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ORIGINAL ARTICLE

Recent growth in occurrences of *Acrida ungarica* (Orthoptera: Acrididae) at the northern margin of the species range: Is it the result of global warming?

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Abstract. The number of records of *Acrida ungarica* in novel habitats and in places where the species was considered extinct, has markedly increased in recent years. We hypothesized that the newly revealed occurrences, on the northern margin of the species range, were not due to an increase in survey effort, but rather a result of the warming climate in the Carpathian Basin. We studied the occurrence data of *Acrida ungarica* and the intensity of Orthoptera surveys over the period of 2002–2022 in 1,840 6 × 5.5 km grid cells of the Central European Flora Mapping System. As background variables, we included macroclimatic data and the vegetation cover of the main potential habitats. The number of grid cells containing *A. ungarica* was significantly higher than the corresponding increase in cells surveyed for orthopterans and the presence of sand and salt steppe habitats, respectively. Furthermore, from 2012 to 2022, significant increasing trends were revealed in effective heat summation above 10°C in the summer months. That the increase in the known distribution of *A. ungarica* is unrelated to the rise in survey intensity indicates that the species distribution seems to be increasing, making it one of the winners from global warming. At the same time, regional rising levels of disturbance (highway networks, large fallow areas) can contribute to the successful horizontal expansion of a species related to open habitats and this species tolerance of disturbance.

INTRODUCTION

It is well known that global climate change has had a significant impact on insect populations (Menéndez, 2007; Löffler et al., 2019; Outhwaite et al., 2022). Ecological responses to global warming vary considerably among taxa and geographic regions (Parmesan & Yohe, 2003; Guo et al., 2009; Chen et al., 2011; Larson et al., 2019; Kolanowska & Michalska, 2023), such that it could be said that there are losers and winners from the recent changes in climate (Samways, 2019). Species adapted to cool temperatures are particularly threatened by global warming (Tayleur et al., 2016), while warm-adapted species can experience record population growth (Lehmann et al., 2020). In Central Europe, climate change has not only led to an increase in average temperature, but also to more frequent and widespread droughts (Bartholy et al., 2009; Spinoni et al., 2016).

Higher temperatures have led to a northern range expansion in several European Orthoptera species, including *Conocephalus fuscus* (Kleukers et al., 1996; Fartmann, 2004), *Roeseliana roeselii* (Gardiner, 2009; Wissmann et al., 2009), *Ruspolia nitidula* (Kaláb et al., 2021), *Phaneroptera falcata*, and *Phaneroptera nana* (Krištín et al., 2022). Furthermore, an increase in relative abundance and area expansion of certain thermophilic Orthoptera species (e.g. *Calliptamus italicus*, *Euchorthippus declivus*, *Omocestus petraeus* and *Platycleis affinis* in western Hungary) has also been observed (Kenyeres et al., 2019). However, it must be noted that many studies do not meet the standards of data sampling and analyses to accurately demonstrate climate-change-induced shifts in species distributions (Taheri et al., 2021).

The highly mobile, thermophilic cone-headed grasshopper, *Acrida ungarica* (Herbst, 1876) is widely distributed and common in its traditional range (Kati et al., 2003). Following a significant reduction in the range of many orthopteran fauna in the second half of the 20th century, there has been a range expansion in recent years that is particularly evident in *A. ungarica*. According to the Hungarian Red List (Varga in Rakonczay, 1990), populations of the species declined significantly in the 1960s due to habitat destruction and the wet summer weather of the period. Similarly in Austria, *A. ungarica* declined significantly after the 1960s and was no longer found at all, becoming extinct in the 1990s (Berg et al., 2005, Bieringer, 2017). In Slovakia it has been ranked as a declining species along the northern border of its range (Krištín et al., 2004, 2020).

