Macedonian Journal of Ecology and Environment
Vol. 23, issue 1
pp. 37 - 48
Skopje (2021)
ISSN 1857 - 8330 (on-line)
ISSN 0354-2491 (print)
Original scientific paper
Available online at www.mjee.org.mk

Distribution and habitat of *Onconotus servillei* (Orthoptera: Tettigoniidae) within its westernmost range (Bulgaria, Romania, Serbia): models and perspectives

Распространување и живеалиште на *Onconotus servillei* (Orthoptera: Tettigoniidae) во најзападниот дел од неговиот ареал (Бугарија, Романија, Србија): модели и перспективи

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Abstract

Degradation and loss of natural habitats as a consequence of anthropogenic activities have resulted in the loss of almost half of the biodiversity on our planet. Habitat specialists are among the species that vanish first and thus they are useful bioindicators for habitat change. One of the biomes subjected to strongest anthropogenic impact is the steppe biome. In Europe, natural steppes are among the most threatened grasslands, especially along their western border along the Lower and Mid Danube. Consequently, many animal species inhabiting steppes have been threatened with extinction.

This study focuses on *Onconotus servillei* – a bush-cricket strongly dependent on the distribution and quality of its steppe habitat and threatened in Europe. It is assessed as Endangered in EU28, Bulgaria and Romania, Critically Endangered in Serbia, and Extinct in Hungary. We collected all known distribution data and model the species ecological niche. Based on confirmed recent observations we compare the model distribution with the species' habitat preferences and current distribution of steppe habitats in Bulgaria, Romania and Serbia. The received pattern is discussed in the light of conservation issues and the species' bioindicator properties to assess habitat quality. We conclude that *O. servillei* should be considered as a good bioindicator species for threatened European habitats and thus as a candidate priority species and species of community interest in need of strict protection of the European Commission Habitats Directive (92/43/EEC) Annexes II and IV.

Key words: ecological niche modelling, conservation, steppe, Natura 2000, bush-crickets, Southeastern Europe

Апстракт

Деградацијата и загубата на природните живеалишта како последица на антропогените активности се причина за загуба на речиси половина од биолошката разновидност на планетата. Видовите

Submitted: 05.04.2021
Accepted: 01.06.2021

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специјалисти кон специфични типови живеалишта се меѓу видовите што први исчезнуваат и од овие причини се корисни биоиндикатори. Еден од биомите кој е најсилно засегнат од антропогено влијание е степскиот биом. Во Европа, природните степи се меѓу најзагрозените тревести екосистеми, особено долж нивната западна граница на распространување покрај Долен и Среден Дунав. Поради тоа, многу животински видови кои живеат во степите се загрозени од исчезнување.

Ова истражување се фокусира на видот *Onconotus servillei* – степски вид скакулец загрозен на европско ниво, кој е силно зависен од распространувањето и квалитетот на живеалиштата во кои се среќава. Видот е проценет како загрозен во ЕУ28, Бугарија и Романија, критично загрозен во Србија и исчезнат во Унгарија. Во оваа публикација се собрани сите познати податоци за дистрибуцијата на видот и врз основа на нив направен е модел за еколошката ниша на видот. Направена е споредба на добиениот модел на дистрибуција со преференците на видот кон хабитатот и со сегашното распространување на степските хабитати во Бугарија, Романија и Србија. Добиените резултати се дискутираат во конзервациски контекст и од аспект на биоиндикаторските својства на видот. Заклучуваме дека *O. servillei* може да се смета за добар биоиндикатор за загрозените европски живеалишта и на овој начин претставува добар кандидат за приоритетен вид и вид од интерес на заедницата за кој е потребна строга заштита според Директивата за живеалишта на Европската комисија (92/43/ЕЕЗ) Анекси II и IV.

Клучни зборови: моделирање на еколошка ниша, конзервација, степа, Натура 2000, долгоантенести скакулци, Југоисточна Европа

Introduction

The natural habitats of our planet are subject to an ever-increasing anthropogenic pressure. As a result, large areas have changed significantly – their natural composition is altered or virtually destroyed. Degradation and loss of natural habitats affect at least 70% of the planet (Watson et al. 2016; Shukla et al. 2019) and have been identified as major contributors to the planet's biodiversity loss (Brondizio et al. 2019), especially affecting habitat specialists that rarely go beyond habitat boundaries with certain characteristics (e.g., Lehosmaa et al. 2017; Cordier et al. 2021). Such species may therefore be considered useful bioindicators for habitat change.

The Palaearctic steppe biome is the second largest continuous biome on Earth, covering 10.3 million km^2, of which 8.9 million km^2, or ca. 6% of the total land surface originally represent steppes (Wesche et al. 2016). Zonal steppes stretch from the northwestern Black Sea coast to northeastern China. West from this area, steppic grasslands are considered extrazonal steppes (Fig. 1), developing where local microclimate, topography, and soil properties provide conditions resembling the macroclimatically driven ones, that define zonal steppes (Wesche et al. 2016). Steppes represent a major carbon sink (Lal 2004), and mesophytic steppes were a major source for highly fertile arable land, which resulted in their vast conversion to cropland in Europe (Deák et al. 2016). Eurasian steppes are among

