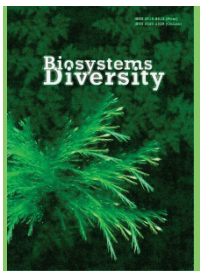

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East and West of the Carpathian Arc: Evidence of postglacial ecological and morphological divergence of *Phytoecia tigrina* metapopulations (Coleoptera, Cerambycidae)

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Phytoecia tigrina Mulsant (1851) is recognized as a species under strict protection EU Habitat Directive, it represents a focal point for conservation efforts across Europe. However, the dearth of comprehensive understanding regarding its biology, ecology, and geographical distribution poses formidable challenges to conservation endeavors. In the current study, we have delineated eight European and two Asian distinct metapopulations of *Ph. tigrina* across its geographic range, with a particular emphasis on elucidating its dispersion within the Circum-Carpathian region. This delineation serves to underscore the species' distribution, niche dimensions and limits of ecological tolerance that illuminate its adaptation capacity to diverse environmental conditions within the range. Our study has unveiled notable differentials in both morphological and ecological traits among *Ph. tigrina* metapopulations, notably between those located on the eastern and western flanks of the Carpathian Arc. Such differentials suggest the influence of divergent evolutionary trajectories, likely influenced by historical climatic changes during the Late Pleistocene and Holocene epochs. Significantly, specimens derived from eastern metapopulations exhibit morphological features of sufficient magnitude to warrant the proposition of a distinct subspecies, *Phytoecia* (*Pilemia*) *tigrina podillica* ssp. nov. This taxonomic delineation underscores the taxonomic complexity inherent within the *Ph. tigrina* species complex. Our investigations have further illuminated the historical dynamics of the species distribution, indicating the presence at least of two refugia during the Last Glacial Maximum (LGM). These refugial enclaves, situated in the Sea of Marmara/Eastern Aegean Sea region and the Pannonian Plain, likely played pivotal roles in shaping contemporary distributional patterns. Moreover, our ecological niche modeling endeavors have elucidated rapid expansions of suitable habitat for *Ph. tigrina* during post-glacial epochs, notably the Preboreal and Boreal periods. These expansions aligned with the rapid dispersion of its host plant *Cynoglottis barrelieri* supplying colonization of new territories in the face of the fast-changing post-glacial environment. Our study underscores the intricate interplay between evolutionary history, environmental dynamics, and imperatives for conservation *Ph. tigrina*. By elucidating these complexities, we endeavor to furnish a robust foundation for future conservation initiatives aimed at safeguarding this emblematic species and its associated habitats.

Keywords: longhorn beetles; niche modelling; GIS; morphology; new taxa; biogeography; evolutionary history; LGM refugia.

Introduction

Phytoecia (*Pilemia*) *tigrina* Mulsant (1851) is an iconic species of longhorn beetle that has been approved for strict protection within both the European Union (Council Directive, 1992) and Ukraine (Red Data Book, 2021). Additionally, *Ph. tigrina* is listed in Resolution 6 of the Berne Convention (Revised Annex I…, 2011). It holds a listing in Annex II and IV of the EU Habitat Directive as a xerophilic meadows habitat indicator species, encompassing the Pannonian, continental, steppic, and alpine realms of Europe. Habitats within the range of *Ph. tigrina* are mandated for inclusion in the Natura 2000 network within EU member states, as stipulated by the EU Habitats Directive. However, the mechanism for such inclusion differs somewhat for the Emerald Network within non-EU countries, such as Ukraine and Moldova, and is rooted in the principles delineated by the Berne Convention. Nonetheless, adequate protection necessitates a profound understanding of the species' biology, ecology, and threats to its existence. Deficiencies exist in the current implementation concerning *Ph. tigrina*, notably in the standard data form, which fails to furnish adequate insight into its biology and ecology, instead focusing solely on threats that may not be readily apparent from the available data (Report…. 2013–2018). Consequently, the assessment of its population status may not accurately reflect reality. To date, Crișan et al. (2017) have provided the most comprehensive information on the biology and habitat preferences of *Ph. tigrina*. However, the characteristics of its ecological niche and the limits of its ecological tolerance remain entirely unknown. This becomes particularly pertinent in light of the discovery of northernmost populations of *Ph. tigrina* in Ukraine (Zamoroka, 2023) and the easternmost populations in Romania and Moldova (Crișan et al., 2017; Bacal et al., 2020), significantly expanding the known range limits. A series of taxonomic changes, culminating in the recognition of several new species along with the introduction of additional synonyms, has further complicated the understanding of both the ecology and biogeography of *Ph. tigrina* (Aurivillius, 1923; Holzschuh, 1984; Özdikmen & Turgut, 2010; Löbl & Smetana, 2010). This holds particularly true for the Balkan Peninsula, Anatolia, and the Middle East. Uncertainty also surrounds the type locality of *Ph. tigrina* (Villiers, 1974; Sama, 2002; Özdikmen & Turgut, 2010). Presently, a confident discussion can be held regarding the spread of *Ph. tigrina* in the following countries: Bulgaria (Gradinarov & Petrova, 2021), Hungary (Kovács & Hegyessy, 2006), Moldova (Bacal et al., 2020), Romania (Crișan et al., 2017), Serbia (Ilić & Ćurčić, 2015), Tür-

kiye (Özdikmen & Turgut, 2010), and Ukraine (Zamoroka, 2022, 2023). In this study, a comprehensive investigation was undertaken encompassing morphological analysis and computational simulation to assess the ecological niche and environmental suitability of *Ph. tigrina* within its Circum-Carpathians range. The study elucidated the ecological disjunctions observed within the range of *Ph. tigrina*. Furthermore, our findings distinctly delineate profound morphological disparities among specimens from the eastern and western metapopulations of *Ph. tigrina*. Subsequent simulations conducted to evaluate climate change dynamics over the past 20 kiloannums (ka) revealed that the probable divergence period of the western and eastern metapopulations aligns with the Pleistocene-Holocene transition.

Materials and methods

Sources and data preparation. Our investigation draws upon original data derived from our own fieldwork, alongside collections procured from various scientific institutions, and an analysis of existing published literature. Our primary dataset was gathered across multiple sites within Romania and Ukraine spanning the period from 2009 to 2023. Furthermore, we meticulously examined specimens housed within esteemed scientific establishments, including the State Museum of Natural History in Lviv, Ukraine (SMNH); the entomological collection at Vasyl Stefanyk Precarpathian National University in Ivano-Frankivsk, Ukraine (PUIF); the Institute of Biological Research in Cluj-Napoca, Romania (ICBCN); the State Museum of Nature of V. N. Karazin Kharkiv National University in Kharkiv, Ukraine (KUMN); and the Halych National Park in Halych, Ukraine (HNP). Additionally, we augmented our dataset with information gleaned from published sources detailing the distribution of *Ph. tigrina*. These data from all three aforementioned sources were collated and geocoded (Table 1) to facilitate subsequent simulation of the species' ecological niche and environmental suitability. Niche and environment suitability modeling. The DIVA-GIS software, version 7.5.0.0 (LizardTech, Inc., and the University of California. U.S., 2012), a Geographic Information System (GIS), was utilized for the purpose of mapping the range of *Ph. tigrina*, conducting ecological niche modeling, and assessing environmental suitability. Bioclimatic data sourced from Worldclim, version 1.3, with a spatial resolution of 2.5 minutes, were employed.

Table 1
Geocoded data on *Phytoecia tigrina* records included into the study

ID	Latitude	Longitude	Country	ID	Latitude	Longitude	Country
1	43.119491	23.409439	Bulgaria	47	46.856962	24.088138	Romania
2	43.093187	23.617066	-//-	48	46.608852	24.133772	-//-
3	42.699986	23.258717	-//-	49	46.441121	21.830414	-//-
4	43.093503	26.718395	-//-	50	44.817360	21.392101	-//-
5	43.173462	27.898620	-//-	51	45.758675	24.129058	-//-
6	41.582351	23.732000	-//-	52	43.273453	20.776053	Serbia
7	41.510799	23.862160	-//-	53	44.778484	20.431001	-//-
8	41.883192	23.108253	-//-	54	43.773569	21.929524	-//-
9	41.715555	23.153432	-//-	55	39.131133	27.183438	Turkey (Asian)
10	42.876103	23.167820	-//-	56	38.603989	27.362948	-//-
11	43.082082	23.504169	-//-	57	38.295151	31.215695	-//-
12	43.080241	23.563534	-//-	58	40.016117	27.040027	-//-
13	46.107989	18.230803	Hungary	59	41.888672	27.228870	Turkey (European)
14	46.751332	18.588814	-//-	60	48.147878	23.069321	Ukraine (Zakarpattia)
15	46.099272	18.080892	-//-	61	46.842369	28.593461	Moldova
16	46.705605	18.486958	-//-	62	46.874721	28.477290	-//-
17	46.334353	21.125588	-//-	63	46.781945	29.472080	-//-
18	46.430447	21.060308	-//-	64	47.196080	27.468221	Romania
19	46.461298	20.956691	-//-	65	47.240609	27.498279	-//-
20	46.501136	21.047916	-//-	66	47.078134	27.747936	-//-
21	46.308582	20.808418	-//-	67	47.067090	27.805091	-//-
22	46.406562	20.896029	-//-	68	47.196080	27.468221	-//-
23	46.277374	21.017705	-//-	69	47.240609	27.498279	-//-
24	46.550767	20.889419	-//-	70	47.078134	27.747936	-//-
25	46.455101	20.894929	-//-	71	47.067090	27.805091	-//-
26	46.336061	21.119859	-//-	72	47.196080	27.468221	Ukraine (Podillia)
27	46.413676	21.045813	-//-	73	47.240609	27.498279	-//-
28	46.160754	18.349587	-//-	74	47.078134	27.747936	-//-
29	46.373522	18.695946	-//-	75	47.067090	27.805091	-//-
30	46.417125	21.108927	-//-	76	46.842369	28.593461	Moldova
31	47.452109	19.075849	-//-	77	46.874721	28.477290	-//-
32	47.511193	19.060642	-//-	78	46.781945	29.472080	-//-
33	46.421462	21.193497	-//-	79	49.321506	24.664678	Ukraine (Podillia)
34	46.481379	21.022440	-//-	80	48.159867	23.051272	Ukraine (Zakarpattia)
35	44.672669	22.299010	Romania	81	48.151885	23.048673	-//-
36	45.888568	22.896149	-//-	82	48.150265	23.043878	-//-
37	45.599075	21.043836	-//-	83	48.133961	23.028171	-//-
38	45.933351	20.893151	-//-	84	48.142954	23.054951	-//-
39	46.833894	23.633346	-//-	85	48.132484	23.069262	-//-
40	46.731580	23.817059	-//-	86	49.223617	24.699652	Ukraine (Podillia)
41	46.699915	23.843392	-//-	87	48.940985	24.792046	-//-
42	46.560253	23.692232	-//-	88	48.924714	24.990425	-//-
43	46.443034	23.586074	-//-	89	46.842369	28.593461	-//-
44	46.276911	23.929377	-//-	90	46.874721	28.477290	-//-
45	43.797284	28.456368	-//-	91	46.781945	29.472080	-//-
46	47.128724	23.860788	-//-	92	47.048877	28.959116	-//-

These data provided insights into the average climatic conditions spanning the period from 1950 to 2000. The model integrated 19 bioclimatic variables, enumerated as follows: BIO1: Annual mean temperature; BIO2: Mean diurnal temperature range (mean of monthly maximum temperature minus minimum temperature); BIO3: Isothermality (BIO2/BIO7 multiplied by 100); BIO4: Temperature seasonality (standard deviation multiplied by 100); BIO5: Maximum temperature of the warmest month; BIO6: Minimum temperature of the coldest month; BIO7: Temperature

annual range (BIO5 minus BIO6); BIO8: Mean temperature of the wettest quarter; BIO9: Mean temperature of the driest quarter; BIO10: Mean temperature of the warmest quarter; BIO11: Mean temperature of the coldest quarter; BIO12: Annual precipitation; BIO13: Precipitation of the wettest month; BIO14: Precipitation of the driest month; BIO15: Precipitation seasonality (coefficient of variation); BIO16: Precipitation of the wettest quarter; BIO17: Precipitation of the driest quarter; BIO18: Precipitation of the warmest quarter; BIO19: Precipitation of the coldest quarter.