A. ungarica is a member of the subtropical genus *Acrida* that reaches the northern limit of its European distribution in the Carpathian Basin (Harz, 1975; Hochkirch et al., 2016). It is listed on the European IUCN Red List as "Least Concern" with a stable population trend (Hochkirch et al., 2016), red-listed as potentially endangered in Hungary (Rakonczay, 1990), as regionally extinct in Austria (Berg et al., 2005), and "Vulnerable" in Slovakia (Krištín, 2020). As a relatively large Central European thermophilic grasshopper (up to 10 cm in length), its specimens require a high average annual heat input for their development (Chappell & Whitman, 1990; Ingrisch & Köhler, 1998). In the Carpathian Basin, *A. ungarica* is found mainly in the lowlands and the adjacent hilly and sub-mountainous areas (Nagy, 2002). Its populations are mainly found in sandy grasslands and salt steppes, but it can be frequently seen in all types of dry and warm grass-rich habitats, dunes, and wastelands (Hochkirch et al., 2016).

The species has recently been found in increasing numbers in Hungary, eastern Austria (recently re-discovered), and the Southwest of Slovakia in areas where it was previously unknown or considered extinct.

We hypothesized that the newly revealed occurrences did not result from increased sampling and searching effort, nor from human-induced introductions from different regions, but rather from the warming trends in the Central European climate. To test our hypothesis, we selected a geometrically and geographically defined study area in the western part of the Carpathian Basin with many current and potential habitats for *A. ungarica*. We analysed the occurrence data using the 6 × 5.5 km grids (1,840 grid cells) of the Central European Flora Mapping System (Niklfeld, 1971) comparing focal species, Orthoptera searching intensity, and potential habitats. Based on the habitat requirements of the species, we also included the macroclimate data of the study period.

MATERIAL AND METHODS

Our rectangular study area was established on the northern edge of *A. ungarica*'s distribution, in the western half of the Carpathian Basin located in four countries (coordinates of the corner points: N48.19962, E16.33161; N48.19963, E20.16498; N46.19966, E20.16525; N46.19970, E16.33167, Fig. 1). According to the species climatic requirements, we delineated the parts of the study area with mean July temperatures of 18–20°C and 20–22°C (Fig. 1). We described regional climate changes using monthly and annual mean temperatures measured in the period 2002–2022, and monthly effective heat sums above 10°C over the past ten years (2012–2022, cf. Fig. 6). Raw macroclimate data were collected by an automatic meteorological station in Fertő-Hanság National Park Directorate (coordinates of data collection: N47.66731, E17.13392 – almost in the centre of the plains in our study area).

For each grid cell, we assigned the year of discovery of *A. ungarica* and the year of published data on the Orthoptera fauna (for data sources see online supplement S1a). The Orthoptera data used in our analyses was not specifically focused on our study species, but on Orthoptera studies and monitoring projects in general.

Based on the initial dates of *A. ungarica* occurrences and published Orthoptera data, we analysed data for four periods (up to 2002, 2002–2012, 2013–2017, and 2018–2022) and three scenarios (Fig. 2): 0 = neither present: i.e. no known presence data of *A. ungarica* and no published data on other Orthoptera species; 1 = Orthoptera only present: i.e. there is published Orthoptera data, so a valid Orthoptera grid cell, but *A. ungarica* absent; 2 = *A. ungarica* present as an existing population in the grid cell. *A. ungarica* has disappeared from some cells in Slovakia and Austria in which it previously occurred (due to landscape conversion: Slovakia: Modrany, Obid, Belá; Austria: Neusiedler See), while some new occurrences seem to be the result of accidental introductions (Slovakia: Nitra, Bratislava; Austria: Wien, Enzersdorf an der Fischa). These are marked on the maps with different icons but were not included in analyses.

