



## The northward spread of the European mantis, *Mantis religiosa* (Mantodea: Mantidae): Data from Lithuania

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**Key words.** Distribution, spreading, COI sequences, meteorological data, seasonality, citizen science

**Abstract.** Geographic distribution of the European mantis, *Mantis religiosa* (Linnaeus, 1758) in Europe covers mostly southern and central Europe, but this species has recently shown a significant northward spread. First reports of *M. religiosa* in Lithuania were in 2008 and now these insects are distributed throughout this country. Information on the spread of *M. religiosa* in Lithuania between 2015 and 2020 are analysed in this paper. The spread of this insect in Lithuania and neighbouring countries can be related to changes in climate, in particular, the increase in average annual temperature and milder winters. Possible routes along which *M. religiosa* spread northwards based on an analysis of mtDNA sequences are presented.

### INTRODUCTION

Insects of the order Mantodea are mostly distributed in tropical areas and only a few occur in the warmer parts of the temperate zone (Kočárek et al., 2005). These insects are predators and are characterized by raptorial fore legs adapted for seizing prey, the mid and hind legs being cursorial.

European mantis, *Mantis religiosa* (Linnaeus, 1758), is the most widespread mantid in Europe and the only native species of Mantidae (Insecta) in Central Europe (Kočárek et al., 2005). It is also present in Africa and Asia and has been introduced to North America (Battiston & Fontana, 2010; Heller, 2013). *Mantis religiosa* is a thermophilic insect (Kočárek et al., 2005; Bolshakov et al., 2010; Breitenmoser, 2016; Linn & Griebeler, 2016) typically inhabiting open and dry landscapes (Liana, 2007; Bolshakov et al., 2010; Durak et al., 2018) and mainly occurs in southern Europe, especially Spain, Italy and the Balkan States (Liana, 2007; Heller, 2013). Until the second decade of the 21<sup>st</sup> century the northern border of the distribution of *M. religiosa* in Europe crossed France, Belgium, Germany, southern Poland, Ukraine and Russia up to 55°N (Bolshakov et al., 2010; Heller, 2013; Zielinski et al., 2018). This species recently spread northwards in several European countries (Landeck et al., 2013; Linn & Griebeler, 2015; Schwarz et al., 2017; Zieliński et al., 2018). One of the main reasons for this expansion can be related to climate change (Kulak, 2009; Linn & Griebelen, 2015; Ostrovsky, 2017).

Increase in economic activity and combustion of fossil fuels over the last century greatly affected the environment, which can be seen in the change in climate. The average global land and ocean surface temperatures have increased linearly by 0.85°C over the period 1880 to 2012 (Pachauri & Meyer, 2014). The year 2008 was the warmest in Lithuania over the period 1778 to 2010, with an average annual temperature of 8.3°C and positive average annual anomaly of 2.1°C (Galvonaite et al., 2013). These climate changes have already affected many natural systems in terms of the timing of seasonal biological events and geographic shifts in the ranges of species (Semenza & Menne, 2009).

During the last few years *M. religiosa* was reported in Lithuania and some even more northerly countries such as Latvia and Estonia for the first time (Pupiņš et al., 2012; Truuverk, 2019). The presence of *M. religiosa* in Lithuania was first reported in 2008 and is now distributed almost throughout the country. Here we present data from Lithuania on the dispersal of these insects over the period 2015–2020. Possible sources of *M. religiosa* based on an analysis of COI sequences of the specimens collected are also presented. This data may be useful for predicting the spread of other insect species, especially in regard to climate change.

### MATERIAL AND METHODS

#### Insect collection and identification

The information on the detection of *M. religiosa* in Lithuania in 2015–2020 was collected using an informative campaign and

questioning inhabitants (389 records), and collecting or observing insects during field studies by the authors in 2008–2020. Field studies included using light traps, observation of habitats at night-time using a head lamp and scanning vegetation in daytime. *Mantis religiosa* has a distinctive appearance, are attracted to city lights at night and are familiar and recognizable, even by non-professionals. Thus, it was possible to use a questionnaire to determine the distribution of these insects. The first information on the presence of this insect aroused the interest of the media and citizens generally, which enabled us to use newspapers, the internet, radio and television to obtain information from the inhabitants of Lithuania. The media requested people to report information on this insect, such as the place seen, habitat, date and a photograph. Additional information was obtained by direct communication. The data (44 records) in the most popular online database the social network for naturalists, “iNaturalist” (available from <https://www.inaturalist.org>, accessed 06 05 2021) were also used. The announcer passed on the captured individuals in some cases. Specimens were identified using the keys of Bey-Bienko (1964), Kočárek et al. (2005) and Shcherbakov et al. (2015). The collected material is deposited in Tadas Ivanauskas Zoological Museum (Kaunas, Lithuania) and in the entomological collections of the Nature Research Centre (Vilnius, Lithuania).

Sixteen insects collected in Lithuania in 2015–2019 and parts of legs of specimens collected in Czech Republic (1 spec.), Belarus (1 spec.) and ootheca (1) from France were preserved in 96% ethanol for the PCR-based investigation.

#### Molecular investigation of the insects collected

DNA from individual tarsi of insects or a piece of ootheca was extracted using the ammonium acetate extraction method (Richardson et al., 2001). The extracted DNA was then dissolved in 100 µL of TE solution. For amplification of Cytochrome oxidase c subunit I (COI) gene fragment, we used primers LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3') and HCO2198 (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3') (Folmer et al., 1994). Thermal PCR conditions were: 94°C for 2 min; 35 cycles of 94°C for 30 s, 49°C for 30 s, 72°C for 2 min; 72°C for 10 min. For the amplification of Cytochrome oxidase c subunit II (COII) gene fragment, we used primers COII-F-leu (5'-TCTAATATGGCAGATTAGTGC-3') and COII-9b (5'-GTACTTGCTTTTCAGTCATCTWATG-3') (Whiting, 2002) and thermal conditions: 95°C for 12 min; 35 cycles of 94°C for 30 s, 52°C for 30 s, 72°C for 45 s; 72°C for 1 min. Thermal cycling was carried out using an Eppendorf thermal cycler (Germany).