Furthermore, simulations were conducted to assess the potential Last Glacial Maximum (LGM) refugia of *Ph. tigrina*. To achieve this, temperature data from Tierney et al. (2020) and precipitation data from Becker et al. (2016) were employed. Additionally, sea level data from Lambeck et al. (2014) were integrated into the final maps. Simulation of changes in the bioclimatic suitability of the environment for *Ph. tigrina* during the Holocene was predicated on climatic data sourced from Mauri et al. (2015) and Peyron et al. (2017).

Microscopy, morphometry and photography. Habitus photographs of complete beetles and their anatomical components were captured using a USB camera, specifically the DLT-Cam PRO 5 MP (China, 2017), affixed to a Nikon SMZ-1 stereomicroscope (Japan, 1999) at magnifications of 20× and 40×. Subsequent to capture, the resultant images underwent alignment and stacking processes utilizing the Helicon Focus 7 software suite, thereby ensuring optimal focus throughout the specimen. Following this, the images underwent enhancement and editing procedures to adhere to the requisite standards for publication.

Morphometric measurements of insect bodies were conducted employing the DLTCamViewer x86, version 3.7.7892 software package, adhering rigorously to standardized methodologies (Fig. 1). A scale calibrated in millimeters (mm) was utilized for length measurements, while curvature measurements were expressed in radians (rad). Specifically, the apical projection of the aedeagus was quantified as the ratio of its width to the length of the tip projection (Fig. 1a). Furthermore, the curvature of the aedeagus was assessed by quantifying the arc of a circle inscribed within the curvature of the ventral lobe of the aedeagus (Fig. 1c). Finally, the size of the parameres was determined by calculating the ratio of their length to the width at the base (Fig. 1b).

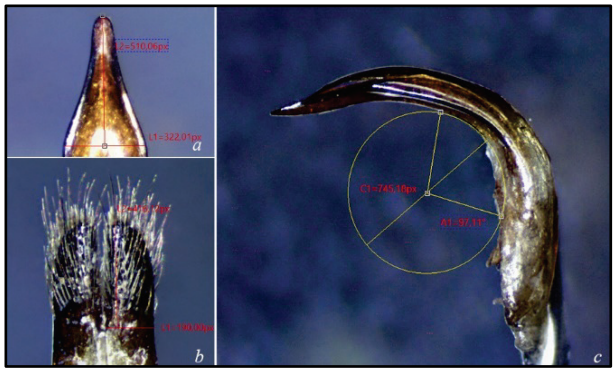

Fig. 1. The scheme of *Ph. tigrina* terminalia measurement

Comparative material: 1 female & 1 male 1929 (SMNH) "Kasova Hora", Burshtyn (49.226625, 24.696203), Ivano-Frankivsk Region, Ukraine, S. Smreczynsky Jun.; ibidem 1 female 07.V.2009 (HNP), A. Zamoroka; ibidem 1 female & 1 male 07.V.2009 (PUIF), A. Zamoroka; ibidem 1 female & 1 male 18.V.2009 (PUIF), A. Zamoroka; ibidem 1 male 09.V.2019 (PUIF), ibidem 10 females 14 males 26.V.2021 (PUIF), A. Zamoroka; 3 females & 7 males 07.VI.2021 (PUIF), Semenivka (48.763754, 25.337067), Ivano-Frankivsk Region, Ukraine, A. Zamoroka; 1 female & 3 males 22.V.2021 (PUIF), Oleshiv (48.925278, 24.990550), Ivano-Frankivsk Region, Ukraine, A. Zamoroka; 1 female & 2 males 17.V.2021 (PUIF), Pidpechary (48.942540, 24.789574), Ivano-Frankivsk Region, Ukraine, A. Zamoroka; 2 females & 2 males 03.VI.2019 (PUIF), "Dubrova", Yunashkiv (49.322404, 24.664579), Ivano-Frankivsk Region, Ukraine, A. Zamoroka; 3 females & 1 male 09.V.2020 (PUIF), "Chorna Hora" Vynohradiv (48.138641, 23.056328), Zakarpattya Region, Ukraine, A. Zamoroka; ibidem 7 females & 6 males 26.V.2022 (PUIF), A. Zamoroka; 1 female without date (KUMN), France, O. Bartenev; 1 female & 1 male 14.V.2021, Fânaţele Clujului (46.83699, 23.61878), Cluj County, Romania, A. Crişan; 1 female & 1 male 24.IV.2021, Baziaş (44.798989, 21.400216), Caraş-Severin County, Romania, F. Prunar; 1 female 29.V.2015, Boju (46.703013, 23.837375), Cluj County, Romania, A. Ruicănescu; 10 females & 10 males 21.V.2017, Comarna (47.059593, 27.815983), Iaşi County, Romania, C. Manci.

Results

Distribution and metapopulations. Our findings indicate that the distribution of *Ph. tigrina* is delineated by the Carpathian Arc into distinct Pannonian (western) and Pontic (eastern) parts (Fig. 2a). Both are connected by a narrow valley along the Danube. Furthermore, attention is drawn to two centers of *Ph. tigrina* documented in literature from Asia Minor, although their current status remains indeterminate (see discussion for comprehensive details). Notably, our investigation exclusively focused on the European range of *Ph. tigrina*, with particular emphasis on its Circum-Carpathian dispersion.

Despite the division of its range into western and eastern sectors, the distribution of *Ph. tigrina* within its confines exhibits heterogeneity, characterized by the formation of distinct metapopulations. Based on levels of isolation and geographical remoteness, we identified eight European and two Asian metapopulations (Fig. 2a). These encompass the following: 1) Zakarpattian (W Ukraine), 2) Transylvanian (C Romania), 3) Banatian (W Romania, E Hungary amd N Serbia), 4) Moldavian (E Romania and S Moldova), 5) Podillian (W Ukraine), 6) Transdanubian (W Hungary), 7) Balkanian (W Bulgaria), 8) Coastal (E Romania, E Bulgaria and NW Türkiye), 9) East Aegean (W Türkiye), 10) Sultanian (CW Türkiye). Our study covered the first five metapopulations from the list.

The distribution of *Ph. tigrina* exhibits disjunctions primarily due to the regional topography. Firstly, the Carpathian Arc acts as a significant barrier, impeding the northward expansion of the species and delineating four substantial metapopulations within the Pannonian Basin, namely the Transcarpathian, Transylvanian, Banatian, and Transdanubian. Furthermore, the Transylvanian metapopulation is the most isolated from the others by the presence of the Apuseni Mountains. To the south, the range of *Ph. tigrina* is constrained by the Dinaric Mountains and the Rila-Rhodope Mountains, while its eastern extent is restricted by the Moesian and North Pontic plains (Fig. 2a). Consequently, this partitioning segregates the Pontic range of *Ph. tigrina* into two distinct segments: the southern segment encompassing the Balkanian and Coastal metapopulations, and the northern segment housing the Moldavian and Podillian metapopulations. Moreover, the continental climate prevailing over the Ukrainian plains acts as an impediment, hindering the species from further eastward dispersion.

We have identified five distinct metapopulations of *Ph. tigrina* within the Circum-Carpathian range, namely the Zakarpattian, Transylvanian, Banatian, Moldavian, and Podillian metapopulations (Fig. 2a). The first three of these metapopulations occupy plains and the lower regions of mountains on the western side of the Carpathian Arc. They extend across the basin of the Tisza River in the north and the Velika Morava River in the south, ultimately reaching the Iron Gate in the Danube Valley to the east. Among these, the Zakarpattian metapopulation of *Ph. tigrina* is the northernmost, identified in several locations within Chorna Hora in the extreme west of Ukraine. This metapopulation is approximately 150 km from the Transylvanian metapopulation and 200 km from the Banatian metapopulation. However, it is crucial to note that despite the absence of recorded occurrences of *Ph. tigrina* between these three metapopulations, they are believed to be interconnected, as corroborated by our simulations (Fig. 3a). The Transylvanian metapopulation of *Ph. tigrina* is the most isolated among the three, bordered to the north and east by the Eastern Carpathians, to the south by the Southern Carpathians, and to the west by the Apuseni Mountains. It likely shares connections with the Banatian metapopulation in the valley of the Mureş River to the south and with the Zakarpattian metapopulation in the valley of the Someş River to the north.

East of the Carpathian Arc, the ecological conditions (see below) are less conducive to the dispersal of *Ph. tigrina*. Unlike the western metapopulations, the eastern metapopulations are located at a considerable distance (50–100 km) from the Carpathians, separated by the Carpathian Highlands with a cool and humid climate (Fig. 2a, 3b).

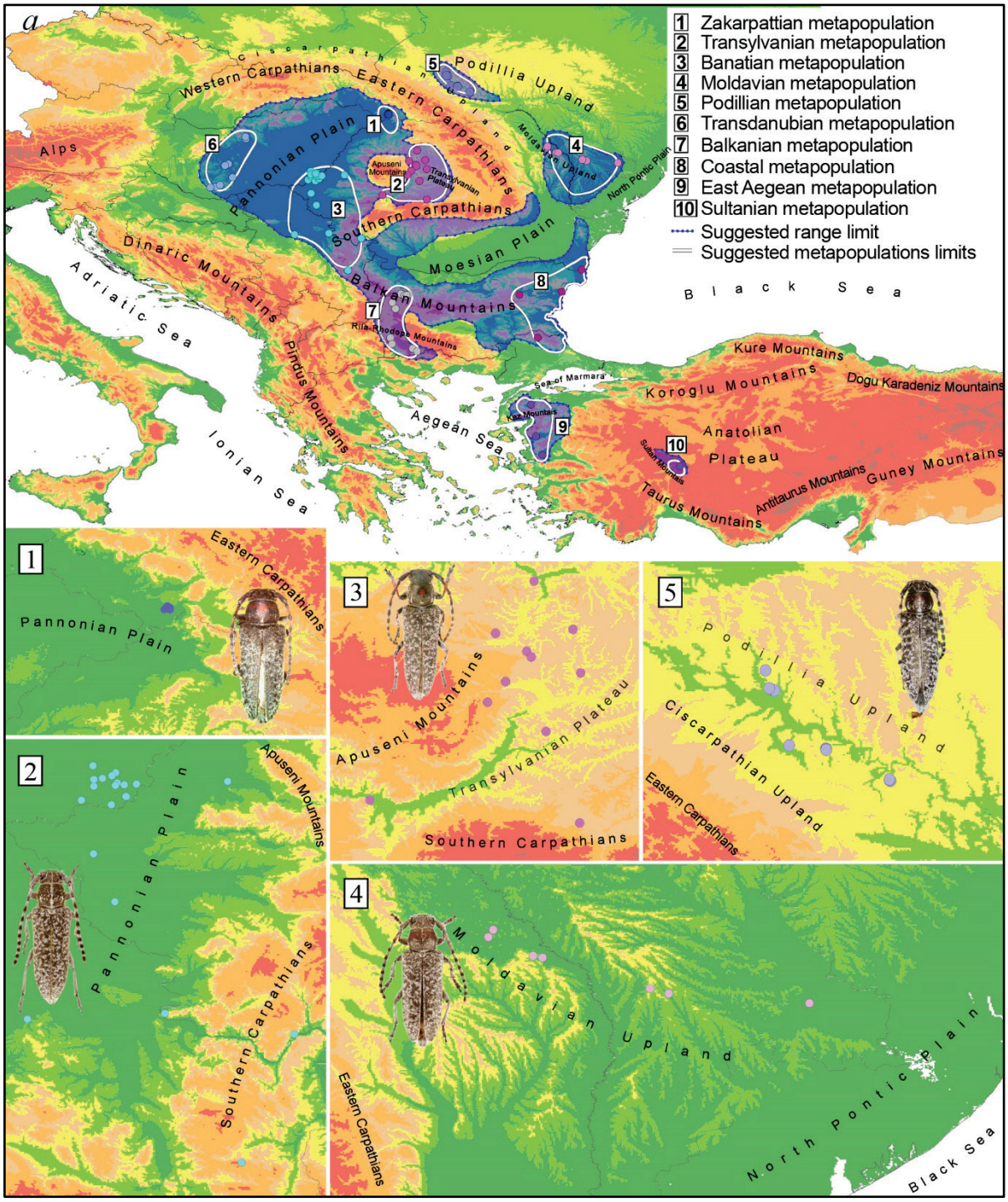

Fig. 2. The currently known range of *Ph. tigrina* (*a*) and with enlarged areas of studied metapopulations (*1–5*)

Furthermore, the range of *Ph. tigrina* is segregated into a northern Podillian metapopulation and a southern Moldavian metapopulation, both of which inhabit the warmest and most humid conditions of the region characterized by a continental climate. The distance between the Podillian and Moldavian metapopulations is approximately 230 km. Our model indicates their complete isolation (Fig. 3a).

