito species of an area in Europe, but each of the faunae has climazonal range. The results revealed that *Culiseta* and *Ochlerotatus* species, those are less implicated in the transmission of human pathogenic agents, are characteristic to the mosquito fauna of the more humid and cold climate areas. In contrast, the diverse *Aedes*, *Anopheles* and *Culex* fauna is characteristic to the mesothermal climate areas. Based on the developed index, the mesothermal-microthermal climate affinity of a given fauna can be determined. The distribution of the mosquito-transmitted arboviruses can be partially correlated with the ranges of the faunae.

Keywords: temperate climate; vector-borne diseases; Mediterranean; Köppen-Geiger; mesothermal; microthermal

INTRODUCTION

Mosquitoes are the potential vectors of several human and veterinary infections causing a serious epidemiological hazard in many countries (HAYES & DOWNS 1980, HUBÁLEK & HALOUZKA 1999, GITHEKO *et al.* 2000, SZÉNÁSI *et al.* 2008, GENCHI *et al.* 2009). More than the one-third of the people of Earth live in malaria-endemic areas. Only this mosquito-borne disease infects more than 200 million and kills about 1 million children annually in each year, in the tropical and subtropical regions of sub-Saharan Africa, South Asia and Latin America (OLUPOT-OLUPOT & MAITLAND 2013, CAMINADE *et al.* 2014). The presence-absence status of the potential vectors predominantly determines the possibility of the occurrence of autochthon vector-borne diseases. While the

vector competence of the different mosquitoes somewhat overlaps with each other, it can usually be stated, that the composition of the mosquito fauna determines the geographical abundance of mosquito-borne diseases. For example, *Plasmodium falciparum* (Welch, 1897) theoretically can be transmitted in humans by females of about 70 anopheline mosquito species (MOLINA-CRUZ *et al.* 2016). Among them, *Anopheles gambiae* (Giles, 1902) is the most prevalent vectors of falciparum malaria, particularly in sub-Saharan Africa. This species and the other competent vectors of *P. falciparum* do not occur to North of the Mediterranean (SINKA *et al.* 2010), which restrict the distribution of this kind of malaria to the subtropical, tropical and equatorial climate areas of the world.

The life cycle and biogeography of mosquitoes are strongly mediated by climate (HAYES & DOWNS 1980, ALTO & JULIANO 2001). The range of many mosquito vectors and pathogens are limited to certain climatic zones or biomes. It is known that multiple environmental factors influence mosquito distribution across areas and mosquito diversity of individual habitats. Besides, the mosquito habitats nowadays are under strong human influence. For example, the size of the waters can influence the mosquito diversity of container habitats as the island biogeography theory suggest (WASHBURN 1995). CHAVES *et al.* (2011) found that the most heterogeneous landscapes harboring the largest mosquito diversity in urbanized areas. JOHNSON *et al.* (2008) proved that land use also has a strong influence on the species-richness of mosquito assemblages. The temporary changes of the mosquito fauna during the year are also a well-known fact. For example, the mosquito fauna is more diverse in the rainy than in the dry season in the Amazonian rain forests (JULIÃO *et al.* 2014). The best predictive factors of the distribution for different mosquito species are not uniform. For example, DIUK-WASSER *et al.* (2006) found that non-forested areas for *Culex pipiens*, surface water, and distance to estuaries for *Culex (Culex) salinarius* (Coquillett, 1904) are the best predictors of distribution. However, these factors explain only the local or medium-scale distribution of the mosquito species.

Climatic conditions have a strong influence on the large-scale range and abundance of insect species. The temperature was previously shown to be positively correlated with mosquito larvae abundance in Sweden (NILSSON & SVENSSON 1995). According to BEKETOV *et al.* (2014), temperature positively affects the number of mosquito larvae, but not the species-richness of the assemblages. BECK-JOHNSON *et al.* (2013) found that mosquito population abundance is more sensitive to temperature than previously thought because the dynamics of the juvenile mosquito stages are also strongly temperature-dependent. The January and July temperature and precipitation values played a key role in the determination of the distribution of vector sandflies. However, the January temperatures have a more important impact on the observed ranges in general (TRÁJER *et al.* 2013). Similar phenomena have been observed in the case of invasive mosquito species. For example, the primary distribution lim-

iting value of *Aedes albopictus* (Skuse, 1894) is the minimum temperature in January (T_{\min} should be more than about -2°C). In turn, the July precipitation also an important factor since *Ae. albopictus* prefers the relatively dry summers (precipitation in July is less than about 6 mm (TRÁJER *et al.* 2014). CAMINADE *et al.* (2012) also used solely climate variables to successfully model the recent and the predicted future distribution of *Ae. albopictus*. It should be noted, that the patterns of biome-scale vegetation areas, which follow the gradients of the climatic variables, also influence the environment and the edaphic factors. It means that the primarily non-climatic factors, like soil, land use, city structure, the available habitats or the natural vegetation, have also climatic background and climate-based zonation patterns. Due to this fact, the observed distribution of certain Mediterranean plant species can help the prediction of the potential distribution of vector arthropods (BEDE-FAZEKAS & TRÁJER 2013).

A relatively few studies were published in the topic of large-scale mosquito faunae. SINKA *et al.* (2012) investigated the global range of dominant malaria vectors by continents. They found five *Anopheles* faunae based on the dominant malaria vectors: four in the mesothermal and one in the microthermal climate regions. Interestingly, KISZEWSKI *et al.* (2004) found different fauna ranges when they studied the dominant malaria vectors of the Old Continent. They determined only three malaria vector faunae based on the dominant *Anopheles* species. Similar studies were not performed in the case of arbovirus vectors mosquito species or the total mosquito fauna of the countries.

In this paper, we aimed to (1) characterize the possibly existing biome-scale mosquito faunae in Europe; (2) determine the character species of the large-scale faunae; (3) determine which Köppen-Geiger climates can be associated with the found biome-scale mosquito faunae; (4) how can we determine the mesothermal/microthermal-related nature of a mosquito fauna using a simple index?

MATERIAL AND METHODS

Mosquito and arbovirus occurrence data

Mosquito occurrence data according to the 2011 status of the European mosquito fauna was derived from the software and database of the *Les moustiques d'Europe (The mosquitoes of Europe)* compiled by SCHAFFNER *et al.* (2001). The database was released on 8 June 2011 and was last updated on 10 October 2011. This database and identifier contain the distribution data of 100 mosquito species presents in Europe, both at the larval and adult stages in 37 geographical domains (counties and islands) of the continent. The database mainly includes the occurrences of the indigenous and some invasive species. It means that the database contains the distribution data of overall 100 mosquito species, but not all species were observed in each geographical unit. Data on diagnostic characters, mapped distribution, biology, medical interest, and bibliography are provided for each species. The resolution of the occurrence database primarily is in county-level, although it separately

contains the data of greater Mediterranean and Atlantic Ocean islands, too. The specific countries/territories were chosen because of the original areal resolution of the dataset. It was also important to handle separately the fauna of the islands from the mosquito fauna of the mainland countries.