All reactions were done in a 25-µL volume for each sample. It consisted of 12.5 µL DreamTag Master Mix (ThermoFisher, Lithuania), 8.5 µL nuclease-free water, 1 µL of each primer and 2 µL of template DNA. The amplification was evaluated by running 2 µL of each PCR product on 2% agarose gel. Fragments were sequenced of both strands with corresponding primers and with the BigDye Terminator V3.1 Cycle Sequencing kit according to the manufacturer's instructions in the Nature Research Centre. Sequences were edited and aligned using the program BioEdit (Hall, 1999). Phylogenetic trees were produced, and intraspecific genetic distances were based on the Kimura 2-Parameter model and calculated using MEGA software.

#### Meteorological variables

Data on the mean annual air temperature (°C), mean January air temperature (°C) and air temperature anomalies compared to climatic norm in Lithuania were obtained from the archive of the Lithuanian Hydrometeorological Service. January air temperature was used because the coldest month in Lithuania is usually January (Galvonaite et al., 2013). The average air temperature

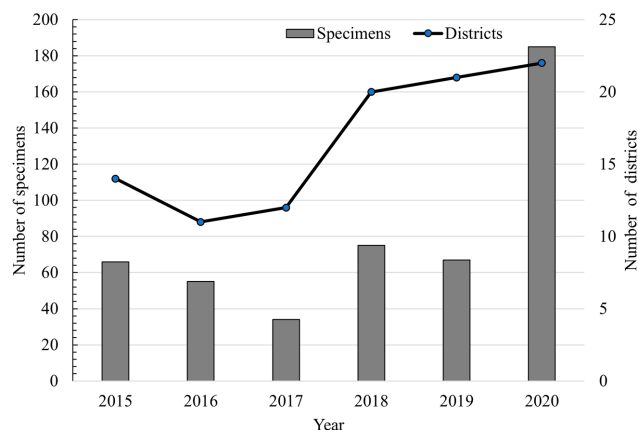


Fig. 1. The numbers of *Mantis religiosa* recorded (columns) and administrative districts (line) in which they were recorded in 2015–2020.

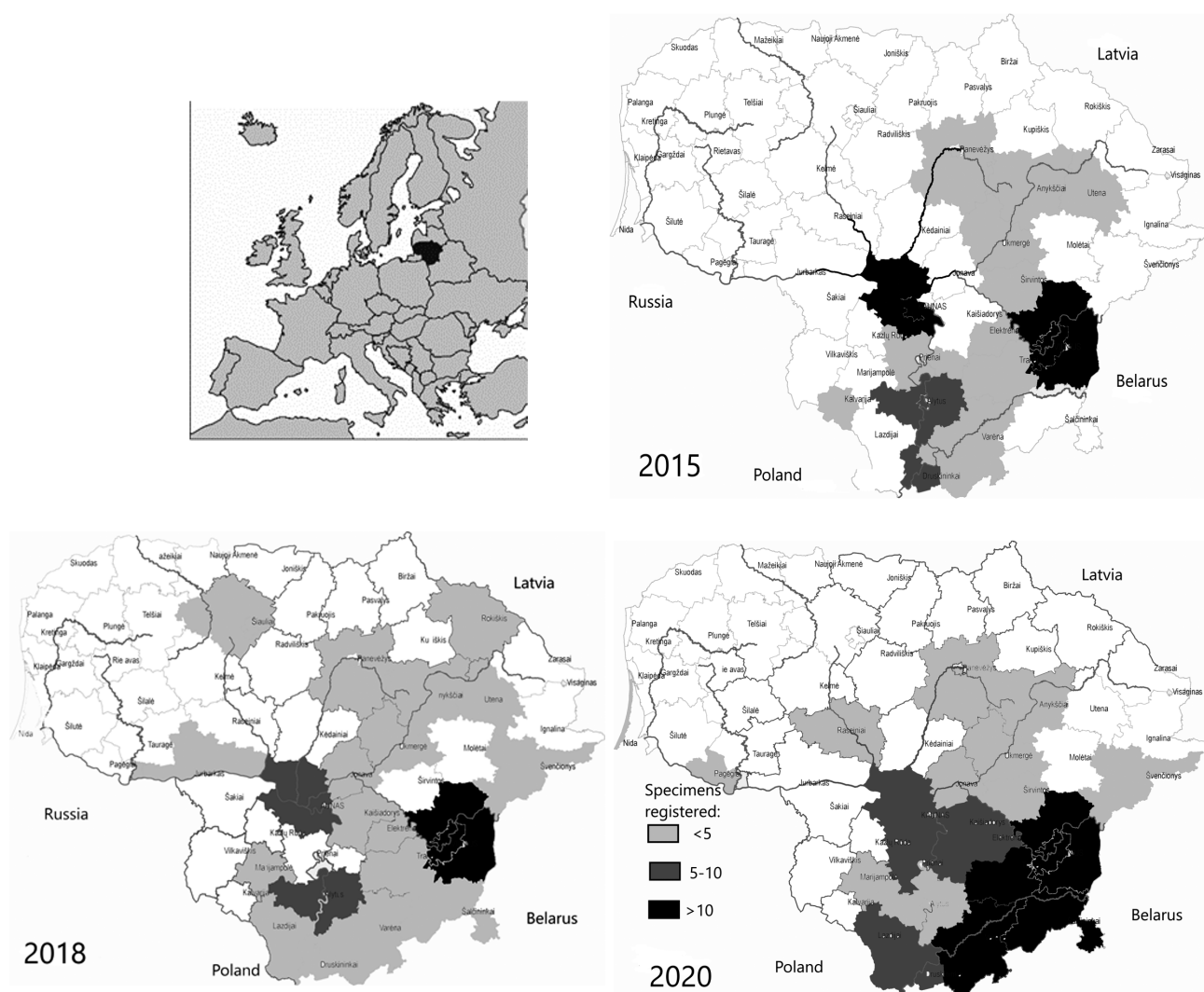
based on the records of four different Meteorological Stations (MS) located in different parts of the country were used: Vilnius (54.626000°, 25.107034°), Varėna (54.248273°, 24.551761°), Kaunas (54.883472°, 23.834990°), Utena (55.515321°, 25.589692°), and the long-term mean annual air temperature compared between two periods: 1961–1980 and 2001–2019. The mean annual air temperature in Lithuania (four MS) were compared with that in Kyiv MS (50.400000°, 30.450000°, Ukraine) and Krakow MS (50.08330°, 19.800000°, Poland), regions where *M. religiosa* were previously naturally distributed, using t test. These data and that from Minsk MS (53.540000°, 27.340000°, Belarus) were obtained from KNMI Climate Explorer (KNMI, 2021).

