The potential effects of climate change on the populations of *Aedes punctor* (Diptera: Culicidae) in Hungary

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Received: 2 July 2021 / Accepted: 21 January 2022 / Published online: 31 January 2022
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Abstract

In Hungary, the boreal-alpine mosquito *Aedes punctor* has a disjunct distribution limited to the Hungarian mid-mountains. The aim of this study was to investigate the potential effect of global warming on the future (2041–2060 and 2061–2080) climatic suitability for the mosquito in Hungary. The results indicate the heterogeneous, but in general, the negative effect of climate change on the distribution area of *Aedes punctor* in this region. The models predict the total loss of mosquito habitat in the Transdanubian mountain ranges (Bakony-Balaton and Mecsek Mts.) for 2061–2080. In the North Hungarian Mountains (in the Mátra Mts.), climatic alterations may result in the habitat contraction, but not total disappearance of the climatically suitable areas for *Aedes punctor* at higher elevations of mountain ranges. It can be concluded that climate change can cause the altitudinal shift of the suitable habitats and the range-contraction of Hungarian middle mountains-inhabiting populations of the mosquito in Hungary in the second half of the twenty-first century assuming that the future climatic needs of the species would remain the same as at present.

Keywords Altitudinal shift · Distribution factors · Mountainous ecosystems · Cold-stenotherm · Survival

Introduction

Climate change is predicted to trigger both the poleward and the altitudinal shift of climate zones and biomes (Harvell et al. 2002). As a part of the future alterations of the fauna, the changing distribution of arthropod species is one of the notable faunistic consequences of the predicted environmental alterations both from an agricultural, veterinary, and human health point of view (Folly et al. 2020; Gu et al. 2018). Due to their vector role, mosquitoes are frequently found in the scope of the current investigations related to climate change (Brugueras et al. 2020; Iwamura et al. 2020; Wang et al. 2020). Global warming already contributed to the spread of invasive, thermophilus mosquito species in the Northern Hemisphere during the last decades, like the Asian tiger mosquito (*Aedes albopictus* Skuse, 1894) (Rochlin et al. 2013) and such temperate mosquito species like the East Asian-origin Asian bush mosquito (*Aedes japonicus japonicus*) (Reuss et al. 2018). Overall, at least five invasive

aedine mosquito species were found in Europe only in the last two decades (Medlock et al. 2012).

Although climatic and meteorological factors form an important part of the factors that influence the mosquito distribution patterns, it should be noted that climate change is not the only cause of the observed northward spread of invasive mosquito species from the subtropical areas to the temperate regions (Trájer et al. 2014). Anthropogenic transport plays a notable role in species migrations (Sáring-Kenyeres et al. 2020). Several other anthropogenic activities like river regulation, long-distance transport can also increase the density and facilitate the spread of mosquito species (Trájer et al. 2015). Due to this fact, the distribution and abundance of mosquito vectors, as well as the incidence of mosquito-borne diseases are in complex relation to climatic and meteorological conditions; and other environmental and demographic factors (Brugueras et al. 2020). In the case of certain areas as well as mosquito species, the joint effect of land cover change and climate change can cause heterogeneous trends in population changes depending on the current land use conditions (Wang et al. 2020). The effect of meteorological conditions on mosquito density varies by factors, regions, and species. While the effect of air temperature up to at least 30 °C on mosquito density is

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generally positive, the effect of the number of rainy days in a month can vary by area (Li et al. 2019).

Among environmental factors, temperature plays a key role in determining the distribution and abundance of mosquitoes (Kobayashi et al. 2002), shaping the annual phenology (Delatte et al. 2009) and population growth (Alto and Juliano 2001). Temperature determines the lifespan of imagoes and influences the dispersal (Roiz et al. 2011), the length of the female gonotrophic cycle (Delatte et al. 2009), mosquito abundance (Bayoh and Lindsay 2003), overwintering (Reuss et al. 2018) and larval survival (Delatte et al. 2009) of mosquito species. It can be concluded that in general, increasing temperatures could enhance the population density and elongate the annual activity seasons of mosquito species (Lafferty 2009). Reversing the logical connection, the decreasing temperature is not favourable for the lowlands-dwelling, thermophilus mosquito species. Due to the tropospheric lapse rate-caused vertical cooling effect, each mosquito species has a specific upper vertical distribution limit in an area which can be seen most clearly in the relation of lowland and mountain habitats (Equihua et al. 2017).