The occurrence of the species' preferred habitats (sand grasslands, salt steppe grasslands) within the 3300 ha (6 × 5.5 km) area was also included in the database with the following codes: 0 = absent; 1 = low (0.1–17 ha); 2 = medium (17.1–140 ha); 3 = significant (> 140 ha). Categories followed the Hungarian Á-NÉR mapping method on habitat data (Bölöni et al., 2011). The occurrence of open sand and salt steppe habitats in grid cells was plotted based on published results (Wiesbauer & Mazzucco, 1999; Viceníková & Polák, 2003; Lájer, 2005; Bauer, 2006; Oberleitner et al., 2006; Molnár & Bagi, 2011; Molnár et al., 2011a, b) (Fig. 3) and our own observations. Cover values of almost all of the habitats have not changed in recent decades, however, we mention in the text the few cases where there have been changes.

A radar chart of the surveyed grid cells and the cells indicating the occurrence of the species in the periods (I–IV) was prepared (cf. Fig. 4). The correlation between the data in cells surveyed for Orthoptera and cells containing *A. ungarica* was tested using the Pearson correlation. The correlations between the cell count of *A. ungarica* occurrences detected in each period (I–IV) and the cell-level event of sand grassland and salt steppe grassland habitats were tested using two-sample paired t-tests (subjects were independent, measurements were obtained from the same subject and normally distributed). We sought statistically significant decreasing or increasing trends in temporal macroclimate data (annual mean temperature, July mean temperature, effective heat sums above 10°C projected in the periods of June, June–July, and June–August) using Mann-Kendall trend tests. Statistical analyses were performed in the Past 3.14. software package (Hammer et al., 2001).