## RESULTS

### Abundance and seasonality of *M. religiosa*

During the five-year investigation (2015–2020) 433 confirmed records of the presence of *M. religiosa* in different parts of Lithuania were reported based on a total of 481 specimens (adults and juvenile), as in some cases several individual insects were recorded for the same locality. *Mantis religiosa* were recorded in 33 different districts and municipalities.

Numbers of districts in which insects were recorded each year varied between 11 (in 2016) and 22 (in 2020), and the number of *M. religiosa* recorded per year was highest in 2020 (Fig. 1). Most were recorded in the east (41.4%) and south (25.8%) of Lithuania, with 12.8% and 11.8% recorded in central and south-eastern parts, and only a few in the northwest (0.2%), west (1.4%), north (1.6%), southwest (2.3%) and northeast (2.7%). Until the year 2017 *M. religiosa* were recorded only from eastern, north-eastern, southern and central Lithuania with most reports for the districts Vilnius and Kaunas (Fig. 2). Since 2018, the number of reports from central Lithuania has increased, with records of *M. religiosa* in Šiauliai district in the north and Jurbarkas district in the west. After 2019 insects were recorded in the west, reaching Pagėgiai district and the Curonian spit on the Baltic Sea in the very west of Lithuania (Fig. 2). Females accounted for 52.5%, males 22.6% and immature individuals 3.8% of all specimens of *M. religiosa* recorded, 21.1% of which the sex was not determined. *Mantis*



**Fig. 2.** Distribution of *Mantis religiosa* in Lithuania in 2015, 2018 and 2020.

*religiosa* of different colours were recorded in Lithuania during the period of this study: green (90.8%) and light brown (9.2%). Of the brown individuals most were female (79.5%), with 15.9% male and 4.5% immature. Of the green individuals, most were female (66.2%), with 28.9% male and 4.9% immature. There was no significant difference in the sex ratio of mantids of the different colours ( $p = 0.06$ ,  $\chi^2 = 3.47$ ).

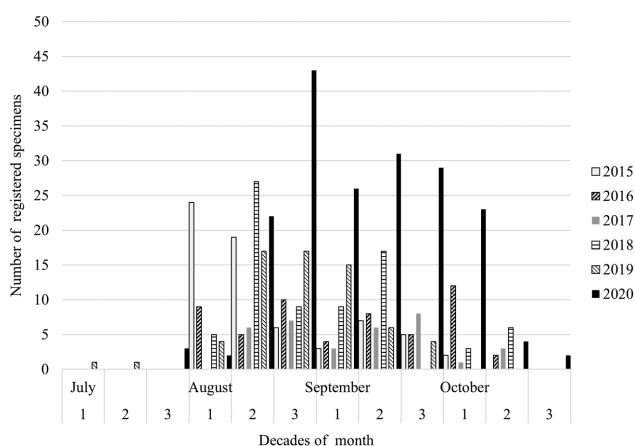
The earliest date on which adults of *M. religiosa* were observed was the 29<sup>th</sup> of July (2020) and the latest the 25<sup>th</sup> of October (2020), they were most abundant (peaks) in August in all years of this study, but 2016 (the first decade of October) and 2017 (the third decade of September) (Fig. 3). Periods when the peaks of *M. religiosa* were recorded in August differed slightly each year and were recorded during the first (2015), the second (2018, 2019) and the third decade of August (2019, 2020) (Fig. 3).

Immature *M. religiosa* (nymph of last instars) were recorded in Lithuania for the first time in 2017. In total there were 15 reports of immature *M. religiosa* from seven districts of southern, eastern and central parts of Lithuania (Fig. 4). Immatures were recorded earlier than adults, with

the earliest reported on the 4<sup>th</sup> (2019, Žuvintas) and 15<sup>th</sup> of July (2019, Vilnius) and the latest on the 16<sup>th</sup> and 12<sup>th</sup> of September (2017, Druskininkai and Vilnius). The highest numbers of nymphs were recorded in the middle of August. Of the nymphs recorded 54% were found in natural and semi-natural habitats (heather, quarries, meadows) and 46% in anthropogenic habitats (homesteads surrounded by a green area or forest).

The locations at which *M. religiosa* were mainly recorded or collected were city streets and walls of buildings where they were possibly attracted to lights, suburban courtyards, and gardens. Some specimens were collected during the trapping of moths using light traps. There are five records of oothecas attached to the walls of buildings and in greenhouses on flowers, with females of *M. religiosa* observed close to the oothecas. There are also reports of females and males mating.