The entomofauna of the mountainous regions seem to be particularly vulnerable to the effects of climate change (Cerasoli et al. 2020). This may have primarily topographical causes. Based on the equilibrium theory of insular biogeography, a smaller area can sustain fewer species (Whitehead and Jones 1969). Due to the exponentially narrowing upward character of mountainous topography in territorial terms, the upward shift of the topographical climate zones causes the rapid decrease of the absolute area of the mountain habitats. While about 12.3% of all terrestrial land area outside Antarctica is mountains, within it, the alpine and nival biogeographic region covers only 2.6% of the total land area (Körner et al. 2011). In other words, the change in the corresponding area of an elevation range is the negative and non-linear (negative exponential) function of the increase of elevation. The effects of climate change may also endanger the regional populations of some mosquito species which prefer the climate of mountain regions. Investigating the topographical distribution patterns of Southern Wyoming, Denke et al. (1996) found that most of the mosquito species can be found on the lower and middle elevation areas in this temperate mountainous region, and there are few species occur in the middle and upper elevations or primarily in the alpine areas like *Aedes punctor* (Kirby, 1837) or *Aedes impiger* (Walker 1848). In hot and seasonally arid regions, mountain forests can be the refugia of mosquitoes. For example, the dry season survival of malaria vector *Anopheles* species in the Kilombero Valley, Tanzania, which can be found in the dry savannah zone of east Africa, is due to the fact that the mosquitoes can find where to lay their eggs on the appropriate wetland habitats along with the

river system throughout the middle of the valley even in the driest and hottest periods of the year (Charlwood et al. 2000). Heat-induced tree mortality and increasing aridity reveal emerging climate change risks for mountainous forests and forest-forming tree species (Allen et al. 2010) as these changes can also negatively affect the fitness of forest-dwelling mosquito populations. This is in contrast to several invasive mosquito species which generally are not tied to a specific vegetation type, many cold-stenotherm species breed in the tree of holes (Sáringier-Kenyeres et al. 2018).

Based on the above-mentioned facts and observations, it can be hypothesized that climate change at the regional level could result in the partial or total area contraction of climatically suitable habitats for mountain mosquito species in the temperate climate zones of the Holarctis. The aim of this study was to model the future (2041–2060, 2081–2100) alterations of the potential climatic suitability patterns of *Ae. punctor* in Hungary, in which mosquito species can be held as an indicator species of boreal-alpine mosquito species related to the effects of global climatic alterations in mid-mountain regions of East-Central Europe.

Material and methods

The modelled mosquito species

Aedes punctor is a typical cold-stenotherm, Holarctic, boreal-alpine distribution mosquito species (Nicolescu et al. 2003). Larvae of this mosquito develop in temporary small acidic waters of different sizes (Edsall et al. 2010). It can even be found in cold areas such as the tundra of the Alaska Peninsula (Frohne 1955) and the bogs and marshes of Estonia and Finland where the species is among the most abundant mosquitoes (Tummeleht et al. 2020; Culverwell 2018). *Aedes punctor* has a circumpolar range in Europe, including the entire Scandinavia where this species is among the most common mosquito species (Fauna Europaea 2017). Outside the boreal areas, the species occurs in the mountains at altitudes dependent on the climate belt. This mosquito species occurs in Western Spain, Romania, and Hungary generally in the mid-mountains and the mid-mountainous regions of the higher mountain ranges (Bravo-Barriga et al. 2021; Nicolescu et al. 2003; Tóth and Kenyeres 2012). The higher elevation areas of the Alpine orogeny belt provide suitable habitats for *Ae. punctor* even in such typical ‘Mediterranean’ countries like Greece (Kaiser et al. 2001). Due to its distribution and environmental requirements, *Ae. punctor* can be considered as an indicator mosquito species related to the investigation of the effects of global warming on mountainous mosquito assemblages.

Outline of the study

Model predictions which were performed to show the potential future changes in mosquito ranges were developed based on bioclimatic (mainly temperature and precipitation-nature data) in most of the cases (Jácome et al. 2019). These kinds of models can be used in areas where notable differences exist in geographical conditions. The transition zones between mountainous areas and lowlands form a typical field of utilization of these kinds of model environments (Wieland et al. 2021; Cunze et al. 2020; Jácome et al. 2019). Due to this fact, the present study was also based on the utilization of bioclimatic variables.

