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ORIGINAL RESEARCH

The Paradox Negative Effects of the mid-Pliocene Warming on the Climatic Suitability of Six Mediterranean Sandfly Species in Europe

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ABSTRACT

The Pliocene era could be the last time when sandfly (Diptera: Psychodidae) species were widespread in Europe. Within the Pliocene, the mid-Pliocene period is an important model period in the investigation of the future effects of anthropogenic climate change. In this study, the mid-Pliocene potential distribution of six Mediterranean sandfly species was modelled based on the M2 mid-Pliocene cold and mid-Pliocene warm paleoclimatic reconstructions. It was found that the cold period's potential occurrence of sandfly species could be notably more extended than the distribution of the taxa in the warm period. The difference is less expressed in the case of the West Mediterranean species, but it is particularly visible in the circum-Mediterranean and East Mediterranean taxa. It can be concluded that not the changes in the mean annual temperature, but the increase of the precipitation patterns and the wetter climate of the mid-Pliocene warm period resulted in the observed differences. The results imply that the use of mid-Pliocene warming as a model of the present climatic changes can be handled with caution in the performing of biogeographic proxies for vector sandflies related to the anthropogenic climate change.

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Introduction

The investigation of past environmental changes on the former occurrence of vector arthropods can help to perform better projections for the potential future distribution of these species. Among vector arthropods, sandfly species are the vectors of leishmaniasis, which is one of the most important parasitic diseases on Earth. In 2018, the so-called cutaneous and visceral forms of leishmaniasis were present in 47 and 43% of the countries of the planet, endangering the health of more than 1 billion people and causing about 30,000-1 million new cases at the annual level (WHO leishmaniasis). Only in Brazil, the average annual age-adjusted mortality rate of visceral leishmaniasis was 0.15 per 100,000 in the period of 2000-2014 (Martins-Melo et al., 2014). In the global level, about 20,000-40,000 deaths occur each year due to leishmaniasis (Alvar et al., 2012). There is consensus among parasitologists that anthropogenic global warming causes the emergence of leishmaniasis (e.g., González et al., 2010; Ready, 2008) and triggers the poleward shift of the vectors and the parasites (e.g., Chalghaf et al., 2018; Cross & Hyams, 1996). Sandfly species are typical subtropical fauna elements (Aspöck et al., 2008) which means that these species have relatively high thermal development and activity thresholds. Global warming creates warmer climatic conditions which can support the future presence of these arthropods in the present-day temperate regions of Europe (e.g., Koch et al., 2017). Although, Mediterranean sandfly species are not only cold-sensitive taxa but several species among them are also sensitive to the wet winters or cool and humid summers (Trájer et al., 2013). The climatic requirements of these species are rooted in their late Paleogene-Neogene evolutionary history. For example, the members of the subgenus *Paraphlebotomus* originated in the hot and dry summer climate regions of South Asia and migrated across the Middle East to Europe in the Miocene era. The arid conditions and the geographical changes of the Messinian Salinity Crisis might support the European and North African migration of sandfly species (Esseghir et al., 2000).

As it was mentioned, several models predict the expansion of the European sandfly species in the 21st century (e.g., Chalghaf et al., 2018; Koch et al., 2017; Trájer et al., 2013). It is a common basis of the model predictions that the environmental suitability of sandfly species is strongly dependent on such climatic factors as the mean temperature and the precipitation conditions. It is because sandfly species are sensitive to atmospheric drought, low thermal conditions and strong solar radiation (Dinesh et al., 2001; Trájer et al., 2018a). The environmental sensitivity of sandfly taxa can be attributed to the habitat preference and the evolutionary history of the species. Ancient *Phlebotomus* species were found in the Cretaceous ambers of Lebanon, France, Jordan and Myanmar (Azar et al., 2003a; Kaddumi et al., 2007; Stebner et al., 2015).

The reconstructions of the paleoenvironment where the resins were buried points to warm tropical climate conditions which were widespread during the Cretaceous epoch (Hinkelman, 2019; Kaddumi, 2007; Azar et al., 2003b). Based on this observation, sandfly species were adapted to the humid tropical-subtropical climatic regions, and it is plausible that this climatic preference was characteristic for sandfly species until the turn of the late Eocene epoch. That time, due to the first glaciation of Antarctica, the global nature of the Earth's climate has undergone substantial changes (Robert & Kennett, 1997). The global cooling and aridification resulted in the contraction of the humid tropical belt and the general aridification of the planet after the Eocene/Oligocene boundary (Liu et al., 2009). However, the adaptation of sandfly taxa to drier and somewhat cooler conditions can be the results of earlier evolutionary development. Based on the fossil sandfly record of the Baltic Amber (Pielowska et al., 2018), sandfly species already colonized the Mediterranean-like climate or a wetter subtropical, but not humid tropical climate areas of northern Europe for the Late Eocene (Priabonian) period (Stuckenberg et al., 1975; Wolfe et al., 2009). Then, parallel to the further cooling trends in the Neogene era, these Mediterranean sandfly taxa colonized the former coastal areas of the Tethys and Paratethys seas in central and western Eurasia (Depaquit et al., 1998). Even until now, a very few species (e.g., *Phlebotomus* (*Larroussius*) *mascittii* Grassi, 1908) were adapted to the climate of such temperate-oceanic climate areas as the territory of Germany (Naucke & Pesson, 2000).

The Pliocene era (2.58-5.333 Ma) could be a key period in the determination of the present occurrences of Mediterranean sandflies. It was the last period in the Neogene era before the Pleistocene glaciations when subtropical conditions were widespread in Europe. Then, the climatic fluctuations should result in the drastic decrease of the sandfly-inhabited areas in Europe and the repeated spread and retreat of sandfly taxa in the Old Continent. In the Pleistocene era, sandfly species suffered notable habitat contractions and repeated habitat dilatations (Mahamdallie et al., 2011; Trájer & Sebestyén, 2019; Kasap et al., 2015). The Pliocene was also a unique period in the aspect that, at the end of the Miocene era, the Pannonian part of the Central Paratethys disappeared in East-Central Europe (Popov et al, 2006), creating similar geographic connections between western and southeastern Europe which can be seen on the present-day continent. Prior to this era, the Paratethys Sea strongly influenced the European climate and affected the speciation (Depaquit et al., 2010) and the adaptation of sandfly species to different climatic regimes (Trájer et al., 2018). Because, at a global level, the geographic configuration of the continents and ocean basins became very similar to the present times in the Pliocene (Haywood et al. 2009a,b), the Pliocene era is frequently held as a model for the future potential effects of the anthropogenic climate change. About 3.5 Ma, the Central American seaway closed (Nesis, 2003), creating such global oceanic circulation regimes that are characteristic of the present times (Yang et al., 2014).