All the adults and immature *M. religiosa* recorded in natural environments by the authors were for dry habitats: dry sandy grasslands, heaths, bushy grassland habitats. The regular findings of adult and immature *M. religiosa* in south



**Fig. 3.** Number of specimens recorded in Lithuania during 2015–2020 in different decades from July to October.

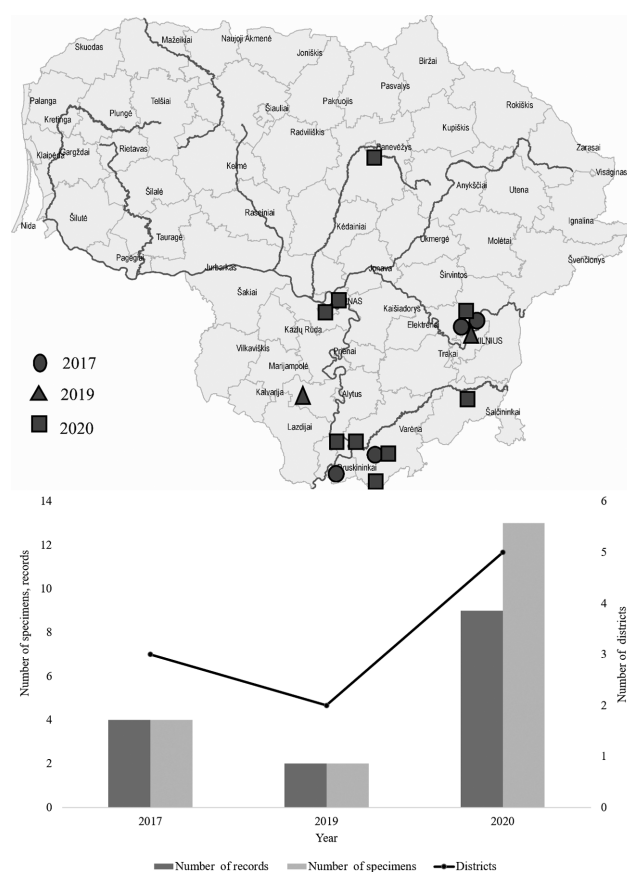
and south-eastern Lithuania in natural habitats indicate the establishment of local populations of the European mantis.

**Molecular analysis**

We obtained COI (643 bp.) and COII (716 bp.) sequences from sixteen individuals of *M. religiosa* collected in Lithuania in 2016–2019 and specimens collected from The Czech Republic, Belarus and France. Four COI and 3 COII haplotypes were recorded in Lithuania. The same COI and COII haplotypes were detected in different years of the study indicating that the origin of *M. religiosa* in different years was the same. Sequences for *M. religiosa* from Belarus differed by 0–0.3% (COI) and 0–0.1% (COII) from those detected in Lithuania and that of material collected in France and The Czech Republic differed by 1.1–2.2% (COI) and 2.5–2.8 (COII). The maximum likelihood phylogenetic trees revealed three (COII) and three (COI) clades (Fig. 5). All specimens collected in Lithuania were in clade A together with a specimen collected in Belarus (M19) and sequences deposited in GenBank from Ukraine (Fig. 5). Sequences of *M. religiosa* collected in France and The Czech Republic clustered in clade B together with sequences from the GenBank obtained from specimens collected in Italy, Austria, Hungary and Slovakia (Fig. 5). The third clade C in the phylogenetic tree included both COI and COII sequences from *M. religiosa* collected in Germany and France.

**Meteorological data**

Annual temperatures in four MS in Lithuania during the period 1961–2019 were not significantly different (varied between  $6.4 \pm 1.1$  (Vilnius and Utena) to  $6.9 \pm 1.1$  (Kaukas)). The mean annual temperatures differed significantly (1961–2019) between Lithuania and two territories in which the presence of mantids was recorded previously: Ukraine (Kyiv,  $p = 0.00$ ,  $t = 9.0$ ) and Poland (Krakow,  $p = 0.00$ ,  $t = 9.4$ ). The air temperatures in Lithuania and Belarus (Minsk,  $p = 0.85$ ) did not differ significantly. During the period 1961–1980 and 2001–2019 average annual air temperature in Lithuania increased more than  $1.5^\circ\text{C}$  from  $5.8 \pm 0.9^\circ\text{C}$  to  $7.4 \pm 0.6^\circ\text{C}$  ( $p = 0.00$ ,  $t = 6.43$ ) and is now similar to that in southern Poland (Krakow,  $7.6 \pm 0.6$ ) and



**Fig. 4.** Map showing the localities and a graph the numbers of immature *Mantis religiosa* recorded in 2017–2020 in Lithuania.