The modelling steps were as follows:

1. The *Ae. punctor*-related mosquito data of the Mecsek Mts., the Bakony-Balaton Mts. and the Mátra Mts. (all of them are Hungarian mid-mountain regions) was selected.
2. The presence and absence UTM grids were identified and georeferenced based on the central coordinates of the 2.5×2.5 km spatial dimension grids.
3. The bioclimatic extrema of the grids was identified for the climate period of 1979–2013 which was held as a reference period.
4. The lower extrema of the precipitation and the upper extrema of the temperature values were determined (for an explanation, see the related part of the Materials and methods section);
5. The selected lower/and or upper bioclimatic extrema were displayed for modelling using the climatic models of 1960–1990, 1979–2013 and the models of the future period 2041–2060 and 2061–2080 according to rcp2.6, 4.5, 6.0 and 8.5 SRES scenarios.

6. The differences between the modelled suitability values of the different future climatic suitability models and the model of the reference period were calculated and depicted.
7. The modelled suitability values of *Ae. punctor* was projected to the relief of the Mecsek, the Bakony, the Mátra and Karancs Mts.

Figure 1 shows the geographical position of the studied area in Europe (Fig. 1.1), as well as the selected Hungarian mid-mountain ranges with the grids for data sampling and the lines which were used in the creation of relief-like models (Fig. 1.2).

Mosquito occurrence data

The occurrence data of *Ae. punctor* was obtained from the monographs of Sándor Tóth (Mátra Mts.: Tóth 2009, Bakony-Balaton Mts.: Tóth 2006 and Mecsek Mts.: Tóth 2011). The surveys were performed by the staff of the Zirc Museum, led by the zoologist Dr. Sándor Tóth in the late 1980s, 1990s and in the first half of the 2000s. The spatial resolution of the data displayed on maps is 2.5×2.5 km.

The monograph contains the data of larvae, pupae, and adults.

Mosquito larvae were captured by collection nets

1. At the waterline;
2. From the surface of submerged stems and shoots, and
3. From the sediment.

Mosquito imagoes were captured by

1. Light traps;

Fig. 1 1.1 The studied regions in Europe. 1.2 The Bakony-Balaton Mts. (A), Mátra (B) and Karancs (C) and Mecsek (D) Mountains in Hungary with the crosslines (red lines) used in the creation of

the relief models of Fig. 6. The source of the satellite map: Google Earth™ Engine (Gorelick et al. 2017). The source of the topographical map: ETOPO global relief model (Amante and Eakins 2009)

2. Directly from the skin by the vacuum-pump collector and occasionally by
3. Carbon-dioxide traps and
4. Net traps.

Figure 2 shows the known occurrences of *Ae. punctor* in the Mecsek Mts., the Bakony-Balaton and the Mátra Mts.

Table 1 summarizes the relevant data about the collections of *Ae. punctor*.

Relief and climate models

The topographical model layer was based on the ETOPO1 2.5 arc-minute spatial resolution global relief model (Amante and Eakins 2009). A total of six climate models were involved in the study (Table 2). Because the observation years of the mosquito cover the late 1980s, 1990s and early 2000s, as a reference period for climatic analysis, the climate model of the 1973–2013 periods was involved in the study. For modelling purposes, as a ‘near past period’,

Fig. 2 The Mátra (1), the Bakony-Balaton (2) and Mecsek (3) Mts. with the presence (yellow points) and absence (red points) 2.5×2.5arc-minutes UTM-based occurrence sites related to *Aedes punctor*. The source of the topographical map: ETOPO global relief model (Amante and Eakins 2009)

Table 1 The details of the collected mosquito material related to *Aedes punctor* in the three regions (s.p. survey period, tot. UTM total number of the UTM grids, pos. UTM total number of the positive UTM grids where *Ae. punctor* where observed, No. c.s. Number of

Region	s.p	tot. UTM	pos. UTM	No. l	No. p	No. im	No. in	rsD%
Bakony-Balaton region	1986–2001	495	25	120	5	1	126	4.81
Mecsek	2003–2007	108	8	25	0	2	27	0.33
Mátra	1991–2007	142	14	244	34	12	290	2.89
Sum		745	47	389	39	15	443	-

