

# Protected remnants of calcareous grasslands bridge the gap in the distribution of a habitat specialist insect – a case of *Cicadetta cantilatrix* Sueur et Puissant, 2007 in the area of Polish Uplands

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**Abstract:** Since the recent application of bioacoustic methods in the research of taxa forming a species complex of mountain cicada *Cicadetta montana* s. l., knowledge of the species diversity and distribution of this group of insects in many European countries has become outdated. This is also true for Poland, where this taxon is rare, and where – of the morphologically cryptic species – only *C. cantilatrix* has been reported and only in the region of Polish Uplands. From 2021 to 2024, we conducted visual and bioacoustic searching to assess the presence of mountain cicadas in 13 remnant patches of dry grasslands (altogether 40.5 ha) protected as Natura 2000 sites and located between two disjunctive locations of known occurrence of *C. cantilatrix*. The presence of mountain cicadas has been confirmed at two sites, in *Inuletum ensifoliae* xerothermic grassland vegetation located on warm and sunny slopes of limestone hills. The two sites found connect the previously known locations of *C. cantilatrix* in the Polish Uplands. Preserving the remnants of dry grasslands that still exist in the landscape of the studied region seems to be essential for maintaining the functional connectivity of this habitat-specialised insect. Due to the still existing knowledge gaps, it is recommended both to search for new localities in suitable xerothermic biotopes and to verify the presence of mountain cicadas at the few sites of old records. The investigation should include both visual observation and bioacoustic search and analysis. A large number of such results would be necessary for unravelling the taxonomic status and geographical distribution of mountain cicadas both in Poland and Central Europe.

**Keywords:** Hemiptera, Auchenorrhyncha, mountain cicada, species complex, species range, landscape connectivity, xerothermic habitats.

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## 1. Introduction

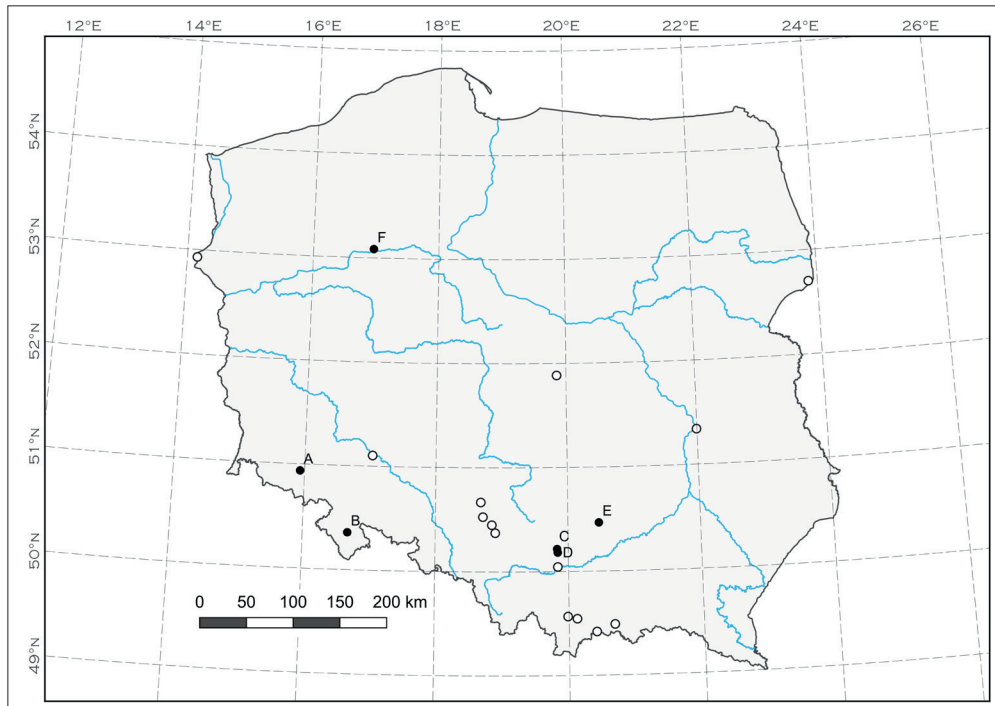
The taxonomic status of species of the genus *Cicadetta* Kolenati, 1857 (Hemiptera: Auchenorrhyncha: Cicadomorpha: Cicadidae) occurring in Europe is still the subject of research and scientific debate. This is particularly applicable to the

mountain cicada *Cicadetta montana* s. l., as recent studies in different parts of the European range have shown that this taxon is a complex of at least 13 different species (Puissant & Boulard, 2000; Gogala & Trilar, 2004; Hertach, 2007; Sueur & Puissant, 2007; Hertach et al., 2016). The individual species within this complex (the equivalent term *C. montana* s. l. was