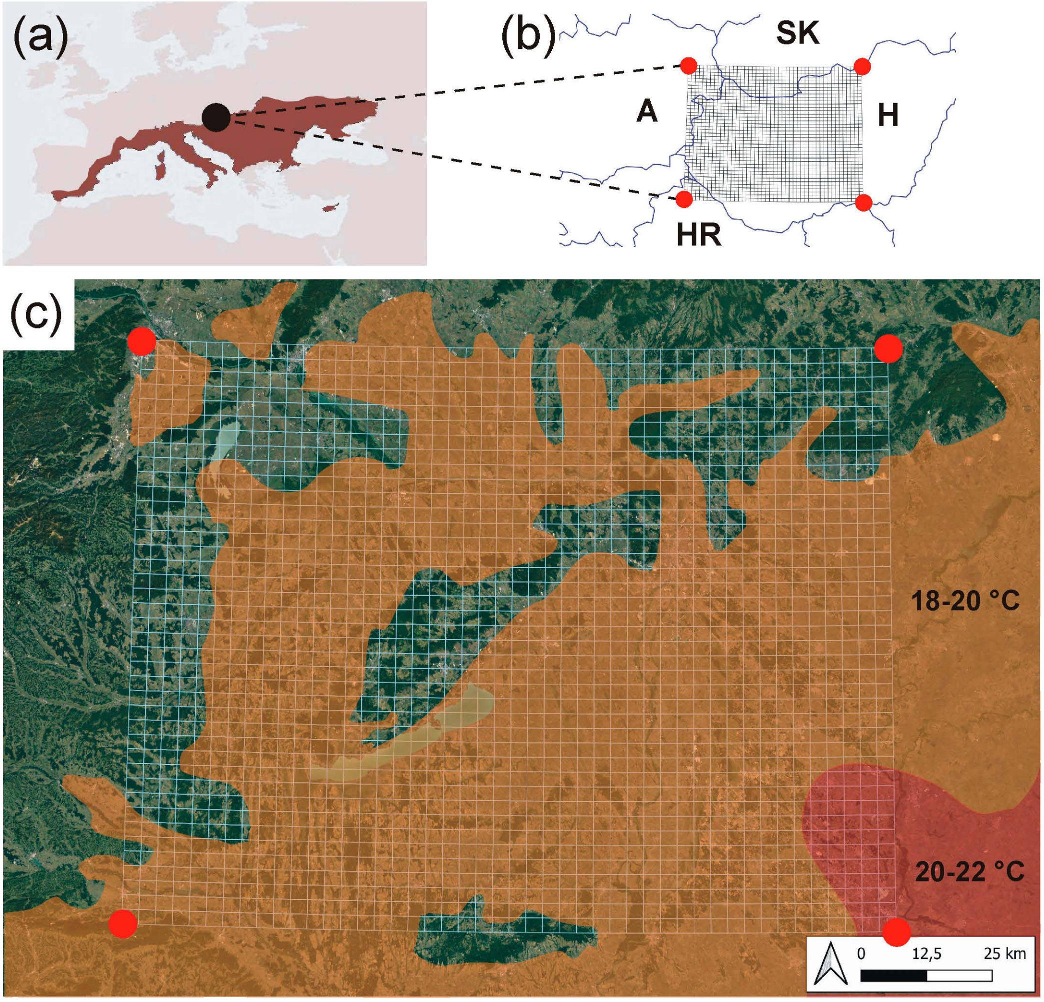

Fig. 1. *Acrida ungarica* distribution within the European species range (ex Hochkirch et al., 2016). (a) – study area with the Central European Flora Mapping 6 × 5.5 km grid cells; (b) – the areas of mean July temperature of 18–20°C (orange); (c) – 20–22°C (red).

RESULTS

Prior to 2002, *A. ungarica* was known from 188 of the 1,840 grid cells in the study area, while orthopterological data were available for 738 grid cells (Fig. 2). In the ten-year period from 2002–2012, the number of orthopteran cells surveyed increased by 12% (to 947), but the number of grid cells containing the study species increased by only 4% (196) (Fig. 2). In the subsequent shorter period, 2012–2017, the number of orthopteran cells increased slightly by 5% (to 992), while the number containing *A. ungarica* increased by 18% (231) (Fig. 2). The most rapid increase in the data occurred between 2018 and 2022 when the number of grid cells examined increased by 9% (to 1,083), but the number of cells with *A. ungarica* increased by 38% (319) (Fig. 2). Overall, the percentage of orthopteran grid cells containing *A. ungarica* increased from 25.5% (188 of the 738 grid cells surveyed) to 29.5% (319 of 1083 grid cells surveyed). That the increase in the number of grid cells containing *A. ungarica* was not a result of more intensive surveying is shown by the Pearson correlation between these two factors being insignificant (Pearson correlation value 0.797, p = 0.202) (Fig. 4).

Table 1. Number of grid cells of sand and salt habitats with the known occurrences of *Acrida ungarica* in the studied time periods.

Habitat	Relative presence	No. of grid cells in the study periods			
		–2002	2003–2012	2013–2017	2018–2022
Sand grasslands	significant	24	24	24	25
	medium	21	21	28	42
	low	54	55	63	78
	all	99	100	115	145
Salt grasslands	significant	49	49	51	56
	medium	30	30	34	38
	low	26	27	34	43
	all	105	106	119	137