Within the Pliocene period, the mid-Pliocene warm period, which lasted from about 3.3 to 3.0 Ma, has become an important model interval for paleoclimate modelling studies (Haywood et al., 2009A). It is also very important in this aspect that the atmospheric carbon dioxide levels were about the same as today. The mid-Pliocene atmospheric carbon-dioxide concentration was about 360-400 ppm (Jansen et al., 2007). At present (2020) it is 412 ppm, and it is still increasing. Because the mid-Pliocene period represents an equilibrium state of a warmer world with a similar carbon-dioxide concentration level, it makes this period the best model for the near-future conditions. On the other hand, the mid-Pliocene is the last geological period when the mean global temperatures were about 2 °C to 3 °C above the pre-industrial temperatures. (Haywood et al., 2009a). Because most of the predicted mean global temperature-increases for the late 21st century fell into this interval, the mid-Pliocene represents the most adequate and accessible example of the near-future atmospheric, oceanic and land surface climatic conditions (Jansen et al., 2007). Due to these facts, several efforts were made to reconstruct the climatic patterns to check the reliability of global climate models (e.g., Jiang et al., 2005; Dowsett et al., 1999).

However, climate models revealed that the mid-Pliocene era should be held with caution when we want to use this period as a model of the predicted future environmental conditions. Notable differences were found between the modelled mid-

Pliocene and the predicted present climatic conditions in the validation process of the models (e.g., Haywood & Valdes, 2004; Haywood et al., 2000; Sloan et al., 1996). Among others, the extension of the tropical-subtropical regions was modelled to receive more annual precipitations sums (Haywood et al., 2000) and the geographical and intensity patterns of the monsoons seemed to be potentially dramatically different from the current conditions (Haywood et al., 2000; Sloan et al., 1996, Chandler et al., 1994). Depending on the model environment, the potential vegetation belt patterns could be different (Haywood et al., 2009A).

Aims and hypothesis

It can be hypothesized that notable differences could exist in the sandfly distribution between the warm and cold periods of the Pliocene era. The mid-Pliocene era was the start of the global cooling which led to the later Pleistocene glacial-interglacial cycles. The aim of this study was to show the effects of the climate of a warm house and cool house periods on the distribution of Mediterranean sandfly taxa.

Materials and methods

The logical frame of the study

The following steps were performed in the study:

1) The 2x7, originally monthly-nature climatic distribution extrema of the selected six Mediterranean sandfly species were converted to bioclimatic-nature values based on the results of Trájer *et al*. (2013).
2) The monthly mean Thornthwaite agrometeorological (aridity) index extrema were calculated for all species and added to the climatic extrema list.
3) The georeferenced monthly mean Thornthwaite agrometeorological (aridity) index values were calculated for the mid-Pliocene cold and warm periods.
4) Then, the selected 2x8 extrema of the selected six Mediterranean sandfly species were displayed in the mid-Pliocene cold and warm period climate models.
5) The difference maps of the two periods were created by species.
6) Finally, the potential diversity maps of the two periods were created according to the studied six sandfly species.

Figure 1 visualizes the workflow of the study.

The species involved in the study

The potential former distribution of the following species was modelled:

1) *Phlebotomus* (*Larroussius*) *ariasi* Tonnoir, 1921 is a typical western, southwestern European and northwestern African sandfly species. This species does not prefer the coastal areas of the western Mediterranean Basin. It is the sandfly of the Mediterranean middle-elevation areas.
2) *Phlebotomus* (*Larroussius*) *neglectus* Tonnoir, 1921 is a member of the Apennine Peninsula, Sicily, Southeast Europe, Asia Minor, and it can also be found in certain areas of the Levant.
3) *Phlebotomus* (*Phlebotomus*) *papatasi* (Scopoli, 1786) is a circum-Mediterranean species with an extended distribution area including both North Africa, Levant, Asia Minor, South and Southeast Europe.
4) *Phlebotomus* (*Larroussius*) *perfiliewi* Parrot, 1930 is a sandfly species which can be found in the coastal areas of the eastern part of the Mediterranean Basin, including also the continental areas of Southeast Europe, Asia Minor and the Caucasus. This species absents in Southwest Europe and the northwestern part of the Atlas Mountains.
5) *Phlebotomus* (*Larroussius*) *perniciosus* Newstead, 1911 can be found in the West Mediterranean Basin and the continental areas of West Europe, also including the Iberian and Apennine Peninsulsa, Sardinia and the northwestern areas of North Africa.
6) *Phlebotomus* (*Larroussius*) *tobbi* Adler and Theodor, 1930 is a member of the East Mediterranean sandfly fauna, occurring also in Southeast Europe, Cyprus, Asia Minor, the Caucasus and Levant.

The brief characterization of the distribution of the species was based on the VECTORNET (2020) occurrence data.

Justification of the applicability of the species involved in the modelling

Before the modelling of the mid-Pliocene ranges of the selected six sandfly species, it is an important circumstance which must be considered whether the modelled species existed or not in the late Neogene era. On the one hand, it is plausible that the evolutionary rate of sandflies could be relatively slow and sandfly species generally could be environment-conservative and cold-sensitive insects also in the past. The following facts confirm these assumptions: 1) The oldest fossil *Phlebotomus* species, namely †*Phlebotomus khludae* Kaddumi 2005, were found in the Albanian, mid-Cretaceous Jordanian amber (Kaddumi, 2007). Based on the paleoclimatic reconstruction of Wu *et al*. (2018), the land, which is Jordan now, had a tropical climate at that time. Their other early occurrences in the fossil record, e.g., the fossil sandflies of the Cretaceous ambers of France and Myanmar (Azar et al., 2003a) also consistently refer to tropical paleoenvironments. Most of the presently existing *Phlebotomus* species and their closest relatives, the Neotropical *Lutzomyia* sandflies are also typical tropical-subtropical fauna elements (Rajesh & Sanjay, 2013). 2) In the present times, sandflies totally lack from the arctic, boreal and extreme continental areas. This occurrence character clearly can be seen in the observed and modelled occurrences of both *Phlebotomus* and *Lutzomyia* taxa (e.g.: Koch et al., 2017; Moo-Llanes et al., 2013). Although fossil *Phlebotomus* species are known from the Late Eocene age Baltic amber (Stuckenberg, 1975) which territory currently has hemiboreal (humid continental) climate (Kottek et al., 2006), this area had a subtropical climate at the time of resin formation (Bogri et al., 2018). 3) Sandflies could be conservative species not only in the sense of their habitat preferences. Fossilized *Leishmania*-like trypanosomatids which were found inside the lumen of the alimentary tract of Cretaceous sandfly larvae in the Burmese amber (Volf et al., 2002) indicates that the parasite-vector coevolution of sandflies and *Leishmania* vectors had already started at least in the early Cretaceous period (Poinar et al., 2007).