also used throughout the paper) differ little morphologically, but are separable on the basis of the specific calls produced by the males (Gogala & Trilar, 2004; Gogala et al., 2008a; Hertach et al., 2016; Trilar et al., 2020). Characteristic for Central Europe is the occurrence of the species *C. cantilatrix* Sueur et Puissant, 2007 (Hertach et al., 2015; Trilar et al., 2020), whose northern limit of known species' range runs through Germany (Meineke, 2012), Poland (Szwedo, 2004; Trilar et al., 2006; Gębicki et al., 2013; Klasa & Bokłak, 2015) and Russia (Benediktov & Mikhailenko, 2017). Due to the significant similarity of the song of *C. cantilatrix* to *C. cerdaniensis* Puissant & Boulard, 2000, both of these species (together with at least two others) are included in a (sub)group within the *C. montana* complex, called the *C. cerdaniensis* group (Gogala et al., 2008a; Hertach et al., 2015; 2016; Benediktov & Mikhailenko, 2017). What is more, *C. montana* species complex includes also *C. concinna* (Germar, 1821), but this is the only species which is visually recognisable, due to distinct morphological differences (Trilar & Gogala, 2007; Hertach et al., 2015). The history of research and changes in taxonomic concepts with regard to mountain cicadas from Europe is presented in many papers (e.g. Gogala & Trilar, 2004; Sueur & Puissant, 2007; Gogala et al., 2008a; Hertach & Nagel, 2013; Klasa & Bokłak, 2015). In Poland, until the beginning of the 21<sup>st</sup> century, two cicada species were reported: *C. montana* (Scopoli, 1772) and *C. concinna* (= *C. podolica* Eichwald 1830) (Nast, 1976; Trilar & Gogala, 2007; Brodacki,

2013; Gębicki et al., 2013; Klasa & Bokłak, 2015). Shortly after it was revealed that *C. montana* is a species complex, bioacoustic studies indicated the occurrence of the species *C. cerdaniensis* in the Polish Uplands (Trilar et al., 2006). Soon after the publication of this paper, another species of mountain cicada has been described in France – *C. cantilatrix*, which calling song is very similar to *C. cerdaniensis*. A re-analysis of previously published data revealed that it is *C. cantilatrix* that occurs in the Polish Uplands (Gębicki et al. 2013; Klasa & Bokłak, 2015). To date, *C. cantilatrix* is the only cryptomorphic species of mountain cicada whose presence in Poland has been confirmed by song analysis. Because of the unresolved taxonomic relationships in the *C. montana* species complex and problems with verification of specimens from museum collections due to bioacoustic species identification (Hertach & Nagel, 2013; but see: Wade et al., 2015 for molecular attempts), the taxonomic assignment of records from many European countries made until the end of the 20th century – including Poland (Smreczyński, 1954; Nast, 1976; Bokłak et al., 2003; Świerczewski & Gębicki, 2003) – remains ambiguous. This is why chorological data on mountain cicadas needs to be updated recently.

In Poland – which, compared to many other central and southern European countries (e.g. Gogala et al., 2008b; Trilar et al., 2012; 2020; Hertach & Nagel, 2013; Hertach et al., 2015; Gogala & Trilar, 2016), is still under-explored – mountain cicadas belong to very rarely observed insects (Fig. 1). Few



**Figure 1.** Distribution of mountain cicada *Cicadetta montana* s. l. observation sites in Poland. Full black circles (A–F; labels as in Table 3) indicate records made in XXI century, empty circles – historical records, not confirmed for at least 50 years. Blue lines – main rivers

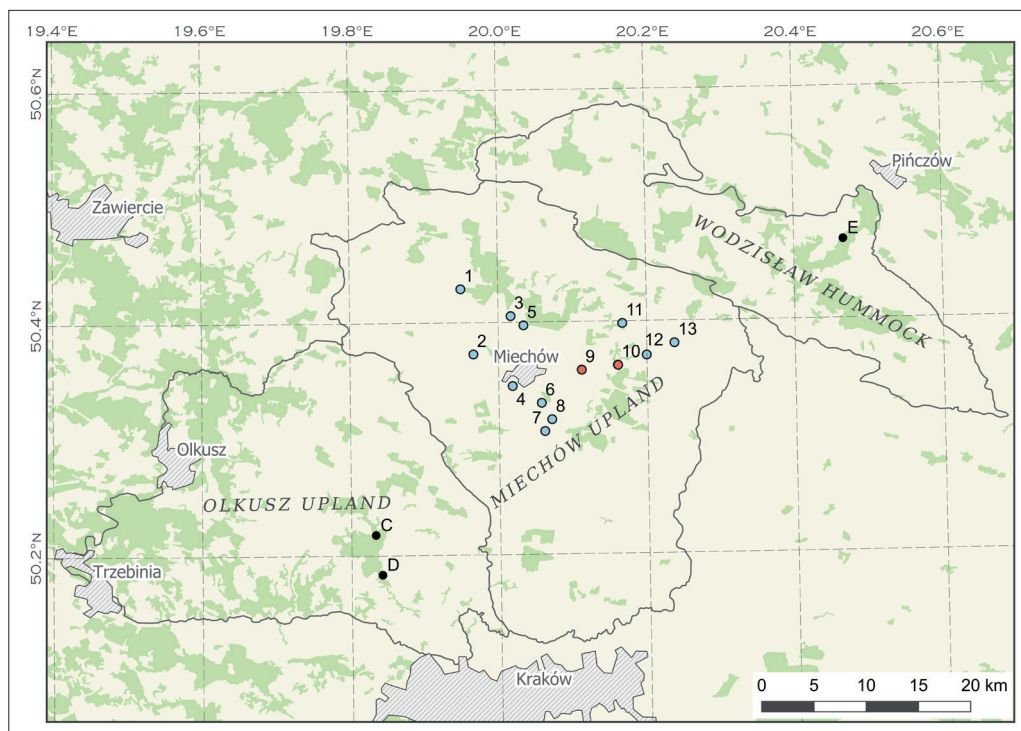
recent localities are known, among others, from the Polish Uplands (site C, D & E in Fig. 1 & Fig. 2), where the presence of *C. cantilatrix* has been confirmed. Because of the taxonomic difficulties described in the paragraph above, it is not clear whether *C. cantilatrix* is the only (besides *C. concinna*, see the paragraph above) species of the *C. montana* complex occurring in Poland. The sites of *C. cantilatrix* located in the Olkusz Upland (Trilar et al., 2006; Klasa & Bokłak, 2015) are separated here by a distance of about 50 km from the closest site from the region of Wodzisław Hummock (Szwedo, 2004; Trilar et al., 2006; Świerczewski & Gruca; 2010) (Fig. 2). These two currently known range islands are separated by the vast Miechów Upland, which is characterised by the presence of numerous patches of xerothermic grasslands and scrub, the most valuable of which are legally protected (Damian & Kus, 2017; Gawroński & Binkiewicz, 2019). And it is important to emphasise that the calcareous xerothermic vegetation formations are considered the preferred habitat for mountain cicadas in Poland (Świerczewski & Gębicki, 2003). On the basis of the above facts it may be assumed that (1) *C. cantilatrix* (or another species from the *C. montana* species complex) may inhabit patches of xerothermic habitats of the Miechów Upland, and (2) the range of this taxon within the Polish Uplands, between the above-mentioned recently known locations, is in fact more continuous than is