Ecology. The resulting ecological niche model for the European range of *Ph. tigrina* (Fig. 4) illustrates a broad range of ecological tolerance, encompassing annual temperatures ranging from 7.3 to 12.8 °C and precipitation levels between 466 and 714 mm. However, its ecological optimum falls within the range of 10–11 °C for temperature and 550–600 mm for precipitation, respectively. Notably, the ecological optima vary for each metapopulation (Table 2), significantly influenced by geographical positioning and regional topography. Particularly, Zakarpattian and Transylvanian metapopulations are characterized by habitats with a notable annual precipitation (Fig. 3d, 3e), albeit with differing temperature conditions (Fig. 3i, 3j). Similarly, significant humidification is observed in the habitats of the Podillian metapopulation (Fig. 3h), accompanied by the coldest conditions (Fig. 3m), not only within the Circum-Carpathian region but also across the entire known range of *Ph. tigrina* (Fig. 4). These distinct characteristics set the Podillian metapopulation apart from the others. Additionally, Banatian and Moldavian metapopulations occupy dry and warm habitats (Fig. 3f, g, k, l). In general, the habitat distribution of *Ph. tigrina* mirrors similar ecological patterns on both sides of the Carpathian Arc, with the primary distinction lying in the fact that the western metapopulations span subxeric temperate continental climates of plains and subxeric cool continental climates of mountain foothills, whereas the eastern metapopulations transition from subxeric cool continental to axeric cool continental climates in uplands distant from mountains (Fig. 3, 4).

Table 2
Bioclimatic features of studied *Ph. tigrina* metapopulations

Bioclimatic variables	Metapopulations (mean ± standard deviation)				
	1. Zakarpattian	2. Transylvanian	3. Banatian	4. Moldavian	5. Podillian
BIO 1	9.34 ± 0.52	8.80 ± 0.76	10.82 ± 0.62	9.52 ± 0.42	7.99 ± 0.08
BIO 2	9.41 ± 0.12	10.33 ± 0.40	9.95 ± 0.34	9.25 ± 0.64	8.68 ± 0.22
BIO 3	29.97 ± 0.01	32.44 ± 0.44	31.46 ± 0.26	28.07 ± 1.38	28.00 ± 0.35
BIO 4	812.51 ± 7.78	799.09 ± 21.21	807.21 ± 15.80	896.58 ± 2.84	835.03 ± 8.09
BIO 5	25.30 ± 0.70	24.68 ± 1.11	27.23 ± 0.81	26.23 ± 0.50	23.81 ± 0.11
BIO 6	–6.10 ± 0.28	–7.15 ± 0.83	–4.40 ± 0.71	–6.71 ± 0.68	–7.17 ± 0.35
BIO 7	31.40 ± 0.42	31.84 ± 1.09	31.63 ± 0.91	32.94 ± 0.70	30.99 ± 0.42
BIO 8	17.50 ± 0.61	16.71 ± 0.94	18.74 ± 0.75	18.58 ± 0.44	16.55 ± 0.10
BIO 9	0.31 ± 0.45	0.12 ± 0.61	2.72 ± 3.48	2.40 ± 2.72	–1.49 ± 0.15
BIO 10	18.86 ± 0.60	18.04 ± 0.94	20.26 ± 0.71	20.02 ± 0.48	17.84 ± 0.10
BIO 11	–1.16 ± 0.38	–1.64 ± 0.60	0.37 ± 0.49	–1.92 ± 0.48	–2.64 ± 0.14
BIO 12	694.50 ± 26.16	619.45 ± 30.48	586.14 ± 48.90	552.86 ± 25.43	666.71 ± 3.40
BIO 13	92.00 ± 4.24	91.91 ± 5.47	79.71 ± 4.62	84.57 ± 9.16	98.00 ± 1.00
BIO 14	39.00 ± 1.41	28.45 ± 2.66	33.57 ± 4.37	27.29 ± 0.76	31.43 ± 0.53
BIO 15	29.32 ± 0.70	43.79 ± 3.57	28.24 ± 1.79	40.05 ± 6.34	44.71 ± 1.51
BIO 16	243.50 ± 10.6	252.64 ± 14.53	203.52 ± 15.54	217.14 ± 19.54	273.86 ± 3.44
BIO 17	126.00 ± 4.24	91.45 ± 7.75	106.86 ± 13.11	93.43 ± 6.53	97.43 ± 1.62
BIO 18	242.00 ± 11.3	243.91 ± 14.37	190.24 ± 10.87	211.14 ± 19.83	266.14 ± 2.61
BIO 19	144.50 ± 4.94	100.91 ± 10.48	123.57 ± 14.11	97.86 ± 10.21	104.00 ± 2.00

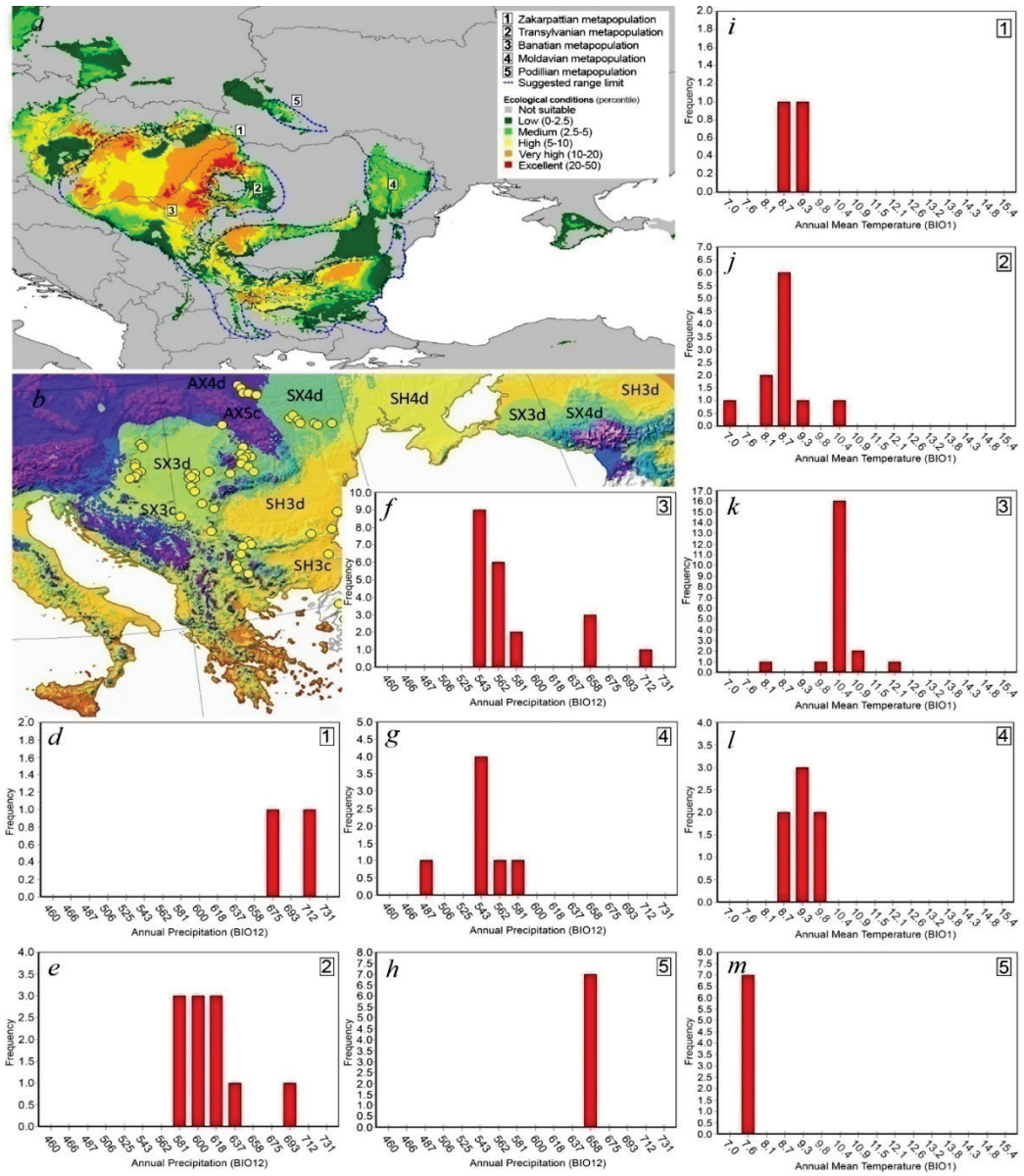

Fig. 3. Ecological features of *Phytoecia tigrina*: modelled environment suitability (*a*); climatic map (*b*) of SE Europe (after Botti, 2018) with records of *Ph. tigrina* (climate labels: AX4d – axeric cool continental; AX5c – axeric cold suboceanic; SX3c – subxeric temperate suboceanic; SX3d – subxeric temperate continental; SX4d – subxeric cool continental; SH3c – subhumid temperate suboceanic; SH4c – subhumid temperate continental; SH4d – subhumid cool continental); the ranked frequency of *Ph. tigrina* occurrence by amount of annual precipitation (*d–h*) and mean annual temperature (*i–m*)

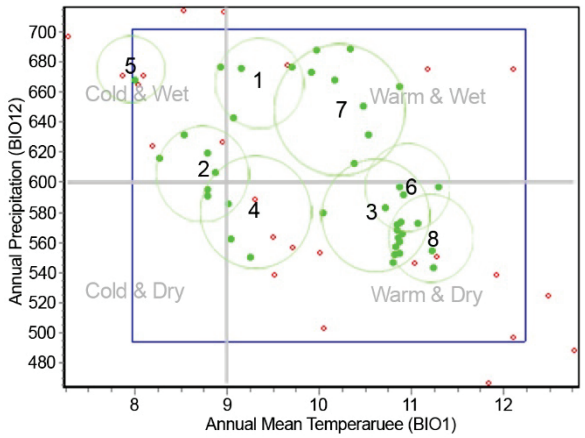

Fig. 4. Temperature-precipitation two-dimensional converting of *Ph. tigrina* observations within metapopulations: (1) Zakarpattian, (2) Transylvanian, (3) Banatian, (4) Moldavian, (5) Podillian, (6) Transdanubian, (7) Balkanian, (8) Coastal; red dots – extreme climatic value for at least one ecological factor outside the envelope; green dots – optimal climatic values by all climatic factors within envelope

Morphology. We found morphological variations of *Ph. tigrina* specimens within the studied metapopulations. Specimens from the metapopulations west of the Carpathian Arc (Zakarpattian, Transylvanian and Banatian) are morphologically very similar to each other. However, specimens of the Moldavian and Podillian metapopulation differ morphologically from those mentioned above. These include variations in head shape and body size in both males and females, as well as differences in the shape of the female pygidium and the size and shape of the male parameres.