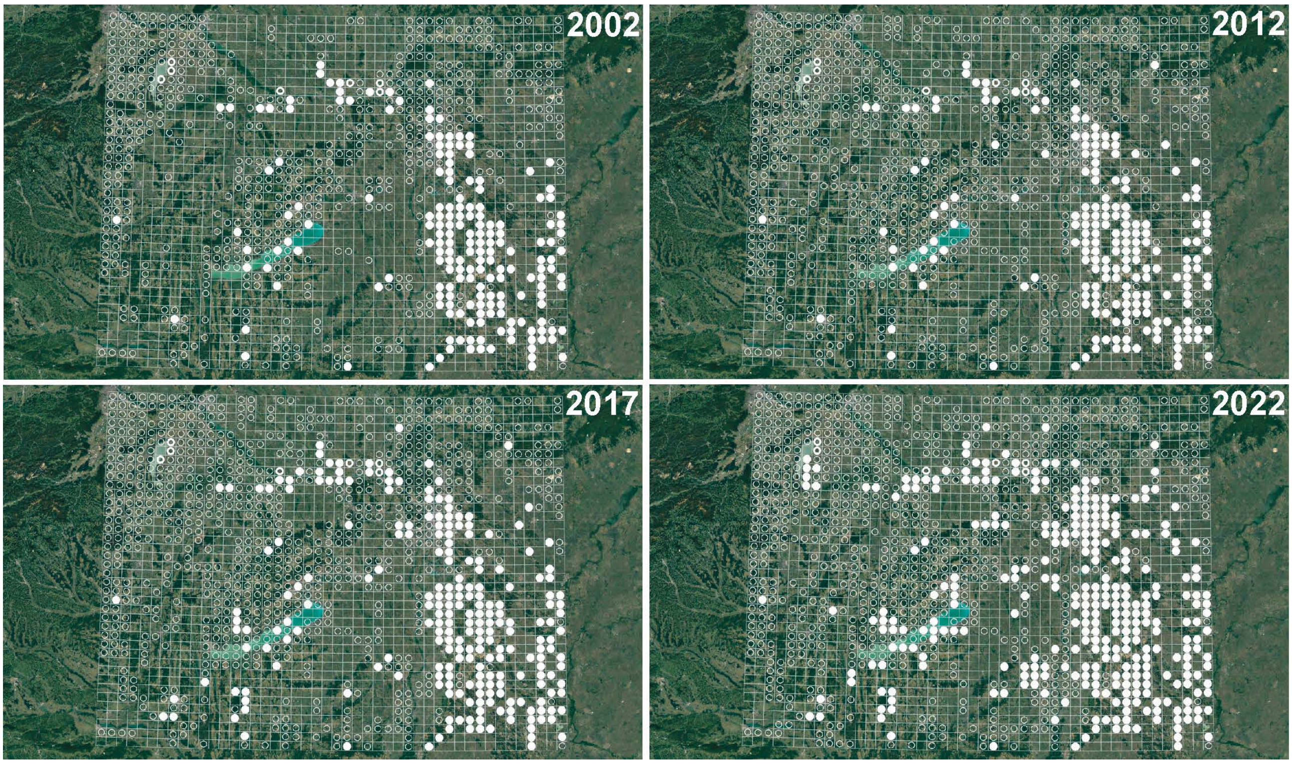

Fig. 2. Increase in the number of grid cells where *Acrida ungarica* has been detected between 2002 to 2022. Grid cells are the 6 × 5.5 km cells of the Central European Flora Mapping System: empty circle – studied grid cells with published Orthoptera records; full circle – grid cell with presence data of *A. ungarica*; full circle with open centre – extinct *A. ungarica* occurrence.