The following geographical domains were used according to the original geographical distribution of the mapped dataset: Albania, Austria, Balearic Islands (Spain), Belgium, Bulgaria, Canary Islands (Spain), Corsica (France), Croatia, Czech Republic, Denmark, Estonia, Finland, the France mainland, Germany, the mainland of the United Kingdom, Greece (including the Aegean Islands, e.g. the Cyclades), Hungary, the mainland of Ireland and North Ireland (United Kingdom), the Italian mainland, Latvia, Lithuania, North Macedonia, Malta, Netherlands, Norway, Poland, the Portugal mainland, Romania, Sardinia (Italy), Serbia, Sicily (Italy), Slovakia, Slovenia, the Spanish mainland, Sweden and Switzerland. Table 1 shows the mosquito species which were involved in the study (the abbreviated forms of the species names were also included).

The European country-level occurrence data of mosquito-transmitted arthropod viruses were based on the work of CALZOLARI (2016).

Advantages and limitations of the used geographical distribution

In veterinary science and epidemiology, the depiction and study of country-wide, territory-wide resolution data are commonly used in the presentation of disease outbreaks and occurrences. This is because in many cases, the exact distribution of pathogens is not known in high resolution. It is also true for the distribution of several mosquito species. It means that such kind of data is suitable for such environmental modeling as climate envelope modeling. However, the area of most European countries does not cover more than two biomes due to their not too large west-east and north-south extension. Based on this fact, the country (and partly territory)-level mosquito data is suitable for biome-scale analyses. Since in the area of the countries can cover several climatic subclasses, both the dominant and the warmest climates were involved in the discriminant analyses.

Climate classification

To characterize the climate of Europe, the widely used Köppen–Geiger climate classification system was applied (KÖPPEN 1884, GEIGER 1961, RUBEL & KOTTEK 2011, 2010). In the Köppen climate system, temperate/mesothermal climates are defined as having an average temperature above -3 or 0°C in their coldest month but below 18°C . This group contains the Mediterranean climates (*Csa*, *Csb*), the humid subtropical climates (*Cfa*, *Cwa*), the oceanic/highland climates (*Cfb*, *Cfc*, *Cwb*, *Cwc*). Continental/microthermal climates are as follows: hot- and warm-summer humid continental climates (*Dsa*, *Dsb*, *Dwa*, *Dwb*, *Dfa*, *Dfb*), subarctic/boreal climates (*Dsc*, *Dsd*, *Dwc*, *Dwd*, *Dfc*, *Dfd*). The used Köppen–Geiger climate classification was based on the ‘Updated world map of the Köppen–Geiger climate classification’ of PEEL *et al.* (2007).

Statistics

For statistical analyses, the statistical tools of Wessa Free Statistics and Forecasting Software Package were used (WESSA 2012). For the comparison of the geographical do-

Table 1. The mosquito species involved in this study.

Genera	Subgenera	Species
<i>Aedes</i>	<i>Aedes</i>	<i>Aedes cinereus</i> (Meigen, 1818)
		<i>Aedes esoensis rossicus</i> (Dolbeskin, Gorickaja et Mitrofanova, 1930)
		<i>Aedes (Aedes) geminus</i> (Peus, 1970)
	<i>Aedimorphus</i>	<i>Aedes vexans vexans</i> (Meigen, 1830)
	<i>Fredwardsius</i>	<i>Aedes vittatus</i> (Bigot, 1861)
	<i>Stegomyia</i>	<i>Aedes aegypti</i> (Linnaeus, 1762)
		<i>Aedes albopictus</i> (Skuse, 1894)
		<i>Aedes cretinus</i> (Edwards, 1921)
	<i>Anopheles</i>	<i>Anopheles</i>
<i>Anopheles atroparvus</i> (Van Thiel, 1927)		
<i>Anopheles beklemishevi</i> (Stegnii et Kabanova, 1976)		
<i>Cellia</i>		<i>Anopheles cinereus</i> (Theobald, 1901)
		<i>Anopheles claviger</i> s. s. (Meigen, 1804)
		<i>Anopheles hyrcanus</i> (Pallas, 1771)
		<i>Anopheles labranchiae</i> (Falleroni, 1926)
		<i>Anopheles maculipennis</i> s. s. (Meigen, 1818)
		<i>Anopheles marteri</i> (Sévenet et Prunelle, 1927)
		<i>Anopheles melanoon</i> (Hackett, 1934)
		<i>Anopheles messae</i> (Falleroni, 1926)
		<i>Anopheles multicolor</i> (Camboulin, 1902)
		<i>Anopheles petragrani</i> (Del Vecchio, 1939)
		<i>Anopheles plumbeus</i> (Stephens, 1828)
		<i>Anopheles sacharovi</i> (Favre, 1903)
		<i>Anopheles sergentii sergentii</i> (Theobald, 1907)
		<i>Anopheles subalpinus</i> (Hackett et Lewis, 1935)
		<i>Anopheles superpictus</i> (Grassi, 1899)
<i>Coquillettidia</i>	<i>Coquillettidia</i>	<i>Coquillettidia richiardii</i> (Ficalbi, 1889)
		<i>Coquillettidia buxtoni</i> (Edwards, 1923)
<i>Culex</i>	<i>Barraudius</i>	<i>Culex modestus</i> (Ficalbi, 1889)
		<i>Culex pusillus</i> (Macquart, 1850)
	<i>Maillottia</i>	<i>Culex deserticola</i> (Kirkpatrick, 1924)
		<i>Culex hortensis hortensis</i> (Ficalbi, 1889)
		<i>Culex hortensis maderensis</i> (Mattingly, 1955)
	<i>Neoculex</i>	<i>Culex impudicus</i> (Ficalbi, 1890)
		<i>Culex martini</i> (Medschi, 1930)
<i>Culex mimeticus</i> (Noè, 1899)		

Table 1 (continued)