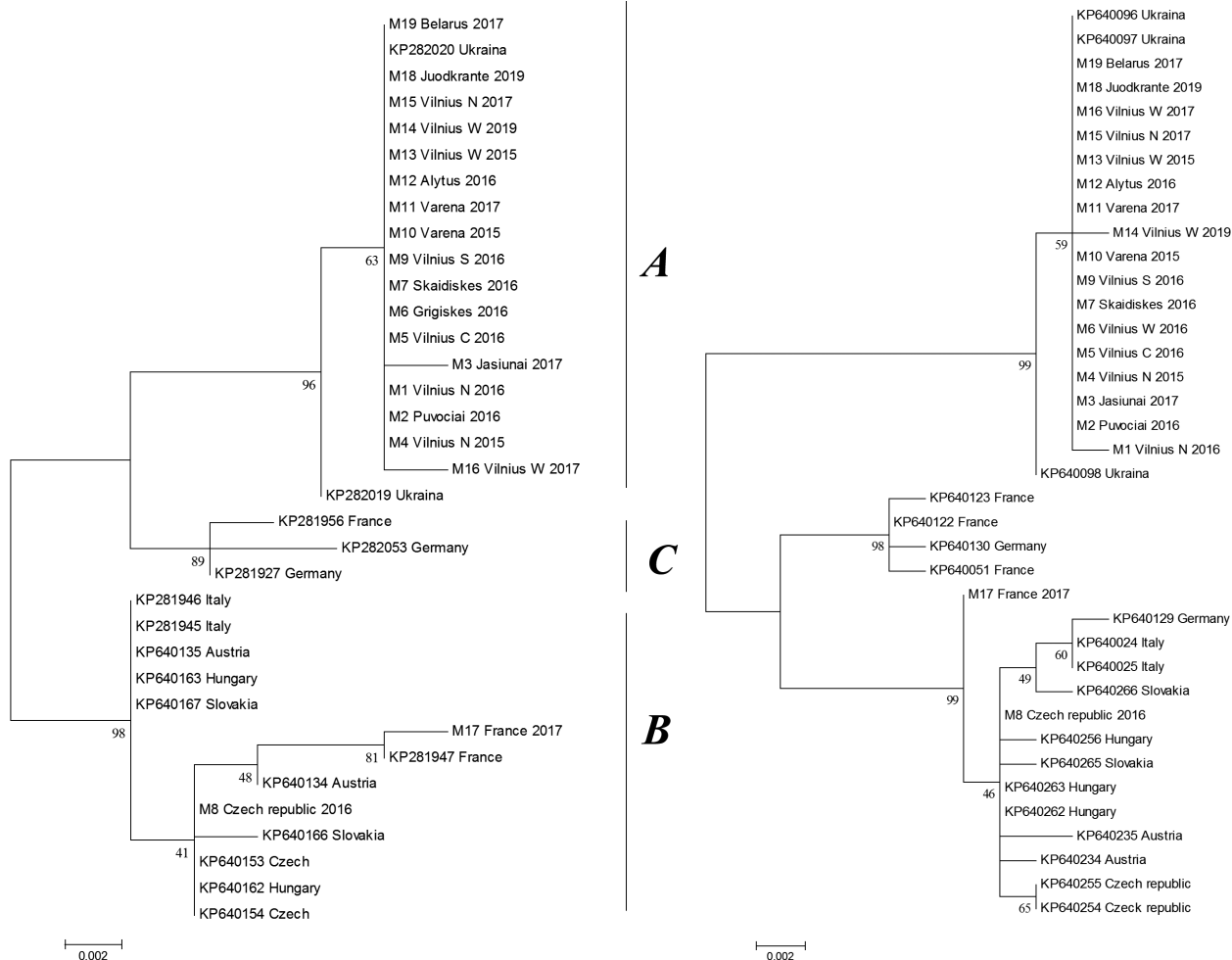
Ukraine (Kyiv,  $7.6 \pm 0.8$ ) in 1961–1980 (Fig. 6). The mean annual temperature in Lithuania over the last few years (2001–2019) and those recorded in Ukraine (Kyiv) and Poland (Krakow) in 1961–1980 do not differ significantly ( $p = 0.34$ ,  $t = 0.96$  and  $p = 0.28$ ,  $t = 1.1$  respectively).

Similarly, the January (coldest month of the year) mean air temperatures have increased in Lithuania since the year 1988 (Fig. 7) thus creating suitable conditions for *M. religiosa* to overwinter.

These temperature changes created opportunities for mantids to spread north into Lithuania both from the south-east (Ukraine) and from the southwest (Poland), where these insects were previously naturally distributed.

**DISCUSSION**

Recent changes in climate, land use and increasing mobility have resulted in range shifts of insects in Europe (Kulak, 2009; Aleksandrowicz, 2011; Linn & Griebel, 2016). The spread and establishment of *M. religiosa* in north-eastern Europe is one such example of the rapid spread of an animal. A number of invertebrate species, a decade ago known only from southern part of Europe, recently spread across Europe and now occur in Lithuania: the moths (Lepidoptera) *Cameraria ohridella* Deschka & Dimić, 1986 (Ivinskis & Rimšaitė, 2006), *Macrosaccus robiniella* (Clemens, 1859) and *Parectopa robiniella* Clemens, 1863 (Ivinskis & Rimšaitė, 2008a), wasp spider *Argiope bruennichi* (Scopoli, 1772) (Arachnida, Araneae)



**Fig. 5.** Maximum likelihood phylogenetic trees, obtained using the Kimura 2-Parameter model (bootstrap 2,000 repetitions) based on the COI (left) and COII (right) gene fragments of *Mantis religiosa* obtained during this study (M1–M19) and those from the GenBank. Data on the specimens investigated in this study are in Table S1.