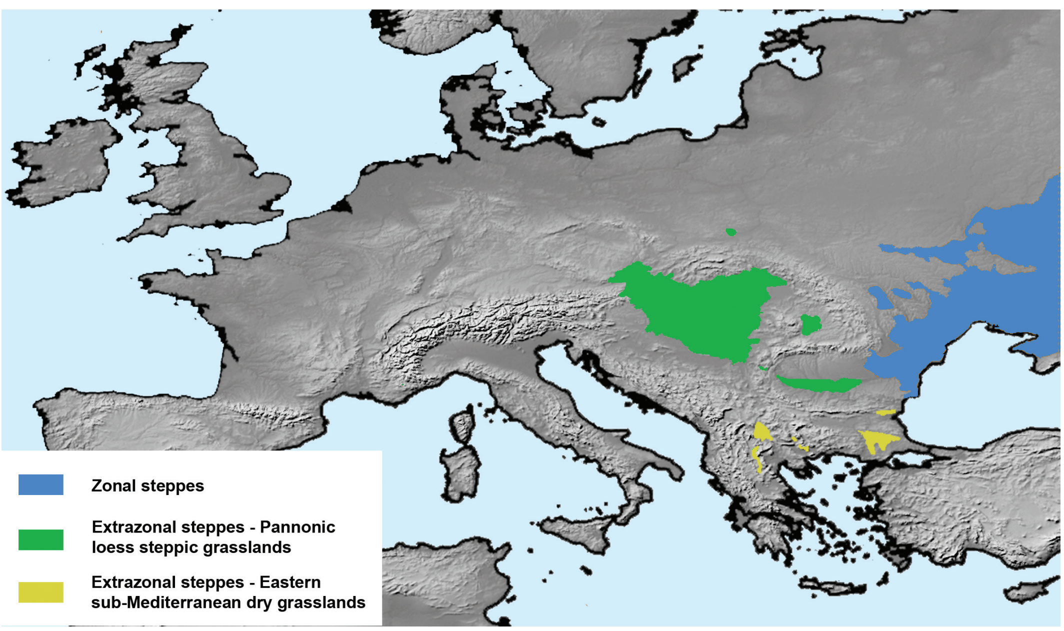

Figure 1. Outline of the distribution of zonal and extrazonal steppes in Southeastern and eastern-Central Europe.