believed. The aim of this study was to confirm the occurrence of mountain cicadas in the Miechów Upland and to explore their distribution in selected, legally protected patches of xerothermic habitats within this region.

## 2. Material and methods

### 2.1. Study area

The study focused on the Miechów Upland, a region covering an area of approx. 1070 km<sup>2</sup>, located in southern Poland and belonging to the Nida Basin macroregion, which is part of the Polish Uplands (Fig. 2). In the Nida Basin the climate is warmer and drier than in the higher neighbouring macroregions, and both summer and the frost-free period last several days longer. The region is strongly insolated, with an average annual temperature of +7.5°C, while for January it is approx. -3°C and for July close to 18°C. Annual precipitation level reaches 550–650 mm (Andrejczuk et al., 2021). The Miechów Upland, whose highest elevations slightly exceed 400 m above sea level, is a gently undulating upland built of chalky marls covered by a layer of loess and, in the river valleys, Pleistocene sands and clays (Andrejczuk et al., 2021). It is an agricultural land with fertile soils, with remnants of



**Figure 2.** Localities surveyed in the Miechów Upland in the course of this research (open circles 1–13, labels as in Table 1), and sites currently occupied by *C. cantilatrix* from neighbouring regions of Polish Uplands (full black circles C–E; Table 3), on the background of selected mesoregion boundaries (after Solon et al., 2018; solid lines, labelled in capital letters), forest patches (green polygons) and main towns (hashed polygons). Red open circles indicate localities where mountain cicadas were found during this study

forests (mainly oak-hornbeam and oak) covering small areas. A characteristic feature of the vegetation is the presence of numerous, although small in area, patches of calcareous xerothermic grasslands and scrub. Their best-preserved fragments are protected in the form of 5 steppe nature reserves and 18 Natura 2000 Special Areas of Conservation, where conservation measures are focused on habitat type 6210 – Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*) (Damian & Kus, 2017; Gawroński & Binkiewicz, 2019; Andrejczuk et al., 2021). Of these, 13 Natura 2000 sites were selected (Table 1), which were then surveyed for the presence of mountain cicadas. The studied calcareous grasslands were distributed over an area measuring 14 by 21 km (Fig. 2). Individual patches of grassland ranged in size from 0.5 to 8.5 ha and covered a total area of 40.5 ha (Table 1).

## 2.2. Field survey and data processing

The study was conducted from 2021 to 2024. The primary method of field surveys was visual searching of selected patches of calcareous grassland for the presence of adult insects and larval exuviae attached to low herbaceous vegetation (Liivamägi & Tarlap, 2017). Complementarily, thorny shrubs were also inspected for larders of the Red-backed Shrike *Lanius collurio* L., 1758, which may contain cicadas captured by this bird (Brodacki, 2013). The observer walked across the grassland on foot at very low speed, frequently pausing and scanning the vegetation

from a low height. Routes were set so densely that the entire area with potentially suitable vegetation structure could be searched, excluding sections heavily overgrown with shrubs and shaded by trees. A varying amount of time was spent searching the grasslands at each location, depending on the degree of variation in the topography and the characteristics and area of potential habitats. To ensure comparability of results, however, it was assumed that at least 1 hour would be required to search 1 ha of grassland at a given location (Table 1). Sites where mountain cicadas were found were inspected several times, but during these additional visits the whole area of the grassland was no longer searched, concentrating on the sections where larval exuviae or adult insects were observed. Searches were conducted on clear, sunny or slightly overcast days with, at most, a slight breeze, between the beginning of the second ten-day period of May and the end of the second ten-day period of June. The aim was to fit into the time period when, the emergence of *C. cantilatrix* adults after a period of subterranean larval life was observed under regional conditions (Trilar et al., 2006; Klasa & Boklak, 2015). The dates for searching for larval exuviae in areas surveyed once were chosen to minimise the risk of insects being undetected due to the later emergence in the season. Therefore, such searches were conducted late, at the end of May and beginning of June (Table 1).