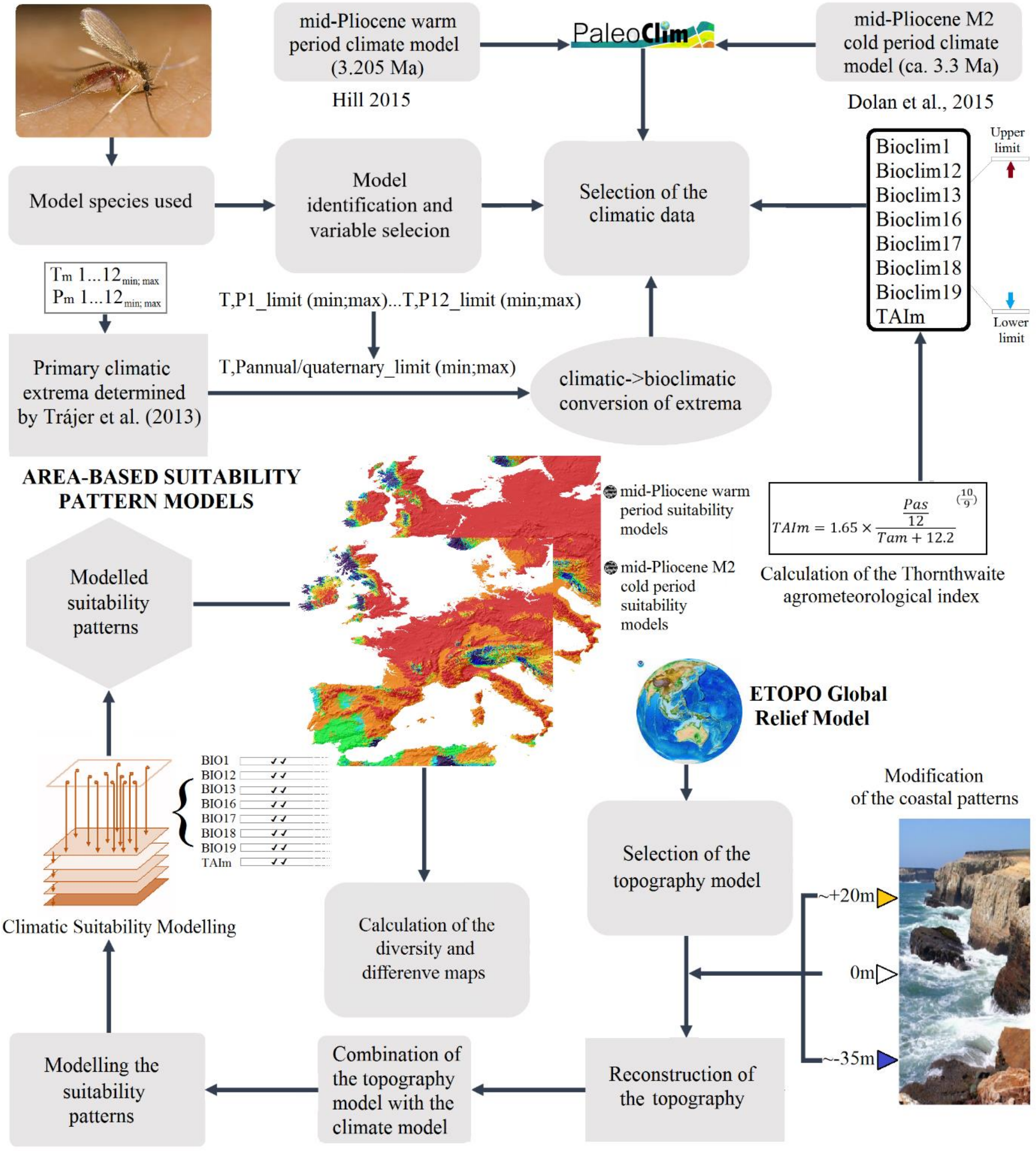

Figure 1. The visualization of the workflow of the study.

On the other hand, phylogenetic evidence suggests that the members of the Mediterranean sandfly fauna could exist before the start of the Pliocene era. Indirect evidence for this hypothesis is as follows: 1) Molecular studies showed that the common ancestors of the Mediterranean Paraphlebotomus species diverged from each other thanks to the existence of the former Paratethys Sea (Depaquit et al., 2002, 2000; Esseghir et al., 2000). This ancient sea played the role of a geographic barrier between North Eurasia and South Asia from the Early Eocene period to the Late Miocene era when the Central Paratethys became isolated from the main sea body (Harzhauser & Piller, 2007). 2) The ITS 2 sequences heterogeneity-based parsimonious phylogram of four Paraphlebotomus species showed that – among others – the divergence of the continental and the Mediterranean island sandfly strains – e.g., the separation of Malta, the Crete and continental Greece strains of *Phlebotomus similis* Perfiliev, 1963 or the Sicily and Morocco populations of *Phlebotomus sergenti* Parrot, 1917 — could happen about at the same time (Depaquit et al., 2002, Fig. 3). There is only one plausible explanation for this phylogenetic phenomenon: the Messinian Salinity crisis-induced paleogeographic changes could induce the parallel, from continent to island migrations and the later divergence of the continental and island sandfly populations of the different species (Kasap et al., 2015; Depaquit et al., 2002) after the Zanclean terminal reflooding of the Mediterranean Basin (Caruso et al., 2020). If this assumption is valid, it should indicate that Paraphlebotomus species already existed in the Late Miocene epoch. Although these species all belong to Paraphlebotomus subgenus, there is no rational argument for assuming that the rate of evolution of the members of Larroussius and Phlebotomus subgenera could be faster. 3) Comparing the climatic requirements of two Paraphlebotomus species, namely of *Ph. sergenti* and *Ph. similis* with the studied six Larroussius and Phlebotomus species, it is striking that their climatic needs are quite similar (Appendix 1-Table 1). This similarity may indicate that sandfly mosquitoes could not have moved significantly away from their ancestors in terms of their ecological needs. This observation can also indicate that the evolutionary rate of the Larroussius and Phlebotomus species would not have been faster than that of the Paraphlebotomus species. Finally, it can be concluded that it is plausible that the studied six sandfly species may also exist in the late Miocene era.

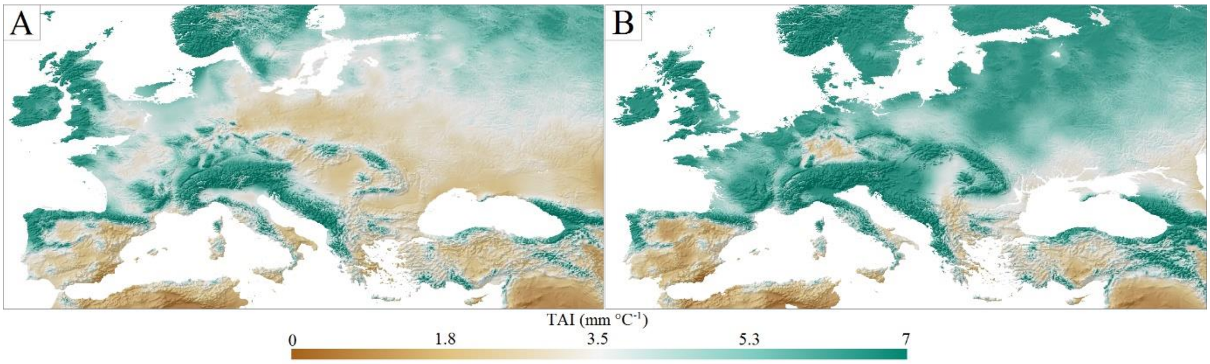

Figure 2. The calculated Thornthwaite Agrometeorological Index values in the mid-Pliocene cold (A) and warm (B) periods.