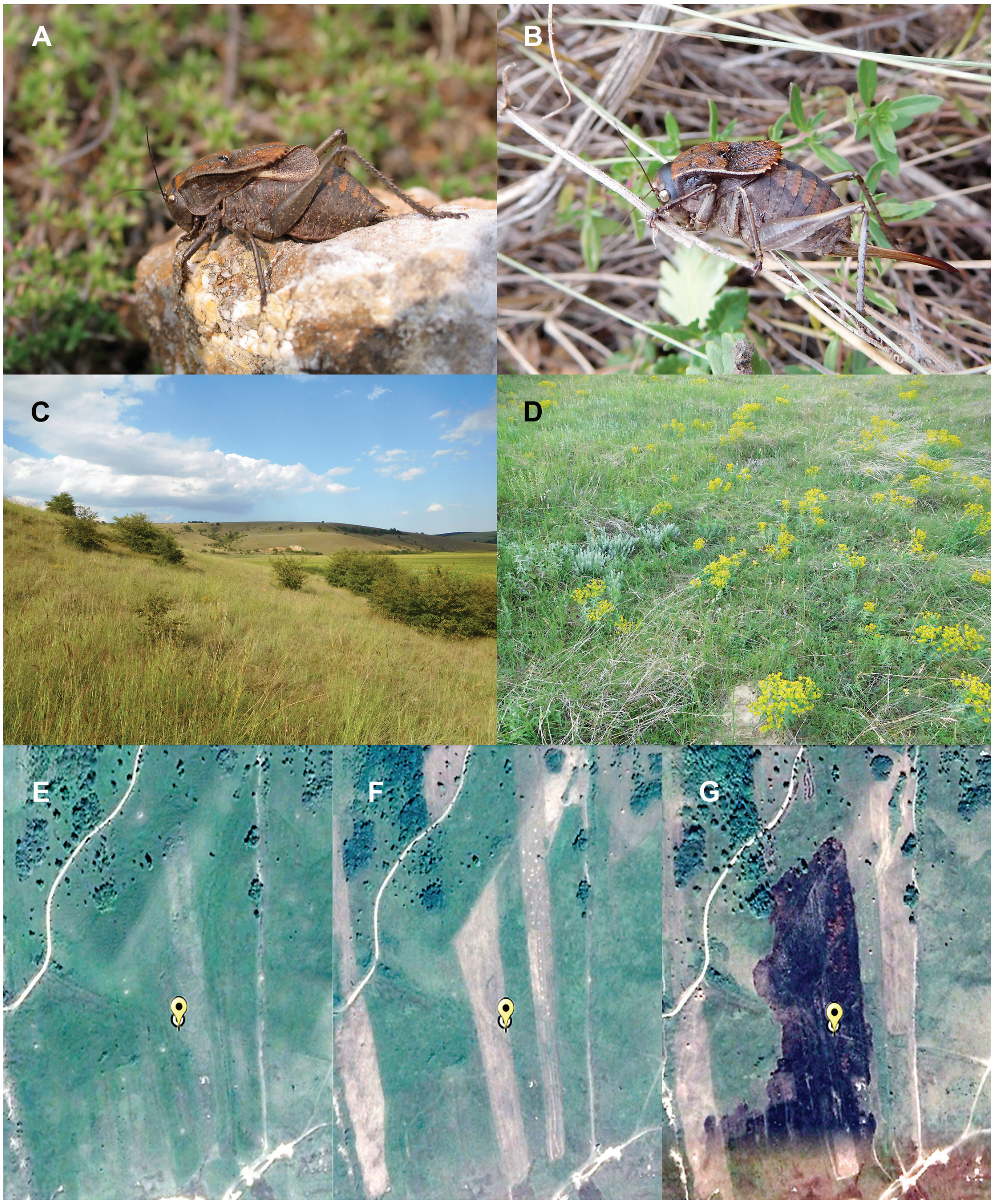

Figure 2. *Onconotus servillei* and its habitat. A – adult male; B – adult female; C – species habitat (Assoc. *Botriochloaetum ischaemi*) near Kapitan Dimitrovo vill. (NE Bulgaria) at the end of July; D – same (close view) at the end of May; E–F – habitat destruction at Paclele (Muntenia, E Romania) viewed with Google Earth 7.3.3. (https://www.google.com/earth/) (E – 5/2017; F – 8/2017; G – 8/2020).

the habitats most vulnerable to degradation (Werger & Staalduinen 2012), and natural steppes are among the most threatened grasslands in Europe among ca. 20 grassland communities requiring protection (Council Directive 92/43 of the European Commission). West of the Pontic area, steppes are distributed along the Danube reaching the Pannonian Basin. Further, smaller steppe patches are scattered over the Mediterranean, Alps and Central Europe. All over that range, this habitat is severely anthropogenically fragmented, and steppe flora and fauna are threatened with extinction not only by abandonment in the last few decades (compare Wesche et al. 2016) but most recently by a variety of anthropogenic factors including severe sedentary grazing intensification (Zólyomi & Fekete 1994; Tzonev et al. 2006; Vassilev & Apostolova 2013).

European extrazonal steppes are considered remnants of a wider distribution during the Holocene Boreal stage (e.g., Palamarev et al. 2002). Subsequent humidification by the middle of the Atlantic stage (ca. 6000 BP) have resulted in a vast replacement of open habitats by forests. And though the influence of the humid climate has been increasingly reversed with the human impact since the Bronze Age, yet, this influence has affected the very steppes as well (Vassilev & Apostolova 2013).

The Lower and Middle Danube Basins provide a route and a westernmost forepost for penetration of the Eurasian steppe into Europe. Though steppes along Danube represent a minute fraction of the Eurasian zonal steppes, their conservation importance is defined by a multitude of factors, including habitat connectivity and diversity at a local and continental scale, landscape diversity, carbon sequestration, support of traditional pastoralism, etc. (e.g., Kirscher et al. 2020).

Although in some countries such as Romania, steppes still occupy significant territories, the Lower Danubian and Black Sea coastal steppes are among the most degraded (e.g., Biserkov et al. 2015; Tzonev 2015; Tzonev et al. 2015; Tzonev & Gusev 2015) and under ever-rising pressure (e.g., Tzonev et al. 2006; Vassilev & Apostolova 2013). Plant associations representing steppes can be temporarily preserved even in small fragments, and steppes are classified as such even under certain habitat pressures (e.g., Vassilev & Apostolova 2013). In the latter case a better picture on the origin and the overall condition of a given habitat may be obtained by examining the distribution and certain population characteristics of model groups of animals that are dependent on a specific combination of macro- and microclimate, soil type and vegetation-composition. However, many habitat specialist animals, occurring in the steppes, are insufficiently studied in terms of their population ecology, population genetics, or even habitat preferences, and their response to habitat fragmentation or deterioration is obscure.

In the present study, we focus on an animal that is known to be narrowly connected with steppe habitats in a broad sense (class *Festuco-Brometea*) – the bush-cricket *Onconotus servillei* Fischer von Waldheim, 1846 (Fig. 2). The species is one of the two known taxa of the genus *Onconotus* Fischer von Waldheim, 1846, occurring in the past from Hungary in the west to southern central Siberia (Tuva) in the east (Cigliano et al. 2021). This species is a shy, short-winged, slow-moving insect with a typical loud male calling song (Korsunovskaya 2008) that makes it easily traceable during its peak activity (own observations). West of the zonal steppes, this cricket is found along the Danube, where it is assessed as Endangered in EU28, Bulgaria and Romania, Critically Endangered in Serbia, and Extinct in Hungary (Golemanski 2015; Hochkirch et al. 2016, 2019; Pavićević et al. 2018; Iorgu et al. in prep.). We use this species as a model for studying the steppes' present condition along the Lower Danube. We collect all confirmed recent locality data for *O. servillei* and model the species ecological niche and distribution. We compare the occurrence probability data with the current distribution of steppe habitats in Bulgaria, Romania and Serbia. The received pattern is discussed in the light of conservation issues and the species' bioindicator properties to assess habitat quality. This study will be a basis for widening our research onto the population genetics and future trends of this peculiar steppe species.

