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ORIGINAL ARTICLE

Abiotic factors associated with the distribution of *Mutilla europaea* (Hymenoptera: Mutillidae) in Northern Europe

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Abstract. The distribution of *Mutilla europaea* (Linnaeus, 1758), has never been carefully investigated in Northern Europe. The density of *M. europaea* is highest along parts of the coast in Northern Europe and its distribution overlaps the border of the temperate zone in this area, which is not surprising, given that it is well documented that temperature regulates the ecology of insect communities (presumably because temperature is associated with several physiological other adaptations and plastic responses). This paper presents new information on its distribution in Northern Europe and reveals that abiotic factors are associated with this species' distribution in the area around the Baltic Sea.

INTRODUCTION

The large velvet ant *Mutilla europaea* (Linnaeus, 1758), is a parasitic mutillid wasp with a widespread distribution from Spain in the west to Japan in the east, and from North Africa in the south to Sweden, Norway and Finland in the north (GBIF, 2020). Most species in the Mutillidae are xerothermophilic and occur in dry habitats, often on sandy ground (Lelej & Schmid-Egger, 2005). The preferences of M. europaea include land used by humans (agricultural fields, pasture, parks, etc.) pine forests, dry meadows, spruce forests, raised bogs, oak forests and wet meadows (Lelej & Shlyakhtenok, 2015). Adult M. europaea are sexually dimorphic, with the females wingless and the males winged. Females are nest parasites and after mating they lay their eggs into the nests of bumblebees (Bombus spp.) or (rarely) honeybees (Apis mellifera). One to three eggs are laid on a single bumbelbee puparium. Hatching occurs three days later, but only one egg successfully hatches on each puparium (Su et al., 2019). After pupation M. europaea adult individuals emerge 16 to 20 days later, which is about six days longer than the 10 to 14 days taken by bumblebees for the same transition (Brothers et al., 2000).

Insect abundance and distribution are often regulated by several abiotic factors, an important one of which is temperature (Savopoulou-Soultani et al., 2012). Effects of temperature on survival, development, and reproduction in insects have been exhaustively explored over several decades (Savopoulou-Soultani et al., 2012). It is well documented that abiotic factors, especially temperature, regulate the ecology of insect communities (SavopoulouSoultani et al., 2012) and also prolong or shorten the life cycle of individual insects (Régnière et al., 2012). The limits to the distribution of insects in temperate zones like Northern Europe are often determined by extremely low temperatures because cooling and freezing greatly disturb the physiology, behaviour, and mechanical functioning of insects (Khaliq et al., 2014). In Northern Europe, males of *M. europaea* die in autumn and females hibernate until the next spring (BWARS, 2021).

Another abiotic factor that affects the distribution of insects is relative humidity (Enjin, 2017). Environmental moisture changes continuously with the seasons, but within seasons, all factors affecting humidity can vary temporally and spatially. Humidity affects the behavior and physiological mechanisms of insects (Khaliq et al., 2014).

Insects are often restricted to specific areas and habitats by biotic and abiotic factors, but the specific pattern is not always easy to explain. The distribution and range of *M. europaea* in Northern Europe is not well known so the objective of this paper is to investigate the records of *M. europaea* in Northern Europe with the goal of better understanding its distribution, especially in terms of abiotic factors, in countries around the Baltic Sea.

MATERIAL AND METHODS

Database

Extensive literature searches of the appropriate faunal databases in eight countries were used to map all the records of M. europaea in Northern Europe around the Baltic Sea (Fig. 1). The coordinates within \pm 100 m of the historical distribution of M. europaea were obtained from the following databases: Den-



mark – Naturbasen (2020); Estonia – Elrikkus (2020); Finland – Laji (2020); northern Germany – Naturgucker (2020); Latvia – Dabasdati (2020); Lithuania – Macrogamta (2020); Norway – Artsdatabanken (2020); and Sweden – Artportalen (2020). The international database Global Biodiversity Information Facility (GBIF, 2020) and the database of international records from the Californian Academy of Sciences and National Geographic were also used (Inaturalist, 2020). Relevant information in all the databases recorded over the period January 1, 1990 to December 31, 2020 was included in this study.