At the sites where mountain cicadas or their larval exuviae were found, listening and recording of calling songs produced by males was conducted on 21.05.2024. It is considered to be an effective method of detecting their presence in

**Table 1.** Localities (Natura 2000 sites) in the Miechów Upland, where patches of xerothermic grasslands (habitat 6210) have been searched for the presence of mountain cicadas *Cicadetta montana* s. l. Survey effort denotes the time spent searching 1 ha of grassland at a given site. The label of each site correspond to those in Fig 2

Site label	Natura 2000 site code	Site name	Latitude (°N)	Longitude (°E)	Area of habitat 6210 [ha]	Field survey dates	Survey effort [hrs/ha]
1	PLH120075	Uniejów-Parcele	50.428904°	19.949789°	0.69	3 VI 2023	02:10
2	PLH120063	Chodów-Falniów	50.374267°	19.965811°	5.76	3 VI 2023	01:04
3	PLH120073	Pstroszyce	50.405249°	20.016902°	2.87	1 VI 2023	01:25
4	PLH120055	Komorów	50.345024°	20.018374°	3.93	4 VI 2023	01:02
5	PLH120076	Widnica	50.397187°	20.034098°	3.42	1 VI 2023	01:11
6	PLH120072	Poradów	50.330272°	20.057409°	8.47	18 VI 2022; 24 V 2024	01:01
7	PLH120062	Kaczmarowe Doły	50.307176°	20.060001°	2.09	30 V 2023	02:47
8	PLH120074	Sławice Duchowne	50.316037°	20.071092°	1.61	29 V 2023	02:29
9	PLH120054	Kalina Mała	50.358362°	20.111768°	3.40	13 VI 2021; 5 VI 2022; 27 V, 4 VI 2023; 12, 21 V 2024	03:55
10	PLH120007	Kalina-Lisinieć	50.362421°	20.160038°	3.11	3 VI 2021; 29 V 2022; 27, 29, 31 V, 4 VI 2023; 12, 18, 21 V 2024	08:36
11	PLH120051	Giebułtów	50.397995°	20.167243°	1.33	5 VI 2022	02:22
12	PLH120053	Grzymałów	50.370511°	20.199613°	0.45	29 V 2022	06:40
13	PLH120049	Cybowa Góra	50.380698°	20.237140°	3.40	13 VI 2021; 15 VI 2022	02:03

field conditions (Hertach, 2007) and, above all, allows determination of the species identity of the insects found (Gogala & Trilar, 2004; Gogala et al., 2008a; Hertach et al., 2015; 2016; Trilar et al., 2020). Listening and voice recording was conducted during the day, in warm, sunny, windless weather. Males emitting voices from shrub branches or low-hanging tree branches were located aurally, approached, and then a recording of several tens of seconds to several minutes in length was initiated. Calling songs were recorded with Tascam DR-07X audio recorder, without external microphone, in PCM 44,1 kHz stereo. The resulting field recordings were further processed in a computer program. Species identification was completed based on the shape and frequency range of the graphs illustrating the recording – a spectrogram and an oscillogram, with the use of a song-based key to taxa belonging to the *C. cerdaniensis* species (sub)group, proposed by Hertach et al., (2015). The graphs were also compared with spectrograms and oscillograms of various species of mountain cicadas available in scientific publications (Trilar et al., 2006; 2020; Sueur & Puissant, 2007; Trilar & Gogala, 2012; Hertach et al., 2015; Gogala & Trilar, 2016; Benediktov & Mikhailenko, 2017) and online resources (Gogala, 2024). Since the representatives of the *Cicadetta*

*montana* species complex sing in a high frequency range (10–18 kHz; Hertach & Nagel, 2013; Trilar et al., 2020), and the field recordings were accompanied by low frequency background noise (e.g. bird singing), the recordings were transformed by filtering out sounds with a frequency lower than 10 kHz, using the high-pass filter function in the software. All audio transformations and visualisation of a spectrogram and oscillogram were performed in Audacity® 3.5.1 software (Audacity Team, 2024).

### 3. Results

Of the 13 localities surveyed, the occurrence of mountain cicadas was confirmed in two: Kalina Mała (Natura 2000 PLH120054, site no. 9) and Kalina-Lisinieć (Natura 2000 PLH120007, site no. 10) (Fig. 2, Table 1). Here insects inhabited calcareous xerothermic grasslands representing the *Inuletum ensifoliae* plant community (Fig. 3), located on warm and sunny slopes of limestone hills, at 320 and 350 m above sea level, respectively. In Kalina Mała the mountain cicada was found only once – in 2022 an imago of a male was found and a larval exuvia attached to a stem of grass. Four



Figure 3. Calcareous xerothermic grassland *Inuletum ensifoliae* in Kalina-Lisinieć Natura 2000 site – the habitat of *C. cantilatrix*, 27 V 2023; photo by R. Bobrek

field surveys of the grassland in this location, carried out in 2023–2024, did not result in any further records of cicadas (Table 2). On the other hand, in Kalina-Lisiniec mountain cicadas were found each year in 2021–2024. A total of 6 adults (3 males, 2 females and 1 individual of unidentified sex) and 43 larval exuviae were recorded between 12 May and 5 June (Table 2, Fig. 4). In both locations, larval exuviae were found at a low height (up to about 20 cm) above the ground, usually attached to herbaceous vegetation (40 out of 44 exuviae), the most common being grass stems (19 ex.) or *Cirsium pannonicum* (L.F.) Link stems (16 ex.). Much less frequently, they were attached to shrub stems (3 ex.), and in one case the found exuvia was lying on the ground surface.