Table 2 The main details of the used climate models

Model	Time	Resolution	Citation
Near past period	1960–1990	2.5 arc minutes	CHELSA
Reference period	1973–2013	2.5 arc minutes	Fick and Hijmans (2017)
CCSM4 rcp2.6	2041–2060	2.5 arc minutes	Hijmans et al. (2005)
CCSM4 rcp4.5	2041–2060	2.5 arc minutes	Hijmans et al. (2005)
CCSM4 rcp6.0	2041–2060	2.5 arc minutes	Hijmans et al. (2005)
CCSM4 rcp8.5	2041–2060	2.5 arc minutes	Hijmans et al. (2005)

the climate model of 1960–1990 was used to investigate the reference period’s disjunct-disperse distribution of the species in the study area. For future modelling purposes, the community climate system model version 4 environment (CCSM4; Gent et al. 2011) and rcp2.6, 4.5, 6.0 and 8.5 SRES scenarios-based climate models (Jubb et al. 2013) for the period of 2041–2060 and 2061–2080 were used. The spatial resolution of the applied climate models is also 2.5 arcminutes. In the studied latitude frame (46 to 48°N), it means that the resolution of the topographical and climatic models is 3.2–3.1 km.

Determination of the climatic extrema

Since the spatial resolution of the mapped mosquito data and the climatic data is quite similar (2.5 and 3.1–3.2 km), the mosquito occurrence data was identified and georeferenced according to the grids of the climatic models. It means 47 individual edge lengths of 3.1–3.2×3.1–3.2 km grids where the mosquito occurs in the Bakony-Balaton, the Mátra and the Mecsek Mts. To gain the bioclimatic values of the grids, the reference period (1979–2013) climate model’s bioclimatic values were sampled. A total of 14 bioclimatic variables were involved. From these, 7 bioclimatic variables have a temperature, and 7 variables have a precipitation nature. In the case of temperature kind

collecting sites, No. l. number of larvae, No. p. number of pupae, No. im. number of imagoes, No. in. number of individuals, rsD% region-specific dominance percentage

of bioclimatic variables (bio1, 5–6, 8–11) the maximum, in the case of the precipitation-nature bioclimatic variables (bio 12–14, 16–19), the maximum values were held as the distribution limiting extrema of *Ae. punctor*. It is due to the observations that this mosquito species is the most abundant in the cooler and humid parts of the Holarctic region as was mentioned in the Introduction. It implicates that low precipitation and higher mean temperature conditions can be unfavourable for this alpine-boreal mosquito species. The identified extrema can be seen in Table 3. The model identification can be found in the Supplementary text.

Results

Model results of 1960–1990 and 1979–2003

The modelled 1960–1990s distribution of the species shows similar patterns although the high suitability value regions form an almost continuous range between the middle and the higher elevation areas including the humid climate Zala Hills in southwestern Transdanubia (Fig. 3). In this period, in the western part of Hungary, the populations of the mosquito could form a continuous range with the east Alpine populations where, at that time, occupying such regions that are no more than about 150–170 m above the sea level.

The modelled distribution of the *Ae. punctor* for 1979–2003 returned the observed abundance patterns: *Ae. punctor* is missing from the lower areas, and it occurs in the middle altitude regions in Hungary (Fig. 4). Comparing the known reference period's occurrences of the mosquito in the studied regions (see Fig. 2), the species did not occur in such areas where the modelled climatic suitability values were less than about 90%. The presence of the mosquito in the second half of the twentieth century was restricted to the central part of the highest elevations of Hungary (the highest peak in North Hungarian Mountains is the Kékes with 1014 m; in the Transdanubian

Fig. 3 The modelled suitability values of *Aedes punctor* in 1960–1990 (1: the westernmost ranges of the Alps, 2: Kőszeg Mts., 3a: outer ranges of the Northwest Carpathians, 3b: inner ranges of the Northwest Carpathians, 3c: outer ranges of the North-Eastern and Eastern Carpathians, 3d: Southern Carpathians, 4: Apuseni Mts., 5: Bakony-Balaton Mts., 6: Mecsek Mts., 7: Mátra Mts., 8: Karancs Mts., 9: Bükk Mts., 10: Zala Hills, 11: Hungarian Great Plain)

Mountains, the highest peak is the Pilis-tető with 756 m) and the westernmost foothills of the Alps (Kőszeg Mountains) where the highest elevation point is the Írott-kő with 882 m. The (lower) elevation limit could be about 171–200 m above sea level.