The western metapopulations are featured by a smaller body size, a short and strongly convex head, notably wide forehead and short mandibles (Fig. 6c–d, g–h). The female's pygidium exhibits a very small and barely noticeable notch (Fig. 7b, d), while the posterior edge of the pronotum displays a small notch in the center (Fig. 7f).

In contrast, specimens from eastern metapopulations are characterized by a larger body size, a significantly elongated head with a flat and elongated forehead, and long mandibles in both sexes (Fig. 6a–b, e–f). The females exhibit a deep notch in the pygidium, similar to that of males (Fig. 7a, c), and a continuous posterior edge of the pronotum (although this minor feature may vary) (Fig. 7e).

The external morphology of males exhibits limited variation. The most variable features in males are the color of the cuticle of the 3rd to 5th antennomeres and tibiae, as well as the size and shape of the genitalia. We observed significant variability in the shape of the male aedeagi. Firstly, the curvature of the aedeagus displays considerable variation (Fig. 8u–y). The curvature ranges from 1.73 rad to 1.88 rad (Table 3). Males from the Podillian and Moldavian metapopulations exhibit the least curved aedeagi, with an arc length of 1.73 ± 0.04 rad and 1.75 ± 0.03 rad respectively (indicated standard deviation). On the other hand, Banatian males are known to have the most curved aedeagi, with an arc length of 1.88 ± 0.02 rad. Secondly, the size of the apical projection of the aedeagi also exhibits significant variation (Fig. 8p–t). The range of this projection is from 0.69 to 1.00 points, with an average of 0.83 ± 0.15. Males from Transylvanian and Banatian metapopulations display the highest values of this index, with 0.98 and 1.00 points, respectively. Conversely, males from the Podillian, Zakarpattian and Moldavian metapopulations exhibit the lowest values of the index, with 0.69, 0.70, and 0.78 points, respectively. Linking male aedeagus morphology to the biogeographic patterns of *Ph. tigrina* distribution remains challenging. In contrast to aedeagus morphology, tegmina vary very little (Fig. 8a–e) within all metapopulations, except for the Podillian. The latter is featured by the average ratio index of paramere width to length which is 1.92 ± 0.03 points. Whereas for the rest of the studied metapopulations, the average value of this this index is 1.56 ± 0.04 (from 1.52 to 1.62).

The external morphological variability in females is higher than in males. They exhibit significant differences in the coloration of the pronotum (Fig. 9) and the shape of its posterior margin (Fig. 7e–f). The intensity of the red spot on the pronotum varies among individuals within all populations, ranging from bright red to barely noticeable dark cherry. Along with color, the shape of the pronotal spot in females also exhibits considerable variation. There are two main forms of the pronotal spot observed in all populations: 1) a rounded central spot and 2) a transverse band. Females with one large central spot and two small lateral spots are rare, and females without pronotal spots are extremely rare.

Table 3
Male genitalia shape variation within the *Ph. tigrina* metapopulations

Metapopulation	Aedeagus curvature, mean ± SD (rad)	Aedeagus tip projection, mean ± SD (r.p.)	Parameres, mean ± SD (r.p.)
1. Zakarpatian	1.80 ± 0.02*	0.70 ± 0.01*	1.52 ± 0.01*
2. Transylvanian	1.81 ± 0.03	0.98 ± 0.20	1.58 ± 0.12
3. Banatian	1.88 ± 0.02	1.00 ± 0.21	1.60 ± 0.15
4. Moldavian	1.75 ± 0.03*	0.78 ± 0.05*	1.62 ± 0.04*
5. Podillian	1.73 ± 0.04*	0.69 ± 0.09*	1.92 ± 0.03*

Note: SD – standard deviation; r.p. – relative points; * – statistically significant value.

The form with one central spot is common in metapopulations westward of the Carpathian Arch. In contrast, females with a transverse red band dominate in metapopulations (both Podillian and Moldavian) located to the east of the Carpathian Arch. The width of the band varies greatly, ranging from very narrow to wide. In some cases, the band widens in the middle and narrows towards the edges. There are also individuals with an extended strip in the center and at the edges.

The shape of the posterior edge of the pronotum also varies (Fig. 7e–f). In eastern metapopulation, the posterior margin of the pronotum is continuous, usually without a notch in the center. Whereas in the western metapopulations, it is with a small notch. It should be emphasized that both forms of the posterior margin of the pronotum occur in all metapopulations but with different frequencies.

Taxonomy. On the basis of the observed geographic isolation, distinct ecology and morphology of eastern metapopulations of *Ph. tigrina* we propose to separate them into distinct subspecies *Phytoecia* (*Pilemia*) *tigrina podillica* ssp. nov. We also redescribed *Phytoecia* (*Pilemia*) *tigrina tigrina* Mulsant, 1851.

Phytoecia (*Pilemia*) *tigrina tigrina* Mulsant, 1851: 134

=*Phytoecia anchusae* Fuss, 1852: 138 (Schlossberg bei Deva, Romania – type locality)

Type locality: vicinity of Grasse (Var), France (Mulsant, 1851) (approx. 43.657369, 6.916162).

Redescription:

Body moderately elongated, subcylindrical, with dense irregular pubescence (Fig. 5c–d). Integument black with clear greenish metallic tint. Head shortened, forehead transverse and convex (Fig. 6c–d, g–h). Genae short, shorter than diameter of the low part of eye. Male antennae quarter longer than in females, as long as 1/3 of elytra length. 3–5th antennomeres dark red colored in both sexes. Pronotum subcylindrical, transverse, laterally convex, anteriorly and posteriorly slightly narrowed (Fig. 7f). Pronotal disc typically with round bright red spot (Fig. 9b, c); rarely with three spots (one central and two lateral) or transverse band (merged three spots). Pronotal spots weak in males. Pronotum with longitudinal median hair strip (often absent). Tibiae dark red (in males 1–2 pairs, in females 1–3 pairs). Elytra moderately elongated, truncated apically. Male pygidium narrowed apically with deep notch. Female pygidium narrowed, apically with shallow notch (Fig. 7b) on dorsal margin. Pygidium apex trilobed (1 wide dorsal and 2 ventral) (Fig. 7d). First and second male ventrites with nonpaired denticles. Fifth ventrite with deep depression in males and longitudinal sulcus in females. Aedeagus median lobe curved (Fig. 8u–w). Dorsal lobe sharply narrowed apically, shorter than ventral lobe; ventral lobe elongated in narrow apical projection (Fig. 8k–m, p–r). Tegmen slightly elongated, parameres short and wide, apically covered with long hairs (Fig. 8a–c, f–h). Body length 10–13 mm (in average for males – 10.5 mm, for females – 12.2 mm).

Diagnosis: Head and mandibles short. Forehead wide and convex. Female pygidium trilobate with shallow notch. Males' parameres short and wide, shallowly separated.

Distribution: Danube basin (? Bulgaria, Hungary, W Romania, Serbia, W Ukraine (Zakarpattya)).

Fig. 5. Habitus comparison of *Ph. tigrina* from eastern (*a*, *b*) and western (*c*, *d*) metapopulations: males (*a*, *c*) and females (*b*, *d*)

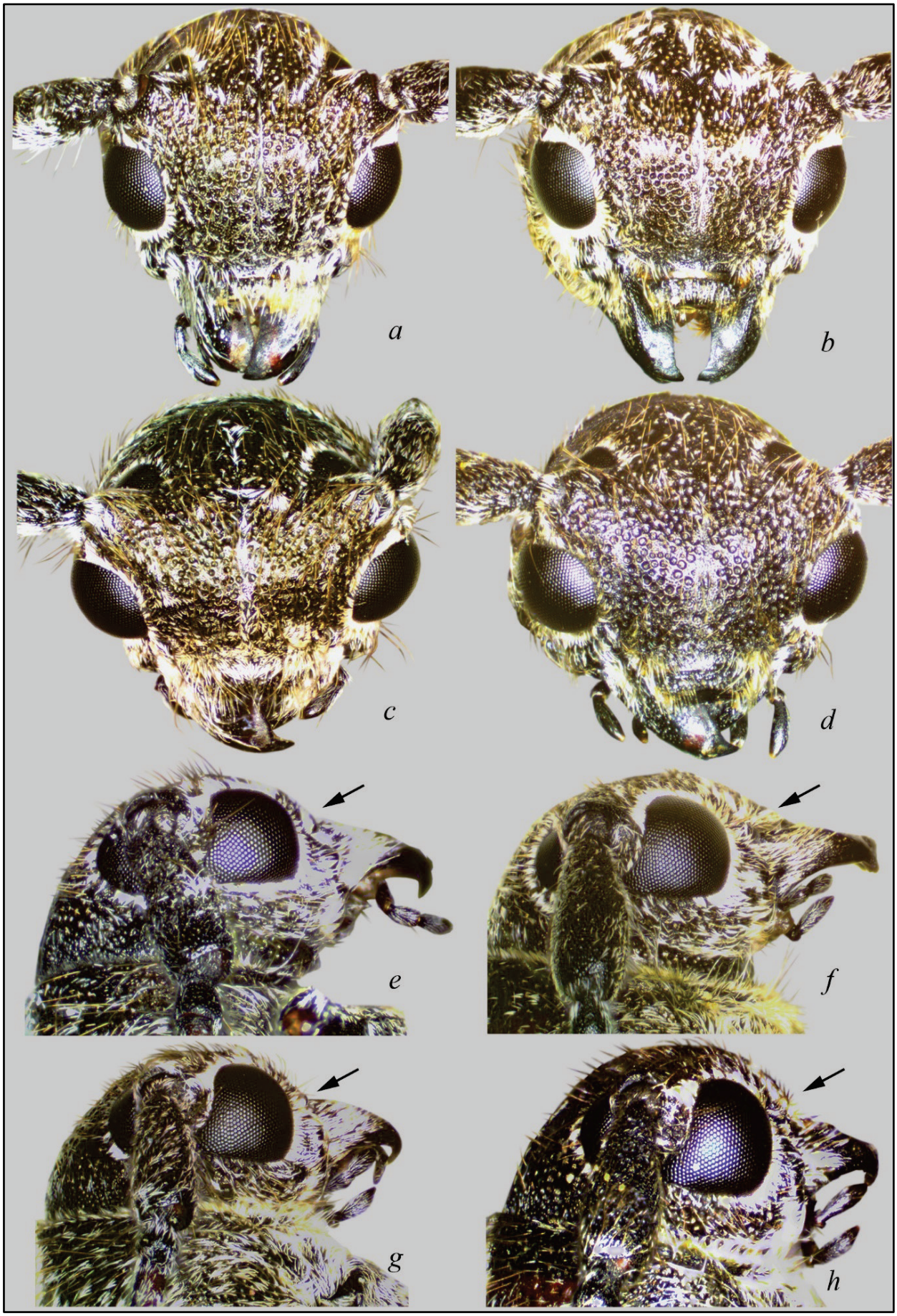

Fig. 6. Comparison of *Ph. tigrina* head morphology from eastern (*a*, *b*, *e*, *f*) and western (*c*, *d*, *g*, *h*) metapopulations: males (*a*, *c*, *e*, *g*) and females (*b*, *d*, *f*, *h*)