Material and methods

Sampling and ecological niche modelling

Our study concentrates on the westernmost part of the range of *O. servillei* on the territory of Romania, Bulgaria and Serbia (mapped area N 42-48.5; E 17.5-30). Occurrence points are based on published and own unpublished data (Table 1). Research focused on its habitat preferences was conducted by the authors in 2020. The species was traced in the field by the male loud calling song produced in the morning and evening hours. In addition to confirmed occurrence points, some unconfirmed literature data from areas where steppe communities still occur were tentatively georeferenced based on expert opinion using Google Earth (www.google.com/earth) and used to feed the ecological niche model providing a better estimation of the ecological requirements of the species. Localities with uncertain geographic position were omitted from the analyses. The occurrence datasets were "thinned" using the R package spThin (Aiello-Lammens et al. 2015) to ensure that the minimum distance between every two points is 1 km. Layers with the 19 bioclimatic variables available at Worldclim v. 1.4 (Hjimans et al. 2005; www.worldclim.org) were downloaded at 30-arc-second resolution. Although these variables are strongly correlated, Maxent shows consistency in regulating redundant variables (Feng et al. 2019), thus we did not eliminate any of the predictors before modelling.

Ecological niche modelling was performed with the presence-only algorithm implemented in Maxent v 3.4.3 (Phillips et al. 2017). Model 'tunning' was performed with the package ENMeval (Muscarella et al. 2014). Different combinations of feature classes and regularization multiplier were compared under the Akaike information criterion (AIC) (Akaike 1974) and the combination with the lowest AICc value was selected for the Maxent settings (see also Warren & Seifert 2011). A set of 10000 random background points was selected. Cross-validation was run with 10 replicates.

Distribution of suitable habitats

The received probability of presence maps were intersected with habitat types following the CORINE Land Cover (CLC) 2018, Ver. 2020_20u1 (https://land.copernicus.eu/pan-european/corine-land-cover) and EUNIS (https://eunis.eea.europa.eu/habitats.jsp), as well as the habitats distribution in Bulgaria (http://natura2000.moew.government.bg/Home/Reports?reportType=Habitats), Romania (https://natura2000.ro/ce-este-re-

Table 1. A synthesis of known locality data of *Onconotus servillei* in Bulgaria, Romania and Serbia. Details on the species habitat when known are provided. Current occurrence points (dark green) and points used to feed the ecological niche model (light and dark green) are noted.

Data used for modelling	Country	Region	Locality	Source	Confirmed occurrence	Latitude	Longitude	Altitude	Date	Habitat area ≤ ha	Syntaxa
yes	Bulgaria	E Danubian plane	Karakouz forest SW of Alfatar	Peshev 1955; Buresch, Peschev 1958; this paper - historic material NMNHS	no	43.905229	27.30561		7/9/1952		
yes	Bulgaria	E Danubian plane	Kanagyol canyon E of Alfatar	this paper - historic material NMNHS	no	43.92348	27.32401		7/7/1952		
yes	Bulgaria	N Black Sea coast	Batova Gora forest near Batovo vill.	Buresch, Peschev 1958; this paper - historic material NMNHS	no	43.43241	27.92444		11.06.1955		
yes	Bulgaria	E Danubian plane	Ognyanovo vill.	this paper	**yes**	43.91657	27.63924	140	8/1/2012	10	
yes	Bulgaria	E. Danubian plane	Alvanovo vill.	this paper	**yes**	43.28686	26.69050	160	7/12/2014	15-19	*Botriochloaetum ischaemi*
yes (2 localities)	Bulgaria	E Danubian plane	Kranovo vill.	this paper	**yes**	44.02345 44.02252 44.01861 44.01092	27.637 27.6351 27.63153 27.6466	35-110	8/1/2012	200	*Botriochloaetum ischaemi*
yes	Bulgaria	E Danubian plane	E of Kapitan Dimitrovo vill.	this paper	**yes**	43.952269	27.706222		28.07.2005 1.06.2020 22.7.2020	60	*Botriochloaetum ischaemi*
yes	Bulgaria	E Danubian plane	E of Debovo vill.	this paper	**yes**	43.58989	24.92618	140	7/18/2020	50-80	*Thymo urumovii-Chrysopogonetum grylli*
yes	Romania	Moldova	Valea lui David	this paper; Mîndru (1960, 1980); Mîndru, Kis (1965); Iorgu et al. (2013)	**yes**	47.19434	27.46758	87	30.06.2016		
yes	Romania	Muntenia	Paclele		**yes**	45.34323	26.70869	304	26.06.2014		
yes	Romania	Dobrogea	Babadag	this paper; Kis (1963); Kis, Lehrer (1981)	**yes**	44.81567	28.71232	119	14.07.2008		
yes	Romania	Dobrogea	Murfatlar		**yes**	44.15790	28.38992	70	30.06.2016		