Future distribution patterns

In general, the models of the 2061–2080 period predict a more severe loss of suitable habitats than the models of the period 2041–2060. It is plausible that *Ae. punctor* potentially will lose most of its habitats in the middle mountain regions of Hungary in Transdanubia. In general, the mean climatic suitability for *Ae. punctor* will not exceed the 0–25% in the lowlands and the 25–60% in the hills. Considering the total area of the Pannonian Basin, higher (90% <) climatic suitability values will only remain in the eastern Alpine regions, in the middle regions of the Carpathian Mountains, in the

Table 3 The determined bioclimatic extrema (*T* temperature-based, *P* precipitation-based) for modelling purposes (*bio1* annual mean temperature, *bio5* max temperature of warmest month, *bio6* min temperature of coldest month, *bio8* mean temperature of wettest quarter, *bio9* mean temperature of driest quarter, *bio10* mean temperature of warm-

Bioclimatic value (T)	bio1 (°C)	bio5 (°C)	bio6 (°C)	bio8 (°C)	bio9 (°C)	bio10 (°C)	bio11 (°C)
Upper extrema	11.0	27.2	-4.1	19.7	2.1	20.5	0.3
Bioclimatic value (P)	bio12 (mm)	bio13 (mm)	bio14 (mm)	bio16 (mm)	bio17 (mm)	bio18 (mm)	bio19 (mm)
Lower extrema	692	95	37	235	125	231	139

est quarter, *bio11* mean temperature of coldest quarter, *bio12* annual precipitation, *bio13* precipitation of wettest month, *bio14* precipitation of driest month, *bio16* precipitation of wettest quarter, *bio17* precipitation of driest quarter, *bio18* precipitation of warmest quarter, *bio19* precipitation of coldest quarter)

Fig. 4 The modelled suitability values of *Aedes punctor* in 1979–2013 (left) and the difference in the modelled suitability values between 1979–2013 and 1960–1990 (right) (1: the westernmost ranges of the Alps, 2: Kőszeg Mts., 3a: outer ranges of the Northwest Carpathians, 3b: inner ranges of the Northwest Carpathians, 3c: outer

ranges of the North-Eastern and Eastern Carpathians, 3d: Southern Carpathians, 4: Apuseni Mts., 5: Bakony-Balaton Mts., 6: Mecsek Mts., 7: Mátra Mts., 8: Karancs Mts., 9: Bükk Mts., 10: Zala Hills, 11: Hungarian Great Plain)

Bükk and Mátra Mts. among the Hungarian mid-mountains, as well as in the higher ranges of the Apuseni Mts. The mosquito will only survive for the second half of the twenty-first century in such regions where the elevation reaches 800–1000 m a.s.l. These regions—excluding the Kőszeg Mts., which range is the easternmost part of the Alps—can be found at the borders of Hungary or in other areas of the Pannonian Basin (Figs. 5,6).

Models showing differences from the reference period also indicate the general future decline of the populations of *Ae. punctor* in Hungary. A minor, only theoretical increase in the suitability values can be seen in certain parts of the Hungarian Great Plain along the Daube valley, which does not mean that the mosquito will colonize this region because of the general climatic suitability of *Ae. punctor* was already low in the reference period. In the middle elevations, the change of the climatic suitability will reach the –45 to –79% change. In the case of the higher (600–800 m) elevations, the change seems to be less expressed, reaching about –30 to –40% and above the 800 m elevations, the slight increase of the climatic values by +15–30% can be predicted, depending on the scenario. Supplementary Fig. 1 and 2 show the predicted differences in the climatic suitability values compared to the values of the reference period (1973–2003).

The comparison of the modelled areal (Figs. 5,6) and vertical (Fig. 7) suitability values of the periods of the past and the future periods indicate that before the potential regional decline of the populations of *Ae. punctor*, climate change causes the fragmentation of the climatically suitable range of the species. This process already started in the second half of the twentieth century and will be accelerated at the turn

of the twenty-first century. Due to the geographical trends in the bioclimatic variables, the suitability zones do not show entirely horizontal features, as can be seen, e.g., in the case of the Mecsek Mts. where a southwest to northeast decreasing suitability trend can be seen in all model results. In the case of the Bakony-Balaton Mts., the direction of the original mild southeast-northwest suitability trend is predicted to reverse to a definitive southeast to northwest decreasing trend between 1960 and 1990 and the future periods (Fig. 7).