During a recording session conducted on 21.05.2024, the calling songs of ca. 5 male mountain cicadas were registered in Kalina-Lisiniec. An exemplary spectrogram and oscillogram of the song recorded then is shown in Fig. 5. On the basis of the analysis of the recordings made, it was identified that the calling male mountain cicadas in Kalina-Lisiniec represent a species of *C. cantilatrix*. The spectrogram covers sounds in the frequency range from approximately 10 kHz to 20 kHz (Fig. 5). The oscillogram shows that the calling song consists of a series of repetitive echemes, characterised by modulated amplitude – initially low (quiet part) and later increasing

Table 2. Number of larval exuviae and number and sex of adult insects recorded at each site and on each survey day when the mountain cicada *Cicadetta montana* s. l. survey was successful. The table presents only the results of visual searches, the number of audio-recorded males is not given. ? – sex of the individual has not been registered

ID	Site label	Site name	Survey date	Search result	
				Exuviae	Adults
1	10	Kalina-Lisiniec	3 VI 2021	5	1♂, 1?
2	10	Kalina-Lisiniec	29 V 2022	2	1♂
3	9	Kalina Mała	5 VI 2022	1	1♂
4	10	Kalina-Lisiniec	27 V 2023	5	-
5	10	Kalina-Lisiniec	29 V 2023	6	-
6	10	Kalina-Lisiniec	31 V 2023	3	-
7	10	Kalina-Lisiniec	4 VI 2023	2	-
8	10	Kalina-Lisiniec	12 V 2024	1	1♀
9	10	Kalina-Lisiniec	18 V 2024	7	1♀
10	10	Kalina-Lisiniec	21 V 2024	12	1♂

significantly (loud part). This feature of the song allows the cicada to be classified into the *C. cerdaniensis* species (sub) group (Hertach et al., 2015; Trilar et al., 2020). The emitted song consists of two alternating phrases, distinguished by their echeme length: P1 and P2 (sensu: Sueur & Puissant,



Figure 4. An emerging male of *C. montana* s. l. in Kalina-Lisiniec Natura 2000 site, 21 V 2024; photo by R. Bobrek

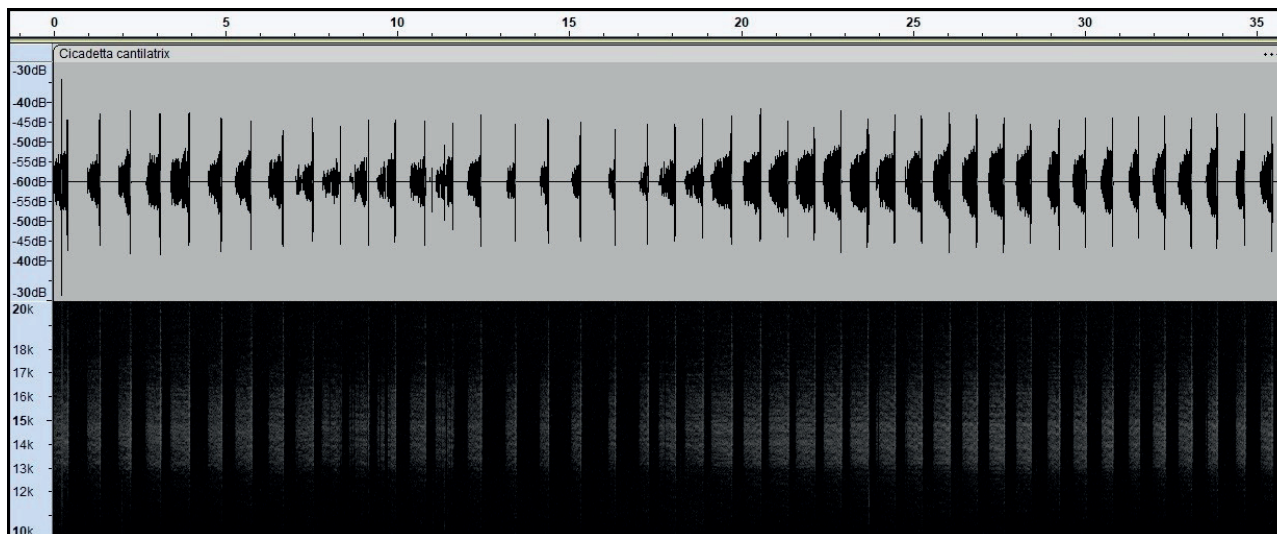


Figure 5. Oscillogram (above) and spectrogram (below) of a 36-second recording of calling song of *C. cantilatrix*, Kalina-Lisiniec Natura 2000 site PLH120007, 21 V 2024. Sound recorded with Tascam DR-07X audio recorder without external microphone, in PCM 44,1 kHz stereo (for clarity only one of the two audio channels is presented)

2007). In Fig. 5, the phrases are arranged in a P2-P1-P2 sequence. The complete absence of phrase P3 (which is a fast-rate series of short echemes) in the recording allows the analysed song to be assigned to *C. cantilatrix*, as it is the only species of the *C. cerdaniensis* species (sub)group in which phrase P3 is missing in its calling song (but not in the courtship song; Hertach et al., 2015). As we were unable to detect and record any calling song in Kalina Mała, it was not possible to determine the species identity of the mountain cicadas inhabiting the site.