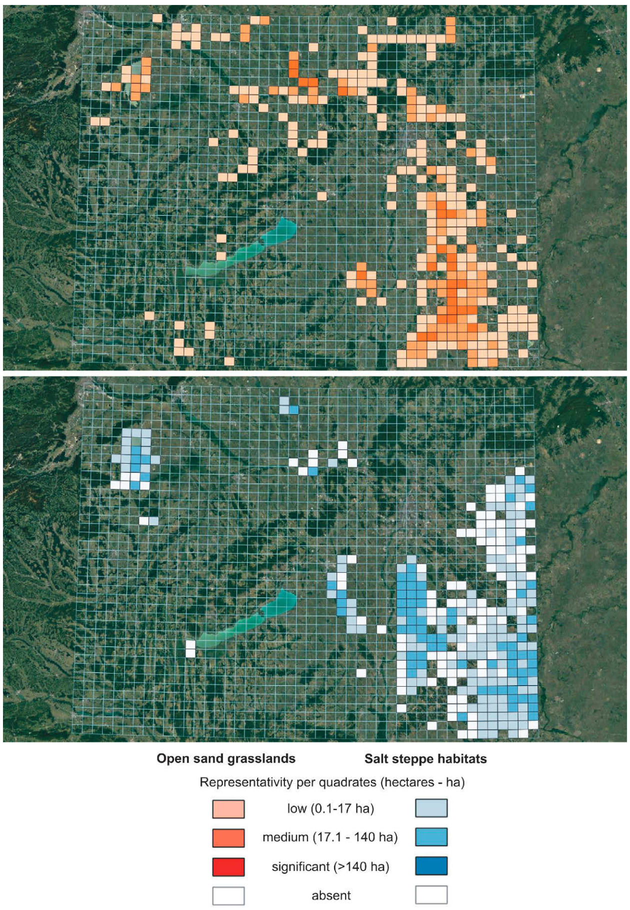

Fig. 3. Surface cover of open sand grasslands (a) and salt steppe habitats (b) in the studied grid cells.

Examination of the grid-level data showed that the greatest increases in new occurrences of *A. ungarica* were not associated with the two habitats considered most suitable for this species: sand grassland and salt steppe (Table 1, Fig. 3). Comparing the data prior to 2002 and from 2018–22, there was a small increase in the cell count of *A. ungarica* in cells with significant sand grassland areas, but a substantial increase in areas with a medium or low number of sandy grassland areas (Table 1). Similarly, there was

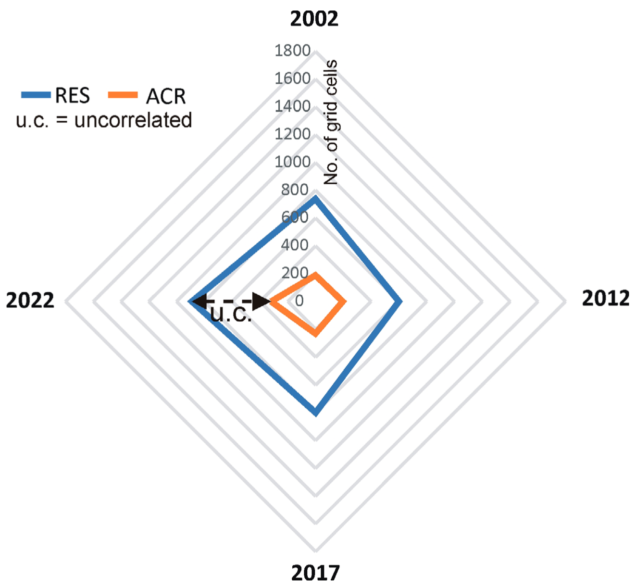

Fig. 4. Radar chart of the increase of the surveyed grid cells (RES) and of the grid cells indicating the occurrence of *Acrida ungarica* (ACR) in the periods ≤2002, 2003–2012, 2013–2017, 2018–2022.

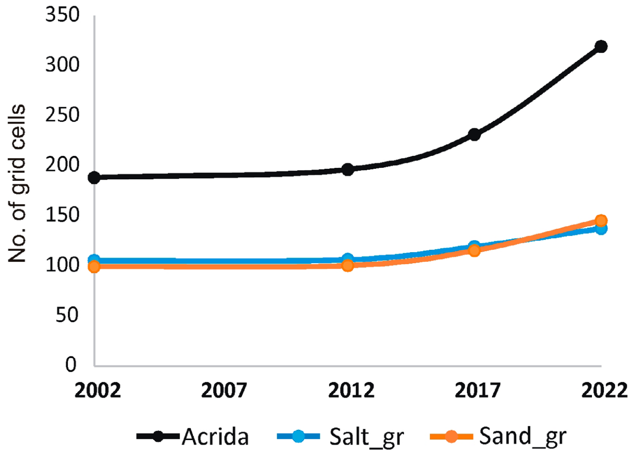

Fig. 5. The number of cells where of *Acrida ungarica* was detected in each time period and the number of surveyed grid cells with occurrence of salt steppe grassland (Salt_gr) and sandy grassland habitats (Sand_gr) showed a significant difference by t-test.

only a slight increase in *A. ungarica* in grid cells with significant salt steppe grasslands, but a substantial increase in areas with few salt steppe grassland areas (Table 1). T-tests of the number of cells where *A. ungarica* was detected in each period (I–IV) and the presence of sand grassland and salt steppe grassland habitats showed a significant difference between the increased data for the species studied and the occurrence of sand grassland and salt steppe habitat types, respectively ($t = 6.158$, $p = 0.001$ and $t = 5.163$, $p = 0.015$) (Fig. 5).