Genera	Subgenera	Species
<i>Culex</i>	<i>Neoculex</i>	<i>Culex territans</i> (Walker, 1856)
	<i>Culex</i>	<i>Culex brumpti</i> (Galliard, 1931)
		<i>Culex laticinctus</i> (Edwards, 1913)
		<i>Culex perexiguus</i> (Theobald, 1903)
		<i>Culex pipiens pipiens</i> Linnaeus, 1758
		<i>Culex theileri</i> Theobald, 1903
		<i>Culex torrentium</i> Martini, 1924
		<i>Culex tritaeniorhynchus</i> (Giles, 1901)
		<i>Culex vishnui</i> (Theobald, 1901)
		<i>Culiseta</i>
<i>Culiseta annulata</i> (Schrank, 1776)		
<i>Culiseta bergrothi</i> (Edwards, 1921)		
<i>Culiseta glaphyoptera</i> (Schiner, 1864)		
<i>Culisella</i>	<i>Culiseta fumipennis</i> (Stephens, 1825)	
	<i>Culiseta litorea</i> (Shute, 1928)	
<i>Allotheobaldia</i>	<i>Culiseta longiareolata</i> (Macquart, 1838)	
<i>Culicella</i>	<i>Culiseta morsitans</i> (Theobald, 1901)	
	<i>Culiseta ochroptera</i> (Peus, 1935)	
	<i>Culiseta subochrea</i> (Edwards, 1921)	
	<i>Ochlerotatus</i>	<i>Ochlerotatus</i>
<i>Ochlerotatus atropalpus</i> (Coquillett, 1902)		
<i>Ochlerotatus behningi</i> (Martini, 1926)		
<i>Ochlerotatus berlandi</i> (Séguy, 1921)		
<i>Ochlerotatus cantans</i> (Meigen, 1818)		
<i>Ochlerotatus caspius caspius</i> (Pallas, 1771)		
<i>Ochlerotatus cataphylla</i> (Dyar, 1916)		
<i>Ochlerotatus coluzzi</i> (Rioux, Guilvard et Pasteur, 1998)		
<i>Ochlerotatus communis</i> (De Geer, 1776)		
<i>Ochlerotatus cyprius</i> (Ludlow, 1919)		
<i>Ochlerotatus detritus</i> (Haliday, 1833)		
<i>Ochlerotatus dorsalis</i> (Meigen, 1830)		
<i>Ochlerotatus diantaeus</i> (Howard, Dyar et Knab, 1912)		
<i>Ochlerotatus euedes</i> (Howard, Dyar et Knab, 1912)		
<i>Ochlerotatus excrucians</i> (Walker, 1856)		
<i>Ochlerotatus exodontus exodontus</i> (Dyar, 1916)		
<i>Ochlerotatus flavescens</i> (Müller, 1764)		

Table 1 (continued)

Genera	Subgenera	Species	
<i>Ochlerotatus</i>	<i>Ochlerotatus</i>	<i>Ochlerotatus hungaricus</i> (Mihalyi, 1955)	
		<i>Ochlerotatus impiger impiger</i> (Walker, 1848)	
		<i>Ochlerotatus (Ochlerotatus) intrudens</i> (Dyar, 1919)	
		<i>Ochlerotatus leucomelas</i> (Meigen, 1804)	
		<i>Ochlerotatus mariae</i> (Sergent & Sergent, 1903)	
		<i>Ochlerotatus nigrinus</i> (Seckstein, 1918)	
		<i>Ochlerotatus nigripes</i> (Zetterstedt, 1838)	
		<i>Ochlerotatus pionips</i> (Dyar, 1919)	
		<i>Ochlerotatus pulcritarsis pulcritarsis</i> (Rondani, 1872)	
		<i>Ochlerotatus pullatus</i> (Coquillett, 1904)	
		<i>Ochlerotatus punctodes</i> (Dyar, 1922)	
		<i>Ochlerotatus punctor</i> Kirby, 1837	
		<i>Ochlerotatus quasirusticus</i> (Torres Canamares, 1951)	
		<i>Ochlerotatus riparius</i> (Dyar et Knab, 1907)	
		<i>Ochlerotatus (Ochlerotatus) sticticus</i> Meigen, 1838	
		<i>Ochlerotatus surcoufi</i> (Theobald, 1912)	
		<i>Ochlerotatus zamittii</i> (Theobald, 1903)	
		<i>Finlaya</i>	<i>Ochlerotatus eatoni</i> (Edwards, 1916)
			<i>Ochlerotatus echinus</i> (Theobald, 1901)
			<i>Ochlerotatus geniculatus</i> (Olivier, 1791)
		<i>Ochlerotatus gilcolladoi</i> (Sanchez-Cosiva, Rodriguez et Guillén, 1985)	
		<i>Ochlerotatus japonicus japonicus</i> (Theobald, 1901)	
		<i>Rusticoidus</i>	
	<i>Ochlerotatus lepidonotus</i> (Edwards, 1920)		
	<i>Ochlerotatus refiki</i> Medschid, 1928		
	<i>Ochlerotatus rusticus</i> Rossi, 1790		
	<i>Ochlerotatus subdiversus</i> (Martini, 1925)		
<i>Orthopodomyia</i>	<i>Orthopodomyia</i>	<i>Orthopodomyia pulcripalpis</i> (Rondani, 1872)	
<i>Uranotaenia</i>	<i>Pseudoficalbia</i>	<i>Uranotaenia unguiculata</i> Edwards, 1913	

main's mosquito fauna, we used a hierarchical cluster analysis with an information theory method (minimum pooled entropy in each new cluster) implemented in the Hierarchical Clustering – Free Statistics Software Calculator tool. To test the equality of the territory- and country-wide diversities of the adjacent large-scale mosquito fauna in genus level, instead of the Student's-test, the Wilcoxon Rank-Sum Test (Mann–Whitney U test) with continuity correction (unpaired) (WILCOXON *et al.* 1970) was used. The Mann–Whitney U test is a robust nonparametric test which can be used instead of the Student's t-test when the population cannot be assumed to be normally distributed. It requires two randomly selected, independent data populations and the Mann–Whitney U test is also less sensitive to

different sample sizes. The discriminant analyses were performed by PAST paleontological statistics software version 3.0 (HAMMER 1999).

RESULTS

The result of the hierarchical clustering

According to the hierarchical clustering, four large-scale fauna regions of European mosquitoes were determined. 1) The Mediterranean fauna covers the countries of the Iberian Peninsula, France, Italy, Albania, North Macedonia, Bulgaria, and Greece. 2) The continental mosquito fauna primarily inhabits the countries of Central and East Central Europe. 3) The boreal mosquito fauna can be found in the countries of Northeast and North Europe. 4) The transitional-insular fauna covers the countries of the British Islands, the Benelux states, Switzerland, Slovenia, and different Mediterranean islands. Both the Mediterranean and transitional-insular fauna covers such geographical domains where the main climates are mesothermal (temperate). Mesothermal climates are the hot-summer Mediterranean climate Cs_a , the warm-summer Mediterranean climate Cs_b , the humid subtropical climate Cw_a and the oceanic climate Cf_b according to the Köppen-Geiger climate classification. The continental and boreal fauna can be found in microthermal areas. The main climates in the geographical domains of the continental fauna are hot-summer and warm-summer humid continental climate Df_a and Df_b . In the land of the boreal fauna, the climate is Df_b and subarctic climate Df_c , although tundra climate ET also occurs in the most northern areas of the Scandinavian countries. The transitional-insular fauna either can be found between the Mediterranean and continental fauna in the continent or in the islands of the Mediterranean Sea. According to the covered climates, the Mediterranean and transitional-insular fauna can be classified as mesothermal, the continental and boreal fauna as microthermal climates according to the main climate categories of the Köppen-Geiger climate classification (Fig. 1).