Discussion

This study provides evidence that climate change could result in the potential regional decline of *Ae. punctor* populations in Hungary in the late twentieth century eliminating the continuity of suitable areas for *Ae. punctor* between the Hungarian mid-mountains and the higher mountain ranges of the Eastern Alps and the Carpathian Mts. This finding suggests that the frequently described general positive impact of climate change on mosquito species (Fischer et al. 2011; Rochlin et al. 2013; Trájer et al. 2014) cannot be generalized for all mosquito species and is predominantly valid for the invasive subtropical-tropical origin species in the continental regions. In the case of mountainous-boreal mosquito species, climate change can cause the regional decline of these species in the mid-mountainous regions. Although the risk of the local and regional mid-mountainous disappearance of the populations of *Ae. punctor* can strongly depend on the climatic alterations, other factors can also play a role in this process. These potential non-climatic elements are as

Fig. 5 The modelled suitability values of *Aedes punctor* in 2041–2060 (A: rcp2.6, B: rcp4.5, C: rcp6.0 and D: rcp8.5) (1: the westernmost ranges of the Alps, 2: Kőszeg Mts., 3a: outer ranges of the Northwest Carpathians, 3b: inner ranges of the Northwest Carpathi-

ans, 3c: outer ranges of the North-Eastern and Eastern Carpathians, 3d: Southern Carpathians, 4: Apuseni Mts., 5: Bakony-Balaton Mts., 6: Mecsek Mts., 7: Mátra Mts., 8: Karancs Mts., 9: Bükk Mts., 10: Zala Hills, 11: Hungarian Great Plain)

follows: (1) the dispersal rate of the species and (2) spatial heterogeneity and the quality of aquatic habitats (Alcalay et al. 2017). The flying dispersal rate of *Ae. punctor* is not known. A notable active dispersal capacity of *Ae. punctor* is contradicted by the fact that it has never been observed far from the modelled, suitable areas in the reference period. The present disjunct distribution of *Ae. punctor* in Hungary can be explained by the assumption that in the former cooler periods (e.g., during the wetter and cooler Maunder minimum; Wanner et al. 1995) the climatic conditions made possible the free dispersal of the mosquito along the mid-elevations of Hungary's Mountain ranges. In the present times, the *Ae. punctor* populations in Hungary occur in island-like mountainous habitats, which in many cases are hundreds of kilometres away from the nearest mountainous areas of the Balkans, the Alps, and the Apuseni Mountains. Comparing the models of 1960–1990 and 1973–2000, it can be said that

the most notable decreases in climatic suitability could occur in the peripheral regions of the Pannonian Basin bordering the high mountains of the Alps and the Carpathian Mts.—including the Apuseni Mts., the outer and inner ranges of the Northwest Carpathians, the: outer ranges of the North-Eastern and Eastern Carpathians, as well as the Southern Carpathians –, and a minor increase could be observed in the hills bordering the Hungarian middle mountains.

The presented future potential climatic suitability conditions predict the further fragmentation and distribution area contraction of the species in the Pannonian Basin. These trends of changes related to an insect species are not unprecedented considering the effects of the late-Neogene and Quaternary environmental processes on the members of the entomofauna. Fossil evidence indicates that while the Quaternary glaciations forced the southward spread of cold-adapted insects of North America and the British Isles, the

Fig. 6 The modelled suitability values of *Aedes punctor* in 2061–2080 (A: rcp2.6, B: rcp4.5, C: rcp6.0 and D: rcp8.5) (1: the westernmost ranges of the Alps, 2: Kőszeg Mts., 3a: outer ranges of the Northwest Carpathians, 3b: inner ranges of the Northwest Carpathians, 3c: outer ranges of the North-Eastern and Eastern Carpathians, 3d: Southern Carpathians, 4: Apuseni Mts., 5: Bakony-Balaton Mts., 6: Mecsek Mts., 7: Mátra Mts., 8: Karancs Mts., 9: Bükk Mts., 10: Zala Hills, 11: Hungarian Great Plain)

warm climate episodes enriched the insect fauna of the same regions with thermophilus species (Elias 2010). It is also known that past changes in climatic conditions significantly impacted the distribution and genetic diversity of mosquito populations (Porretta et al. 2012; Morgan et al. 2011). Model results showed that the climatic fluctuations of the last 3.3 Mys could also result in the repeated spread and retreat of the mesothermal mosquito fauna of Western Eurasia (Trájer and Padisák 2019). In the case of such Transdanubian members of the Middle Hungarian Mts. like the Bakony-Balaton and the Mecsek Mts., the decrease in the suitability values for 2061–2080 seems to be so notable that it is very plausible that *Ae. punctor* will disappear from the Transdanubian part of Hungary.