While the mean annual and July temperature in the study area showed a slight, but non-significant upward trend between 2002 and 2022 (online supplement S1b), significant increasing trends were revealed by Mann-Kendall trend tests in effective heat sums above 10°C projected in the periods of June, June to July and June to August (Fig. 6).

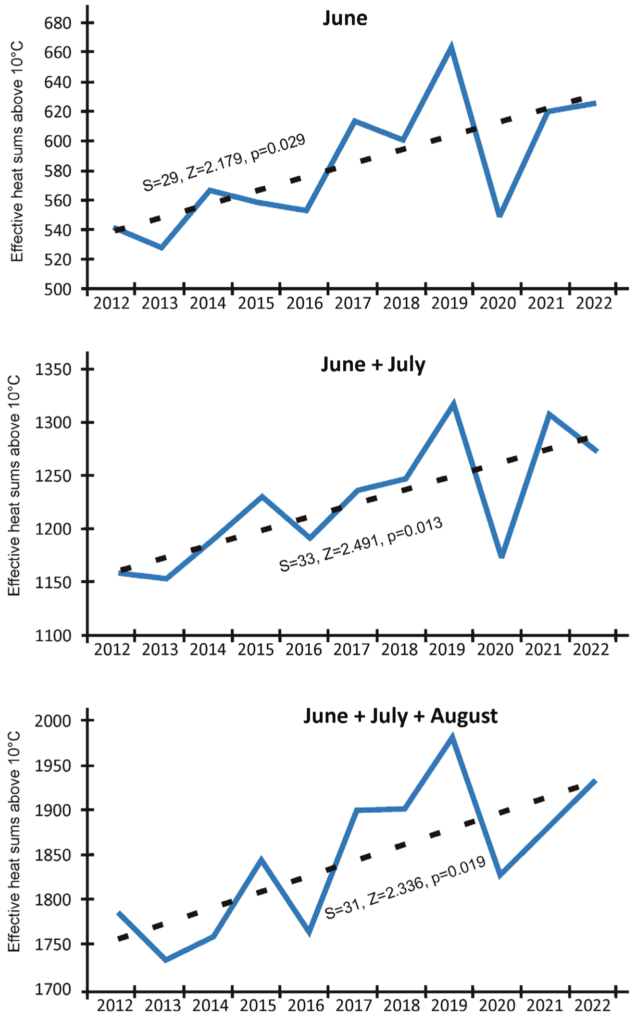

Fig. 6. In the 2012–2022 interval, significant increasing trends were revealed by the Mann-Kendall trend test in effective heat sums above 10°C projected in the periods of June, June–July, June–August.