The border between the mesothermal and microthermal mosquito fauna area extends between Bulgaria and Albania. In the West Mediterranean-Atlantic basin, this line stretches from the northern coasts of the Adriatic Sea to the British Isles in the southeast to northwest direction. The observed recent bordering patterns between the mesothermal and microthermal mosquito fauna areas is close to the border of the temperate-oceanic Cf_b , cool oceanic Cf_c and humid continental climates Df_a and the temperate Mediterranean climate Cs_b , temperate oceanic climates Cf_b . The boreal group covers also some of the areas where ET (tundra climate) occur that indicated the use of 'term' boreal instead of 'cold temperate'. Within the microthermal continental-boreal zone,

the border between the continental-boreal and boreal mosquito fauna also runs in the northwest to the southeast direction (Fig. 2).

The discriminant analysis according to the warmest Köppen-Geiger climate categories showed that Estonia, Finland, Latvia, Lithuania, Norway and Sweden which countries dominantly have $Df_{a,b}$ climates, form a well separated group. The $Cf_{a,b}$ and $Cs_{a,b}$ climate groups overlap with Malta and North Macedonia. Slovakia, Romania and Poland which has about in similar or comparable territorial extension $Df_{a,b}$ and $Cf_{a,b}$ climates, form a minor group partly within the $Cf_{a,b}$ climate group. Italy, which has in equal extension $Cs_{a,b}$ and $Cf_{a,b}$ climate areas, is near to the $Cs_{a,b}$ climate group. The presence of several *Ochlerotatus* species is characteristic to the mosquito fauna of the $Cf_{a,b}$ and $Df_{a,b}$ climate areas. In contrast, the rich *Anopheles* fauna is characteristic to the $Cs_{a,b}$ climate areas (Fig. 3).

The discriminant analysis of the mosquito fauna of the territorial domains according to their dominant Köppen-Geiger climate categories shows that Estonia, Finland, Latvia, and Lithuania have dominantly humid continental $Df_{a,b}$ climates form a well-separated group. The countries of the hot-

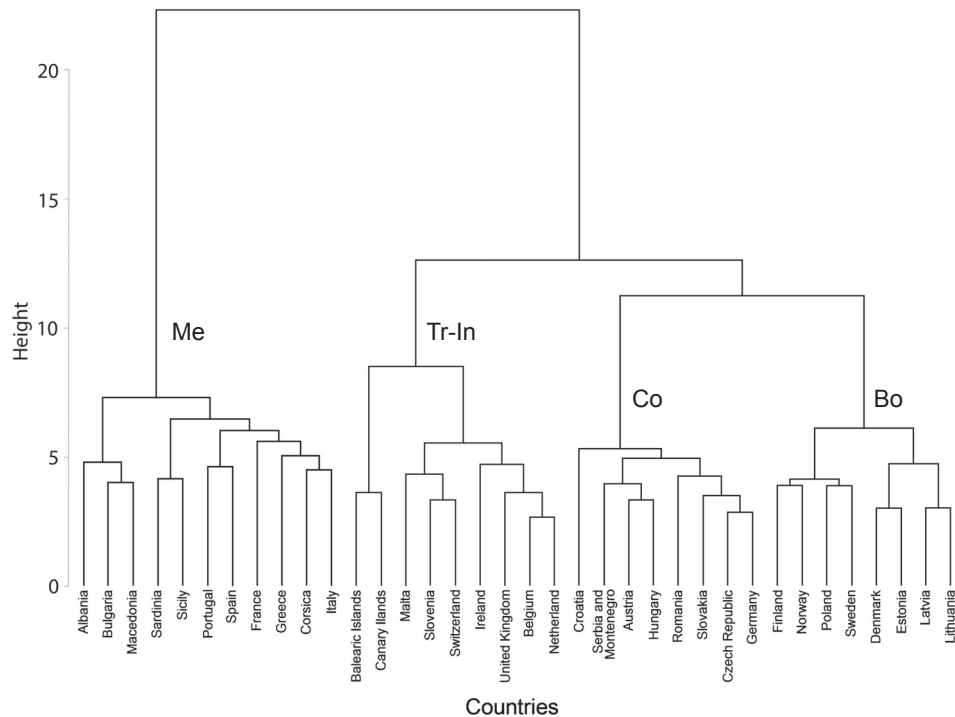


Fig. 1. Cluster analysis for certain European countries and territories based on their mosquito species. Dash line shows the 5% significance level (Me = Mediterranean, Tr-In = transitional-insular, Co = continental, Bo = boreal; Macedonia = North Macedonia)

summer and warm-summer Mediterranean $Cs_{a,b}$ and humid subtropical and oceanic $Cf_{a,b}$ dominant climate areas overlap with Croatia, Malta, the United Kingdom, and The Netherlands. Spain, which also has cold semi-arid climate Bs_k climate areas, can be found within the $Cs_{a,b}$ climate group (Fig. 4).

The character species of the fauna

From the involved 100 mosquito species, 47 is the member of the temperate, 45 of the Mediterranean, 38 of the boreal and 24 of the transitional-insular mosquito fauna areas. It was proposed that the presence of a mosquito species is characteristic for a fauna if the species can be found in at least in the 80% (ratio: $0.8 \leq$) of the geographical domains of the mosquito fauna or a fauna