Climatic, climatic extrema and topographic data

The mid-Pliocene climatic data were gained from the PleoClim climatic database. The following climate models were used for modelling: Pliocene: mid-Pliocene warm period (3.205 Ma) (Hill, 2015), v1.0 and mid-Pliocene marine isotope stage M2 cold period (3.3 Ma) (Dolan et al., 2015), v1.0. The used spatial resolution was 2.5 arc-minutes. The topographic data was based on the ETOPO 1 arc-minute global topographic model (Amante & Eakins, 2009). In accordance with the original models, the used seashore mask was +25 and -35 meters in the case of warm and cold periods. The climatic extrema used in the suitability modelling process were based on the study of Trájer *et al.* (2013). The authors determined the lower and upper climatic distribution limiting values of the Mediterranean sandfly species based on the known occurrences of the sandfly species in Europe and the REMO climate model (Jacob & Podzun, 1997). The original data was given in monthly extrema values. Because the Pliocene climatic models provided so-called bioclimatic variables (Brown et al., 2018) it would be necessary to convert the monthly data into annual and quarterly values. The determined and used climatic extrema can be found in Appendix 1-Table 1.

The used climatic factors

The used climatic variables for suitability modelling purposes were as follows: the lower and upper limits of the annual mean of the temperature ($Tam_{limit.min,max}$; °C; Bioclim1), the lower and upper limits of the annual precipitation sum ($Pas_{limit.min,max}$, mm; Bioclim12), the lower and upper limits of the precipitation of wettest month ($Pwm_{limit.min,max}$, mm;

Bioclim13), the lower and upper limits of the precipitation of wettest quarter ($Pweq_{limit.min,max}$, mm; Bioclim16), the lower and upper limits of the precipitation of driest quarter ($Pdq_{limit.min,max}$, mm; Bioclim17), the lower and upper limits of the precipitation of warmest quarter ($Pwaq_{limit.min,max}$, mm; Bioclim18), the lower and upper limits of the precipitation of coldest quarter ($Pcq_{limit.min,max}$, mm; Bioclim19). To make the model aridity-sensitive, the lower and upper limits of the mean monthly Thornthwaite agrometeorological (aridity) index ($TAIm_{limit.min,max}$, mm°C-1) was added to the factors which can be derived from the temperature and precipitation values (Kemp, 1990). Because the Mediterranean sandfly taxa are sensitive to the low atmospheric humidity conditions (Trájer et al., 2018~~a~~; Elnaiem et al., 1998), the use of this factor seems to be important.

The equation of the mean monthly *TAI* index modified with the nomenclature of the used factors was as follows:

$$TAIm = 1.65 \times \frac{\frac{Pas}{12}^{\left(\frac{10}{9}\right)}}{Tam + 12.2}$$

where

TAIm is the monthly mean Thornthwaite agrometeorological (aridity) index in mm°C^{-1},

Pas is the annual precipitation sum in mm,

Tam is the monthly mean temperature in °C.

Model identification

Each of the distribution-limiting factor values is climate model-independent. This means 8x2 climatic factors in the model in the case of each species that is an adequate factor number for climate envelope modelling purposes. Modelling was based on the binary logic of the Boolean algebra (Whitesitt, 2012) according to the flowing formalism:

$$1(Tam) = \begin{cases} 0 & if \quad Tam_{limit.min} > Tam > Tam_{limit.max} \\ 1 & if \quad Tam_{limit.min} \leq Tam \leq Tam_{limit.max} \end{cases}$$

$$1(Pas) = \begin{cases} 0 & if \quad Pas_{limit.min} > Pas > Pas_{limit.max} \\ 1 & if \quad Pas_{limit.min} \leq Pas \leq Pas_{limit.max} \end{cases}$$

$$1(Pwm) = \begin{cases} 0 & if \quad Pwm_{limit.min} > Pwm > Pwm_{limit.max} \\ 1 & if \quad Pwm_{limit.min} \leq Pwm \leq Pwm_{limit.max} \end{cases}$$

$$1(Pweq) = \begin{cases} 0 & if \quad Pweq_{limit.min} > Pweq > Pweq_{limit.max} \\ 1 & if \quad Pweq_{limit.min} \leq Pweq \leq Pweq_{limit.max} \end{cases}$$

$$1(Pdq) = \begin{cases} 0 & if \quad Pdq_{limit.min} > Pdq > Pdq_{limit.max} \\ 1 & if \quad Pdq_{limit.min} \leq Pdq \leq Pdq_{limit.max} \end{cases}$$

$$1(Pwaq) = \begin{cases} 0 & if \quad Pwaq_{limit.min} > Pwaq > Pwaq_{limit.max} \\ 1 & if \quad Pwaq_{limit.min} \leq Pwaq \leq Pwaq_{limit.max} \end{cases}$$

$$1(Pcq) = \begin{cases} 0 & if \quad Pcq_{limit.min} > Pcq > Pcq_{limit.max} \\ 1 & if \quad Pcq_{limit.min} \leq Pcq \leq Pcq_{limit.max} \end{cases}$$

$$1(TAIm) = \begin{cases} 0 & if \quad TAIm_{limit.min} > TAIm > TAIm_{limit.max} \\ 1 & if \quad TAIm_{limit.min} \leq TAIm \leq TAIm_{limit.max} \end{cases}$$

The equations were displayed as areal-based reconstructions. The potential area-based suitability patterns were determined according to the following mathematical formalism:

$$A(Tam; Pas; Pwm; Pweq; Pdq; Pwaq; Pcq; TAIm) = Tam \bigcap Pas \bigcap Pwm \bigcap Pweq \bigcap Pdq \bigcap Pwaq \bigcap Pcq \bigcap TAIm$$

Where *A(Tam;Pas;Pwm;Pweq;Pdq;Pwaq;Pcq;TAIm)* shows the potential distribution area of the given species, which contains the remaining areas after taking into consideration the annual mean of the temperature limitations, and precipitation limitations, as well as the limitations of the mean monthly Thornthwaite agrometeorological (aridity) index. Summarizing the used climatic factors, a total of 16 variables was involved. The models were displayed in QGIS version 3.2.3. with Grass 7.4.1. software (Lacaze et al., 2018) as suitability heat maps where the satisfied 16 climatic extrema mean the 100%; 0 completed factor is equal to the 0% environmental suitability value.