DISCUSSION

Reviewing the extensive literature data on climate-related range shifts has shown that despite gradual improvements over time, there is scope for improving standards in data and methods for analysing climate-change-induced changes in species distributions. Accurate reporting is essential because policy responses depend on it (Taheri et al., 2021). Our approach and results showed that the increase in the known distribution of *A. ungarica* at the northern boundary of its range in Central Europe is not related to the increase in sampling and searching intensity. Further, the species (in its southern form *A. u. mediterranea*) is now able to survive in the novel northern areas even after introduction outside its regular breeding range (see example in the Czech Republic: Holuša et al., 2013, 2017; Vlk et al., 2014). However, the many new occurrences revealed in recent years in our study area are indeed unrelated to introductions but from vertical and horizontal expansion of thermophilic species as a result of global warming, which has been described in a number of areas in recent years (Breitenmoser, 2015; Kettermann & Fartmann, 2018; Kenyeres et al., 2019; Kaláb et al., 2021; Krištín et al., 2022; Illich & Zuna-Kratky, 2022; Starka et al., 2022). With regard to *A. ungarica*, we have shown that there has been substantial horizontal expansion northwards, which means this species seems to be one of the winners from global warming, the occurrence of which is demonstrated by the significantly increasing trends in effective heat sums above 10°C in the study area. The spread of *A. ungarica* has been aided by its high mobility, by its being less sensitive to disturbance than other regional grasshoppers, due to high ecological plasticity (Nagy, 2002; Kenyeres, 2018), and by its apparent tendency to be more of a generalist. Previous studies indicated that *A. ungarica* was something of a habitat specialist, preferring sand and salt steppe grasslands (cf. Menéndez et al., 2007; Löffler et al., 2019), but we found that the expansion of this species was in grid cells that contained fewer of these habitats. This apparent shift from a specialised habitat-selection to a more generalist lifestyle triggered by climate warming has also been observed in other species, such as *Ruspolia nitidula* in Austria and Czechia (Lechner, 2017; Kaláb et al., 2021). As a result, *A. ungarica* sometimes occurs in high numbers in more disturbed and man-made habitats (e.g., quarries, roadside ditches, dry grasslands, agricultural landscapes, Erdős et al., 2021; Arnóczkyné Jakab & Nagy, 2022), and, according to our results, in many atypical habitats such as short dry grasslands and secondary grasslands. An increase in the frequency and distribution of the species has also been reported in Romania (Sas-Kovács & Sas-Kovács, 2019). Furthermore, it has to be noted that citizen science contributed to the growth of occurrences because *A. ungarica* is a relatively conspicuous species with large-bodied individuals.

From a conservation perspective, it is noteworthy that *A. ungarica* seems to be less sensitive to disturbance than expected, at least in the core areas of its range in the Hungarian part of the Carpathian Basin. However, previous studies by some of our group (Krištín et al., 2020) revealed several examples where the conversion of grasslands to arable land (with a predominance of large-scale corn and rapeseed fields) and the intensification of land and pesticide use can cause a complete decline of the focal species. Eutrophication and abandonment, which led to denser vegetation and a detrimental microclimate, can also result in a decrease in occurrences (Bieringer, 2009, 2017).

Our experience on the Hungarian side of Lake Fertő (a new occurrence detected in 2022) showed that moderate land use can benefit populations. The local habitat of *A. ungarica* was formerly intensively grazed, but in order to preserve natural values, less intensive land management (reduced grazing, alternating mowing, and grazing) was introduced some years before the first observation of *A. ungarica*. The modified management scheme provided a much more abundant food supply and a more suitable habitat structure for the species.

The monitoring of newly discovered populations is essential to detect natural fluctuations in the northern area margin and assess land management priorities for the species (e.g. Bieringer et al., 2018). In addition, presence-absence studies of potential sand and salt steppe grassland habitats and their surrounding degraded dry grasslands may further increase our knowledge of how distributions can change as a result of global warming. On the basis that the species currently has a broader ecological range in terms of habitat selection, the search for new occurrences in the Croatian part of our study area (where the main habitats of the species are not present at all) seems particularly promising, even though survey efforts in the area have not been sufficiently intensive thus far.

CONCLUSIONS

Newly revealed populations of *A. ungarica* have been observed in areas where the effective heat sums above 10°C of the summer months has increased in the past decade. According to our results, the expansion of *A. ungarica* at its northern range limit is not related to an increase in sampling and searching intensity, but is due to changes in regional climatic conditions. At the same time, rising levels of disturbance (highway networks, investment areas, large fallow areas) may also contribute to the successful expansion of a species, which has high mobility and is tolerant of disturbance, related to open habitats. Therefore, we suggest that *A. ungarica* does not require special conservation measures, although reducing disturbance to moderate levels (grazing or mowing with low intensity) has been shown to favour this species.

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