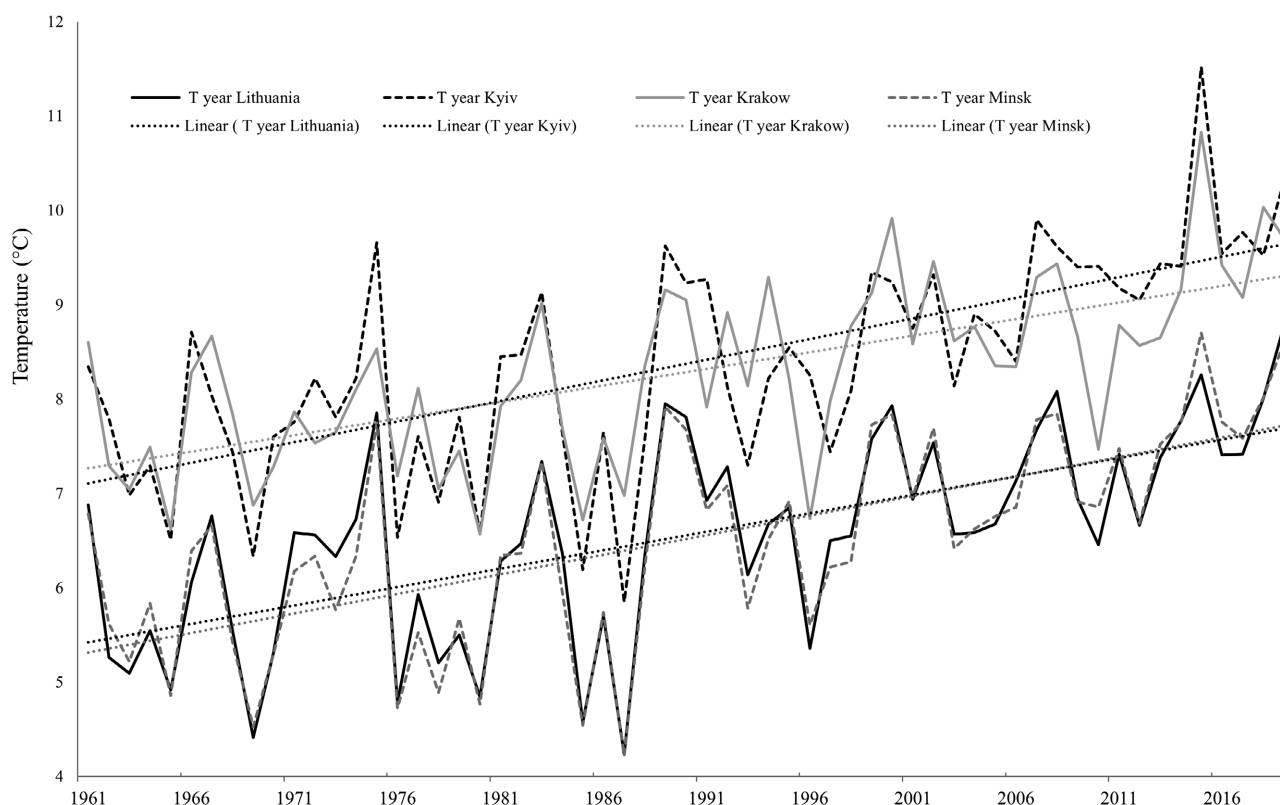
(Ivinskis & Rimšaitė, 2002; Biteniekytė, 2005), dragonflies (Odonata) *Aeshna affinis* Vander Linden, 1820 (Bernard, 2005) and *Orthetrum brunneum* (Fonscolombe, 1837) (Bernard & Ivinskis, 2004) and the bush-cricket *Phaneroptera falcata* Poda, 1761 (Orthoptera) (Ivinskis, Rimšaitė, 2008b).

Targeted questionnaires were used to study the distribution of *M. religiosa* in Lithuania, a method that was successfully used in Poland and Latvia (Liana, 2007; Pupiņš et al., 2012; Zielinski et al., 2018). A similar method was used to collect information on the distribution of the invasive mantids *Hierodula patellifera* Serville, 1839 in France (Moulin, 2020) and *H. tenuidentata* Saussure, 1869 and *Sphodromantis viridis* (Forskål, 1775) in Italy (Battiston et al., 2018, 2019). Surveys based on questionnaires gather a lot of information about the spread of a target species from all over a country, but do not confirm the presence of vital subpopulations and lack information on habitats.

The spread of *M. religiosa* in Lithuania began in 2008 (Rimšaitė et al., 2017), when five adult females were found in different parts of Vilnius for the first time. The localities where most of these insects were first recorded (2008–2015) in Lithuania were near highways and transport cor-

ridors and only three specimens were recorded at the edges of pine forests or peat bogs (Rimšaitė et al., 2017). This indicates that *M. religiosa* may be transported on vehicles along transport corridors. During the first period of this study (2008–2015) the highest numbers of records were for the surroundings of Vilnius and southern part of the country (Rimšaitė et al., 2017). The European mantis spread during the period 2015–2020 from south, south-east and east Lithuania to south-west and west Lithuania. The largest numbers of reports were for the biggest towns, which can be explained by the specificity of the data collection, due to the large number of respondents in metropolitan areas and not to the fact that they are population hotspots.

*Mantis religiosa* inhabited regions in south-eastern Poland until 2007 (Liana, 2007) and recently spread northwards in this country (Durak et al., 2018; Kadej et al., 2018; Zieliński et al., 2018), as is reported in Germany and The Czech Republic (Landeck et al., 2013; Linn & Griebelen, 2015; Mückstein, 2016). One individual *M. religiosa* was recorded for the first time in Latvia at Lielvārde in 2008, the same year as in Lithuania and several individuals were also found in 2010 (Pupiņš et al., 2012). This species reached Estonia ten years later, in 2019 (27<sup>th</sup> of August), the



**Fig. 6.** The mean annual temperatures in Lithuania (average based on Vilnius, Kaunas, Varėna, Utena MS), Krakow MS, (South Poland), Kyiv MS (Ukraine) and Minsk MS (Belarus) for the period 1961–2019 and their linear trends (straight lines).