Data used for modelling	Country	Region	Locality	Source	Confirmed occurrence	Latitude	Longitude	Altitude	Date	Habitat area ≤ ha	Syntaxa
yes	Romania	Dobrogea	Ivrinezu Mic		**yes**	44.24371	28.01930	26	1.08.2019		
yes	Romania	Muntenia	Comana	this paper - historic material MGAB	**yes**	44.15275	26.15967	62	3.07.2019		
yes	Serbia		Kladovo - near Vayuga vill.	this paper; Pančić 1883 as Kladovo surroundings	**yes**	44.56038	22.63547	75	7/18/2019		
no	Bulgaria	N Black Sea coast	Balchik	Buresch, Peschev 1958	no						
no	Bulgaria	E Danubian plane	Borovo	Buresch, Peschev 1958	no						
no	Bulgaria	E Danubian plane	Russe surroundings	Nedelkov 1908	no						
no	Bulgaria	E Danubian plane	Shoumen	Buresch, Peschev 1958	no						
no	Bulgaria	M Danubian plane	Svishtov surroundings	Nedelkov 1908	no						
no	Bulgaria	M Danubian plane	Pleven	Nedelkov 1908	no						
no	Bulgaria	N Black Sea coast	Varna	Nedelkov 1908; this paper - historic material NMNHS	no				[07]		
no	Bulgaria	N Black Sea coast	Varna	this paper - historic material NMNHS	no				7/3/1943		
no	Bulgaria	M Danubian plane	Peychinovo vill. (as Burumliy)	this paper - historic material NMNHS	no				17.06.1932		
no	Romania	Moldova	Ciric	Mîndru (1960); Mîndru, Kis (1963)	no	47.18928	27.596437	72			
no	Romania	Muntenia	Cernica	this paper - historic material MGAB	no	44.41688	26.29238	58	1954		
no	Romania	Dobrogea	Macin	this paper - historic material MGAB	no	45.23842	28.202453	291			
no	Serbia		Čamurlija	Pančić 1883	no						
no	Serbia		Moravica	Us 1938	no						

teaua-natura-2000/) and Serbia (own habitat selection) to select for the habitat type. Further, plant communities in a few confirmed occurrence points of *Onconotus servillei* were classified phytosociologically (Braun-Blanquet 1964) (Table 1) and physiognomically.

Results

After the thinning procedure, a total of 16 localities were retained for modelling (Table 1). The lowest AICc was obtained with a regularization multiplier (RM) of 1.5 and linear, quadratic and hinge features. The mean area under curve (AUC) from the 10 replicate models of *Onconotus servillei* was 0.89. Among the variables with the highest contribution to the model were BIO9 Mean Temperature of Driest Quarter, BIO10 Mean Temperature of Warmest Quarter, BIO12 Annual Precipitation, BIO13 Precipitation of Wettest Month, BIO16 Precipitation of Wettest Quarter, BIO18 Precipitation of Warmest Quarter (Fig. 3). The highest gain from a single variable was obtained with BIO16. The model (Fig. 4) highlighted suitable conditions for *O. servillei* along the northwestern Black Sea coast North of the Burgas Bay in Bulgaria up to ca. 46.5° latitude north and westwards along the Danube up to Central Hungary ca. 47.5° latitude north, with an interruption in the forested zone of the Carpathians and Balkan Mountains. The highest probability is concentrated in the Dobroudzha/Dobrogea region, covering northeasternmost Bulgaria and easternmost Romania, bordered to the west by the Danube and to the east by the Black Sea. Suitability and occurrence frequency recedes towards the Carpathians and sharply decreases in a relatively large area along the Danube river between Vidin and Corabia.

Localities of the species in Bulgaria generally fit the habitat 6250 (Pannonic loess steppic grasslands) and partly 6240 (Sub-Pannonic steppic grasslands) of the EUNIS classification and fall into the CORINE Biotopes type “Pastures”. Yet, 6240 covers far too extensive areas largely overgrown with scrub or ruderalized, which, compared to the occurrence points of *Onconotus servillei*, makes the result of omission of this habitat here negligible. Therefore, as a first step, we measured overlap between the available maps of habitat 6250 or similar habitat types (a 1x1 km grid for Bulgaria, outlines for the steppe associations within the Natura 2000 network for Romania, and manually outlined steppe habitats for Serbia) and the CORINE Biotopes habitat type Pastures. The result (Fig. 5A) recovered 826 km^2.