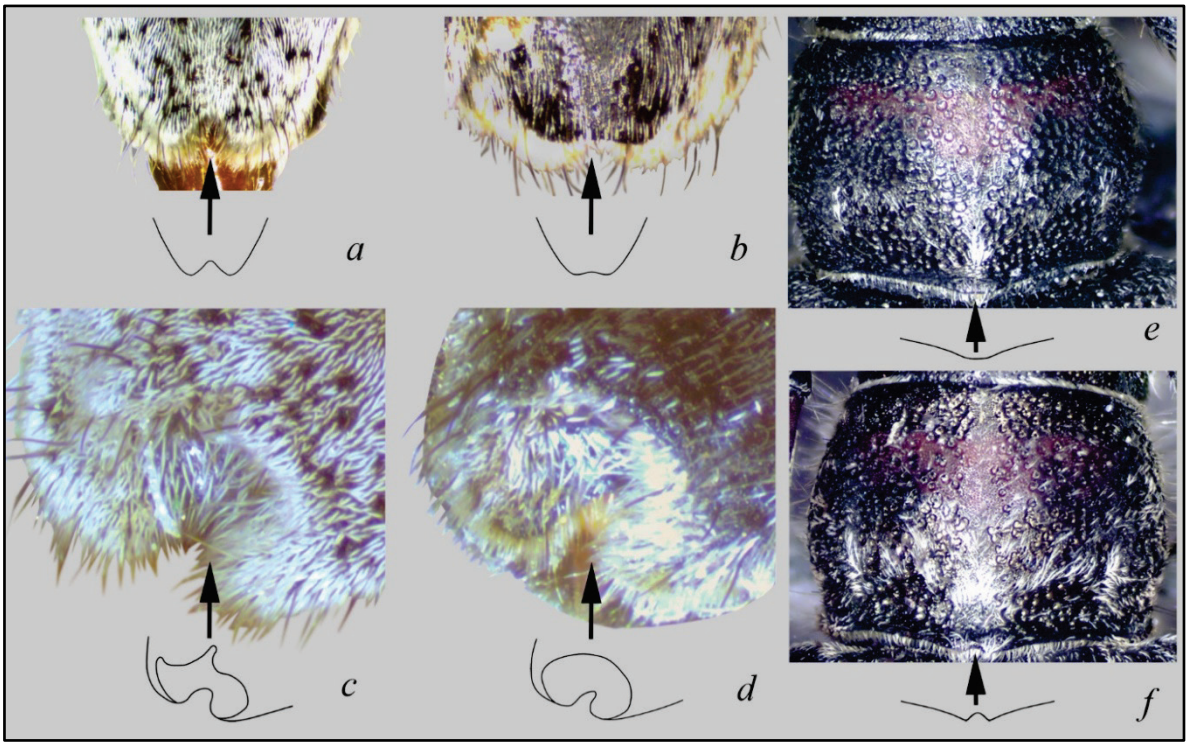

Fig. 7. Morphological comparison of female pygidia (*a*–*d*) and pronota (*e*–*f*) of *Ph. tigrina* from eastern (*a*, *c*, *e*) and western (*b*, *d*, *f*) metapopulations

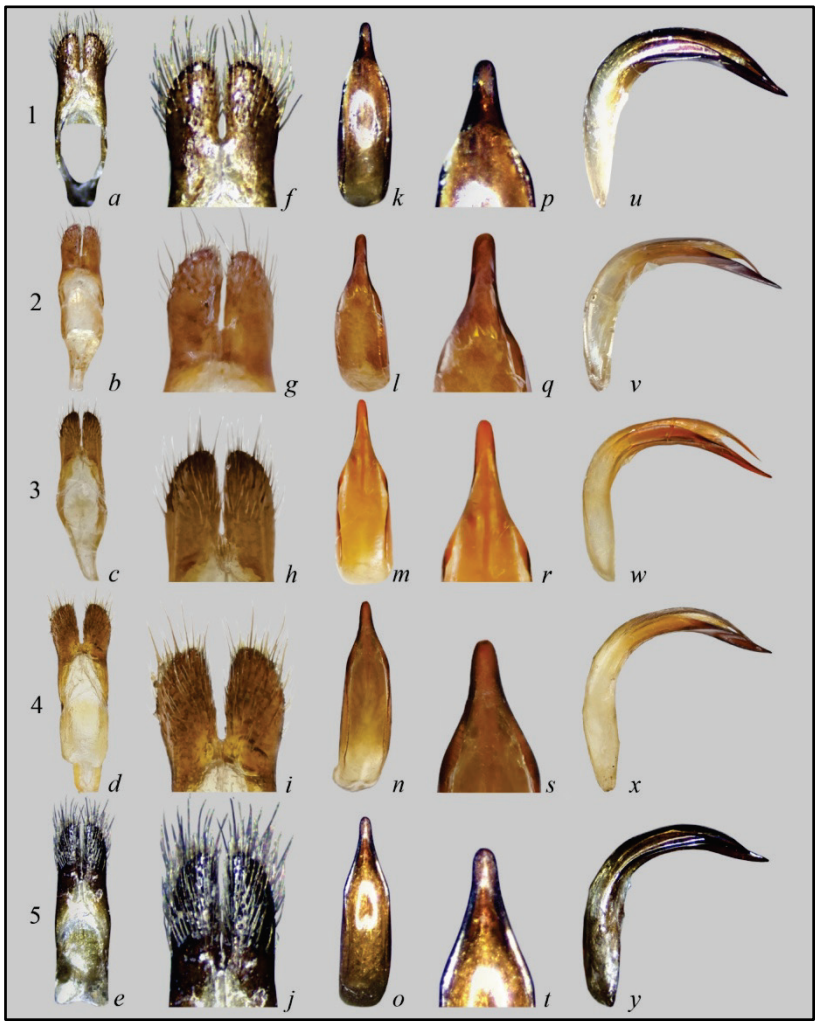

Fig. 8. Comparison of *Ph. tigrina* male terminalia including dorsal view of tegmen (*a*–*e*), enlarged dorsal view of parameres (*f*–*j*), dorsal view of aedeagus (*k*–*o*), enlarged dorsal view of the aedeagus apical process (*p*–*t*), lateral view of aedeagus (*u*–*y*) within the studied metapopulations: Zakarpatian (1), Transylvanian (2), Banatian (3), Podillian (4), Moldavian (5)

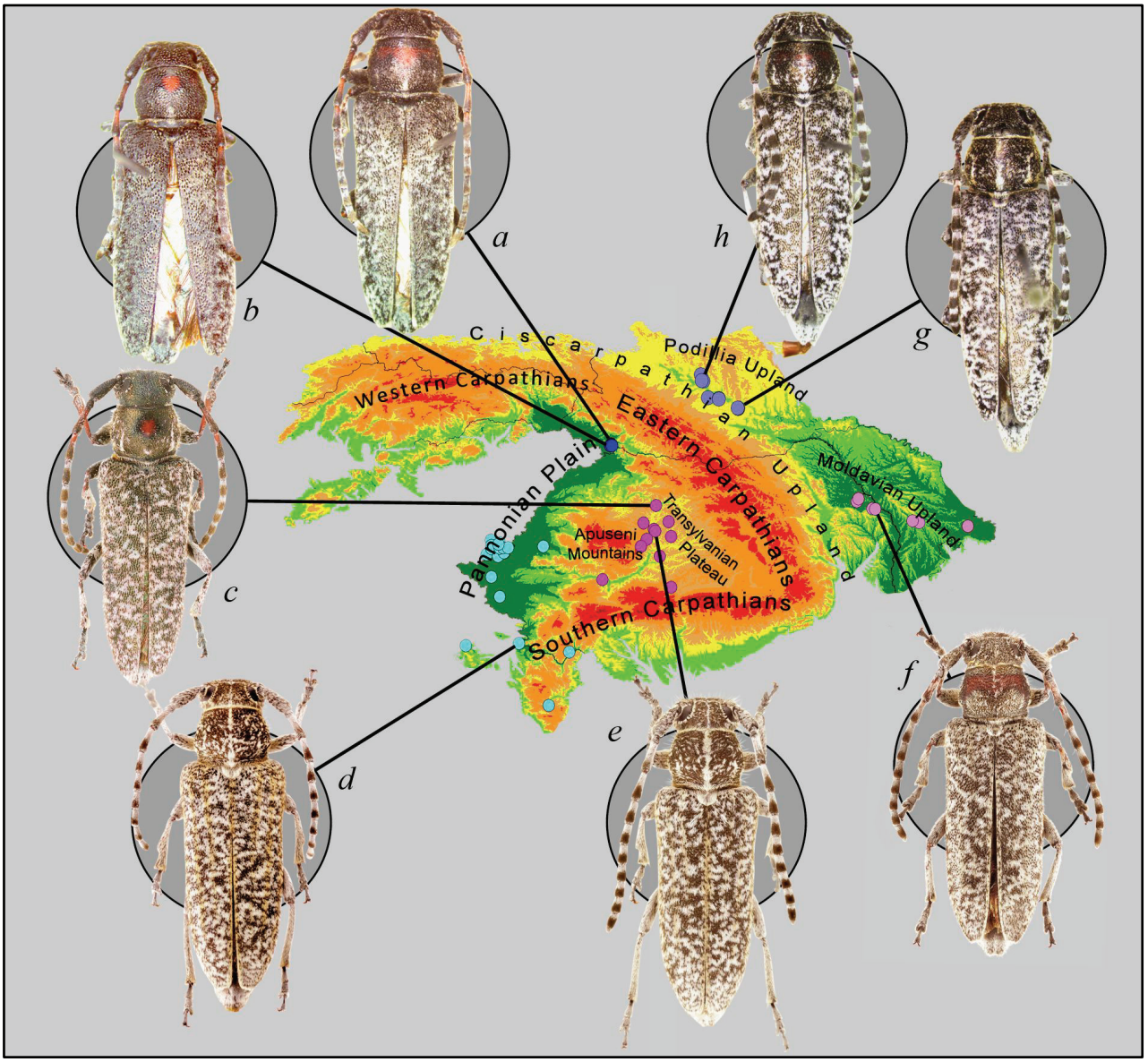

Fig. 9. Female habitus comparison of *Ph. tigrina* from different parts the range: Zakarpatian (*a*, *b*); Transylvanian (*c*, *e*); Banatian (*d*); Moldavian (*f*); Podillian (*g*, *h*)

Remarks: The presence of *Ph. tigrina* in France remains uncertain and speculative due to the absence of recent confirmatory records.

Phytoecia (*Pilemia*) *tigrina podillica* ssp. nov.

Description:

Holotype – male (Fig. 5a), 11 mm long. Body subcylindrical, moderately elongated with dense irregular pubescence. Integument black with very weak metallic tint. Head moderately elongated, coarsely and sparsely punctated, with dense pubescence. Forehead elongated, slightly narrowed, almost flat (Fig. 6a, e). Mandibles elongated. Genae elongated, as long as diameter of lower part of eye. Male antennae as long as 3/4 of elytra length. Bases of 3–11th antennomeres covered by dense white pubescence. Cuticle of base of 3–5th antennomeres slightly red colored. Pronotum subcylindrical, transverse, laterally convex, anteriorly and posteriorly slightly narrowed, with irregular dense light pubescence and longitudinal median hair line. Pronotal disc with unclear red colored transverse spot and sparsely punctated with big and small dots. Scutellum wide, rounded, with dense pubescence. Legs black, densely pubescent. Cuticle of the base of pro- and mesotibia dark red colored. Elytra moderately elongated, almost parallel, slightly narrowed posteriorly, apically truncated, densely and coarsely punctated. Pubescence irregular and ripple of white, light rusty and black hairs. Pygidium apically narrowed with deep notch. I and II ventrites with nonpaired denticles. V ventrite with deep depression. Abdomen covered by dense lying hair. Aedeagus median lobe curved (Fig. 8x, y). Dorsal lobe sharply narrowed apically, shorter than ventral lobe. Ventral lobe elongated in narrow apical projection (Fig. 8n, o, s, t). Tegmina vary from short (Fig. 8d, i) to elongated (Fig. 8e, j), entirely pubescent, densely punctated (Fig. 8d, e).