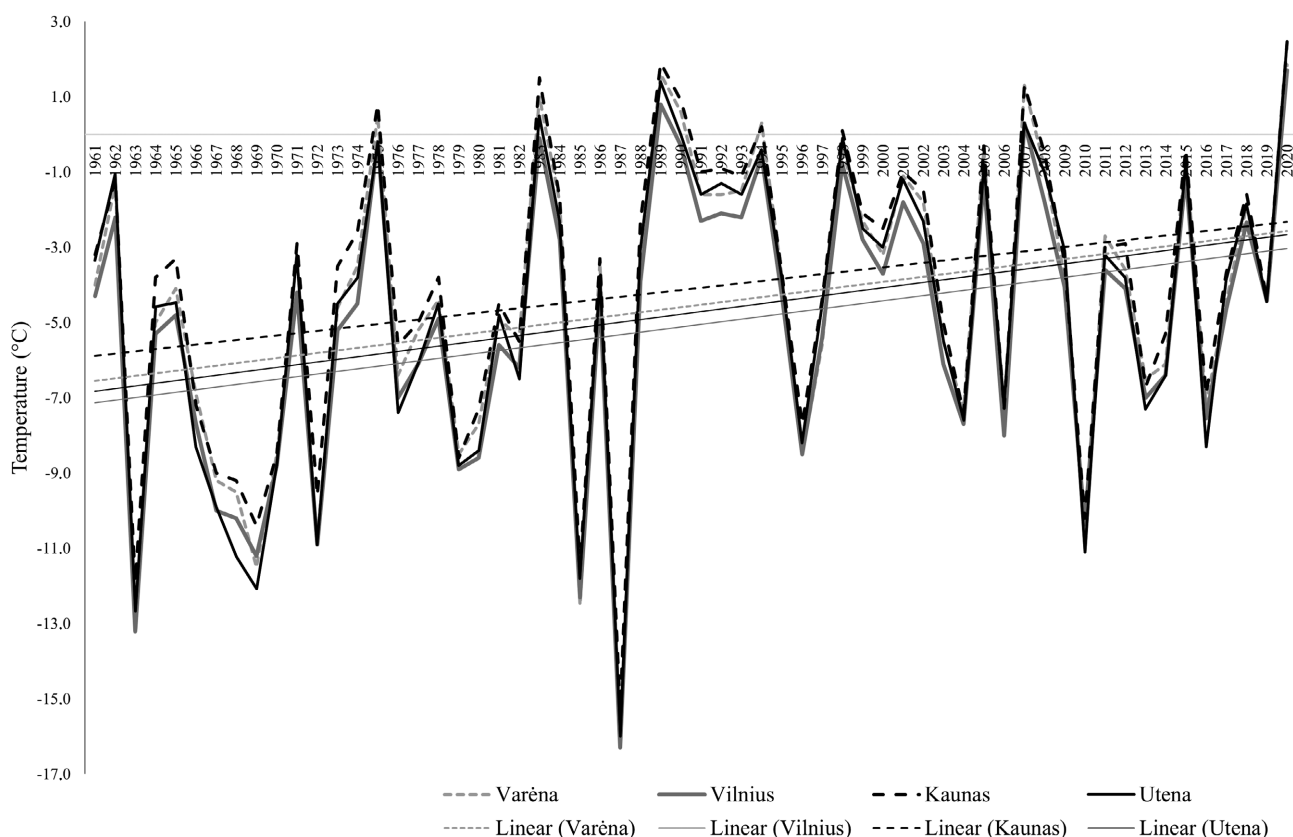
first adult female was recorded close to Pärnu (58.27831, 24.579328) (Truuverk, 2019) and this is now the northernmost record for *M. religiosa*. Before this the northernmost record for *M. religiosa* was in Russia at Severnoje in the Kostroma distr. (58.03002, 41.42999) (Bolshakov et al., 2010). In Belarus and Russia, the spread of this species to the north also started in 2008 (Kulak, 2009; Aleksandrowicz, 2011; Ostrovsky, 2017; Serzhantova et al., 2017, 2019).

Development time and moulting periods of *M. religiosa* differ in different countries because the temperatures there also differ (Liana, 2007; Linn & Griebeler, 2016). Adult *M. religiosa* emerge in May in warm Mediterranean regions, whereas nymph development is typically completed in late July or August in colder countries such as Poland and Germany (Liana, 2007; Linn & Griebeler, 2016). The same periodicity in the appearance of imagines was recorded in Lithuania, with the first adults recorded in the first decade of August and only one record of an adult mantid at the end of July in 2020, while juveniles were observed from the first decade of July. The phenology of the life cycle of the perennial and viable populations in Germany and Poland confirms that it is likely this species will adapt to local conditions in Lithuania.

Habitats of *M. religiosa* in Central Europe are similar to those of other xerophilous or xerothermic insects, such as bush-crickets *Phaneroptera falcata* (Liana, 2007; Bolshakov et al., 2010; Landeck et al., 2013). Orthoptera usually form an important part of the adult diet of *M. religiosa* (Landeck et al., 2013; Breitenmosen, 2016). Bush-

crickets were recorded in south Lithuania in 2008 for the first time (Ivinskis & Rimšaitė, 2008b), the same year as *M. religiosa*. Now bush-crickets are distributed throughout Lithuania and were recorded in south-eastern Latvia in 2011, 300 km north-east of the locality of the first record in Lithuania. This indicates that the speed of spread of this species can be approximately 100 km per year (Budrys et al., 2015), although other authors indicate a much lower speed (Kočárek et al., 2008).

Typical localities of *M. religiosa* in Poland are clearings coniferous forests or grasslands at the edges of these forests, where the microclimate is warmer (Liana, 2007). Due to climate change and increase in temperature the role of such habitats become less important as it is currently colonizing new suitable habitats – waste and fallow lands (Liana, 2007). Studies on the habitat requirements of *M. religiosa* in Germany and Italy indicate the importance of microhabitats: females prefer solid substrates with high heat-storing capacities for egg deposition, as it results in faster egg development (Batististon & Fontana, 2010; Linn & Griebeler, 2016). As *M. religiosa* locates more suitable habitats, local populations will become established and as a consequence the species will spread further northwards. Across Europe air temperatures have been increasing since the 20<sup>th</sup> century, the European average temperatures indicate that 7 of the top 10 warmest years were recorded in the period starting in the year 2000 and there is a clear upward trend in annual average temperatures over the last few decades (van der Schrier et al., 2013). In this period, winters and springs were warmer (~1.7–2.0°C), whereas



**Fig. 7.** Mean air temperatures (°C) in January in four MS (Vilnius, Kaunas, Varėna, Utena) in Lithuania over the period 1961 to 2019 and their linear trends (straight lines).

summer and autumn temperatures changed less. The last decade of the 20<sup>th</sup> century was distinguished by a unique climatic phenomenon of several successive warm winters (1988/1989–1994/1995). For the last two hundred years, eastern Europe has never experienced such a long series of anomalously warm winters (Bukantis, 2001). This creates the preconditions for the establishment of overwintering populations of southern species of insects in this region.