#### 4. Discussion

Mountain cicadas of the *C. montana* species complex have been reported from a wide area of southern and central Poland, including mountainous and upland areas, and from single sites in lowlands (Nast, 1976; Gębicki et al., 2013). Sites that can currently be considered historic (where the presence of mountain cicadas has not been confirmed for at least half a century) included the Carpathian Mountains (Nowy Targ Basin, Beskid Sądecki Mts., Pieniny Mts. and Gorce Mts.; Nast, 1976), Kraków and surroundings of Ojców (Smreczyński, 1954), upland parts of Silesia (Bytom, Tarnowskie Góry, Tworóg and Lubliniec; Boklak et al., 2003), Lublin Upland (Bochotnica; Nast, 1976) and lowland sites located in the Mazovian Lowland (Hulanka near Brzeziny; Nast, 1976), Silesian Lowland (Wrocław; Letzner, 1886 after: Struś & Malkiewicz, 2015), Białowieża Forest (Karpiński, 1958; Nast, 1976) and the Bieleń nature reserve at the Lower Odra River Valley (Celiński & Filipek, 1957; Nast, 1976). Present (discovered or confirmed after 2000) localities

of *C. montana* s. l. have been recorded only in three regions: (1) in the Middle Noteć River Valley (site F on Fig. 1, where the presence of *Cicadetta* sp. was incidentally mentioned; Ruta, 2007), (2) in the Sudety Mts. (Miłek Mountain in the Kaczawskie Mts. and the Krowiarki Range in the Śnieżnik Massif; Struś & Malkiewicz, 2015; sites A & B on Fig. 1) and (3) in the area of the Polish Uplands. In the latter region, based on analyses of calling songs, the occurrence of *C. cantilatrix* has been confirmed – on two sites in the Ojców National Park (Olkusz Upland; Trilar et al., 2006; Klasa & Boklak, 2015; sites C & D on Fig. 2) and at single site in the Polana Polichno nature reserve (Wodzisław Hummock; Szwedo, 2004; Trilar et al., 2006; Gębicki et al., 2013; site E on Fig. 2). Within the present study two further localities of *C. montana* s. l. were found in the area of the Polish Uplands (Fig. 2) – in the Natura 2000 sites Kalina Mała (site 9) and Kalina-Lisiniec (site 10), with *C. cantilatrix* confirmed in the latter area. Despite the fact that different species of the *C. montana* complex may occur sympatrically, sometimes even at a single site (Gogala & Trilar, 2004; Hertach, 2007; Sueur & Puissant, 2007), given the habitat structure similarity of both newly discovered sites (*Inuletum ensifoliae* xerothermic grassland) and the current occurrence in the Polish Uplands of other sites colonised by *C. cantilatrix*, it is most likely that the site at Kalina Mała is also occupied by this species. Of course, further research using bioacoustic techniques is required to confirm this, as the presence of other species of cicada in both localities cannot be entirely ruled out. It should be noted that the results obtained regarding the presence of mountain cicadas at particular sites should be treated as minimal, due to the relatively small amount of search effort in some locations, especially those surveyed only once (Table

1). More intensive, repeated searches over a period of several years might result in the detection of a larger number of occupied sites, especially when the local abundance is low. This is due to rather low detectability of these insects in the field (see last paragraph of the discussion). Their specific bionomics also play a role, as these insects may appear on the ground in varying numbers and with different phenology in subsequent years.

Two new mountain cicada localities found in the Miechów Upland are placed between previously known disjunctive localities of *C. cantilatrix* in the Polish Uplands, forming a sort of link between them (Fig. 2). The ephemeral nature of the Kalina Mała site (where the insect was recorded in only one of the four years of the study; Table 1 & 2) combined with the scatter of relatively small (in relation to the area of the study region) patches of xerothermic grasslands in the landscape may suggest the existence of 'extinction and colonization' dynamics characteristic of taxa functioning in a metapopulation system (Hanski, 1994; Fischer & Lindenmayer, 2007). Grassland patches could then be considered as habitat- and bioclimatically favourable areas for larval development, in contrast to generally unfavourable, intensively farmed landscape (matrix; Fischer & Lindenmayer, 2007; Lindborg et al., 2014; Olsen et al., 2018). In the case of flight-able animals, despite the lack of spatial continuity of the habitat, even small patches that are scattered over the landscape and spatially isolated can provide the necessary genetic contact within a population, as long as they are not too far from each other (Saura et al., 2014). This is also supposed to apply to mountain cicadas (Hertach, 2007). The dispersal stage in these insects is the imago, which has the ability to fly. This allows adult cicadas, including probably fertilised females, to potentially cross the habitat matrix to reach favourable xerothermic habitats. However, the distance between patches of favourable habitats cannot be too great. Although there are no precise estimates of the range of such dispersal in mountain cicadas, they are generally considered incapable of long-distance flight due to the low endurance of their wing muscles (Hertach et al., 2025). On the other hand, the presence of trees and shrubs scattered in the generally open arable landscape of the Miechów Upland may facilitate reaching patches of xerothermic grasslands, where conditions offer the chance for successful larval development. Thus, preserving the remnants of xerothermic habitats that still exist in the landscape of the Miechów Upland seems to be essential for maintaining the functional metapopulation connectivity of this habitat-specialised, stenobiotic insect. And this is despite the generally small area of such habitats that remains in the landscape (Dzwonko, 2013; Hanczaruk & Bąba, 2019), and especially their limited area in the studied region that is under legal protection (only about 50 ha, European