The second criterium of Alcalay et al. (2017) is related to the larval and general habitats or, in other words, the realized ecological niche of the species. However, at the first step,

because this second criterium assumes niche conservatism that may not necessarily occur, the possibility of a niche shift should be discussed. The shift in the climatic niche of a mosquito could happen, e.g., via the alteration of the timing of the laying eggs and egg hatching, the length of the activity and the diapausing season. Changes in such kinds of adaptation strategies were observed in the case of *Ae. albopictus* in Italy at the time of the Italian invasion of the species (Luciano et al. 2003), however, it is not known what adaptation responses are expected from *Ae. punctor*.

The plasticity of the feeding behaviour can also be important. In the case of the previously mentioned invasive *Ae. albopictus* it is known that while in the rural areas of the province of the Italian capital the mosquito rather prefers the blood of domestic ungulate mammals than humans, in urban sites, including Rome, the females of the mosquito dominantly feed on humans (Valerio et al. 2010). The ability

Fig. 7 The difference between the modelled suitability values of 2041–2060 (A: rep2.6, B: rep4.5, C: rep6.0 and D: rep8.5) and 1979–2013 (1: the westernmost ranges of the Alps, 2: Kőszeg Mts., 3a: outer ranges of the Northwest Carpathians, 3b: inner ranges of the Northwest Carpathians, 3c: outer ranges of the North-Eastern and Eastern Carpathians, 3d: Southern Carpathians, 4: Apuseni Mts., 5: Bakony-Balaton Mts., 6: Mecsek Mts., 7: Mátra Mts., 8: Karancs Mts., 9: Bükk Mts., 10: Zala Hills, 11: Hungarian Great Plain)

to switch between blood source organisms can be of great importance when a mosquito species loses its former, rather rural, or sylvatic habitats due to climate change. In Hungary, females were also collected by traps and from the skin (Tóth 2004) indicating that the mosquito has the capacity to switch between the non-human and human blood source organisms. Renshaw et al. (1995) showed that females of *Ae. punctor* are willing to feed on a human host only two days after the emergence and can synthesize lipid after only one day. These laboratory observations can explain the early initiation of host-seeking of this species and show that *Ae. punctor* can adapt to anthropogenic environments. It is also known that larger females of *Ae. punctor* enjoy greater reproductive success than do smaller females and it may be altered by environmental factors (Packer and Corbet 1989). In the case of *Ae. albopictus* it was found that in the generally warmer and drier urban sites, decreased larval survival, smaller body sizes, and lower per capita growth rates of mosquitoes compared to the populations of the suburban and rural areas. However, there are no data about the correlation between climatic suitability and other environmental factors (e.g., urban/rural habitat status) and the size and fitness of the females of *Ae. punctor*, it can be hypothesized that the disturbed urban environment can be less advantageous mosquito-like than more natural environments (Murdock et al. 2017). These facts call into question the assumption of niche conservatism of this species. However, despite the theoretical possibility of niche shift, the question remains as to why this adaptation has not taken place in Hungary so far in the areas adjacent to the mosquito's habitat if it would be possible.

Climatic forecasts predict about a 20–35% increase of the winter precipitation in the studied Hungarian middle mountain regions for 2071–2100 (Bartholy et al. 2011) which at first glance may seem favourable for the mosquito. However, the same study predicts that average winter temperatures will increase by 3–4 °C. It is also very likely that due to climate change, the length of the snow season, as well as the accumulated snow depth are predicted to notably decrease over the entire European continent in the twenty-first century (Solomon et al. 2007). These climatic trends can be disadvantageous for *Ae. punctor* because their larvae hatch during the snowmelt and require the cool and acidic water of puddles formed after snow melting (Kaiser et al. 2001). On the other hand, it is also known that the adults of this mosquito rarely leave the shaded and wind-protected space that is formed under the canopy of the trees (Kaiser et al. 2001). The larvae of *Ae. punctor* were found in the Hungarian middle mountains mainly in shady habitats, most often in blunt-type natural small water and swamp-type natural stagnant water (Tóth 2004). These kinds of habitats characteristically can be found in the mid-mountain beech forests and mixed beech-hornbeam forests in Hungary. In this regard,