Allotype – female (Fig. 5b), 14 mm long. The female allotype is similar to the male holotype except featured patterns of head, pronotum and abdomen. Forehead slightly wider than in male (Fig. 6b). Antennae shorter than in male; 3–5th antennomeres clearly dark red colored on their bases. Pronotum with clear transverse red band (Fig. 7e). Pronotal posterior margin continuous, without median notch (Fig. 7e). First and second pairs of legs dark red colored. Pygidium narrowed, apically with deep notch on dorsal margin, as deep as in male; quadrilobed (2 dorsal lobes and 2 ventral lobes) (Fig. 7a, c). First and second ventrites usually without denticles. In paratype series, three of ten females had very small denticle on the middle of the 1st ventrite (gynandromorphism?). Fifth ventrite with median longitude sulcus.

Diagnosis: Head and mandibles elongated. Forehead narrowed and flattened. Female pygidium with deep notch, quadrilobed. Male parameres elongated, narrowed and deeply separated.

Variations. Females are more variable than males. The male body size ranges from 11 to 15 mm (mean: 12.2 mm); for female it is 11–16 mm (mean: 13.1 mm). The pubescence of the body varies greatly; near quoter of paratype series specimens covered by very sparse hair. The sha-

pe and color intensity of the red pronotal spot of females also varies. In the most typical case, it is a transverse band (merged 1 central and 2 lateral spots). Individuals with one central or three separate pronotal spots are extremely rare.

Etymology. A new subspecies is named after the physiographic region of Podillia (West Ukraine), where it was collected for the first time.

Type material. Holotype (1 male, 09.V.2019. Kasova Hora, Burshtyn, Ukraine) and 24 paratypes including allotype (10 females and 14 males, 26.V.2021. Kasova Hora, Burshtyn, Ukraine) of *Phytoecia* (*Pilemia*) *tigrina podillica* ssp. nov. deposited in the PUIF collection.

Type locality. "Kasova Hora" (49.226625, 24.696203), 310 m a.s.l., Burshtyn, Ivano-Frankivsk Region, Ukraine (Fig. 10).

Distribution: Dnister and Prut basins (Moldova, E Romania, W Ukraine (Podillia)).

Evolutionary history and probable refugia. The discernible morphological and ecological distinctions observed within each subspecies of *Ph. tigrina* suggest independent evolution in separate geographical regions during the Pleistocene-Holocene climate oscillations. Our modeling (Fig. 11) of the suitability of bioclimatic conditions for the existence of *Ph. tigrina* delineates the position of its probable refugia during the Last Glacial Maximum (LGM) of the Pleistocene (~24.5–19.0 ka) and its subsequent post-glacial expansion in the Holocene (~10.3–0.0 ka). In essence, the dynamics of bioclimatic suitability, and consequently the range of *Ph. tigrina*, exhibit a pulsating nature characterized by periods of expansion and contraction.

Fig. 10. Type locality of *Ph. tigrina podillica* ssp. nov.: general view of Kasova Hora (*a–e*); *Cynoglottis barrelieri* a foodplant of *Ph. tigrina* (*f*); adult beetle of *Ph. tigrina podillica* ssp. nov. feeding (*g*) and ovipositing (*i*) on *C. barrelieri*; the nick with egg of *Ph. tigrina podillica* ssp. nov. on the stem of *C. barrelieri* (h)

Our model illustrates two significant declines in the range of *Ph. tigrina* during the Last Glacial Maximum (LGM) (~25.4–19.0 ka) and the Atlantic time (~7.5–5.0 ka). During the LGM, mean annual temperatures were approximately 6 °C lower than present, accompanied by a drier climate (Tierney et al., 2020; Toucanne et al., 2022). Tundra and xerocryosteppe dominated most of Europe, with the northern boundary of forests (the taiga biome) reaching approximately 45–50 degrees north latitude (Shao et al., 2018; Davis et al., 2022). It is highly probable that there were two LGM refugia for *Ph. tigrina*. The first was situated in the region of the Sea of Marmara and the Eastern Aegean Sea, while the second was located in the Pannonian Plain (Fig. 11a). During the LGM, sea levels were around 150–200 m lower than present (Lambeck et al., 2014), resulting in the existence of two or more land bridges connecting the Balkan Peninsula and Asia Minor. This historical connection may explain the presence of *Ph. tigrina* in Asia Minor. The refugium in the Northern Aegean Sea area was likely linked to numerous thermophilous microsite refugia within the Danube valley and the Pannonian Plain. Conversely, the territories to the east of the Carpathians were likely unsuitable for the existence of *Ph. tigrina*, and the species may have been absent there. However, it is worth noting an intriguing hypothesis proposed by Kajtoch et al. (2016), suggesting the existence of scattered microsite refugia for thermophilic biota in xerocryosteppe conditions within the periglacial zone during the last glaciation. While such extrazonality may have occurred in the past, today there are similar examples of refugium microsites for thermophilic insects in the boreal zone (Egorov et al., 2022). At the moment, we cannot confirm the validity of this idea regarding *Ph. tigrina*. Vitali & Schmitt (2017) proposed the presence of large refugia in the Balkans and Anatolia, a notion supported by our models for *Ph. tigrina*.

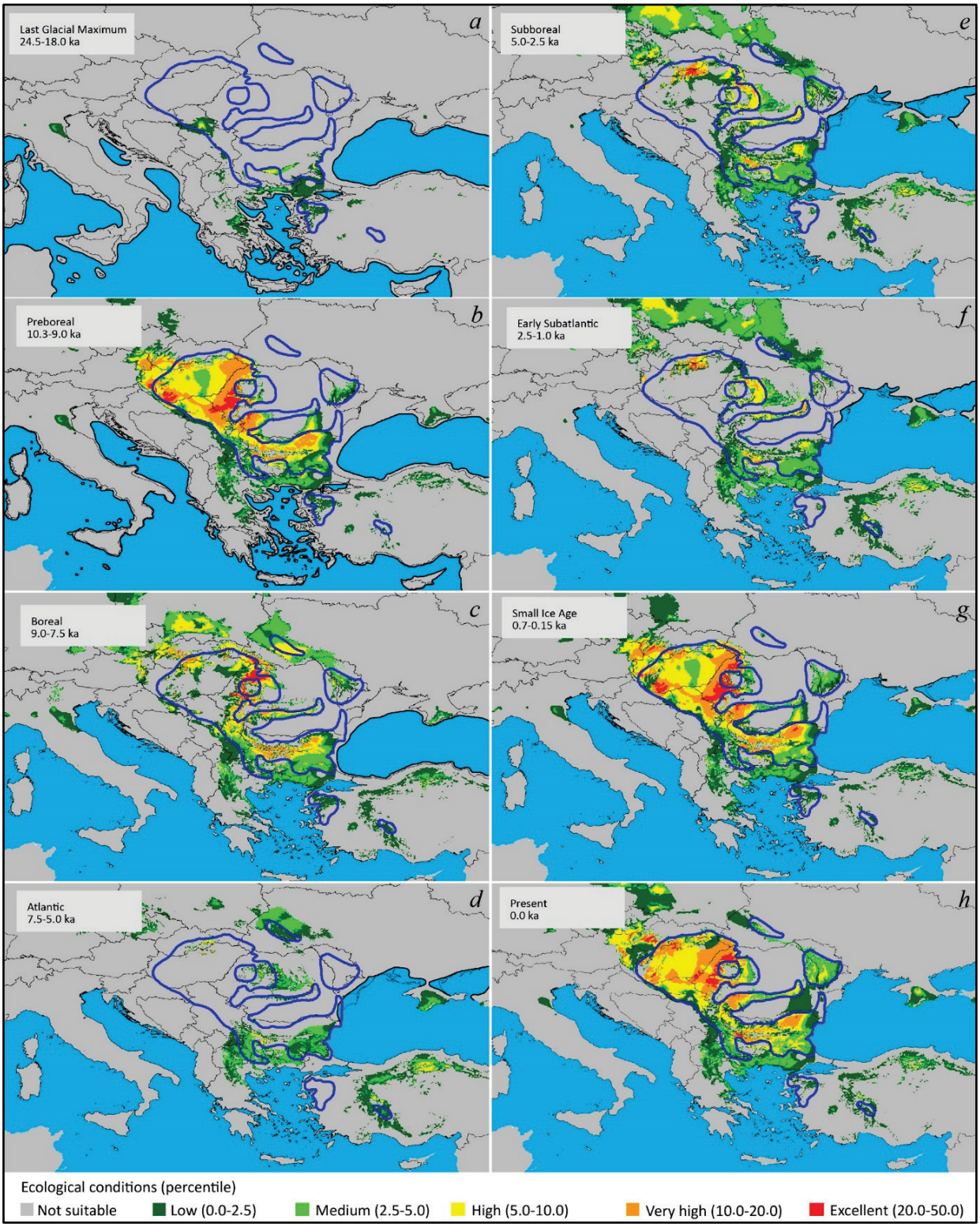

Fig. 11. The bioclimatic modeling of environment suitability for *Ph. tigrina* during Last Glacial Maximum of Pleistocene and Holocene climate oscillations; the current known range of *Ph. tigrina* is outlined by blue line

Our model illustrates a rapid expansion of favorable conditions (Fig. 11b) for the existence of *Ph. tigrina* in the territories of the Balkans and Pannonia during the Preboreal period (~10.3–9.0 ka). It is presumed that the expansion of *Ph. tigrina* range within the Pannonian Plain occurred much earlier than the extensive expansion of forests in the region. This scenario is highly plausible, considering the current rapid expansion of certain Cerambycidae species associated with herbaceous plants due to climate warming (Zamoroka & Mateleshko, 2016; Zamoroka & Hleba, 2019; Viznovych & Zamoroka, 2022; Babytskiy et al., 2023). Additionally, it is important to acknowledge the potential significant contribution of ancient anthropogenic activities, such as fire disturbances of the environment (Dietze et al., 2018), to the rapid spread of *Ph. tigrina* during the Preboreal period. The mass migrations of wild ungulates, as proposed by the forest-pasture hypothesis (Sandom et al., 2014), likely supported open and semi-open landscapes, further aiding in its spread.

The eastward expansion of *Ph. tigrina* likely occurred during the Preboreal period (10.3–9.0 ka), initially spanning the Moldavian Upland and later the Podillian Upland in the Boreal time (~9.0–7.5 ka) (Fig. 11c). A significant contraction of the range of *Ph. tigrina* was observed during the Atlantic time (~7.5–5.0 ka) (Fig. 11d). The Atlantic time represents the

climatic optimum of the Holocene, characterized by average annual temperatures approximately 3 °C higher than modern times and a drier climate (Jensen & Vorren, 2008; Mauri et al., 2015; Moossen et al., 2015; Peyron et al., 2017). During the Atlantic time, the northern limit of forests extended beyond 65 degrees north latitude, and thermoxerophilic species spread much further north (MacDonald et al., 2000; Jensen & Vorren, 2008; Zamoroka et al., 2019). The drier climate during the Atlantic time likely resulted in the Circum-Carpathian disjunction of *Ph. tigrina* range and the divergence of its eastern and western metapopulations. It is evident that subsequent climatic fluctuations during the second half of the Holocene (~5.0–0.0 ka) did not lead to the reconnection of the ranges of both subspecies (Fig. 11e–h), contributing to their long-term isolation, as observed in many other species of animals and plants (Zamoroka et al., 2018; Zamoroka, 2019).