Data sources

The bioclimatic data consisting of 19 variables that was included in the analysis was downloaded from the World Climate WorldClim2.0 Database (http://www.worldclim.org). A species distribution model was developed using abiotic inputs. An old map with records up to 1964 (see Erlandsson, 1964) was compared with the new records from the databases. The map for 1964 shows only the records for Denmark and Fennoscandia (Sweden, Norway, Finland and the Kolapeninsula). ArcGIS 10.8 software was used to transform the old map into a new map with the new records added (Fig. 1).

Museum collections

To analyse the size and colour variation of individual insects, the collections of the National Museum of Natural History in Stockholm, the National Museum of Natural History in Gothenburg, and the Museum of Biology in Lund were used. All the specimens were caught in Sweden between about 1850–2023. These animals were studied under a microscope at each one of the museums. The animals at the National Museum of Natural

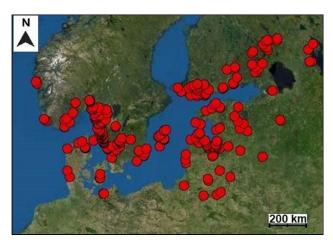


Fig. 1. Distribution of M. europaea in Northern Europe.

History in Stockholm were measured, using the measuring stick in the microscope.

RESULTS

Distribution of M. europaea in Northern Europe

Fig. 1 is a GIS map showing the 1990 to 2020 distribution of records of *M. europaea* in Northern Europe.

Fig. 2 shows the distribution of this species on historical records (black spots) and modern records (red spots) in Fennoscandia and Demark interesting pattern. Up until

Table 1. The climate variables associated with the distribution of *M. europaea*.

Conditional model	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-7.63931	1.31639	-5.803	6.50e-09 ***
poly(wc2 0 bio1 amt, 2)1	-250.33272	55.66063	-4.497	6.88e-06 ***
poly(wc2_0_bio1_amt, 2)2	-105.78294	22.39259	-4.724	2.31e-06 ***
wc2 0 bio2 mdrt	-2.64078	0.33983	-7.771	7.80e-15 ***
wc2 0 bio3 iso	0.79863	0.12351	6.466	1.00e-10 ***
wc2 0 bio9 mtdq	0.14729	0.03853	3.823	0.000132 ***
poly(wc2_0_bio10_ttwew, 2)1	725.97515	102.32115	7.095	1.29e-12 ***
poly(wc2 0 bio10 ttwew, 2)2	-168.21789	44.03282	-3.820	0.000133 ***
poly(wc2_0_bio12_ap, 2)1	-64.40637	31.49200	-2.045	0.040838 *
poly(wc2 0 bio12 ap, 2)2	-45.90483	21.11393	-2.174	0.029694 *

Table 2. The 19 investigated bioclimate variables.

Code	Description	Associated with M. europaeas' range	
Bio1	Annual Mean Temperature (°C)	Yes	
Bio2	Mean Diurnal Range [Mean of monthly (max temp-min temp)] (°C)	Yes	
Bio3	Isothermality (BIO2/BIO7) (× 100)	Yes	
Bio4	Temperature Seasonality (standard deviation × 100)	No	
Bio5	Max Temperature in Warmest Month (°C)	No	
Bio6	Min Temperature in Coldest Month (°C)	No	
Bio7	Temperature Annual Range (BIO5-BIO6) (°C)	No	
Bio8	Mean Temperature in Wettest Quarter (°C)	No	
Bio9	Mean Temperature in Driest Quarter (°C)	Yes	
Bio10	Mean Temperature in Hottest Quarter (°C)	Yes	
Bio11	Mean Temperature in Coldest Quarter (°C)	No	
Bio12	Annual Precipitation (mm)	Yes	
Bio13	Precipitation in Wettest Month (mm)	No	
Bio14	Precipitation in Driest Month (mm)	No	
Bio15	Precipitation Seasonality (Coefficient of Variation) (mm)	No	
Bio16	Precipitation in Wettest Quarter (mm)	No	
Bio17	Precipitation in Driest Quarter (mm)	No	
Bio18	Precipitation in Hottest Quarter (mm)	No	
Bio19	Precipitation in Coldest Quarter (mm)	No	