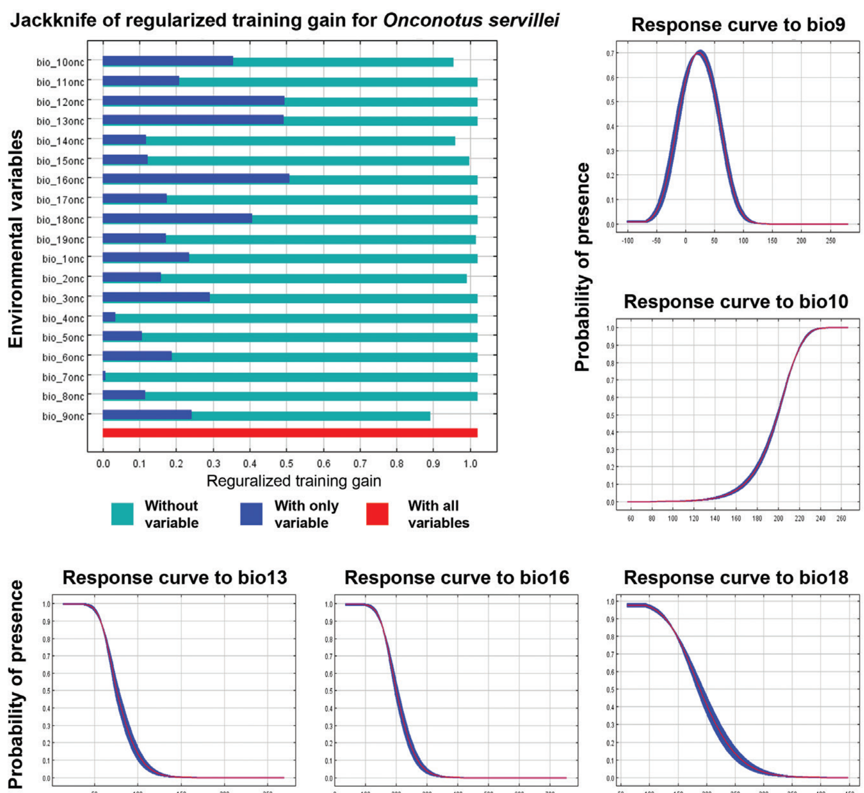

Figure 3. Contribuion of the 19 bioclimatic variables from Worldclim v. 1.4 to the ecological niche model of *Onconotus servillei*. Jackknife test graph of the contribution of the variables used to the model is presented in the upper left corner; response curves for selected variables with higher contribution are presented at the right and bottom sides of the figure.

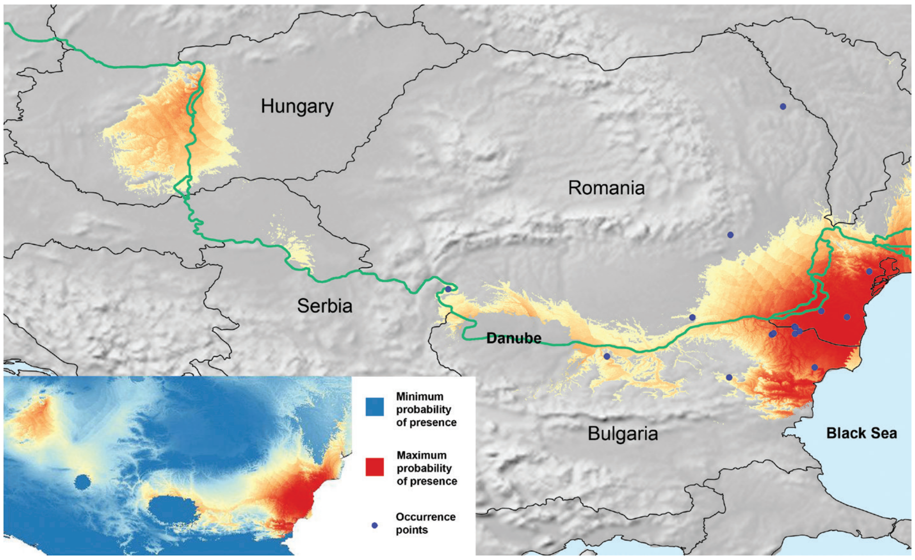

Figure 4. Spatial visualization of the >0.5 probability of occurrence model of *Onconotus servillei*. Blue dots represent occurrence points used. Green line represents the Danube River. The panel in the lower-left corner of the figure represents the full-spectrum of the model.