Discussion

Our observations of significant morphological and ecological distinctions among metapopulations of *Ph. tigrina* from the eastern and western sides of the Carpathian Arc suggest their disparate evolutionary trajectories during at least the Late Pleistocene and the entirety of the Holocene. This distinction facilitated their classification as two separate subspecies. To the west of the Carpathians, the widespread subspecies *Ph. t. tigrina* (details regarding the typical location are discussed below), while the subspecies *Ph. t. podillica* ssp. nov. spreads to the east of the Carpathians. Our simulations indicate that during the Last Glacial Maximum (LGM) period (24.5–18.0 ka), there were two probable refugia for *Ph. tigrina*, namely the Aegean and Pannonian regions (Fig. 11a). However, it is likely that *Ph. tigrina* was entirely absent to the east of the Carpathian Arc during this period. Its migration to this area presumably occurred during the Preboreal time (10.3–9.0 ka), with simulations suggesting that the migration route followed the western coast of the Black Sea from the Aegean refugium (Fig. 11b). Presently, *Ph. tigrina* is documented along the western coast of the Black Sea (Coastal metapopulation) and the adjacent highlands (Fusu et al., 2015; Gradinarov, 2016; Crişan et al., 2017; Georgiev, 2020; Gradinarov & Petrova, 2021). However, we lack specimens from this area available for the study, thus hindering our ability to assess the degree of morphological similarity between the Moldavian and Coastal metapopulations. It is noteworthy that Holzschuh (1984) conducted a comparison of *Ph. tigrina* specimens collected in Hungary, [W] Romania, and Bulgaria (without specifying the locality), noting no discernible differences among them. Additionally, the female pygidia photographs published by him (Holzschuh, 1984: 172–173) resemble closely the specimens examined by us from western metapopulations and are notably distinct from those found in the eastern regions. This suggests that, at least in (?Western) Bulgaria, the prevalent subspecies is *Ph. t. tigrina*.

It should also be acknowledged that despite the notable morphological resemblance of *Ph. tigrina* specimens from the Moldavian and Podillian metapopulations, they exhibit differences in the morphology of the males' parameres (Fig. 8). Specifically, males from the Podillian metapopulation display elongated and slender parameres (Fig. 8e, j), whereas those from the Moldavian metapopulation exhibit shorter and broader parameres (Fig. 8d, i). The latter closely resemble the parameres of males from western metapopulations, suggesting a potential zone of introgression between the two subspecies south of the Carpathian Arc. Interactions between subspecies may occur through a hypothetical South Carpathian metapopulation, the existence of which is inferred from our simulations (Fig. 3a); however, specimens from this region remain entirely undocumented.

In general, the comprehension of the range limits of *Ph. tigrina* remains incomplete due to the absence of recent reliable records to substantiate historical data. This issue gained particular significance following a series of publications that uncovered inaccuracies in defining the typical locality (Villiers, 1974), the delineation of several new taxa from *Ph. tigrina*, previously regarded as a singular species (Aurivillius, 1923; Holzschuh, 1984), and a succession of synonymies (Özdikmen & Turgut, 2010; Löbl & Smetana, 2010). Moreover, there have been apparent instances of misidentifications of *Ph. tigrina*, further complicating the understanding of its present distribution. Consequently, various interpretations of the zoogeography of *Ph. tigrina* have been proposed. For instance, Özdikmen & Turgut (2010) characterized its range as Turano-European (Turano-Sarmato-Pannonian) based on Miroshnikov's (1990) publication, which reported a sighting of *Ph. tigrina* in Armenia (specifically, Tsaghkadzor [Darachichag]). However, we believe that Miroshnikov erroneously identified a female of *Phytoecia* (*Pilemia*) *annulata* (Hampe, 1852) as *Ph. tigrina*. *Phytoecia annulata* is widespread in Armenia, Azerbaijan, Iran, Syria, and Turkey. Subsequently, Tezcan et al. (2020) referred to the range of *Ph. tigrina* as "East-European," which is incorrect since the species is entirely absent in Eastern Europe. Additionally, Danilevsky (2020) proposed the presence of *Ph. tigrina* in the southern region of Russia (?Caucasus); however, the basis for this assumption remains unclear to us as confirming specimens are unavailable. Our data indicates that *Ph. tigrina* is a subendemic Ponto-Pannonian species spanning the basins of the Danube and Dnister in Europe and mountains in the West of Asia Minor (Fig. 2a). An overview of the published data on the distribution of *Ph. tigrina* is presented in Table 4.

Table 4
Evaluation of *Ph. tigrina* range

Geographic part	Country	Source	Status
Balkan Mountains	Bulgaria	Nedlyakov (1905), Kantardzhyeva-Minkova (1934), Gradinarov (2016), Gradinarov & Petrova (2019; 2021)	Reliable
Balkan Peninsula	Greece	Pic (1952), Heyrovsky (1967)	Doubtful
Bükk Highland	Hungary	Hegyessy & Kovács (2003), Kovács (2005), Kovács & Hegyessy (2006)	Reliable
Caucasus	Armenia, Russia	Miroshnikov (1990), Löbl & Smetana (2010), Danilevsky (2020)	Doubtful
Dunántúl Highland	Hungary	Merkl & Szél (2012)	Reliable
East Aegean–Marmara	Türkiye (Asian)	Demelt & Alkan (1962), Demelt (1963), Gül-Zümreoğlu, (1975), Özdikmen & Turgut (2010), Tezcan et al. (2020), Danilevsky & Tavakilian (2022)	Reliable
Guney Mountains	Türkiye (Asian)	Özdikmen & Hasbenli (2004), Danilevsky & Tavakilian (2022)	Doubtful
Maritime Alps (Type locality)	France	Mulsant (1851), Holzschuh (1984)	Doubtful
Mecsek Highland	Hungary	Kuthy (1897), Kaufmann (1914), Kaszab (1971), Holzschuh (1984), Hegyessy et al. (1999), Hegyessy & Kovács (2003), Kovács (2005), Kovács & Hegyessy (2006), Csathó (2009), Tóth et al. (2016)	Reliable
Moldavian Upland	Moldova, Romania	Miller & Zubowsky (1917), Medvedev & Shapiro (1957), Dascălu (2002), Popescu (2013), Csathó (2014), Derjanschi et al. (2016), Tóth et al. (2016), Crişan et all. (2017), Bacal et all. (2020), this study	Reliable
Middle East	Syria, Lebanon, Israel	Pic (1891), Sama (2002), Ozdikmen (2008)	Doubtful
Pannonian Plain (Tisza–Danube–Velika Morava)	Hungary, Romania, Serbia	Kuthy (1897), Kosanin (1904), Kaszab (1971), Ieniştea (1975), Holzschuh (1984), Ádám (1988), Kovács (1998), Hegyessy et al. (1999), Hegyessy & Kovács (2003), Kovács (2005), Kovács & Hegyessy (2006), Csathó (2009), Tatole et al. (2009), Serafim (2010), Serafim & Chimiliu (2010), Ilić & Ćurčić (2015), Tóth et al. (2016), Crişan et all. (2017), this study	Reliable
Podillia Upland	Ukraine	Zamoroka & Panin (2011), Zamoroka and al. (2012), Zamoroka (2022, 2023), this study	Reliable
Rila–Rhodope Mountains	Bulgaria	National Scientific Program (2018)	Doubtful
Sultan Mountains	Türkiye (Asian)	Özdikmen & Hasbenli (2004), Özdikmen & Turgut (2010)	Reliable
Transylvanian Plateau	Romania	Fuss (1852), Panin & Săvulescu (1961), Serafim (2010), Crişan et all. (2017), this study	Reliable
Volcanic Mountains	Ukraine	Zahaykevych (1961), Zamoroka (2022, 2023), this study	Reliable
West Black Sea Region	Bulgaria, Romania, Türkiye (European)	Özdikmen (2008, 2010), Fusu et al. (2015), Gradinarov (2016), Crişan et all. (2017), Georgiev (2020), Gradinarov & Petrova (2021)	Reliable

The presence of *Ph. tigrina* in France remains a matter of contention. Initially described by Mulsant (1851) from the vicinity of Grasse, no subsequent evidence has emerged to substantiate its occurrence in the designated type locality. Eventually, Villiers (1974) concluded that the reference to Grasse as the type locality for *Ph. tigrina* was erroneous. In subsequent publications (Villiers, 1978), *Ph. tigrina* was excluded from the fauna of France. However, it is noteworthy that Holzschuh (1984) referenced a female specimen labeled "Gallia merid." apparently collected in the southern region of France. During a brief visit to Kharkiv (Ukraine) in 2019, we had the opportunity to examine Bartenev's collection (KUMN) of Cerambycidae. Among the specimens, we discovered a female *Ph. tigrina* (Fig. 12) labeled "France" in Russian; however, the exact collection locality, date, and collector were unspecified. Unfortunately, we were unable to conduct an in-depth examination of this specimen. It is imperative to acknowledge that ongoing hostilities in the City and Region of Kharkiv since February 24, 2022, have severely impeded the continuation of our research. Nevertheless, while the specimen of *Ph. tigrina* from Bartenev's collection may originate from France, meticulous verification and confirmation with new reliable data are necessary.

Fig. 12. Female specimen of *Ph. tigrina* from O. Bartenev's collection, deposited in KUMN with label "France" (in Russian)

The understanding of the Asian (e.g., Türkiye) part of the *Ph. tigrina* range remains incomplete. This is attributed to the separation of several species previously classified as *Ph. tigrina*, notably highlighted in Holzschuch's seminal work (1984). Presently, there exists no comprehensive review of the collected reliable samples from this region. Contemporary publications often either reference older works, which in turn cite even earlier sources (Özdikmen & Hasbenli, 2004; Özdikmen & Turgut, 2010; Danilevsky & Tavakilian, 2022), or lack any data pertaining to species in the region altogether (Löbl & Smetana, 2010; Danylevsky, 2020). Sama (2002) and Pic (1891) presented data on *Ph. tigrina* from the Middle East, potentially expanding the recognized boundaries of the species range; however, these records are contentious. Some of the older records of *Ph. tigrina* may pertain to subsequently described species, including *Phytoecia breverufonotata* Pic, 1952; *Phytoecia griseomaculata* Pic, 1891; *Phytoecia halperini* Holzschuh, 1999; *Phytoecia smatanai* Holzschuh, 2003; *Phytoecia samii* Özdikmen & Turgut, 2010. Just two decades ago, these were all regarded as a single species (Sama, 2002). Therefore, the records of *Ph. tigrina* from Asia Minor warrant meticulous review to ascertain their accurate classification. The Asian range of *Ph. tigrina* likely encompasses the basins of the Aegean and Marmara Seas and several isolated regions, such as the Sultan Mountains (Özdikmen & Turgut, 2010; Tezcan et al., 2020). Our models (Fig. 3a) precisely illustrate such distribution patterns.

The distribution of *Ph. tigrina* appears to align closely with the range of its host plant, *Cynoglottis barrelieri* (All.) Vural & Kit Tan (Fig. 13a). Nonetheless, there are numerous regions where *C. barrelieri* thrives, yet *Ph. tigrina* remains undocumented. These areas encompass the Apennine Peninsula, Maritime Alps, the western and southern parts of the Balkan Peninsula, most parts of Asia Minor, and the Ukrainian plains. This observation underscores the interplay of biotic factors (such as the presence of host plants) and abiotic factors (including climate) in constraining the spread of *Ph. tigrina*.

Our niche modeling analysis (Fig. 3a) indicates that the environmental conditions in the Dinaric and Pindus Mountains of the West Balkans are unsuitable for *Ph. tigrina*, despite the widespread occurrence of *C. barrelieri* in these regions. *Ph. tigrina* may only inhabit microhabitats within river valleys in these areas. Despite the prevalence of *C. barrelieri* in the Italian mountains, *Ph. tigrina* sightings are lacking (Fig. 2a). Our hypothesis is that the Apennine populations of *C. barrelieri* may have dispersed independently from distinct refugia during the Last Glacial Maximum (LGM), compared to populations in Anatolia, the Balkans, Pannonia, and Podillia.