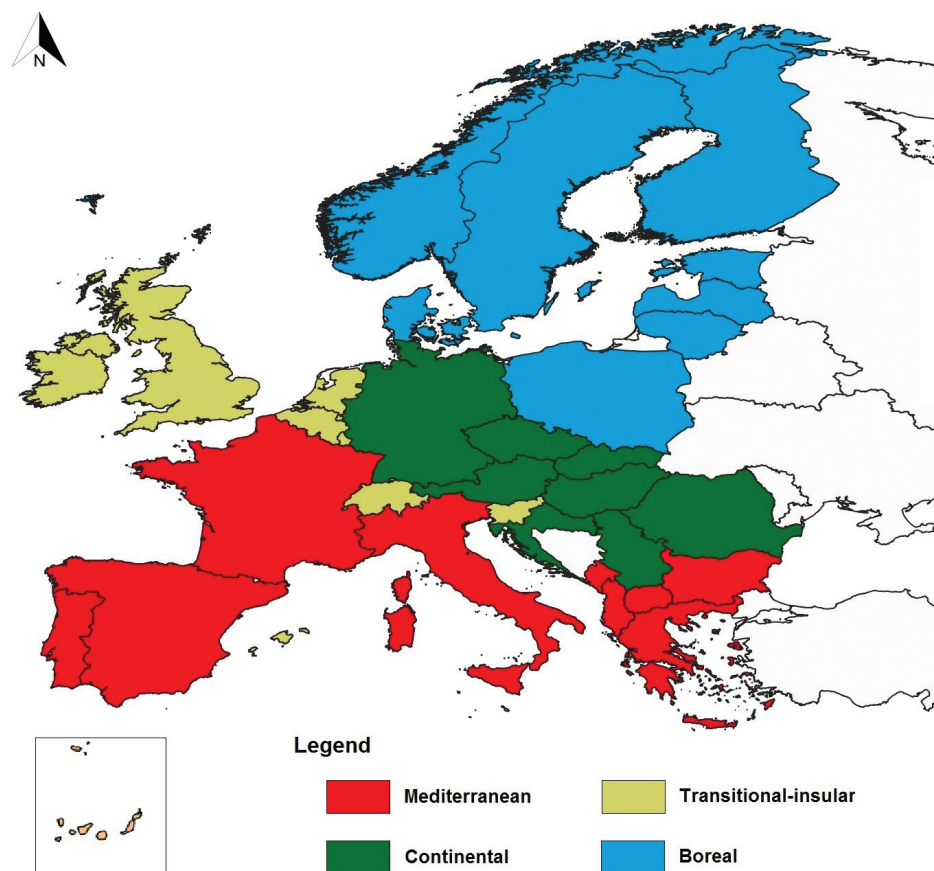


Fig. 2. The ranges of the determined mosquito fauna in Europe according to the HCA results (white = not studied; in the frame = The Canary Islands)

Table 2. The character species of the mosquito fauna (Me = Mediterranean, Tr-In = transient-insular, Co = continental and Bo = boreal)

Species	Me	Tr-In	Co	Bo
<i>Uranotaenia unguiculata</i>	1.0	0.1	1.0	0
<i>Anopheles algeriensis</i>	1.0	0.2	0.8	0.1
<i>Culex martini</i>	0.2	0.1	0.9	0
<i>Culex mimeticus</i>	1.0	0	0.2	0
<i>Culex perexiguus</i>	0.8	0	0	0
<i>Ochlerotatus echinus</i>	0.8	0	0	0
<i>Culiseta glaphyroptera</i>	0.1	0	0.8	0.1
<i>Ochlerotatus leucomelas</i>	0.2	0.1	0.9	0.8
<i>Ochlerotatus excrucians</i>	0.1	0.2	0.9	0.9
<i>Aedes rossicus</i>	0	0	0.8	0.1

A total of 13 mosquito species exclusively or almost exclusively (80%≤ of the cases) belongs to the mesothermal and 23 the microthermal fauna. Most of the mosquitoes of the microthermal fauna is *Ochlerotatus* species (20/23). The most numerous mosquitoes of the mesothermal fauna belong to the genera *Culex* or *Ochlerotatus* (3-3/13; Table 2).

Inversely, it was also proposed that if the inhabited domains of a mosquito belong to at least in 80% of a single fauna, the mosquito belongs to this kind of mosquito fauna. Based on this criterion, a total of 25 species inhabits exclusively or almost exclusively (80%≤ of the cases) the Mediterranean, 1 the transitional-insular, 6 the continental and 9 the boreal geographical domains. The insular-transitional fauna has no character species. It indicates that this is a collective group of such areas which can be found between the Mediterranean and continental zones or on the islands of the Mediterranean Sea. Both Table 2 and 3 shows, the transitional-insular fauna is a heterogenic group where

Table 3. The ratio of mosquitoes according to their participation in the different mosquito fauna (Me = Mediterranean, Tr-In = transient-insular, Co = continental and Bo = boreal)

Species	Me	Tr-In	Co	Bo
<i>Aedes aegypti</i>	1.0	0	0	0
<i>Aedes cretinus</i>	1.0	0	0	0
<i>Aedes rossicus</i>	0	0	0.8	0.2
<i>Anopheles beklemishevi</i>	0	0	0	1.0
<i>Anopheles cinereus</i>	0.8	0.2	0	0
<i>Anopheles marteri</i>	1.0	0	0	0

Bold numbers: found in at least in 80% of the geographical domains

Table 3 (continued)

Species	Me	Tr-In	Co	Bo
<i>Anopheles melanoon</i>	0.8	0	0.2	0
<i>Anopheles multicolor</i>	1.0	0	0	0
<i>Anopheles sacharovi</i>	0.8	0	0.2	0
<i>Anopheles sergentii sergentii</i>	1.0	0	0	0
<i>Anopheles subalpinus</i>	0.8	0	0.2	0
<i>Anopheles superpictus</i>	0.8	0	0.2	0
<i>Culex brumpti</i>	1.0	0	0	0
<i>Culex deserticola</i>	1.0	0	0	0
<i>Culex impudicus</i>	0.9	0	0.1	0
<i>Culex mimeticus</i>	0.8	0	0.2	0
<i>Culex perexiguus</i>	1.0	0	0	0
<i>Culex pusillus</i>	1.0	0	0	0
<i>Culex tritaeniorhynchus</i>	1.0	0	0	0
<i>Culex vishnui</i>	1.0	0	0	0
<i>Ochlerotatus eatoni</i>	0	1.0	0	0
<i>Ochlerotatus echinus</i>	1.0	0	0	0
<i>Ochlerotatus gilcolladoi</i>	1.0	0	0	0
<i>Ochlerotatus japonicus japonicas</i>	0	0	1.0	0
<i>Ochlerotatus lepidonotus</i>	1.0	0	0	0
<i>Ochlerotatus nigrinus</i>	0	0	0	1.0
<i>Ochlerotatus quasirusticus</i>	1.0	0	0	0
<i>Culiseta glaphyroptera</i>	0.1	0	0.8	0.1
<i>Culiseta bergrothi</i>	0	0	0	1.0
<i>Ochlerotatus behningi</i>	0	0.2	0	0.8
<i>Ochlerotatus subdiversus</i>	0	0	1.0	0
<i>Ochlerotatus punctodes</i>	0	0	0	1.0
<i>Ochlerotatus pionips</i>	0	0	0.2	0.8
<i>Ochlerotatus mariae</i>	0.9	0.1	0	0
<i>Ochlerotatus impiger impiger</i>	0	0	0	1.0
<i>Ochlerotatus hungaricus</i>	0	0	1.0	0
<i>Ochlerotatus hexodontus hexodontus</i>	0	0	0	1.0
<i>Ochlerotatus euedes</i>	0	0	0	1.0
<i>Ochlerotatus berlandi</i>	0.8	0	0.1	0.1
<i>Ochlerotatus atropalpus</i>	1.0	0	0	0

the island-effect and the climatic transition conditions between the mesothermal and microthermal climates could cause the heterogenic fauna patterns.