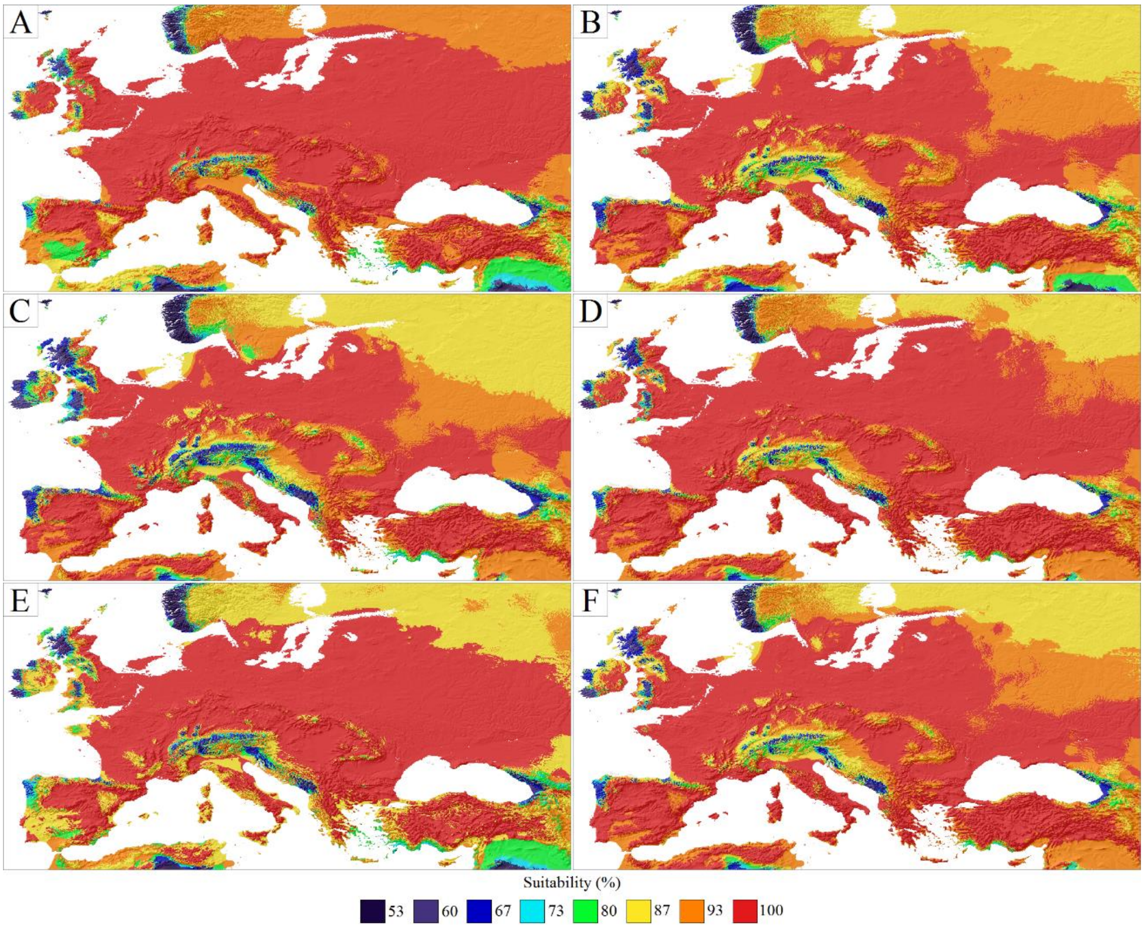

Figure 3. The potential suitability patterns of six sandfly species in the mid-Pliocene cold period (A: *Ph. ariasi*, B: *Ph. neglectus*, C: *Ph. papatasi*, D: *Ph. perfiliewi*, E: *Ph. perniciosus*, F: *Ph. tobbi*).

Results

Differences in the aridity index

It was found that the TAI patterns of Europe were largely different in the warm and cold mid-Pliocene periods. In general, the climate of Europe was wetter in the warm period. The differences in the aridity index are the most notable in the East and East-Central, but it can also be seen in the continental areas of western Europe (Fig. 2A). There are no notable differences between the TAI values of the Mediterranean Mountains, the coastal areas of the west part of the Mediterranean Basin, in the British Isles and the higher parts of southwest Scandinavia (Fig. 2B).

The modelled suitability values of the cold period

In contrast to the warm period, the modelled M2 mid-Pliocene cold period suitability patterns of the studied sandfly species are quite similar. In general, the potential distribution of the species includes almost whole continental Europe, the Atlantic coasts, the Apennine Peninsula, the Mediterranean Islands, Southeast Europe and Asia Minor. The suitability patterns of the species show varying conditions in South Scandinavia and the Apennine and Iberian Peninsulas. The species shows low suitability values in the western coastal areas of the British Isles, Southeast Iberian Peninsula and along with the higher ranges of the Alpine Orogeny Belt (Fig. 3).

The modelled suitability values of the warm period

The modelled suitability values of the studied sandfly species vary by species. The present-day western Mediterranean *Ph. ariasi* and *Ph. perniciosus* shows large and similar potential distribution which includes large areas in the continental parts of Europe, western Europe, the higher elevations of Asia Minor and the Mediterranean Ranges, the Carpathian Basin and certain parts of the British Isles and southwest Scandinavia. The potential distributions of *Ph. neglectus*, *Ph. papatasi*, *Ph. perfiliewi*, *Ph. perniciosus* and *Ph. tobbi* includes the northern ranges of the Iberian Peninsula, the Atlantic and Mediterranean coastal territories of France, the Apennine Peninsula, the eastern part of the Carpathian Basin, Southeast Europe, Asia Minor and the North Pontian and Caspian areas of East Europe (Fig. 4).