We found adult *M. religiosa* of both sexes and since 2017 also juveniles, which indicates this species can successfully overwinter in Lithuania. The presence for several years of juveniles and adults in the same natural areas in south and south-eastern Lithuania indicate that there are local population of *M. religiosa* in Lithuania and this species is now established here and continues to spread.

As in its distribution elsewhere there are two colour forms of *M. religiosa* in Lithuania: grass-green and brown shading from yellow to dark brown. The different colours are possibly related to the places where they can be well-hidden and indirectly related to climatic conditions and colour of the substrate (Battiston & Fontana, 2010), but not to sex (Lopez, 1998), which is in accordance with our results. Our data revealed that females dominate both colour forms of the European mantis.

Genetic diversity, based on mtDNA, of the *M. religiosa* in Lithuania is poor with only few haplotypes, which indicates they all originated from the same locality. Possible routes followed by *M. religiosa* in its northward spread in Europe are reported by Linn & Griebelen (2015). They

analysed four mtDNA genes of European mantis throughout Europe, except for Northern Europe and the Baltic countries, and detected three main clades of *M. religiosa* in Europe. The first clade (A), called the East lineage, includes those from the Ukraine the sequences of which are similar to those of the Lithuania and Belarus specimens in the present study. This indicates that *M. religiosa* spread from Ukraine and Belarus to Lithuania. The second clade (B) determined by Linn & Griebelen (2015) includes all central European, Italian and east German haplotypes, hereafter called the Central lineage (in the present study it includes sequences from mantids collected in France and The Czech Republic). The third clade (C) includes the French and west German haplotypes, hereafter called West lineage. This clustering reflects genetic isolation by distance during glacial periods (Hewitt, 1999) and the major ice age refugia (Linn & Griebelen, 2015). As presumed, *M. religiosa* spread to Lithuania from one direction, the southeast (Ukraine). In contrast, the German populations of the European mantis originate from two directions: eastern France (West lineage) and central Europe (Central lineage).

The haplotype diversity reported in populations of *M. religiosa* is very low and possibly the result of colonization by a small number of individuals (Taberlet et al., 1998; Hewitt, 1999; Dlugosch & Parker, 2008) as in the case of Lithuania.

Climate change is one of the reasons for the current northward spread of *M. religiosa* and other species from

southern Europe, but not the only one. The distribution of *M. religiosa* in central Europe was also limited by environmental conditions (Liana, 2007) and the spread of this species has been possible because of new types of suitable environment. Further research on *M. religiosa* in Lithuania is needed to clarify which habitat features are favourable for these insects and which microhabitats it colonizes first.

**ACKNOWLEDGEMENTS.** We are grateful to all the respondents that sent us records of the presence of *M. religiosa* throughout Lithuania. The authors acknowledge the help of O. Machač (Czech Republic) and D. Vincheuski (Belarus) in providing material for PCR-based studies and valuable information. We also thank V. Bačianskas, R. Ferenc, G. Gulbinienė, R. Markevičiūtė, J. Mackevičius, S. Paltanavičius, A. Petrašiūnas, A. Pranaitis, G. Smailytė, L. Šveistytė and T. Ūsaitis for providing additional records of *M. religiosa* and G. Vaitonis for help in preparing the distribution maps. We are very grateful to anonymous reviewers for their valuable comments and suggestions.

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Received March 8, 2022; revised and accepted July 25, 2022

Published online August 16, 2022

**Table S1.** *Mantis religiosa* individuals used for molecular investigation.

	Collection date	Collection locality	District	Country
M1_Vilnius_N_2016	2016 08 23	Santariškės, North Vilnius	Vilnius	Lithuania
M2_Puvociai_2016	2016 08 29	Puvočiai	Varėna	Lithuania
M3_Jasiunai_2017	2017 08 30	Jašiūnai	Šalčininkai	Lithuania
M4_Vilnius_N_2015	2015 09 04	Santariškės, North Vilnius	Vilnius	Lithuania
M5_Vilnius_C_2016	2016 09 30	Central Vilnius	Vilnius	Lithuania
M6_Vilnius_W_2016	2016 09 15	Grigiškės, West Vilnius	Vilnius	Lithuania
M7_Skaidiškės_2016	2016 08 29	Skaidiškės	Vilnius	Lithuania
M8_Czech_republic_2016	2016	Czech republic	Czech republic	Czech republic
M9_Vilnius_S_2016	2016 09 14	Pavilnys, South Vilnius	Vilnius	Lithuania
M10_Varena_2015	2015 08 09	Varėna	Varėna	Lithuania
M11_Varena_2017	2017 08 17	Kapiniškiai	Varėna	Lithuania
M12_Alytus_2016	2016 10 03	Alytus	Alytus	Lithuania
M13_Vilnius_W_2015	2015 08 10	Lazdynai, West Vilnius	Vilnius	Lithuania
M14_Vilnius_W_2019	2019 08 29	Lindiniškės, West Vilnius	Vilnius	Lithuania
M15_Vilnius_N_2017	2017 09 10	Balsiai, North Vilnius	Vilnius	Lithuania
M16_Vilnius_W_2017	2017 09 12	Skatulė street, West Vilnius	Vilnius	Lithuania
M17_France	2016	France	France	France
M18_Juodkrantė_2019	2019 09 01	Juodkrantė	Neringa	Lithuania
M19_Belarus	2017	Belarus	Belarus	Belarus