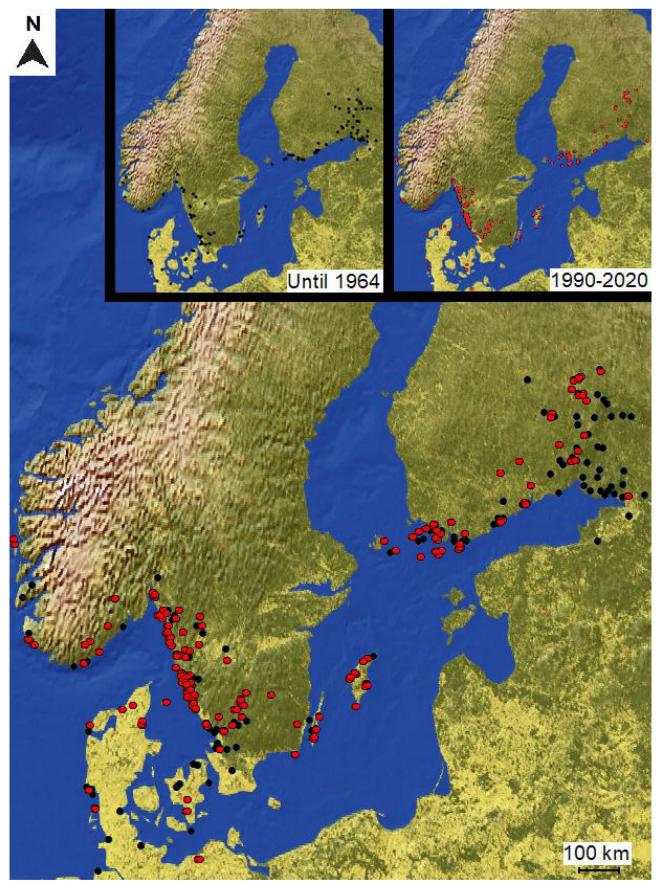


Fig. 2. Distribution of *M. europaea* in Northern EuropeThe black dots are old records and the red are modern records. There is some overlap in the distribution of red and black dots.

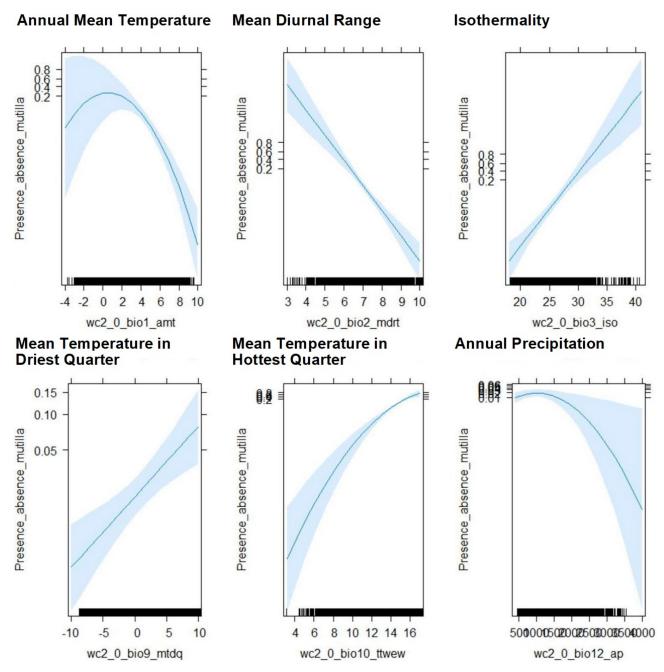


Fig. 3. Several of the climate variables are statistically significantly associated with the distribution of M. europaea.

1964, the distribution in Denmark and Fennoscandia clearly overlaps the modern distribution, indicating that the range of the population of *M. europaea* has been stable for some decades. It is possible that the apparent disappearance from eastern Finland is a result of poor sampling in modern times rather than actual disappearance of the species (the area became a part of Russia after World War II).

Of the 19 climate variables included in this study, six were significantly correlated with the distribution of *M. europaea* in Northern Europe (Fig. 3, Tables 1 and 2).

Results of the study of the collections of insects in museums

A total of 175 museum specimens from the Scandinavian peninsula were examined, 120 females and 55 males.