Mosquito diversity by genera and climate

Based on the results of the Wilcoxon Rank-Sum Test, a significant difference ($p = 0.02$) was found between the number of *Anopheles* species of the Mediterranean ($n = 10$, median = 9.5) and temperate ($n = 9$, median = 6) areas. A non-significant difference ($p = 0.83$) was found between the number of *Aedes* species of the Mediterranean ($n = 10$, median = 3) and temperate ($n = 9$, median = 3) areas. Significant difference ($p = 0.02$) was found between the number of *Culex*

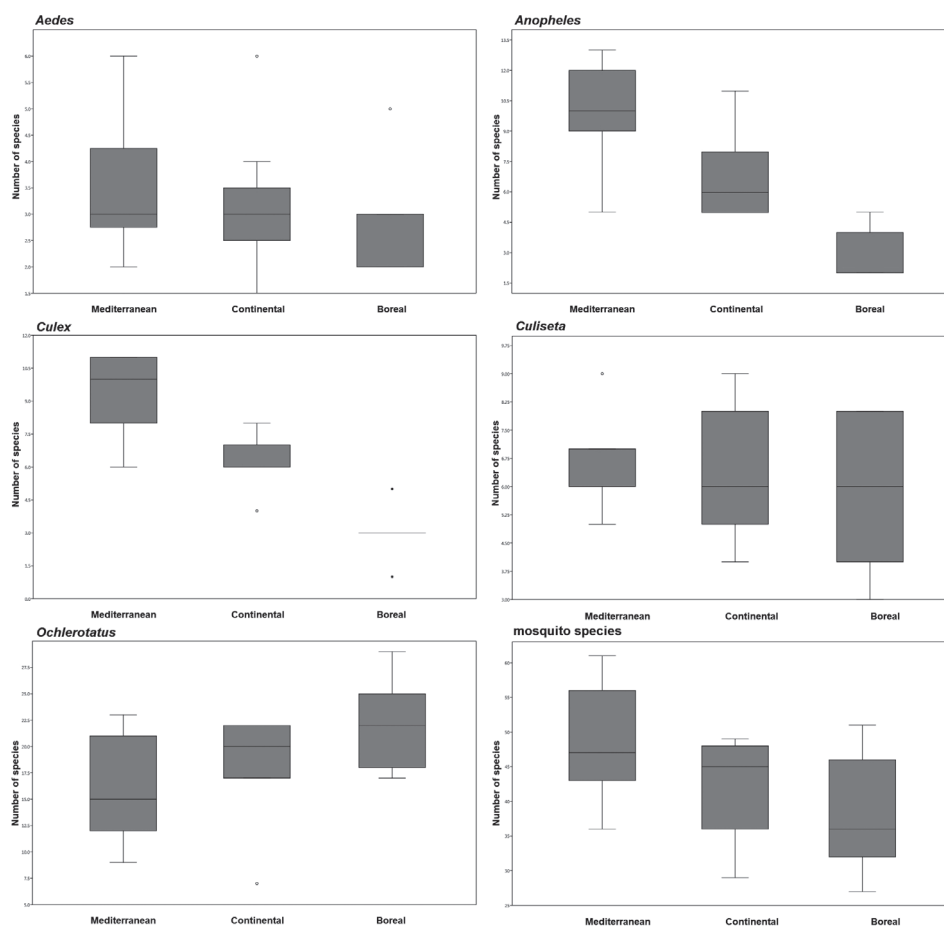


Fig. 5. The comparison of the taxonomical composition and total species number of the Mediterranean, the temperate and the boreal mosquito faunae

species of the Mediterranean ($n = 10$, median = 10) and temperate ($n = 9$, median = 6) areas. Also, no-significant difference ($p = 0.40$) was found between the number of *Culiseta* species of the Mediterranean ($n = 10$, median = 6) and temperate ($n = 9$, median = 6) areas. In contrast, significant difference ($p = 0.01$) was found between the number of *Ochlerotatus* species of the Mediterranean ($n = 10$, median = 15) and temperate ($n = 9$, median = 20) areas. No-significant difference ($p = 0.14$) was found between the total mosquito number of the Mediterranean ($n = 10$, median = 46) and temperate ($n = 9$, median = 45) areas. Significant difference ($p = 0.01$) was found between the number of *Anopheles* species of the temperate ($n = 9$, median = 6) and boreal ($n = 8$, median = 2.5) areas. Marginally significant difference ($p = 0.07$) was found between the number of *Aedes* species of the temperate ($n = 9$, median = 3) and boreal ($n = 8$, median = 2) areas. Significant difference ($p = 0.01$) was found between the number of *Culex* species of the temperate ($n = 9$, median = 6) and boreal ($n = 8$, median = 3) areas. In contrast, no-significant difference ($p = 0.35$) was found between the number of *Culiseta* species of the temperate ($n = 9$, median = 6) and boreal ($n = 8$, median = 6.5) areas. No-significant difference ($p = 0.21$) was found between the number of *Ochlerotatus* species of the temperate ($n = 9$, median = 20) and boreal ($n = 8$, median = 22.5) areas. No-significant difference ($p = 0.19$) was found between the total mosquito number of the temperate ($n = 9$, median = 45) and boreal ($n = 8$, median = 37) areas (Fig. 5).

According to the above-described results, the affinity of the mosquito fauna of an area for mesothermal or microthermal climates can be quantified according to the proportion of the rather mesothermal climate preferring mosquito genera (*Aedes*, *Anopheles* and *Culex*) and the rather microthermal climate preferring genera (*Culiseta* and *Ochlerotatus*). The mesothermal climate affinity index can be calculated according to the following formula:

$$McA_i = \frac{\sum_3^{i=1} (N_{Ae} \cdot N_{An} \cdot N_{Cx})}{\sum_2^{i=1} (N_{Cs} \cdot N_{Oc})}$$

MCA_i : mesothermal climate affinity index
 N_{Ae} : number of *Aedes* species
 N_{An} : number of *Anopheles* species
 N_{Cx} : number of *Culex* species
 N_{Cs} : number of *Culiseta* species
 N_{Oc} : number of *Ochlerotatus* species

Mean of the MCA index of Mediterranean, temperate and boreal fauna are as follows: 1.11 (SD: 0.19; median: 1), 0.66 (SD: 0.1; median: 0.6) and 0.33 (SD: 0.05; median: 0.3). The mean MCA_i value of the transitional-insular fauna is 0.83 with a notable SD which is 0.82, the median is 0.5. According to the results of the Wilcoxon Rank-Sum Test, significant differences were found in the MCA_i values between the Mediterranean and temperate ($p < 0.001$), Mediterranean and boreal ($p < 0.001$) and temperate and boreal ($p < 0.001$; Fig. 6).