Environment Agency, 2022). However, even those patches of grasslands that are legally protected – because of their secondary origin – are gradually deteriorating due to the cessation of traditional forms of agricultural use and the initiation of secondary succession of vegetation (Mazur & Kubisz, 2000; Gawroński & Binkiewicz, 2019; Hanczaruk & Bąba, 2019). Locally in the studied region, also the creation of open-cast mines of mineral materials, intensification or change in agricultural use, high fertiliser application rates on surrounding agricultural land, or physical damage caused by vehicles may pose a threat to the existence or quality of these grasslands (Kubisz et al., 2025). In the context of biodiversity protection, every patch that still exists is valuable, and halting the process of their loss in the landscape is an important task. It is not only because they are potentially inhabited by extremely scarce mountain cicadas, but also by a whole range of other endangered, sensitive, stenobiotic plants and animals that use the calcareous xerothermic habitats (e.g. Mazur & Kubisz, 2000; van Swaay, 2002; Dzwonko, 2013; Lyons et al., 2018; Kubisz et al., 2025). Therefore, it is important to implement active protection measures on the xerothermic grasslands of the Miechów Upland, which has already taken place in certain localities (Damian & Kus, 2017; Gawroński & Binkiewicz, 2019; Kubisz et al., 2025). Such measures generally aim to protect the grassland from tree and shrub expansion while maintaining the open character of the xerothermic vegetation at the site (Mazur & Kubisz, 2000; Hanczaruk & Bąba, 2019). However, it is important that conservation measures balance the objectives of long-term preservation of xerothermic vegetation (protection of plant communities) and conservation of insect populations that inhabit them, as these are not always compatible (Kubisz et al., 2025). From the point of view of the ecological requirements of mountain cicadas, the ecotone between grassland and forest should not be over-simplified (by e.g. intensive shrub removal), nor should all trees and shrubs, especially solitary ones, be eliminated from the grassland (Hertach, 2007), as these play an important role as singing posts for males. When prioritising areas for the implementation of active protection, however, it is worth taking into account not only the current state of the habitat within the individual sites, but also their relative distribution in space. It is imperative to try to maintain the highest possible degree of landscape connectivity between patches of favourable habitat (Lindborg et al., 2014; Olsen et al., 2018), e.g. by actively protecting patches acting as stepping stones (Fischer & Lindenmayer, 2007; Saura et al., 2014) located between the best-preserved sites. This would maximise the chances of survival for those xerothermophilic species that function in the region as an archipelago of subpopulations and for which landscape connectivity is a critical precondition for their long-term conservation (see e.g. Kubisz et al., 2025).

In central Europe (including Poland), typical habitats of mountain cicadas include xerothermic vegetation, especially warm, sunny hillsides covered with grassland or scrub with oak *Quercus* spp. and blackthorn *Prunus spinosa* L. as well as the ecotone zone between sparse forests (pine or deciduous) and dry meadows (Świerczewski & Gębicki, 2003; Trilar & Gogala, 2012; Hertach & Nagel, 2013). These views on habitat preference are confirmed by the most recent records of mountain cicadas in Poland (five reported in the literature and two obtained in the present study), made in the 21<sup>st</sup> century (Table 3). Indeed, they were recently found in dry and warm, calcareous xerothermic grasslands of the class *Festuco-Brometea*, represented by the communities *Inuletum ensifoliae*, *Origano-Brachypodietum* or *Thalictro-Salvietum pratensis*. The grasslands at these sites were located on sunny slopes of calcareous hills with predominantly southern (SW-SE) exposure, covered to varying degrees with thermophilic

scrub communities and surrounded by deciduous or mixed forests. In the case of sites located in the Sudety Mts. (A & B; Fig. 1, Table 3), the xerothermic vegetation developed in the excavations of disused limestone quarries. Also in Hungary, *C. cantilatrix* has been observed in a similar habitat – on thermophilous grassland overgrown with bushes located on the southern slope of a hill (Trilar & Gogala, 2012). In Switzerland, on the other hand, *C. cerdaniensis* s. l. (taxon including *C. cantilatrix* and *C. cerdaniensis* s. str.) most typically inhabited very sparse, periodically wet *Molinio-Pinetum* on marl, edges of the forest (hedges, shrubs) located along extensively used, dry meadows (e.g. *Mesobromion*), and sunny and sparse sites with *Fraxino orno-Ostryon* (Hertach, 2007). These habitats are generally similar in the structure of vegetation, although are distinctly more mesophilous compared to xerothermic grasslands typically occupied in Poland. This difference may be related to the fact

**Table 3.** Vegetation characteristics of the most recent (recorded in the 21<sup>st</sup> century) *Cicadetta montana* s. l. sites in Poland. For each site, the year and the cicada species recorded, data on location on the slope and its aspect, description of the grassland, thicket and forest vegetation and the source of the data are given. The label of each site correspond to those in Figs. 1 & 2. \* – located in an excavation of an inactive limestone quarry. \*\* – The occurrence of *Cicadetta* sp. was mentioned in the referenced paper, but the species was not specified. However, it can be assumed that it was a representative of *Cicadetta montana* s. l. ns. – not specified