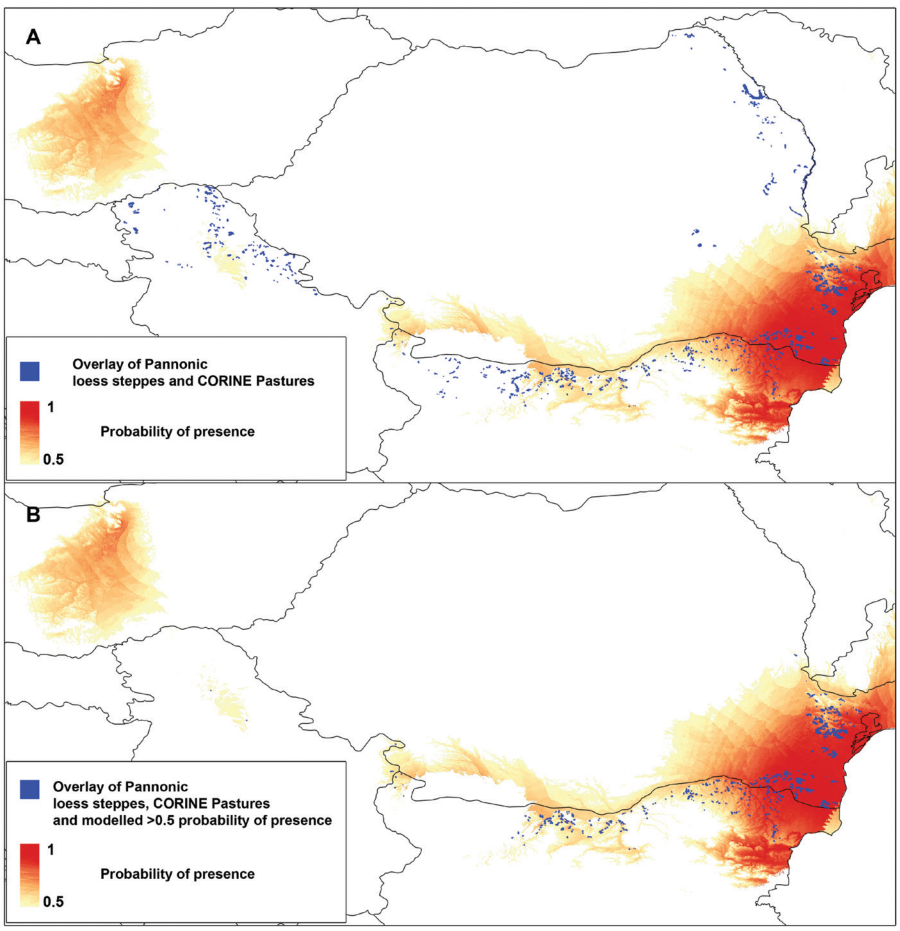

Figure 5. Distribution of the habitat of *Onconotus servillei*. A – an overlap of the Pannonic loess steppic grasslands and CORINE Biotopes type "Pastures" (blue pattern) presented over the >0.5 probability of occurrence model of the species; B – an overlap of the Pannonic loess steppic grasslands, CORINE Biotopes type "Pastures", and the modelled >0.5 probability of occurrence of the species, presented over the >0.5 probability of occurrence model of the species (blue pattern).

The ecological niche model outlined large areas with suitable conditions, though these are predominantly covered by agricultural lands, settlements, other infrastructure etc., thus being unavailable for the species. Therefore, we superimposed areas with a probability of presence for *O. servillei* over 0.5 and the overlapped CORINE and EUNIS selected habitats. The latter resulted in a set of polygons with a total area of 370 km^2, of which 261 km^2 in Romania, 107 km^2 in Bulgaria, and 2 km^2 in Serbia (Fig. 5B).

The Pannonic loess steppic grasslands generally agree with the distribution of the alliance *Festucion valesiacae* Klika, 1931 of the class *Festuco-Brometea* Br.-Bl. et Tüxen ex Soó, 1947 (Fig. 2C, D). Details on plant associations from sampled habitats with the currently registered occurrence of *O. servillei* are provided in Table 1. Our field studies confirmed the occurrence of *O. servillei* from two syntaxonomic plant associations (Table 1) of the alliance *Festucion valesiacae* forming typical loess steppes within the habitat type 6250 (Pannonic loess steppic grasslands). However, the species habitat was further defined by physiognomy as nearbyn associations of the syntaxon *Thymo urumovii-Chrysopogonetum grylli* Tzonev, 2013 (Tzonev 2013) with different plant diversity and cover were either inhabited or not by *Onconotus servillei*, which had a strict preference towards species-rich dense vegetation with a developed dead grass layer. The species was not located in any checked plots of the habitat 62C0 Ponto-Sarmatic steppes.

Discussion

Recently, Kirscher et al. (2020) postulated remarkable conservation value of the European extrazonal steppes, recovering independent evolutionary history and high phylogenetic diversity with characteristic species-specific distribution of a few steppe inhabitants. Kirscher et al. (2020) revealed (in five out of six study cases) a genetic gap between the Alpine and Central European populations on the one hand, and the (North-) Balkan and Pannonian populations on the other, the latter showing closer genetic relationships with populations from the Eurasian zonal steppes. Yet, their study involved ecologically tolerant organisms with a wide distribution beyond steppe grasslands (i.e., *Omocestus petraeus*, inhabiting also Mediterranean scrub and stony mountain meadows, and *Stenobothrus nigromaculatus*, occurring from humid and ruderal meadows in the lower mountain belt to 2500 m asl in the subalpine belt of the high Balkan mountains; e.g., Chobanov 2009), that might have survived Pleistocene glaciations in a wide range of refugial habitats (for alternative case results see Kajtoch et al. 2016 but the discussion here targeted geographic areas instead of species origin and ecological preferences). On the other hand, habitat specialists confined to steppes are strictly limited to habitats defining this biome (Dengler et al. 2014). *Onconotus servillei* is such a species, narrowly connected with typical steppe habitats (partly Sergeev 2021; Hochkirch et al. 2016, 2019; this paper). In modern times, its vast range stretched from Western Siberia to Hungary (l.c.), covering the European (and partly the Middle Asian) steppe region including the steppe fractions of the Pannonian Basin in central Hungary. Yet, it has never been found in steppe fractions west of this area, which, based on the much larger historic sampling record in Central and Western Europe, brings to the conclusion that it either never occurred there or disappeared from that area after the Mid Atlantic stage. The last record of this species from Central Europe (Hungary) dates over 130 years ago (Pungur 1899), and thus it is considered extinct from that area (Hochkirch et al. 2016, 2019). The species was only recently confirmed still occurring in a small area of northeastern Serbia (Ivković et al. 2020) after over 80 years since its last record from this country (Us 1938). Though being far more numerous and larger, Bulgarian and Romanian populations are also largely fragmented due to fragmentation of their habitat (both natural – by forested or humid areas, and anthropogenic – far more severely – by agricultural and urban territories). As the species is flightless, slow-moving, and has a short monovoltine cycle (adults present from mid-June usually to the end of July), small populations (e.g., the only known population in Serbia) may be considered under potential risk of extinction as a consequence of environmental and demographic stochasticity.