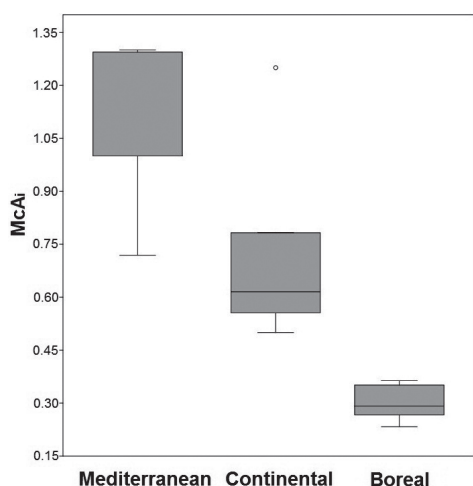


Fig. 6. The comparison of the McA_i index of the Mediterranean, temperate and boreal mosquito fauna

Based on its McA_i value (0.86), the mosquito fauna of the Balearic Islands is wedged into the Mediterranean fauna, while the mosquito fauna of Belgium, Ireland, the Netherlands, Slovenia, the United Kingdom (McA_i : 0.60-0.53) are more the part of the temperate fauna. The McA_i value of Switzerland (McA_i : 0.50) can be found between the temperate and boreal mosquito faunas. The McA_i value of the European countries and islands shows a northeast to southwest increasing trend (Fig. 7).

Comparison of the distribution of large-scale mosquito faunas with the occurrence of mosquito-transmitted arthropod viruses

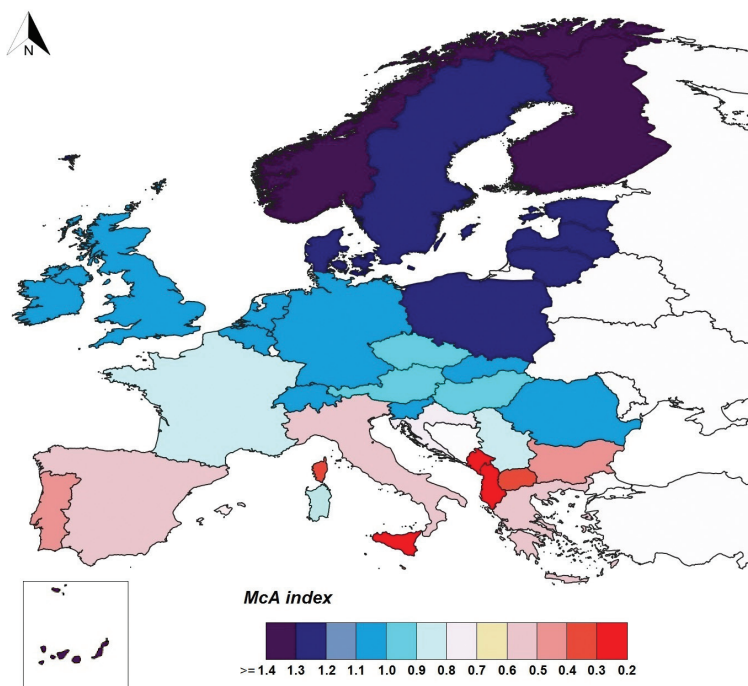


Fig. 7. The McA_i index of the studied European countries and islands

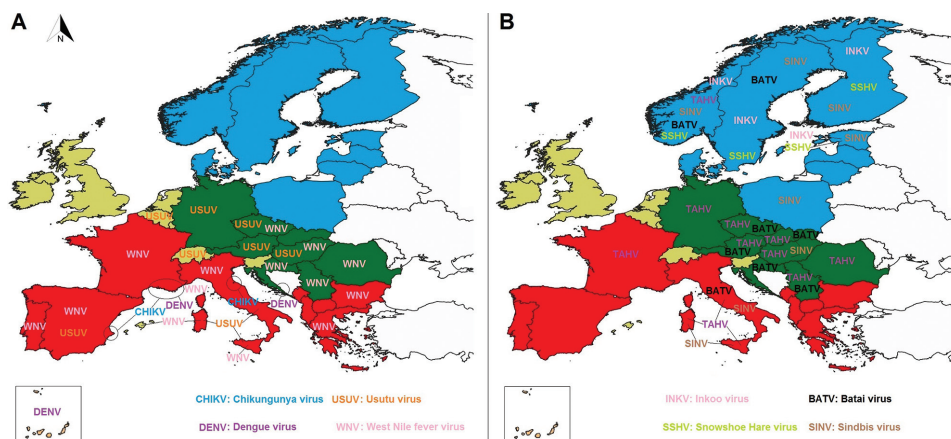


Fig. 8. The distribution of mosquito-transmitted arboviruses according to CALZOLARI (2016) projected on the map of the found large-scale mosquito faunae. A = arboviruses with southern occurrences, B = arboviruses with northern occurrences (white = not studied; in the frame = The Canary Islands)

According to their European occurrences, the mosquito-borne arboviruses can be divided into two major groups. The arboviruses of the first group predominantly occur in the Mediterranean, transitional-insular and continental mosquito areas. The Usutu and West Nile viruses are the characteristic members of this group (Fig. 8A). The arboviruses of the second geographical group can be found in the boreal and temperate mosquito fauna areas (Fig. 8B). The introduced Chikungunya and Dengue virus-caused infections occur only in the coastal Mediterranean mosquito areas. In contrast, the Snowshoe and Inkoo viruses can be found in the area of the boreal mosquito fauna. The Sindbis, Tahyna and Batai viruses predominantly occur in the boreal and temperate mosquito areas, but these viruses also can be found in some Mediterranean territories.

DISCUSSION

This is the first study which was conducted to determine the biome-scale mosquito fauna of Europe, comparing the distribution of large-scale mosquito faunae with the occurrence of mosquito-transmitted arthropod viruses in Europe. At first reading, it may seem like that the geographic resolution of the used database is too coarse for any climatic inference since only within one country, very different climate areas can be found. For example, mainland Italy goes from arctic climate in the high mountains in the Alps to the dry Mediterranean summer-like climate of Apulia, and the average values

of the climatic variables do not capture the spatial heterogeneity. However, it should not be forgotten that the aim of this study was the studying of the large-scale, biome-level investigation of the mosquito fauna and not the local level evaluating of the climatic requirements of the mosquito fauna, or the medium-range modeling of the distribution of mosquito assemblages. The present work is clearly macroecological, and it was neither aimed to analyses the distribution limiting climatic factors of the fauna or re-model the distribution the involved mosquito species. For such purposes, niche modeling is one of the most frequently applied method (e.g. FERRIER & GUIBAN 2006) or the use of feed-forward artificial neural network (ANN) techniques (BEDE-FAZEKAS *et al.* 2015).