Site label	Year	Name	Cicada species	Slope	Aspect	Grassland	Thicket	Forest	Data source
A	2014	Miłek Mountain (Góra Miłek)	<i>C. montana</i> s. l.	yes	SW	xerothermic grassland: unspecified*	-	deciduous: birch and willow grove with domination of <i>Salix caprea</i>	Struś & Malkiewicz, 2015
B	2003	Krowiarki Ridge (Pasma Krowiarki)	<i>C. montana</i> s. l.	yes	SW	xerothermic grassland: unspecified*	-	mixed: with a high share of <i>Fagus sylvatica</i>	Struś & Malkiewicz, 2015
C	2006-2014	Górkowa Rock (Górkowa Skała) in Ojcowski NP	<i>C. cantilatrix</i>	yes	SSE	xerothermic grassland: <i>Origano-Brachypodietum</i>	thermophilous thicket	deciduous: oak-hornbeam forest	Klasa & Boklak, 2015
D	2005-2014	Krzyżowa Rock (Krzyżowa Skała) in Ojcowski NP	<i>C. cantilatrix</i>	yes	SE	xerothermic grassland: <i>Origano-Brachypodietum</i>	thermophilous thicket	deciduous: lime-hornbeam forest <i>Tilio cordatae-Carpinetum betuli</i>	Trilar et al., 2006, Klasa & Boklak, 2015
E	2003	Polichno Clearing (Polana Polichno)	<i>C. cantilatrix</i>	no	-	xerothermic grassland: <i>Thalictro-Salvietum pratensis</i> and <i>Inuletum ensifoliae</i>	thicket of <i>Juniperus communis</i>	deciduous: oak forest	Trilar et al., 2006
F	2001-2006	Byszewice Hills	<i>Cicadetta</i> sp.**	ns	ns	ns	ns	ns	Ruta, 2007
9	2022	Kalina Mała Natura 2000 PLH120054	<i>C. montana</i> s. l.	yes	NW	xerothermic grassland: <i>Inuletum ensifoliae</i>	thermophilous thicket	deciduous groves	this study
10	2021-2024	Kalina-Lisiniac Natura 2000 PLH120007	<i>C. cantilatrix</i>	yes	SW	xerothermic grassland: <i>Inuletum ensifoliae</i>	thermophilous thicket	mixed forest	this study

that macroclimatic conditions in Poland are less favourable for the species than in Switzerland, which is located to the southwest. It can be hypothesised that in order to neutralise the impact of macroclimatic differences, in Poland (hence at the northern edge of its range in Europe) *C. cantilatrix* prefers warmer and drier sites than closer to the centre of its range.

In Switzerland, also *C. montana* s. str. and *C. cerdaniensis* s. l. differ in their habitat preferences and to a certain degree can be segregated according to habitat niche. All mountain cicada species inhabiting Switzerland prefer warm and dry climate and sun exposed sites with sparse vegetation. Nevertheless *C. montana* s. str. is the most eurytopic species, occurring also in mesophilous or higher-elevated (mountainous) habitats, while *C. cerdaniensis* s. l. – the most stenotopic one, inhabiting the warmest locations (Hertach, 2007). These conclusions are interesting in the context of older observations of cicadas from Poland. Although most of them lacked detailed information on the vegetation structure of the sites (Smreczyński, 1954; Nast, 1976; Boklak et al., 2003), some certainly differed significantly in character from xerothermic grasslands (e. g. mountain forest, pine forest; Nast, 1936). Thus, it is conceivable that the habitat differentiation of reported sites (forests vs. xerothermic grasslands with sparse woody vegetation) in which mountain cicadas were observed in Poland (thus in a rather small part of its European range) may be due to at least two reasons. The first may be, of course, the sufficiently high plasticity in habitat selection and/or changes that have occurred over the years in the taxon's habitat preferences. The second may be the different species identity of some of the former records (cf. Szwedo, 2004), compared to up-to-date sites from the Polish Uplands, where the presence of *C. cantilatrix* has been documented in extremely warm xerothermic grasslands (Table 3). However, it is important to be aware that the habitat niches of different mountain cicada species may overlap to some extent, so that they may even sympatrically inhabit the same sites. This has been recorded in Switzerland in the case of ecotone habitats between forest and dry grassland, where both *C. montana* s. str. and *C. cerdaniensis* s. l. were found (Hertach, 2007). Also in Greece, *C. montana* s. str. and *C. cantilatrix* occupied the same sites (Gogala et al., 2008b). Hence, habitat selectivity, although useful to some extent, cannot be the only criterion used to distinguish these cryptic species.

Detection of mountain cicadas under field conditions should be considered quite difficult, due to the subterranean life mode of the larvae, the secretive nature of the adult insects and the high frequencies of their acoustic emissions. Calling songs are audible with the unaided ear only to some, especially younger, people (Gogala & Trilar, 2016). Therefore, when conducting bioacoustic search for cicadas in the field,

it is important to ensure that the researcher (or assisting person) is able to hear high-frequency sounds (even close to the upper range of human hearing, approx. 10–20 kHz). If not, the use of an ultrasonic detector set to signals in this frequency range is highly recommended during the search (Gogala & Trilar, 2016). It is also difficult to detect larval exuviae, which are placed low on herbaceous vegetation and blend in colour with the substrate. All these characteristics of the species, combined with the lack of exploration of other xerothermic grassland patches – which are numerous in the studied region and provide potentially suitable habitat for these insects – implies that the actual distribution of *C. cantilatrix* in the Polish Uplands may be wider than reported in this paper. Because of the fragmentary and partly outdated (regarding the data from the past century) knowledge on the occurrence of mountain cicadas in Poland, it is recommended both to search for new localities in suitable xerothermic biotopes as well as to verify the presence of this taxon in the areas of old records. Attention should be paid to the presence of larval exuviae and, above all, to the search for adult insects using bioacoustic methods. Such results would at least partly fill the existing gaps in knowledge and at the same time provide the necessary basis for unravelling the taxonomic status and geographical distribution of mountain cicadas inhabiting this part of Central Europe.

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