In Türkiye, *C. barrelieri* is abundant, yet reliable records of *Ph. tigrina* are scarce. The taxonomic classification of the Turkish *Ph. tigrina* population warrants comprehensive and distinct scrutiny. In Ukraine, *C. barrelieri* is prevalent in the forest-steppe sub-biome, whereas *Ph. tigrina* is only documented in the westernmost parts of Podillia and Zakarpattia (Zamoroka, 2022, 2023).

Of particular significance are our simulation outcomes, which indicate a high likelihood of *Ph. tigrina* spread in the Southern Carpathians (Romania) (Fig. 3a). However, no reports of *Ph. tigrina* from this area have come to our attention. Furthermore, simulations suggest that *Ph. tigrina* should also inhabit Southern Slovakia, the Czech Republic, and Eastern Austria (Fig. 3a), despite the absence of corroborating data. We posit that *Ph. tigrina* may be more widespread than currently documented, and further investigations may reveal its presence in the aforementioned regions.

We have observed that the distribution of *Ph. tigrina* is notably fragmented, comprising distinct metapopulations. Within its European range, we have identified eight metapopulations, five of which were thoroughly investigated in our study. Our findings unequivocally reveal that the fragmentation of the *Ph. tigrina* range primarily stems from climatic factors.

In the southern expanse of its range, *Ph. tigrina* is predominantly confined to mountain valleys. Conversely, in the northern regions, it extends into the foothill uplands. Of particular interest is the northernmost Podillian metapopulation of *Ph. tigrina*, which reaches nearly 50 degrees north latitude. This metapopulation spans areas characterized by a cool (7.5–8.0 °C) and humid (650–700 mm) climate (Fig. 3h, 3m, 4). Additionally, its contribution to the overall statistics of the ecological niche of *Ph. tigrina* suggests a shift towards the lower ecological limits for temperature values (Fig. 14a, b) and the upper ecological limits for annual precipitation (Fig. 14c, d). Such a shift strongly indicates its ecological isolation, serving as additional evidence, alongside morphological features, for its classification as the subspecies *Ph. t. podillica* ssp. nov. Conversely, the contribution of the southernmost Anatolian metapopulations to the general statistics of the ecological niche of *Ph. tigrina* contrasts sharply with that of the Podillian metapopulations (Fig. 14). Both represent two extreme values that delineate the ecological limits of the species in the southern and northern regions, respectively.

Conclusions

In conclusion, *Ph. tigrina* emerges as a species of significant conservation concern, underscored by its designation for strict protection and the limited understanding of its biology, ecology, and distribution. Our study identifies eight distinct metapopulations within its range, with a particular focus on its dispersion within the Circum-Carpathian region. We observe notable morphological and ecological differentiations among metapopulations, particularly between those situated east and west of the Carpathian Arc, leading to the proposal of a distinct subspecies, *Phytoecia* (*Pilemia*) *tigrina podillica* ssp. nov. Furthermore, our research sheds light on the historical dynamics of the species, indicating the presence of two Last Glacial Maximum refugia and rapid expansions of favorable habitats during key post-glacial periods. Moving forward, efforts to deepen our understanding of *Ph. tigrina* ecology, biology, and population dynamics are essential for effective conservation strategies. Additionally, ongoing monitoring and adaptive management approaches will be crucial to ensure the long-term survival of this iconic species and the preservation of its habitat amidst ongoing environmental changes. In addition to the insights

gained from our morphological and ecological investigations, future molecular studies hold immense importance for achieving a comprehensive understanding of the nature of *Phytoecia tigrina*.

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The authors declare that the research was conducted in the absence of any commercial or other relationships that could be construed as a potential conflict of interest.

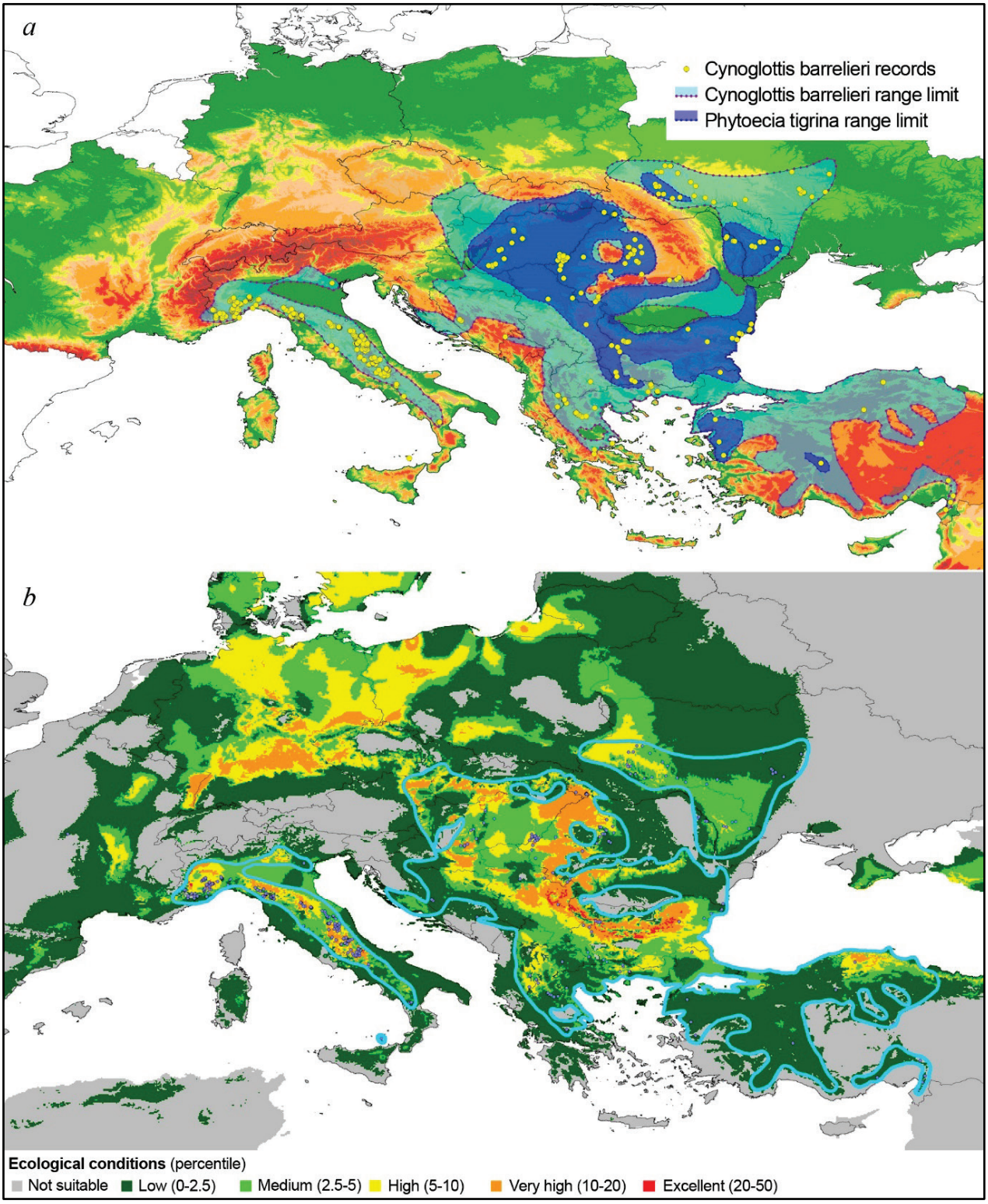

Fig. 13. The current range of *C. barrelieri* a host plant of *Ph. tigrina* (*a*) and its niche simulated environmental suitability in Europe and Asia Minor (*b*)

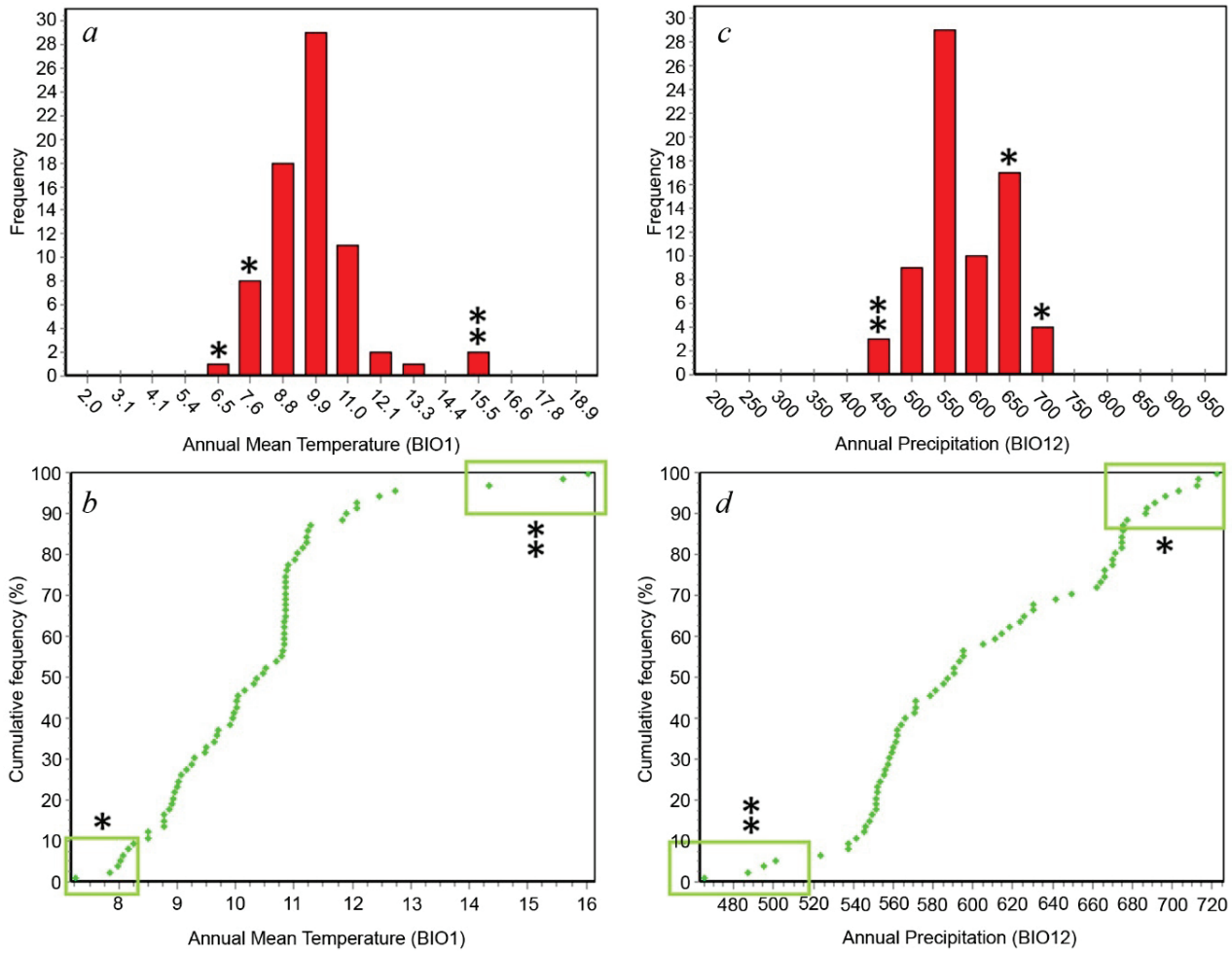

Fig. 14. General ecology of *Ph. tigrina*: ranked (*a*, *c*) and cumulative (*b*, *d*) frequency of specimens' occurrence by annual mean temperature (*a*, *b*) and amount of annual precipitation (*c*, *d*); the contribution of Podillian (one asterisk) and Turkish (two asterisks) metapopulations in general ecological statics of *Ph. tigrina*

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