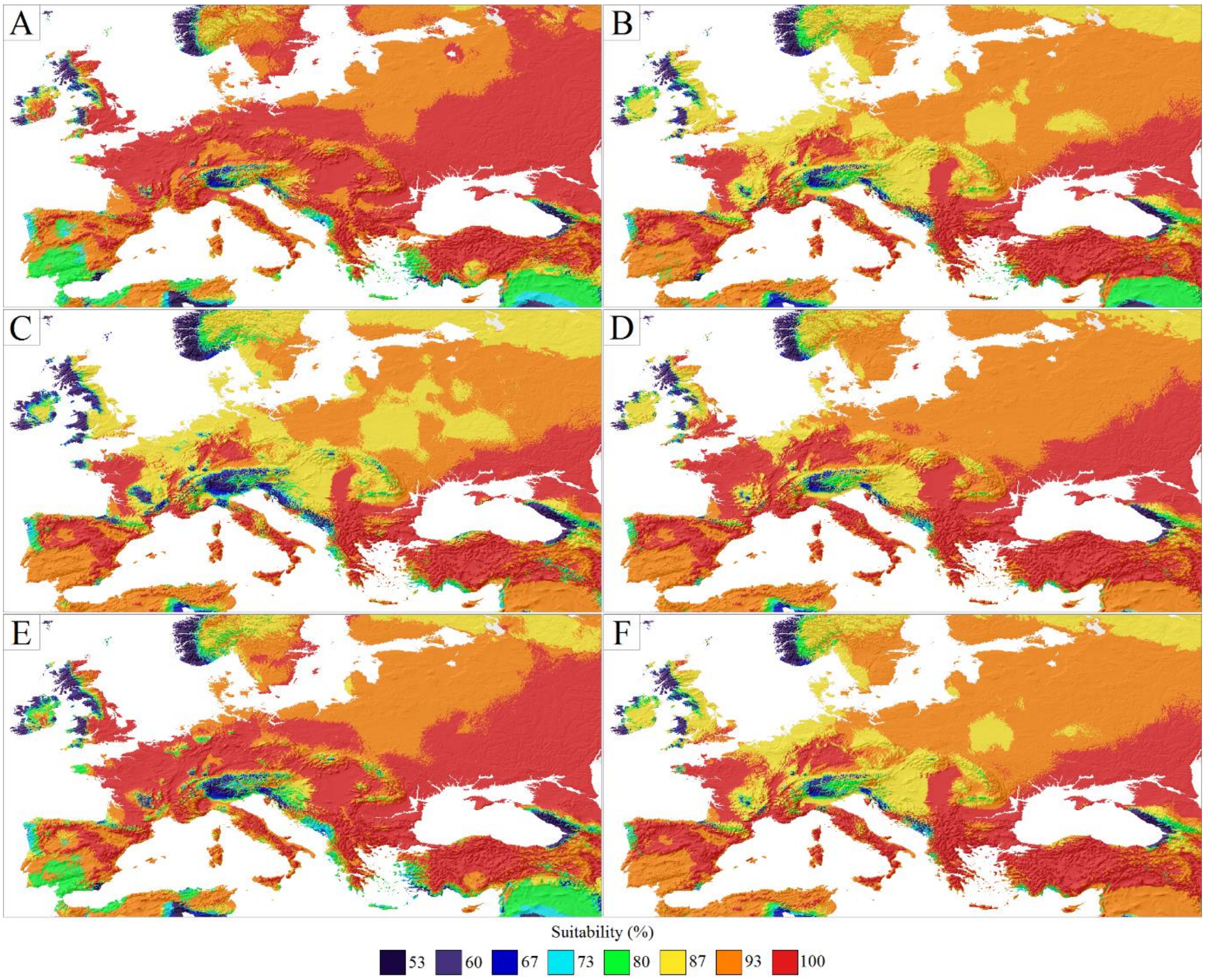

Figure 4. The potential suitability patterns of six sandfly species in the mid-Pliocene warm period (A: *Ph. ariasi*, B: *Ph. neglectus*, C: *Ph. papatasi*, D: *Ph. perfiliewi*, E: *Ph. perniciosus*, F: *Ph. tobbi*).

Differences in the warm and cold period models

Considering the 100% suitability value of the areas as the modelled distribution of the species, in the northern parts of continental Europe, the potential occurrence of sandfly taxa generally could be higher in the M2 mid-Pliocene cold period than in the mid-Pliocene warm era. This difference is also expressed in the case of *Ph. ariasi* and *Ph. perniciosus*, but it is particularly visible in the case of *Ph. neglectus*, *Ph. papatasi*, *Ph. perfiliewi*, *Ph. perniciosus* and *Ph. tobbi*. In the M2 mid-Pliocene cold period, the potential distribution of the studied sandfly species could only be somewhat smaller in certain parts of Scandinavia and East Europe. The models indicate that the changing climatic conditions which led to the mid-Pliocene warm period triggered the retreat of the sandfly-colonized areas in continental Europe. It should be added that the observed distributions are partly the consequence of the different sea level-induced topographic conditions in the northern areas of Europe (Fig. 5).

The diversity patterns seem to be relatively homogenous in the mid-Pliocene cold period and more heterogenous in the mid-Pliocene warm era. In the cold period, hight diversity areas can be seen in Central Europe, in large areas of southern Europe and Asia Minor (Fig. 6A). In the warm period, the highest diversities can be seen mainly in the North Pontic area, southeast Europe, the Apennine Peninsula and Asia Minor, as well as in certain parts of the Iberian Peninsula, Central Europe, the Atlantic coasts of western Europe and the extended areas of eastern Europe (Fig. 6B).