European steppes and specifically steppes along the Danube suffered large scale destruction as a result of massive transformation to cropland (Wesche et al. 2016; Biserkov et al. 2015; Tzonev 2015; Tzonev et al. 2015; Tzonev & Gusev 2015; own observations) and recently, after a short period of desolation, pressure over steppes is rising again (e.g., Tzonev et al. 2006; Vassilev & Apostolova 2013). Sedentary overgrazing, illegal ploughing, frequent arson and illegal burning, afforestation, mining and oil/gas drilling were reported as major factors for recent loss of steppe habitats (summarized by Wesche et al. 2016). All over the European steppes levels of steppe conversion to agricultural land are very high (Wesche et al. 2016), reaching enormous amounts in Central Europe. In Hungary, ploughing, afforestation, the invasion of shrubs and trees, the building activity and the establishment of open water surfaces were main factors for the 15% decrease of non-cultivated sand, steppe and riverine vegetation in recent years (Biró et al. 2008). At a broader time scale, 94% of 18th Century open sand grasslands and about 99% of closed sand grasslands in Hungary have disappeared (Biró et al. 2008). The latter numbers throw light on the probable reason for the disappearance of the westernmost populations of *O. servillei*. Along the Lower Danube, such precise data is missing. And though by the mid 20th Century, the existence of large-scale agricultural lands was not a common phenomenon in Southeastern Europe (the former Ottoman Empire), in the 1950s, the trend of enlargement and intensification of agriculture as a consequence of land nationalization reached the levels in Europe and USSR (e.g., Enyedi 1967). The latter, together with the use of DDT (Dichlorodiphenyltrichloroethane) as an insecticide, had detrimental effects on specialized insects, and the disappearance of certain bush-cricket species in Bulgaria has been noted in the 1950s (Buresch & Peschev 1958). As a consequence, steppes were largely destroyed and fragmented with small isolated patches remaining either on the verge of agricultural land, usually on steep slopes, or on rocky ground, where mechanical tillage was hindered. The latter is commonly the case with remnants of Ponto-Sarmatic steppes, while Pannonic loess steppes, developing on thicker soils, remained mostly on sloping terrains between fields.

Our field studies confirmed a strong preference of *O. servillei* towards rich dense vegetation cover, where animals usually hide most of the time or jump into when disturbed. The species was missing from patches within areas of the same habitat, dominated by a significant share of bare ground. Therefore, preference towards dense vegetation may not only ensure shelter but may have a major role in the species‘ water balance regulation. This must be the reason why the species was not located in plots of the habitat type 62C0 Ponto-Sarmatic steppes, even though historical records exist for the occurrence of *O. servillei* along the Black Sea coast, where this habitat is dominant.

We infer that currently publicly available regional geospatial distribution data of the EU Habitats Directive habitat types (e.g., http://natura2000.moew.government.bg/Home/Reports?reportType=Habitats; https://natura2000.ro/ce-este-reteaua-natura-2000/) are not precise enough for scientific purposes. By overlaying the latter data with CORINE Land Cover data (https://land.copernicus.eu/pan-european/corine-land-cover), confirmed occurrence data, and the distribution model for *O. servillei,* we provide rough estimates of the suitable habitat coverage of the species or its possible area of occupancy (IUCN 2012) in Serbia, Bulgaria and Romania. Yet, the species' narrow ecological preferences towards specific microclimate and vegetation composition suggest smaller actual area of occupancy.

Ongoing worrying negative trends of the species habitat are the increased cases of ploughing, arson and illegal burning (Fig. 2E–G), as a response to available subsidies from the European agricultural fund for rural development under the Rural Development Program (based on the European Union's rural development objectives). The latter mostly harm the Ponto-Sarmatic steppes (e.g., https://www.riosv-varna.org/docs/IPU-Kaliakra-draft-26-06-2017.pdf) but was also documented for the Pannonic loess steppic grasslands in Bulgaria (local authorities, pers. comm.) and inner steppes in Romania (Fig. 2E–G). Overgrazing as a result of sedentary pastoralism that has recently peaked due to the European Union's rural development objectives is an additional factor fragmenting and destructing the species' habitat.

Small bordering populations of *O. servillei*, occurring in areas with low probability of occurrence (see the two northernmost isolated localities in Romania on Fig. 4), are possibly survivors of a climatically induced habitat shift and thus are particularly vulnerable to habitat change. Anthropogenic influence may have severe negative effect on these populations and easily bring them to extinction. Hence, special attention should be paid on such populations in order to better understand the intrinsic and extrinsic factors defining the future of this species.

Our study is an initial step towards understanding the habitat preferences and trends and thus the future of *Onconotus servillei*. We reveal the potential of this peculiar bush-cricket as a model bioindicator species with strong preference to habitat type, physiognomy, and quality. Its strong link with habitat type 6250 Pannonic loess steppic grasslands provides opportunities to use it as a tool for monitoring the habitat quality and defines it as a candidate priority species and species of community interest in need of strict protection of the European Commission Habitats Directive (92/43/EEC) Annexes II and IV. Further studies on the population ecology and genetics of *O. servillei* would refine our understanding of the processes ruling the evolution and trends of steppe-specialist species.

Acknowledgements

We thank Petar Dimov (IBER-BAS) for technical consultations concerning geospatial data. We appreciate the valuable comments and corrections of two anonymous reviewers that helped improving the quality of this paper.

This study is part of grant KP-06-N31/13 to Dragan Chobanov by the National Science Fund of the Ministry of Education and Science of Bulgaria. Research on *Onconotus servillei* in Serbia by Slobodan Ivković was funded by the grants program for supporting the Orthoptera Species File.

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