As it was described, three major natural mosquito faunae were found in Europe: a Mediterranean, a temperate and a boreal. The transitional-insular, fauna is not a separate climatic fauna as consisting of mosquito assemblages of e.g. the Balearic and British Islands and some European countries, which are in the bordering zone of the two-main mosquito fauna having Mediterranean or Atlantic climate or can be found in the Mediterranean Sea or the Atlantic Ocean (Canary Islands). In the Canary Islands, only a total of 11 species of Culicidae was observed (BAEZ & FERNANDEZ 1980) which can be partly consequent on the distance from the mainland, the lack of the extended freshwater habitats and the relatively small area of the islands. In the case of Malta also, the above-mentioned factors can explain the relatively small number of mosquito species since only nine mosquito species are currently known from the islands of Malta (GATT *et al.* 2009). In the other hand, some endemic mosquito species also exist in the Mediterranean islands (*An. sergenti* in the Canary Islands and Sicily, *Cx. brumpti* in Corsica and Sardinia, *Oc. eatoni* in the Canary Islands, Madeira and *Cx. hortensis maderensis* in the Canary Islands) where the glacial episodes did not extinct the local mosquito fauna as it happened e.g. in the British Islands where although about 34 mosquito species exist. MACARTHUR and WILSON (1967) have shown in *The theory of island biogeography* that the dynamics of colonization and extinction events in the islands are in equilibrium, but the extinction rates depend on the size of islands (GILPIN & DIAMOND 1976). It should indicate that the islands have fewer mosquito species in general. The case of Great Britain is special since during the last glacial up to 6,000 years ago, the main British land had direct contact with the continental landmass of Europe. In contrast, even during the peak of the last glacial maximum, Sicily, Malta and the Balearic Islands were separate landmasses in the Mediterranean Sea and enjoyed the temperate climate (BECKER *et al.* 2015).

The discriminant analysis results showed that the mesothermal mosquito fauna is attached to the Mediterranean-subtropical (*Csa*, *Csb*) and the warm-temperate (*Cfa*, *Cfb*) climate areas. In contrast, the microthermal mos-

quito fauna lives under cold-temperate climate conditions (*Dfa*, *Dfb*, *Dfc*). Since climate change results in the northward shift of the biomes, it is likely that the distribution of mosquito fauna will follow the changing climatic patterns. Synthetizing of our results with the modeled shift of the Köppen-Geiger climatic zones by RUBEL and KOTTEK (2010) it can be projected that at the end of the 21st century, the border between the mesothermal and microthermal mosquito fauna will run from Scandinavia to the Caspian Sea covering almost the entire area of continental Europe. To make correct predictions, the preformation of a complex, niche modeling would be required. The developed mesothermal mosquito fauna-affinity index is useful in the determination of the mesothermal or microthermal nature of the studied mosquito fauna. This index can resolve the problem of the somewhat confusing 'insular-transient' mosquito fauna. For example, the McA_i value of the mosquito fauna of the Balearic Islands is high that can be the logical consequence of the fact that these islands can be found in the West Basin of the Mediterranean Sea. In contrast, the index of Switzerland's mosquito fauna is low, which can be explained by the fact that this European country can be found in the main massifs of the Alps which area has expressly mountainous character.

It requires further investigation whether and how the characteristic vegetation determines the large-scale distribution patterns of the mosquito fauna, although both could depend on similar climatic factors. It is known that e.g. *An. plumbeus* prefers to breed in the hole of certain tree species, but these mosquitoes also can breed in several other small water types (TÓTH 2006). The type of vegetation influences several other biotic and abiotic factors as the chemistry of the waters, the taxonomic composition of aquatic and bird predators, shading, the diurnal variance of temperature, wind, and humidity. Climate change also can strongly influence these factors altering the hydrology and nutrient chemistry of waters (VÖRÖSMARTY & MEYBECK 2004). The pine forest of North, the mixed and deciduous forest of Central Europe, the Mediterranean shrublands provide a very different environment of mosquitoes. There is evidence that vector arthropods and vegetation can respond parallel to the changing climatic conditions in the sense of the similar magnitude and direction shift of their distribution ranges (BEDE-FAZEKAS & TRÁJER 2013). The permanency and the seasonal accessibility of the available breeding habitats can also be different. In the boreal areas, winter freezing of the waters can determine the length of the mosquito larva season, while in the arid and semi-arid areas the lack of the available waters can limit the mosquito populations.

The European occurrences of mosquito-borne arboviruses show more or less correspondence to the geographical patterns of the found mosquito fauna. The occurrence of some arboviruses shows a direct correlation to certain mosquito fauna areas. For example, Chikungunya and Dengue viruses

occur solely in the area of the Mediterranean mosquito fauna. The Chikungunya virus is predominantly transmitted by *Ae. albopictus* in Europe (WHO 2016), which mosquito is a subtropical fauna element (DELATE *et al.* 2008). The earlier introduction of *Ae. albopictus* from the Far East and the introduction of Chikungunya virus from India to Italy in 2007 created the conditions of the outbreak of the first Chikungunya fever epidemic in the Mediterranean Basin (REZZA *et al.* 2007, BONIALURI *et al.* 2008). The Snowshoe Hare virus occur solely in the areas of the boreal mosquito fauna. It can be simply explained by the boreal distribution area of the European vectors of the virus. For example, *Oc. hexodontus* (EVANDER *et al.* 2016) occur only in the boreal areas. The distributions of the mammalian hosts (e.g. *Clethrionomys rutilus* (Pallas, 1779) or *Dicrostonyx torquatus* (Pallas, 1778) are also clearly boreal animals (HUBÁLEK 2008). The case of the Inkoo virus is very similar. The main vectors of the virus (*Ochlerotatus communis* (De Geer, 1776), *Oc. punctor*, and *Oc. hexodontus*) inhabit the boreal and the mountainous areas of Europe. For example, *Oc. communis* is a typical sylvatic species (SCHAFNER *et al.* 2001). This mosquito inhabits the pine forests and less abundant in deciduous woods (RETTICH *et al.* 1978). Larvae of the species prefer the acidic water of peatlands (BECKER *et al.* 2003). The most important vertebrate host of Inkoo virus is *Lepus timidus* Linnaeus, 1758 which is a Palearctic hare. The quasi Pan-European distribution of Tahyna virus can be the consequence of the wide range of the potential mosquito vectors. For example, *Ae. vexans*, which is one of the most frequent mosquito species in Europe, can transmit the Tahyna virus (HUBÁLEK 2008). The vectors of Sindbis virus (e.g. *Cx. pipiens*, *Oc. communis* and *An. hyrcanus*; HUBÁLEK 2008) has also wide distribution area. While the West Nile virus lacks from the boreal and the cool summer Atlantic areas, the most important vector *Cx. pipiens pipiens* is present almost in entire Eurasia. In Western Europe, the primary distribution limiting factor of West Nile fever is the minimum temperature in July. West Nile fever occurs only in those regions where the June to September mean temperature reaches the 22 °C and the precipitation in July are less than 80 mm (TRÁJER *et al.* 2014). It can be concluded that the distribution of the mosquito vectors only one factor which determines the occurrence of mosquito-borne arbovirus infections.

*

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