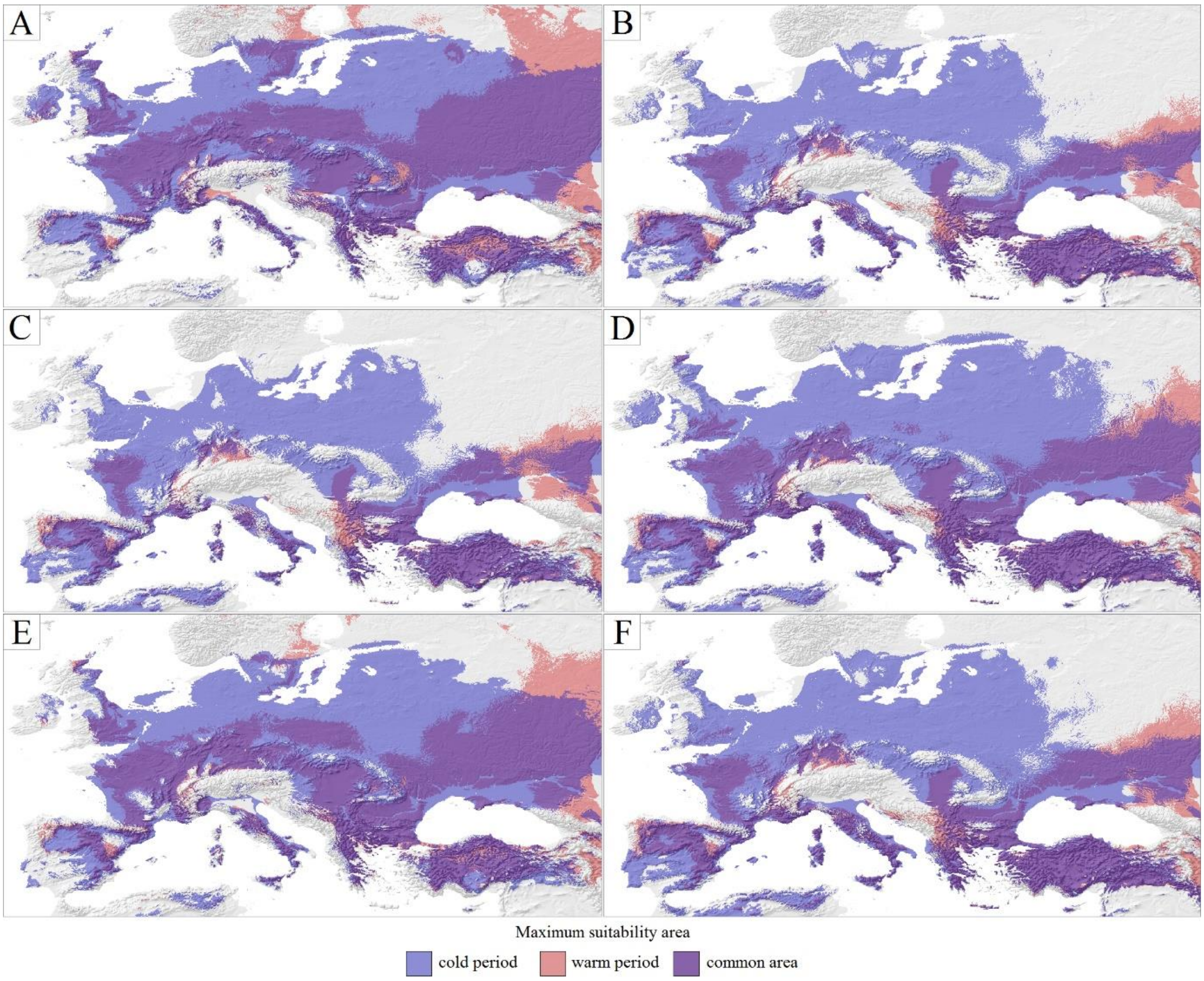

Figure 5. Differences in the potential suitability patterns of six sandfly species in the mid-Pliocene cold and warm periods (A: *Ph. ariasi*, B: *Ph. neglectus*, C: *Ph. papatasi*, D: *Ph. perfiliewi*, E: *Ph. perniciosus*, F: *Ph. tobbi*).

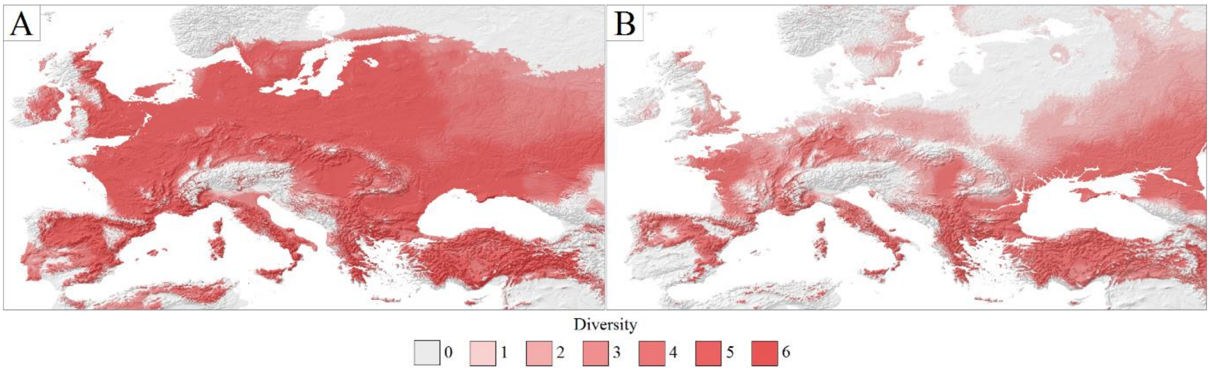

Figure 6. The potential sandfly diversity based on the modelled six species in the mid-Pliocene cold (A) and warm (B) periods.

Discussion

It was found that contrary to expectations, the mid-Pliocene warming of Europe could result in the notable southward retreat of the Mediterranean sandfly species that is the opposite of what future projections suggest based on the present climatic trends and greenhouse gas emissions (e.g., Chalghaf et al., 2018; Koch et al., 2017; Trájer et al., 2013). In the background of the apparent contradiction, that fact can be found that the nature of the mid-Pliocene warming was different from the present climatic trends. That time, global warming caused the excessive increase of the annual precipitation sums in almost the entire territory of Europe based on the paleoclimatic reconstructions which caused more humid conditions on the entire continent. The model results are supported by the coexistence approach-based climatic reconstructions. For, example, in Gérce, western Hungary, the mid-Pliocene precipitation sums can reach the annual 843-1160 mm interval (Erdei et al., 2007) which is only 607 mm today. However, wet summer conditions in general are unfavourable for the Mediterranean sandfly species (Trájer et al., 2013). As partial exceptions, *Ph. ariasi* and *Ph. perniciosus* can be mentioned, those species were adapted to the wetter and more Atlantic conditions of western and southwestern Europe. In contrast, the typical circum-Mediterranean species like *Ph. papatasi* and the members of the East Mediterranean sandfly fauna were adapted to the summer hot and dry subtropical conditions during the Tertiary period (Trájer et al., 2018b). These species could respond to the wetter, mainly wet subtropical and wet temperate conditions of the mid-Pliocene warm period with a large-scale retreat in the continental parts of Europe as the results of this study show.

It is problematic to validate the modelled suitability values with observed occurrences because fossil Psychodidae insects are not known in the Pliocene age fossil record of Europe. One of the richest Pliocene fossil sites of insects in the Old Continent is the alginate strata of the about 4 Ma-formed Pula maar crater in western Hungary. In the sediment of the former crater lake, Psychodidae species were not found. Among the fossil insect species, relatively large (4 mm) *Hispa atra* Linnaeus, 1767 (Coleoptera: Chrysomelidae) individuals were found. This size is characteristic to the present-day, Mediterranean populations of the insect in Bulgarian (Krzeminski et al., 1997) and not to the temperate Central-European populations, confirming that the mid-Pliocene climate was warmer than it is today in this area. This finding was also confirmed by the paleobotanical investigations (e.g., Erdei et al., 2007).

As it was mentioned, it is plausible that Phlebotomine sandflies have a tropical origin. However, the present members of the European sandfly fauna were rather adapted to the summer hot and dry conditions of the Mediterranean parts of the continent. It could happen in the Neogene period, but the evolutionary process itself could already start earlier, plausibly in the late Eocene era, based on the fossil Psychodid record of Baltic Amber which was deposited under hot summer subtropical climatic conditions (Stuckenberg, 1975). The production of the ancient resin by pines was also tied to the altering climatic conditions, and it could be forced by the stress of the trees due to global cooling and aridification trends after the Eocene climatic optimum (Wolfe et al., 2009). The fossil insect fauna of the Baltic amber is a puzzle of thermophilic and temperate insect taxa (Bogri et al., 2018). This circumstance could refer to the transitional former geographical position of the amber sedimentation area between the typical tropical and temperate climate areas. While in the late Miocene era, Southeast Europe could have Mediterranean-like hot and dry summer climatic character (Erdei et al., 2007), *Ph. ariasi* and *Ph. perniciosus* adapted to the humid subtropical climate of western Europe (Trájer et al. 2018 B).

It is plausible that certain sandfly species, which were adapted to the hot and wet tropical/subtropical climate areas of Paleogene Europe, might die out in the last 35 million years. If this hypothesis is correct, the extinction of the thermophilus taxa could be stepwise between 4-0.5 Ma, related to the major climatic deteriorations in 2.7-2.4 and 0.9-0.8 Ma as it was found in the case of plant taxa (Martinetto et al., 2017). In parallel, the ancestor of *Paraphlebotomus* species, another important sandfly subgenus in Eurasia, might adapt to the hot and dry summer but cooler winter condition of South-Central Asia and the evolution of this subgenus could be strongly influenced by the Alpine orogeny (Alten, 2010). Based on the plausibly better pre-adaptation of *Paraphlebotomus* species, it can be hypothesized that these taxa have over competed and replaced the original thermophilus sandfly fauna of Europe during the Late Neogene-Quaternary eras.