There was no significant difference in the size of females and males $[P(T \le t) \text{ two-tail} = 0.578614014]$. Individuals of *M. europaea* collected in Sweden, on the other hand, varied greatly in size from 9–21 mm.

There is some degree of variation in colour in *M. europaea*. Males have black heads and dark red to red brown mesonotum, or are completely black. Females have black (most often) or dark red heads (less often) (Fig. 6). The mesonotum of the females varies from red to dark red and brown (Figs 4, 5). There is no distinct border between the colours. In this study, most of the females had dark red cuticles (Fig. 6). At the Museum of Biology in Lund, there were 48 females of which two had a red mesonotum, in 40 it was dark red and in six brown. Of these, 41 had black heads, three brown and four dark red. Only one male was



Fig. 4. The variation in colour of the mesonotum of *M. europaea* varies from red (far left) to dark red (second from left) and brown and black.

completely black. At the National Museum of Natural History in Gothenburg, there were 50 females, of which three had a red mesonotum, in 35 it was dark red and in twelve brown. All females had black heads and there was no black males in the collection.

DISCUSSION

The map showing both historical and modern records of *M. europaea* in Fennoscandia (Fig. 2) indicate that this species has lived in the same areas over the last few decades. The results of the climatic analysis (Table 2) indicate that six climate variables are associated with the distribution of *M. europaea*: one humidity variable (annual precipitation) and five temperature variables. The populations in Fennoscandia live at the limits of where this species can occur.

Insects are poikilotherms and do not have the ability to regulate their own body temperature, and rely on external factors, like sunshine, to increase their temperature. Factors like size, shape, colour, and orientation determine the effect of solar radiation on insect body temperature. Large size and thermal inertia are associated, and larger bodied animals can maintain body temperatures above ambient for longer (Potter et al., 2009).

Some species of Mutillidae are sexually dimorphic in terms of size, with either significantly larger females or males. Sex-biased size variation may be associated with host-seeking or courtship behaviour (Deyrup & Manley, 1986). Other species (including *M. europaea*) have equal-



Fig. 6. A pinned female of *M. europaea* with dark red head and mesonotum.

sized females and males, but there can be a large size difference in size between individuals of the same sex (see Results). The difference in size are associated with differences in nutrition, temperature, genes, etc. In Addition, in *M. europaea* adult size is associated with the size of its host with individuals that parasitized honey bees generally smaller than those that parasitized bumblebees (BWARS, 2021).

Abiotic components of the environment can act as ecological filters and selective forces determining the colour of the body of velvet ants (Lopez et al., 2021). The pigmentation of individuals of Mutillidae is consistent with the photoprotection hypothesis and Gloger's rule, which states that in endotherms, more heavily pigmented forms tend to be found in more humid environments, and that species with a dark colouration occupy habitats with dense vegetation, high humidity and UV-B radiation (Lopez et al., 2021).

Insect colours can have important biological functions, such as thermoregulation (Stuart-Fox et al., 2017), predator avoidance via camouflage (crypsis and mimicry) (Skelhorn & Rowe, 2016), warning (aposematic) colouration



Fig. 5. Two pinned females of M. europaea, the one on the left has a red mesonotum and the one on the right a brown mesonotum.

(Stevens & Ruxton, 2012), or colour can be a secondary sexual characteristic (Jorge García et al., 2016). It has long been recognized that many Hymenoptera have a recurring pattern of black head, orange/red mesosoma, and black metasoma (BOB colouration). Orange to red colouration is very common in female Mutillidae, although there are several patterns. BOB colouration appears to be less common in male Mutillidae, although it is found, for example, in both sexes of the Palearctic species *M. europaea* and *Smicromyrme rufipes* (Fabricius, 1787) (Mora & Hanson, 2019). The results of this study indicates that colour varies in *M. europaea*; however, more research is needed to account for this variation in colour, since it is not clear in what habitat the specimens in the museum collections were collected.

If the weather in Northern Europe becomes hotter and more extreme because of climate change, the abiotic factors will also change, which could result in the distribution of *M. europaea* changing. A change in its distribution has not yet been record (Fig. 2), but climate change could affect the future distribution of the *M. europaea*.

CONCLUSION

The distribution of *M. europaea* in Northern Europe has apparently been the same for some decades. Distribution is associated mainly with two abiotic factors, temperature and humidity.

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