it is important to consider that floristic studies project the drastic reduction in suitable areas for European beech (*Fagus sylvatica* L.) dominated forests in Hungary (Czúcz et al. 2011). Although it cannot be stated that the presence of *Ae. punctor* is tightly correlated with the presence of beech since this species occurs also, e.g., in the spruce forests in the boreal regions of Europe (Pestov and Paniukova 2013), the acidotic soils, the closed forest canopy and the accumulation of snow are more characteristic of the beech-dominated forests in Hungary. By the end of the twenty-first century, the present-day temperate beech and mixed forests will be replaced by thermophilus mixed broad-leaved forests, and the fitness of beech forests will decline in this region (Brandl et al. 2018). This projection is in good agreement with the projected enormous biome shift in Hungary modelled by Bergengren et al. (2011) that indicates that *Ae. punctor* will lose most of their suitable habitats in Hungary till the end of the twenty-first century. Because the larva season of the species starts as early as the start of March and the annual peak can be observed in mid-April in Hungary (Tóth 2004), these facts also indicate that the larvae of this univoltine mosquito species prefer fresh, cold, stagnant waters.

The decreasing area of the European beech and the related mountainous habitats may cause the parallel shift of *Ae. punctor* populations to the higher elevations and the significant habitat loss of the mosquito in Hungary, although it should be noted again that the presence of the species is not related to the presence of European beech. Modelling the potential effect of climate change on mosquito diversity in a certain area is a complex methodological problem. Several factors affect the distribution of the mosquito population, and in certain cases, temperature plays an important but relatively controversial role (Rochlin et al. 2016). Due to this fact, rather than the simple climatic values, the so-called bioclimatic values were used that is closely related to the criteria of the climatic classification systems and commonly used input data in environmental modelling (Jácome et al. 2019). The evaluation of short-time observations (e.g., faunistic surveys) requires specialized statistical techniques, such as, e.g., maximum entropy or MaxEnt algorithms in general (Mwey et al. 2013). In the present case, such procedures were not necessary because mosquito collecting surveys covered a relatively longer observation time window and mosquito collections were performed in three individual regions. What cannot be easily fit to the ecological forecasting models is the environmental plasticity of mosquito species. Aedine mosquitoes are generally thought of as a genus that could adapt very well to new or changed circumstances. One of the well-known examples for this fact is *Aedes aegypti* (Linnaeus in Hasselquist, 1762), which originally inhabited the tropical forests of Africa, first adapted to the human environment, and then reached the boundaries of the temperate and continental belt because of

adaptation to the cooler climates and human transport (Powell and Tabachnick 2013). Regarding the adaptability of *Ae. punctor*, its large Holarctic distribution area demonstrates that this mosquito species has a high degree of adaptability in boreal-cool continental areas, but this does not mean that *Ae. punctor* is certainly able to be competitive with thermophilus mosquito species if in their original habitats the monthly mean temperatures notably increase due to climate change. It is a good example of this vicariant distribution that—may be caused by both climatic and biotic factors—in those sites where *Ae. punctor* is present, generally, *Aedes* (*Ochlerotatus*) *annulipes* (Meigen 1830) is absent and vice versa in Hungary (Tóth 2006, 2004).

Conclusions

The presented model results can be summarized by that *Ae. punctor* plausibly will persist in large areas of the Holarctic, including the higher regions of the Central European mountains in the future, but it is very likely that populations in the lower mid-mountains will disappear or be reduced to small areas in Hungary. Proper forest management and protection of the habitats of the mosquito species may allow the species to survive in the cool northern valleys in its current habitats in Hungary that are becoming extrazonal areas for this mosquito species in the second half of the twenty-first century.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10841-022-00378-3>.

Author contributions The Author planned, prepared, and wrote this work.

Funding Open access funding provided by University of Pannonia. This work was supported by the Széchenyi 2020 project of the Hungarian Ministry of Innovation and Technology under Grant Number NKFIH-471-3/2021 project.

Data availability The data related to the results of the study can be requested from the author. The primary mosquito data used in the study is available in the cited monographs.

Code availability Not applicable.

Declarations

Conflict of interest The author has no conflict of interest which should be reported.

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