Considering the results of this study, it is an interesting question which should be answered that if in the mid-Pliocene cold period, all the modelled sandfly species could inhabit large areas of Europe, why certain *Larroussius* and *Phlebotomus* species are restricted presently in either the west or the east part of the Mediterranean Basin. It is known that the glacial-interglacial fluctuations could have strong effects on the populations of the substantially primarily thermophilus Mediterranean sandfly taxa. In the ice age, sandfly populations could suffer a notable genetic bottleneck effect (Mahamdallie et al., 2011; Esseghir et al., 1997). Trájer and Sebestyén (2019) showed that in the last glacial maximum, the potential extension of the sandfly refugees in Europe could be very small.

These refugees could be restricted to the very narrow coastal areas of the southern Iberian Peninsula, the Mediterranean islands, the Apennine Peninsula and the Aegean Archipelago. However, not only abiotic factors could influence the persistence and extinction of sandfly species in an area in the last 3 million years. Very little can be known about competition between sandfly species. Ibrahim *et al.* (2005), investigating the distribution and population dynamics of sandfly species, found that larval competition could exist between certain species, although this observation was not confirmed. It was showed that the presence of certain typical ligneous plant species strongly coincides with the occurrence of Mediterranean sandfly species (Bede-Fazekas & Trájer, 2013). Although sandflies are not tied directly to plant species, they can be related to certain microhabitats like the barks of trees (Hanson, 1961) or the burrows of rodent species (Yaghoobi-Ershadi, 2001). These are important potential breeding habitats of sandfly species, and it is not known whether the changing distribution of the characteristic habitats was parallel to the altering distribution of sandfly species or not in the past.

It can also be hypothesized that sandfly species were not able to respond to the improving climatic conditions by rapid spread during the warming phases of the interglacials. Modelling the potential future distribution of sandfly species, Fischer *et al.* (2011) showed that sandflies would not be able to occupy their climatically suitable habitats entirely in the future due to their limited natural dispersal capacity. The active dispersal capacity of sandfly species is low among flying arthropods. For example, male and female individuals of *Ph. papatasi* could travel about 1,200-1,500 meters after 13 nights (Doha et al., 1991) which is equal to 92-115 meters per night dispersal rate. The longevity of the adult *Ph. papatasi* individuals increases as the ambient temperature decreases, and at 15°C, it is about 9-35 days under laboratory conditions (Kasap & Alten, 2006). Considering these dispersal rates, it is important to know that *Ph. papatasi* individual was not captured under 24°C in the Aegean islands, indicating that the real active potential dispersal rate of sandflies could not be notable during their entire adult lifespan (Tsirigotakis et al., 2018). It should be added that the potential activity period of such sandfly species as *Ph. neglectus* is short at the northern border areas, which implies that the annual generation numbers can also be low (Trájer, 2019).

The combination of low annual generation numbers and low active dispersal rate values resulted in weak dispersal abilities. It is also important that all climate models represent average values. It means that even in the mid-Pliocene climatic maximum and later times, the short cooler periods might have a strong impact on the realised occurrence patterns and the potential local extinctions of sandfly species. Each of the recently established suitability models was based on only short reference periods. For example, in the models of Koch *et al.* (2017) and Trájer *et al.* (2013), the reference period was equal to the general base period of climatic models, which is equal to 1960-1990. It is the consequence of a forced compromise because the history of the systematic, pan-European surveillance of sandfly species has relatively short history. It implies that suitability models which are based on the mean climatic values of a given period could not be able to give back short, but devastating climatic events as rapid, but short climatic fluctuations. Although it would be very important in the case of such taxa which have a relatively bad dispersal capacity as *Phlebotomus* species. A recent example can be used to demonstrate the effect of short-term climatic fluctuations on the occurrence of cold-sensitive Mediterranean sandfly species. In Central Hungary, after a longer warm period in the late 19th century and the first half of the 20th century, *Ph. perfiliewi* was observed in Budapest (Lőrincz & Szentkirály, 1933). After the cold winter years of the mid-20th century, this species has been no captured again in the Hungarian Capital. *Phlebotomus neglectus* and *Ph. mascitti* might have again colonized the agglomeration of the city only at the turn of the 20th/21st centuries (Trájer, 2017) when the climate of Central Hungary became again hostile to sandfly species due to warming.

Conclusions

It can be concluded that not the increasing thermal conditions, but the decreasing aridity could result in the retreat of the Mediterranean sandflies in the mid-Pliocene era. It indicates that the Pliocene climatic alterations could be handled with caution when it is used to approximate the effects of near-future climatic changes. It is a very important difference in the characters of the mid-Pliocene warming and the anthropogenic climate change, that while the first one caused the notable increase in the precipitation sums in Europe, the second one is projected to cause the increase of the aridity of Europe in the future due to the parallel decrease of the precipitation sums in the continental and south parts of Europe and by the increasing temperature conditions.

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Conflict of interest statement

The author declares that he has no conflict of interest.

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Appendix 1

Table 1. The distribution-limiting values of the sandfly species. The distribution limiting climatic extrema of the studied sandfly species. **PAria**: *Ph. ariasi*, **PNegl**: *Ph. neglectus*, **PPap**: *Ph. papatasi*, **Pperf**: *Ph. perfiliewi*, **PPern**: *Ph. perniciosus*, PSerg: *Ph. sergenti**, PSim: *Ph. similis**, **PTob**: *Ph. tobbi*. *: these species were only included to the discussion.

Species	month	bio1	bio12	bio13	bio16	bio17	bio18	bio19	TAI
PAria	min	7.0	207	21	69	18	18	69	1.5
	max	16.6	1629	156	483	264	264	483	9.2
PNegl	min	7.9	141	24	69	3	3	69	0.9
	max	18.4	1377	171	489	162	162	489	7.2
PPap	min	8.9	105	18	51	0	0	51	0.6
	max	18.7	1239	138	426	153	153	426	6.3
PPerf	min	7.3	108	18	54	0	0	54	0.7
	max	18.7	1521	171	507	198	198	507	7.9
PPern	min	8.0	168	21	60	12	12	60	1.1
	max	17.9	1434	126	432	240	240	432	7.6
PSerg*	min	9.0	105	18	51	0	0	51	0.6
	max	18.9	1140	135	450	96	96	450	5.7
PSim*	min	9.4	144	24	72	3	3	72	0.9
	max	18.0	1038	150	414	87	87	414	5.3
PTob	min	7.7	108	18	54	0	0	54	0.7
	max	19.0	1422	174	507	171	171	507	7.3